

LOBSTERS: BIOLOGY, MANAGEMENT, AQUACULTURE AND FISHERIES

Second Edition

Edited by

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Preface

The stimulus for the 2006 version of this book was the publication of the *Biology of Freshwater Crayfish*, edited by David M. Holdich, in 2002, published by Blackwell Science Ltd. The Holdich book was different to most other texts dealing with similar material, in that although there are topics such as growth, nutrition and reproduction and behaviour, the full material for the commercial species is presented under each separate genera, rather than under fisheries, countries or topics such as management, aquaculture or conservation. In the 2006 edition and again in the current edition I have followed the same approach, except for a few minor instances where it was appropriate to make comparisons for clarity.

Not all genera of marine lobsters are covered in this volume. In selecting the material I have chosen those genera with the most commercially important populations. All species have been dealt with together under genera. Readers will no doubt find gaps in the topics examined. Space limitations precluded the inclusion of additional material.

The 2006 edition of the book was well received and the publishers were delighted. At their request I undertook to prepare a revised version, concentrating on the vast number of publications since 2005. I also took the opportunity to add additional

chapters on Lobsters in Ecosystems; Genetics of Wild and Captive Populations; Translocating Lobsters to Improve Yield and Value of the Fisheries; Climate Change; Systems to Maximize Economic Benefits in Lobster Fisheries; Ecolabelling of Lobsters and Essential Habits and Microhabitats for Tropical Spiny Lobsters, all of which are topics of special interest. To fit these new chapters into the book, some biological material presented in the 2006 edition was incorporated into the chapters dealing with specific genera in this revised edition. Chapter 1 Lobsters in Ecosystems was presented as a Key Note talk at the 9th International Conference and Workshop on Lobster Biology and Management in Bergen, Norway, in June 2011.

Many people contributed to the development and production of this book. They are not acknowledged individually because of space availability, but all authors wish to thank the many colleagues who assisted them with their contributions.

Bruce F. Phillips

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Chapter 1

Lobsters as Part of Marine Ecosystems – A Review

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Abstract

Lobsters are the focus of valuable fisheries worldwide; they are often regional icons, and mainly because of this are among the most researched animals on earth. As fishery management moves globally from a single-species to an ecosystem-based emphasis, it remains important to understand the role of species functions in marine ecosystems. Despite the wealth of research on lobsters, our understanding of their role in marine ecosystems is patchy. As mid-trophic-level consumers, lobsters function in the transfer of energy and materials from primary producers and primary consumers to apex predators. They are large-bodied and conspicuous, and can comprise a considerable proportion of the collective consumer biomass. Still, the nature and strength of interactions, and the relative importance of top-down and bottom-up effects to their productivity is murky. Australia, the USA, the European Union, Canada and New Zealand are beginning to implement ecosystem-based fishery management. Here, we review two case studies from dramatically contrasting ecosystems: the spiny (rock) lobster *Panulirus cygnus* in subtropical Western Australia, and the American lobster *Homarus americanus* in cool temperate eastern North America. Our analysis identifies knowledge gaps and takes a first step in evaluating the consequences of differing ecosystem-based management approaches to these and other lobster fisheries.

Key Words: lobsters; *Panulirus cygnus*; *Homarus americanus*; ecosystem; fisheries management; large marine ecosystems

1.1 Introduction

Ecosystem-based management (EBM) first developed as a concept in terrestrial systems, using the principles of outcome-based management (Grum-

bine, 1994). Lubchenco (1994) and Sherman & Duda (1999) subsequently laid the foundation for the emergence of the marine EBM movement. Table 1.1 (after Lubchenco 1994) is used as the basis of this chapter. We focus here on ‘Individual

Table 1.1 The single-species to ecosystem-based management paradigm shift from Lubchenco (1994).

From	To
Individual species	Ecosystems
Small spatial scale	Multiple scales
Short-term perspective	Long-term perspective
Humans: Independent of ecosystems	Humans: integral parts of ecosystems
Management divorced from research	Adaptive management.
Managing commodities	Sustaining production potential for goods & services

Species to Ecosystems' but comment at times more broadly on the question of ecosystem management in marine systems and lobster fisheries.

Over the last 10 years ecosystem-based fisheries management (EBFM) has emerged as an approach to natural resource management that is more comprehensive than focusing only on a single species. Marine ecosystems are considered to be a dynamic complex of animals, plants and micro-organisms with their associated non-living environment of water, air and sediment, interacting as a functional unit (from Article 2, UN Convention on Biological Diversity). Marine ecosystems may be identifiable and exist across a range of spatial scales, from ocean basin scale, such as the Eastern Tropical Pacific region, to local area scale of a few hundred metres or less, such as an individual estuary or embayment. It is in this context that the EBM of fisheries is conducted. To be effective, EBFM reverses the order of management priorities from starting with objectives for the target species to starting with objectives for the ecosystem, or at least objectives for a species assemblage consisting of multiple trophic levels and the environmental factors related to that assemblage. The movement toward EBM of marine living resources rather than single species management of target stocks further broadens the expectations of EBFM, and is in line with international agreements, most recently as expressed through the Johannesburg and Reykjavik Declarations, and supported by the UN Food and Agricultural Organization through the Code of Conduct for Responsible Fisheries (FAO, 2003).

In the USA, EBM has been mandated by National Ocean Policy (The White House Council on Environmental Quality, 2010). Ecosystem-based research initiatives in the USA include the CAMEO (Comparative Analysis of Marine Ecosystem Organization) programme jointly sponsored by the US National Science Foundation and the National Oceanic and Atmospheric Administration, and the US integrated modelling to service the EBFM approach (Link *et al.*, 2011).

There are many versions of the ecosystem approach to management, including EBM (Ward *et al.*, 2002); EBFM (Brodziak & Link, 2002); ecosystem approaches to fisheries management (EAFM) (Garcia *et al.*, 2003); and integrated oceans management (IOM) (NOO, 2004). Such a large number of terms can be confusing, but it is important to recognize that they are all variations on a theme (Fletcher, 2006). All of these approaches require that in addition to managing the target stocks and the impacts of fishing, the key trophic and habitat interactions, the spatial scale of connectivity among stocks and the other species dependent on the target species, as well as the socio-economic outcomes of fishing activities, are all given consideration within the management system to allow objectives for the broader ecosystems to be met. 'Ecosystem-based fishery management recognizes the physical, biological, economic, and social interactions among the affected components of the ecosystem and attempts to manage fisheries to achieve a stipulated spectrum of social goals, some of which may be in competition.' (Marasco *et al.*, 2007). When implemented effectively, EBFM is a subset of EBM, which for ocean ecosystems where fishing operates encompasses all forms of human activities, some of which will also interact with the fisheries.

We have chosen to focus this review on two contrasting species of lobster: the sub-tropical spiny lobster, *Panulirus cygnus* of Western Australia, and the temperate clawed lobster, *Homarus americanus* of the US Northeast and Atlantic Canada. The shelf waters of the Western Australia and Eastern North America are strikingly contrasting environments. Australia's western rock lobster occupies a geographic range that is subtropical and characterized by a gentle north-south gradient in

Table 1.2 Large marine ecosystems.

	Large Marine Ecosystem 44	Large Marine Ecosystem 7	Large Marine Ecosystem 8	Large Marine Ecosystem 9
Area km ²	543,577	674,862	308,554	303,029
Shelf area km ²	61,032	322,093	238,843	100,016
Inshore fishingarea km ²	66,437	137,688	124,784	73,112
Coral Reefs % of world	0.4	0.0	0.0	0.2
Sea Mounts % of world	0.0	0.0	0.0	0.0
Primary production mgCm ⁻² day ⁻¹	476	809	1,536	721

Data from Sea Around Us Project, <http://www.searroundus.org/lme/44.aspx>.

sea surface temperature (SST). By contrast, the geographic range of the American lobster in the western North Atlantic has the steepest latitudinal gradient in SST on the planet and large seasonal extremes.

These two species of lobsters are currently demonstrating opposite trends in catch – the annual catch of *H. americanus* is increasing in its most productive areas while that of *P. cygnus* is declining. Both species have been the subject of extensive research and both species are the basis for fisheries that have received Marine Stewardship Council (MSC) certification, at least for sections of, if not the entire fishery. This also means that extensive and current reviews of the literature pertaining to these species are available.

We refer to the large marine ecosystems (LMEs) relevant to the lobster species in question as described by Sherman & Duda (1999) and accepted by the US National Oceanic and Atmospheric Administration (NOAA) and endorsed by the White House Council on Environmental Quality (2010). The world-wide classification of LME is available at <http://www.lme.noaa.gov>. *Panulirus cygnus* predominantly occurs in the West-Central Australia LME 44 in Western Australia. The geographic range of *Homarus americanus* spans the Northeast US Continental Shelf LME 7, the Scotian Shelf LME 8, and the Newfoundland–Labrador Shelf LME 9. While *H. americanus* occupies a smaller geographic range than that of *P. cygnus*, it traverses a much steeper latitudinal gradient in SST and range of environmental conditions. The basic details of the LMEs used in this study are shown

in Table 1.2. The data are from Sea around Us project: <http://www.searroundus.org/lme/44.aspx>.

Plate 1.1 presents a general overview of some of the main ocean activities in lobster fisheries which need to be considered in ecosystem management. In this chapter we have attempted to examine the material that is available on lobsters in these ecosystems over the last 30 years.

1.2 Species overviews

1.2.1 Western rock (spiny) lobster *Panulirus cygnus*

Life history, geographic range, depth, habitat and fishery

The western rock lobster occurs only in the Indian Ocean on the western seaboard of Australia and is found in commercial quantities from Augusta in the south to Shark Bay in the north, along approximately 1000 km of coast (Plate 1.2A). The distribution of the population is greater than LME 44, but the majority of the fishery for this species falls within this LME. The offshore movement of the phyllosoma larvae takes them well beyond LME 44, and this large spatial scale of the distribution of the small lobsters makes EBM of the fishery difficult.

A full review of the species is provided in Chapter 10 and earlier data is available in Phillips (2006). After hatching, the Stage I phyllosoma larvae rises to the surface and they are rapidly dispersed offshore in a wind-driven surface layer of

the Indian Ocean. As they are transported offshore in the plankton they develop through a series of moults, increasing in size. Nine to 11 phyllosoma stages have been defined.

Much of the larval life of the lobster is spent in the open ocean and by May/June each year most have grown to Stages VI–VIII. By this time most of the phyllosoma are more than 200 km from the coast. They become widely distributed in the south-eastern Indian Ocean and have been found at least as far as 1500 km offshore at 99°E and between 13°S and 34°S, which is the limit of sampling that has been conducted. The area in the Indian Ocean where the larvae are found is an area of low plankton density characterized as a marine desert (Tranter, 1962). The highest abundances occurred between 26°S and 32°S, west of the centre of the adult population along the coast. After developing through the early and middle stages offshore, late-stage phyllosoma are returned towards the continental shelf by the deeper circulation. There is a geostrophic inflow from the ocean towards Western Australia in the upper 2 or 3 m as a result of a strong alongshore pressure (Clarke & Li, 2004). By September/October/November each year there are large numbers of late Stages VIII and IX phyllosoma (which are about 35 mm total in length) near, but offshore from, the continental shelf. The late stage phyllosoma (Stages VI–IX) tend to occur lower in the water column than early and mid-Stage larvae and are found at 0–60 m at night and descend to 60–140 m during the day (Phillips & Pearce, 1997).

The final Stage IX phyllosoma metamorphoses into the puerulus stage (the post-larva) in the slope region beyond the shelf break (Phillips *et al.*, 1978; McWilliam & Phillips, 1997, 2007; Phillips & McWilliam, 2009). The puerulus is a transitional stage short (3–4 weeks) which bridges the planktonic and benthic phases of the life cycle and swims 40–60 km across the continental shelf toward shore, where it settles in holes and crevices in the shallow coastal reefs.

When the puerulus settles, it molts after a few days into a benthic juvenile stage, which has the form and structure of the adult lobster. These post-pueruli are usually found in shallow coastal reefs where they remain for 3–5 years. Larger juveniles

migrate offshore in November to January each year. It is in these depths of 30–150 m that they reach maturity, mating takes place and the life cycle is completed.

Rocky reefs are an important habitat type in the near-shore coastal waters of LME 44, supporting a diverse assemblage of benthic macroalgae and associated fish and invertebrates. The rocky reef communities are a key component of coastal productivity, provide habitat and food for marine fauna, contribute to biogeochemical cycles, and can exert influence over nearby habitats such as seagrass meadows. In many places, these reefal habitats are offshore, and they protect the shallower inshore waters from wave energy, creating more protected inshore lagoon habitats and providing a wide variety of soft and hard substrata for a diverse marine fauna and flora.

Early juvenile spiny lobsters tend to be solitary in the small holes or dens that they choose, but as they grow they become gregarious. For example Fitzpatrick *et al.* (1990) showed that in *P. cygnus* over 95% of newly settled pueruli and post-pueruli (6–10 mm carapace length (CL)) were solitary, but less than 20% of animals that had been settled for about a year (i.e. 20–25 mm CL) were solitary. Their gregarious behaviour is considered an effective anti-predator strategy (Butler *et al.*, 1999). Nonetheless, natural mortality rates of lobsters, and particularly those of juvenile animals, are extremely high. Herrnkind & Butler (1994) estimated mortality of *P. argus* to be 96–99% in the first year after settlement, while Phillips *et al.* (2003) found similarly high rates of natural mortality (80–96%) for *P. cygnus* juveniles at the end of their first year after settlement. In the case of *P. cygnus*, as few as 3% of settling pueruli are estimated to survive to recruit into the fishery, 3.5 years after they first settled as pueruli (Phillips *et al.*, 2003).

Waddington (2008) and Waddington *et al.* (2010) used stable isotope analysis and gut content analysis to determine the diet and trophic position of western rock lobsters from mid-shelf coastal ecosystems (35–60 m depth) at three locations. Lobsters were primarily carnivorous, and no consistent differences in diet were detected with varying lobster size, sex or among locations. The main components of the diet were bait (from the fishery) and

small crustaceans – crabs and amphipods/isopods. Foliose red algae, bivalves/gastropods and sponges were minor contributors to diet. The diet of lobsters in these mid-depth coastal ecosystems differed from the results of other studies of diets of lobsters from shallow coastal ecosystems (MacArthur *et al.*, 2011). In particular, coralline algae and molluses – important prey in studies of lobsters from shallow coastal ecosystems – were found to be minor components of the diet. These differences are likely to reflect differences in food availability between these systems and, potentially, differences in choice of prey by lobsters that inhabit deeper water. Given the high contribution of bait to lobster diet in both shallow and deep waters, bait is likely to be subsidizing lobster production in deep coastal ecosystems during the fishing season (Waddington & Meeuwig, 2009; MacArthur *et al.*, 2011).

Bellchambers *et al.* (2010) and Bellchambers (2010) examined the relationship between abundance and size of western rock lobster and benthic habitats in deep water (35–60 m) based on the annual independent breeding stock survey and benthic towed video transects conducted near Dongara, Jurien Bay and Lancelin in Western Australia between 2005 and 2007. Abundance of western rock lobster was found in these studies to be partly related to benthic habitat, with high abundances associated with high cover of mixed assemblage and the macroalga *Ecklonia* sp. Lobster size was more strongly associated with habitat, with larger lobsters found in mixed assemblages with sponges, and smaller lobsters associated with mixed assemblages with *Ecklonia* sp.

The spatial complexity and quality of habitats where the lobsters live is also likely to have an influence on their nutrition and possibly their growth rates. Coralline algae were recorded as the major component of lobster guts sampled from reefs across the central area of LME 44, indicating an important trophic role for these algae and their habitats in lobster productivity. However, animal prey may provide more nutrition when it is available (MacArthur *et al.*, 2011). This infers that these lobsters may benefit significantly by choosing habitat that has a broad range of structures and supports a diverse array of flora and fauna prey items.

Fisheries in the LME 44

This LME has a very narrow continental shelf, and primary and secondary production is limited by low levels of nutrient-rich upwelling. As a result, fish stocks in the West-Central Australia LME are limited. Many of the targeted species are endemic to Australia or Western Australia. There are small but locally important commercial fisheries for rock lobster, abalone, pink snapper, shark, crabs, pilchards, prawns and scallops. Constantly changing ocean conditions affect the abundance and distribution of all species in the marine food chain, including both targeted and non-targeted species.

There have been a number of dramatic changes in the lobster fishery in recent years. These changes are described in detail by Phillips *et al.* (2010) including the new management arrangements, the status of the stocks and the current economic and social situation of the fishery. Here, we summarize the major changes in the fishery and discuss aspects relevant to this study of the ecosystem. For earlier details on fishery see Phillips *et al.* (2007) and Phillips *et al.* (2010).

The EBFM study by Fletcher *et al.* (2010) reported that this fishery is currently facing a number of significant issues, including recent persistent reductions in recruitment levels, and major reductions in the allowable catch have been designed to prevent breeding stock levels from being adversely affected. In addition, the income levels for fishers are being affected by relatively low prices due to overseas market conditions and high currency exchange rates, which are exacerbating the impacts of increased costs associated with fuel and labour. This combination is generating significant social issues for the catching and processing sectors, and there are flow-on economic impacts to the dependent human communities and service groups.

Annual commercial catches of *P. cygnus* since the mid-1980s have fluctuated between about 8000 and 14,400 t, but on average have yielded around 11,000 t. Catches from 1945–6 to 2009–10 for *P. cygnus* are shown in Chapter 10 (Fig. 10.3). After almost a decade of good to average levels of puerulus settlement, below average and very low pueruli settlements of this species have been observed since the 2006–7 fishing year, including the latest

available data (2011–12). There is a close relationship between pueruli settlement levels and recruitment into the fishery 3 and 4 years later (Phillips, 1986; Caputi *et al.*, 1995a,b). This relationship and the low levels of settlement provides the driver for concern for the stock, and is expressed in the reduction in catch levels enforced in the fishery from 2008–9 to 2011–12.

There are two major research and management issues associated with the series of low puerulus settlements. First, understanding the causes that have led to the low puerulus settlement, and second, devising management measures that are required to deal with the effects of the low settlement. These low settlement years commencing 2006–7 will have had a major impact on recruitment into the fishable stock, commencing with the 2009–10 fishing season. Without management actions being taken to significantly reduce exploitation on the rock lobster stock, the recent years of low puerulus settlement would also have the potential to result in much lower breeding stock levels 4–6 years after settlement, and then possibly have major ongoing consequences for the fishery.

Catches since the mid-1980s, and increasingly in the last 5 years, have been constrained by management measures which have been introduced to limit effort in the fishery. The 2008–09 fishing season, for example, was predicted to catch 9200 t, but through a range of management measures taken to reduce fishing pressure, the actual catch was reduced to 7600 t (Fig. 1.1A). The fishery was then constrained in the 2009–10 season to a target catch of 5500 t and this target level has been applied for the following 3 years. In 2008/09, the 7600 t fishery was estimated to be worth A\$191 million and the 5500 t catch in 2009/10 was worth about A\$156 million.

The management measures introduced to constrain the fishery are extensive and complex, and have been applied at the same time as the fishery prepares to move from a mainly input set of controls to a hybrid system of management controls that are based on catch quotas. As a result of the management measures, the number of boats declined in 2009–10 by about 20%. In the northern zone (zone B) of the fishery, for example, in December 2008 there were 89 boats authorized to

fish, but in 2009/10 there were 71 authorized vessels. Rules about how the pots can be used in the fishery have also changed. The number of ‘licensed pots’ has not changed, but fishers will only be able to fish with 40% of the pots they own, only on weekdays, and only on 4 days of the week. The numbers of days of closure will be adjusted to ensure that the target catch is achieved, pending the introduction of a system of specific catch quotas. Recreational fishers, although they only take a small proportion of the overall catch, will also be constrained to fishing only within specified seasons, and by pot limits, pot requirements, lobster minimum size limits and other constraints, possession limits, and a range of locally closed areas. All of these controls are designed to limit effort and catch in the fishery to thereby ensure that the breeding stock level is not further depleted. The controls are also intended to smooth the catch in the commercial fishery and reduce the economic impact of the low puerulus settlement years.

A workshop (Brown, 2009) which focused on examining the ‘likelihood’ of factors that could have caused the recent decline in puerulus settlement concluded that the decline could have been caused by either changes in environmental conditions and productivity in the eastern Indian Ocean, by overfishing causing a decline in the abundance of the rock lobster breeding stock, particularly in the northern region of the fishery, or by a combination of these two factors. The uncertainty regarding the cause of the low puerulus settlements represents a high risk to the fishery.

Environmental factors such as the Leeuwin Current (influenced by the El Niño–Southern Oscillation (ENSO) cycle, represented by the Southern Oscillation Index – SOI) and westerly winds in late winter–spring significantly affect the inshore puerulus settlement *P. cygnus*. A major concern regarding the recent low puerulus settlements was that the longstanding numerical relationship between puerulus recruitment and these environmental conditions, which had previously provided a good explanation of the variations in settlement (Caputi *et al.*, 2001), no longer provided an adequate explanation of the recent settlement patterns, particularly the very poor settlement of 2008/09 (Fig. 1.1B). The relationship between the strength of the SOI,

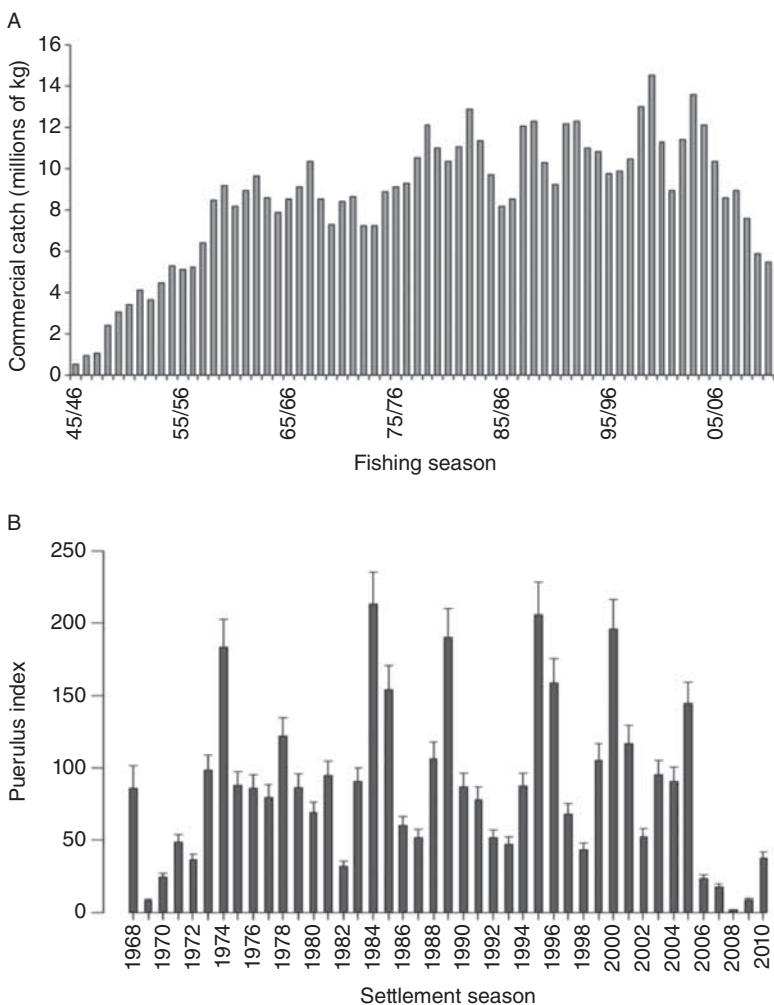


Fig. 1.1 (A) Seasonal catches in the commercial western rock lobster fishery for *Panulirus cygnus* from post war years to 2009/10, and (B) puerulus settlement index in the central region of the western rock lobster fishery for *Panulirus cygnus* (Dongara and Jurien) from 1968 to 2008/09. (From Phillips *et al.*, 2010, with permission from the Journal Marine Biological Association of India).

the Leeuwin Current and the levels of puerulus settlement appears to have been eroded over the last few years (Fig. 1.2).

The main cause for the decline in puerulus settlement is still unclear, but changes in the ecosystem are affecting the pelagic part of the *P. cygnus* life cycle, and overfishing of the breeding stock is still a possible contributing factor. A small increase in the puerulus settlement level in 2011/12 has been taken as a good sign for the fishery. However, it remains to be seen if this new level of settlement is sustained and if it carries through into increased adult abundances in future years. This situation emphasizes the need for knowledge of ecosystem scale changes

in the environment and the ecological interactions in sub-legal stages of the lobster to understand what is influencing the decline in puerulus settlement and provide for a more robust ecosystem-based approach to management of this fishery.

1.2.2 The American lobster *Homarus americanus*

Life history, geographic range, depth, habitat and fishery

The American lobster *H. americanus* occurs in the coastal waters from Labrador, Canada, to New

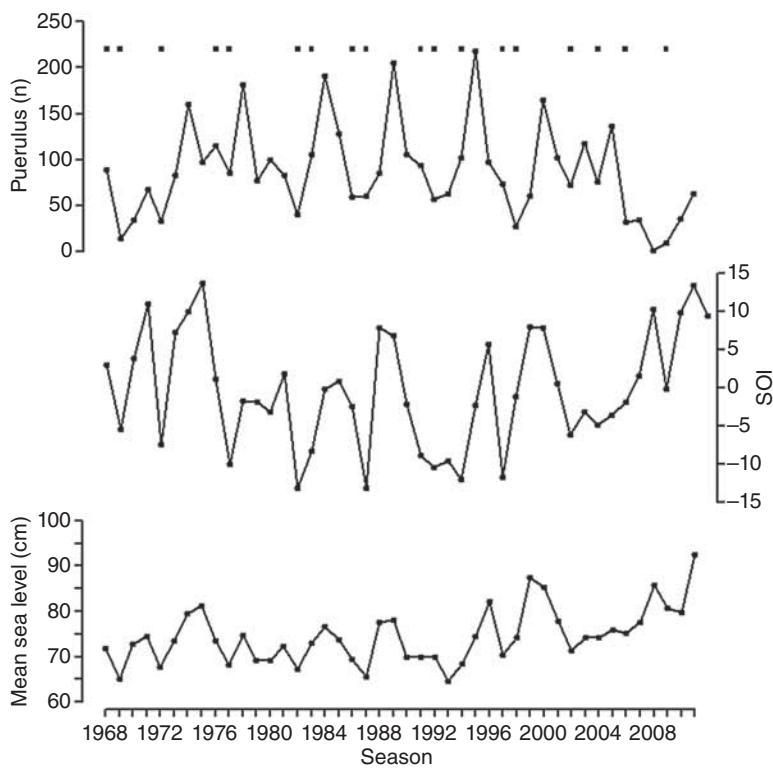


Fig. 1.2 Diagram illustrating the relationship between the Southern Oscillation Index (SOI; denoted by ~), Fremantle sea level (mm) (which is an indicator of the strength of the Leeuwin Current; denoted by ■), and the puerulus settlement at Dongara in Large Marine Ecosystem 44. (Updated from Pearce and Phillips 1988). ENSO Events are shown along the top of the diagram.

Jersey, USA, although the southern extent of its range departs from shallow coastal waters and extends into deeper shelf waters as far south as North Carolina on the US continental shelf. The life history, ecology and fishery of *H. americanus* are reviewed in detail elsewhere (Factor, 1995; Phillips, 2006; Chapter 8 of this volume). The range of *H. americanus* in the western North Atlantic spans the greatest latitudinal gradient in SSTs of any oceans (Plate 1.3 and Plate 1.4). Over the distance of a few hundred kilometres summer maximum temperatures range from the mid-20s centigrade in coastal southern New England, USA, to just over 10°C in the Bay of Fundy, Canada. At the northern limit of the *H. americanus* range in Atlantic Canada, the lobster is largely restricted to waters less than 50 m deep. In the middle of its range *H. americanus* is more broadly distributed from the coast to deep-water canyons on the continental shelf break. The southern limit of the species' coastal distribution is Long Island Sound and the northern Mid-Atlantic

Bight, USA, but even further south it becomes increasingly restricted to deeper, cooler water out to the edge of the continental shelf off Virginia and North Carolina. Consequently the commercial fishery transitions from predominantly near-shore in the north to predominantly offshore in the south.

The shelf waters of the Northwest Atlantic have been warming rapidly in recent decades (Steneck *et al.*, 2011). As the climate warms, the coastal environments at the southern end of the *H. americanus* range are becoming increasingly physiologically stressful during the summer, whereas those in historically cooler regions may be becoming more favourable (see Chapters 4 and 8). The thermal gradient is associated with a biogeographic shift in the diversity and composition of associated marine fauna, and this may have implications for the nature of trophic interactions across the lobster's geographic range (Frank *et al.*, 2007; Wahle *et al.*, in press). Essential elements of the American lobster's life history and fishery are provided here, and a full

review of the species is provided in Chapter 8. *Homarus americanus* has three planktonic larval instars and one post-larval instar that is the transition from a pelagic to benthic existence. The first three larval stages distribute over a range of depths, but the post-larva is neustonic and therefore more prone to wind-driven transport. The post-larva is also a capable swimmer and swimming behaviour plays an important role in vertical and horizontal movements. About half-way through the post-larval stage they become competent to settle and begin diving to select appropriate shelter-providing habitat, typically in relatively shallow zones above the summer thermocline. Following settlement, early juveniles are cryptic and remain strongly associated with rocky shelter. As they grow they undergo an ontogenetic shift in behaviour and habitat use and they range increasing distances from shelter and become seasonally migratory between inshore and outer coastal waters (Wahle & Steneck, 1991; Lawton & Lavalli, 1995). Unlike spiny lobsters, clawed lobsters are not social – shelters are typically used by a single individual except during mating. Sexual maturity comes sooner and at a smaller size for males than females, but males larger than the female tend to have greater mating success (Atema & Voight, 1995). Maturation size and age varies regionally, most probably with thermal regime – females in the warmer southern New England, for example, mature in 4–5 years, whereas those in the colder Bay of Fundy mature at 8 or 9 years.

There are fisheries for *H. americanus* in both US and Canadian waters, and together they extend through most of the *H. americanus* geographic range. The US fishery is mostly near-shore (<100 m) within the Gulf of Maine (Area 1), and offshore (>50 m) in the south, including Georges Bank (Area 2), the southern New England shelf and Mid-Atlantic Bight (Area 3). In the USA, the lobster fishery within 3 nautical miles of shore is managed by the respective state marine resource agency. From 3 to 200 nautical miles offshore (the boundary of the Exclusive Economic Zone) the fishery is managed by the federal National Marine Fisheries Service (NMFS) and the Atlantic States Marine Fisheries Commission, a consortium of all lobster-producing states.

The Canadian lobster fishery is managed by the Department of Fisheries and Oceans and is divided into 41 Lobster Fishing Areas (LFA). In Canada, there is no division between provincial and federal waters as there is in the USA. To date only Canada's LFA 41 lobster fishery is certified by the Marine Stewardship Council (see also Chapter 6).

Lobster fishing is characteristically a near-shore coastal fishery in Atlantic Canada and the Gulf of Maine, where it does not extend much beyond 100 m depth. In southern New England and the mid-Atlantic states of the USA, it becomes more of an offshore, deeper water fishery, especially targeting the banks and canyons along the edge of the continental shelf. Harvesting is almost exclusively conducted by trap, although some lobster by-catch is permitted in trawl fisheries that operate in these areas.

Over the past three decades landings of the American lobster have increased dramatically, but not uniformly across the various areas. In the Gulf of Maine and maritime Canada lobster grounds, for example, lobster landings are experiencing historic highs, while the lobster fishery in southern New England is near historic lows. These changes are of great concern to the industry and managers alike. For the first time in history, fishery managers have been considering a moratorium on lobster harvesting in southern New England. The scientific consensus to date suggests that these dramatic changes in catch reflect changes in abundance that have less to do with changes in fishing effort and more to do with a widespread alteration of the physical and biotic environment, as we discuss below.

The total fishery catches from LMEs 7, 8 and 9, while collectively about 10-fold higher than those from LME 44, have been severely depleted of fin-fish. This has been followed by an increase in lobster and other crustacean landings (Fig. 1.3) especially in northern sectors (Worm & Myer, 2003; Frank *et al.*, 2006, 2007; FAO 2003).

LME 7

Much has been published on Northeast U.S. Shelf LME fisheries, including resource population assessments (Sherman *et al.*, 1996; Kenney *et al.*, 1996; Mavor & Bisagni, 2001) and the status of living marine resources in 'Our Living Oceans'

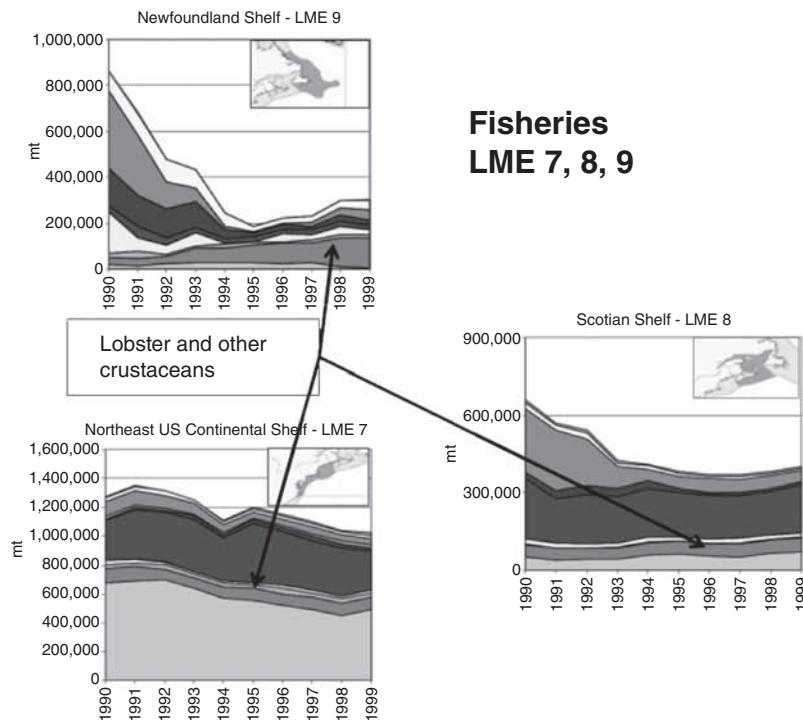


Fig. 1.3 *Homarus americanus* and other crustaceans caught in Large Marine ecosystems 7, 8, and 9. Data from FAO (2011).

(NMFS, 1996) and in the NEFSC Status of Stocks reports. The catch composition of this LME is diverse, and comprises demersal fish (groundfish) dominated by Atlantic cod, haddock, hakes, pollock, flounders, monkfish, dogfish, skates and black sea bass, pelagic fish (mackerel, herring, bluefish and butterfish), anadromous species (herrings, shad, striped bass and salmon) and invertebrates (lobster, sea scallops, surfclams, quahogs, northern shrimp, squid and red crab). In the late 1960s and early 1970s there was intense foreign fishing within the US Northeast Continental Shelf LME.

The precipitous decline in biomass of fish stocks during this period was the result of excessive fishing mortality (Murawski *et al.*, 2000). Total reported landings declined from more than 1.6 million t in 1973 to less than 500 000 t in 1999, before increasing to just less than 800 000 t in 2004. The value of the reported landings reached US\$1.8 billion (expressed as 2000 US dollars) in 1973 and in 1979, and has maintained a level above US\$1

billion except for the 3-year period between 1998 and 2000. Among the most valuable species are lobster, sea scallops, monkfish and summer flounder (Sherman & Hempel, 2009).

LME 8

Commercially exploited species in LME 8 include cod, haddock, pollock, silver hake, halibut, white hake, and turbot. Pelagic species include the Atlantic herring and the Atlantic mackerel. Invertebrates include snow crab, northern shrimp and short fin squid. Both snow crab and northern shrimp prefer cold water and the increased landings for both those species coincide with the cooling of the eastern shelf (Zwanenburg, 2003). Systematic fishery surveys of the shelf made between the 1960s and the present are the most consistent source of information available concerning this LME.

Total reported landings recorded a peak of 889 000 t in 1970 and declined to less than a quarter of this level or 213 000 t in 2004. Major changes

include a dramatic decline in landings of cod, silver hake and redfish. However, the value of the reported landings reached its peak of US\$1.2 billion (in 2000 US dollars) in 2000, as a result of high value commanded by its landings of crustaceans.

LME 9

Commercially exploited fish species in LME 9 include cod, haddock, salmon, American plaice, redfish, yellowtail and halibut. Also harvested are lobster, shrimp and crab. Historic records of catches of Atlantic cod can be reconstructed back to 1677 (see Forsey & Lear, 1987). Total reported landings, dominated by cod until the 1990s, exceeded 1 million t from 1967 to 1970, but declined to 525 000 t by 2004.

1.3 How far have we come in thinking about lobsters as part of the ecosystem?

1.3.1 *Panulirus cygnus*

Ecosystem structure and foodweb

The shelf waters of Western Australia and the east coast of North America are strikingly contrasting environments. Australia's western rock lobster occupies a geographic range that is subtropical to temperate and characterized by a gentle, although sometimes complex, north–south gradient in SSTs and ambient temperature. The West-Central Australia LME 44 extends from Cape Leeuwin (about 34.5°S), at Australia's south-west edge, to North West Cape (22°S). The LME owes its unity to the West Australia Current, a north-flowing current coming from the circulation pattern of the counter-clockwise Indian Ocean Gyre and West Wind Drift. But it also has a southward-bound band of warm water close to the continental margin known as the Leeuwin Current, which delivers warm waters to the coast in the Austral winter, permitting tropical and sub-tropical reefs systems to flourish in the shallow coastal waters at 29°S, the most southerly occurrences of hard coral reefs in the Indian Ocean. Biodiversity of the two regions is also very different (Plate 1.5).

The LME has an extremely narrow shelf, and much of the environment comprises cool, temperate waters with complex, diverse and abundant reefal, seagrass and algal communities, much of which is in good condition (DSEWPAC, 2011). The region is an important nursery area for the Antarctic-feeding humpback whale, and home to many species of other mammals (such as dolphins and sea lions) sharks, including the whale shark, and seabirds associated with the coastal islands and reefs. As with the targeted species, many species of flora and fauna are endemic to Western Australia, and the ecological values of these ecosystems are consequently high. Some elements of this biodiversity, such as the seagrass and algal assemblages, are of global significance, because of their substantial abundance, rich species diversity and extensive endemicity. For example, Shark Bay and Ningaloo Reef, which are at the northern end of LME 44, are both World Heritage listed for the outstanding universal significance of their natural marine ecosystems (DSEWPAC, 2011).

The region has a Mediterranean climate, with mild wet winters and hot dry summers. There are only few major rivers delivering land-based nutrients, and nutrient-rich upwellings from the deep ocean waters are mainly limited to small shelf-edge canyons, which are the focus for significant local production, and attract large mammals and pelagic fish. The dominant feature of the shallow water ecosystems is the gradation between tropical and temperate flora and fauna, from the north to the south of the region, the low nutrient status waters, and the extensive system of barrier reefs running south to north that establish the inshore lagoonal ecosystem along much of the length of LME 44.

Ecosystem modelling

The trend in number of primary publications dealing with ecosystem approaches to fisheries and developing or applying ecosystem modelling for fisheries management was evaluated by Christensen & Walters (2011). They included results for the 20-year period from 1999 to 2009, and found 2785 ecosystem and multispecies modelling publications, of which 391 were publications developing, applying or reviewing ecosystem modelling

approaches. The results indicate an approximately 19% growth per year in the annual number of model publication since 1995.

Ecopath/EcoSim modelling (Christensen *et al.*, 2000) is a mass-balanced energetic modelling approach of ecosystem function that has gained increasing application. We are aware of Ecopath models applied to both the *P. cygnus* and *H. americanus* ecosystems. There have been two Ecopath studies in sections of the LME 44 and another modelling study attempted to identify indicators for the effects of fishing using a range of alternative models. None of these models were for the whole ecosystem, and they do not answer all the questions which might be asked, but they do provide a useful synthesis of some aspects of the problem, and some of the relevant data.

Jurien Bay Marine Park

Loneragan *et al.* (2010) and Lozano-Montes *et al.* (2011) used an Ecopath model to characterize the structure and function of the Jurien Bay marine ecosystem in temperate Western Australia ($\sim 30^{\circ}\text{S}$) and to explore the ecosystem impacts of fishing in the Jurien Bay Marine Park (area 823 km^2), a protected area with several levels of management zoning, including no-take areas. Jurien Bay Marine Park is not a protected area for the western rock lobster, and fishing, both commercial and recreational, is permitted in most areas of the park. Estimated total catches of all species in the marine park by the commercial sector (340 t in 2006) and recreational fisheries (56 t), were dominated by western rock lobster (*P. cygnus*) ($\sim 70\%$ of total catches).

A mass-balance Ecopath model was developed by Lozano-Montes *et al.* (2011) to quantify the interaction of prey, predators and the rock lobster fishery in Jurien Bay Marine Park. The model contained 250 species that were aggregated into 80 functional groups based on similar functional ecosystem roles or significance to fishing. A set of model parameters including biomass, consumption rates (Q/B), production per unit of biomass (P/B) and diet composition were used in the analysis.

The functional species groups covered more than four trophic levels (TLs). Sharks occupied the highest trophic level of the ecosystem, whereas

primary producers, detritus and other non-living groups (e.g. detached algae and bait) represented the lowest level (TL1). Owing to the nature of the adult rock lobster dietary characteristics (generalist feeders that feed on a range of plants and animals) the TL of adult lobsters was taken to be 2.7. Jurien Bay Marine Park was found to be dominated by the lowest trophic levels (TL1 and TL2) as the majority of functional species groups had a trophic level lower than 3.5 and comprised 80% of the total biomass ($1229\text{ t km}^{-2}\text{ year}^{-1}$).

The mixed trophic impact (MTI) analysis showed that several of the ecosystem functional groups ($>60\%$) were influenced by changes in the biomass of benthic groups (e.g. *Ecklonia*, seagrasses, macroalgae, phytoplankton and benthic invertebrates). When the biomass of *Ecklonia* increased, the biomass and trophic flows for groups such as post-puerulus rock lobster, juvenile rock lobster and crabs also increased. The overall relative change in MTI (biomass and energy flow) of post-puerulus, juvenile and adult rock lobsters was 0.22, a change almost double the magnitude of change in *Ecklonia* production. A possible explanation for this strong response by lobsters to changes in biomass of *Ecklonia* could be attributed to the food substrata and shelter the seaweed provides for lobsters. The MTI analysis also investigated the trophic role of adult rock lobsters and showed that even a small simulated increase in the MTI of adult lobsters resulted in a theoretical increase in lobster catch (18%) and a small decline of biomass and trophic flows of lobster prey (e.g. coralline algae, small gastropods, epifauna, crabs and small grazers) as well as a decrease in biomass and trophic flow to juvenile lobsters. The increase in adult lobsters also resulted in a small theoretical increase in biomass and trophic flow of lobster predators such as small sharks, rays, octopus and sea lions.

The results of these studies indicate that Jurien Bay Marine Park in its present condition is a dynamic ecosystem (Primary Production : Biomass ratio = 1.68) showing low recycling rates and is dominated by benthic functional groups (biomass of benthic : pelagic groups = 1.27). This domination by benthic communities suggests a greater importance of bottom-up processes than top-down interactions, driven primarily by *Ecklonia*, seagrasses

and macroalgal communities that are the main habitat and food source for many invertebrates and fish species in the marine park. This study did not simulate the ecosystem structure that may have existed in the absence of fishing, and so it is unclear how the natural (unfished) ecosystem would have been structured or have functioned in the presence of natural abundances of the various age classes of lobsters that would exist within the marine park (puerulus of *P. cygnus* settle in high abundances in this region, and in suitable habitat in this marine park). Also, the study did not consider in detail the potential effects of input of settling lobsters originating outside the study area. The relative importance of the benthic processes, the ecological function of the lobsters and the high-level predators may be somewhat different in the natural condition from that reported in these Ecopath studies for this ecosystem.

Lobster structuring of benthic communities

Moore & Hynes (2011) reported that although there has been over 30 years of research into the biology, ecology and behaviour of *P. cygnus*, there was still little quantitative information on potential flow-on trophic effects on the structure and functioning of benthic marine assemblages resulting from the removal of *P. cygnus* by this fishery. They undertook a project to quantify the impact, if any, of the western rock lobster fishery on trophodynamics within shallow-water assemblages.

The results demonstrate that *P. cygnus* may influence the abundance of the numerically dominant gastropod grazer *Cantharidus* spp. However, they showed no evidence of flow-on effects through the food web or any evidence that *P. cygnus* plays a role in structuring benthic assemblages as a whole and they could find no evidence that *P. cygnus* plays a ‘keystone’ role anywhere in its biogeographic range. Based on these investigations of the role of *P. cygnus* density, diet and behaviour in influencing assemblage structure, it was concluded to be unlikely that the western rock lobster fishery has a significant structuring impact on shallow-water benthic assemblages, or is a bottleneck through which large amounts of shallow water biomass and energy passes. However, this conclu-

sion has been challenged by MacArthur *et al.* (2007), who consider that there is little evidence to determine if the western rock lobster is or is not playing a major ecological role in community structuring. They point to the better studied examples of lobsters in other parts of the world where such ecological structuring roles are more evident (e.g. *P. interruptus*: Robles, 1987, 1997; Robles & Robb, 1993; Lafferty, 2004; *Jasus edwardsii*: Babcock *et al.*, 1999; Babcock, 2003; *J. lalandii*: Barkai & McQuaid, 1988) and conclude that the hypothesis for western rock lobster remains to be tested in any convincing manner. MacArthur *et al.* (2007) also further conclude that while the western rock lobsters may not be demonstrated to be keystone species, they are likely to be important components of the energy cycling in both shallow- and deep-water areas, and hence represent important grazers and predators, respectively, and provide an important prey source for many species of coastal fish, sharks and other large invertebrates such as octopus. This conclusion about the likely important role of the lobsters in energy cycling and trophic structure of shallow water ecosystems has been further reinforced by subsequent studies of the diet and nutrition in shallow waters near patch reefs in the region (MacArthur *et al.*, 2011).

Larval advection modelling

Caputi *et al.* (2010) have developed a model to assess the relative contribution of larval production from different areas of the breeding stock to the abundance and spatial distribution of puerulus settlement using a larval advection model. It is hoped that this model will assist in developing an understanding of the space and time factors influencing the advection of puerulus, and contribute to a better understanding of the causes of the low puerulus settlements in recent years.

Effects of fishing

The identification of indicators of the indirect effects of fishing is often an issue for fisheries management, particularly if only commercial catch data (i.e. direct effects of fishing) are available. Complex, intermediate and simplified qualitative models,

including aspects of uncertainty and aggregation error, were produced for two fishery case studies off Western Australia to identify potential indicators of change caused by fisheries extraction and bait input (Metcalf *et al.*, 2011). The two sites studied were in the West Coast Bioregion (WCB) between 20 and 250 m depth. High levels of both recreational and commercial effort in the WCB, particularly in the metropolitan zone near Perth, have been identified to be responsible for a decline in the abundance of several species of fin-fish, including dhufish and pink snapper (Fletcher & Santoro, 2010). Commercial and recreational rock lobster fishing also occurs in this bioregion. The study also explored the indirect ecological impacts of lobster fishing (*P. cygnus*) and focused on a smaller study area within the coastal zone (40–

60 m) of the WCB, off Jurien Bay. This region was selected as it is located towards the centre of the lobster fishery's distribution and has been demonstrated to be representative of the wider fishery in terms of habitats, fishing effort and lobster catch (Bellchambers, 2010).

Models of intermediate complexity (Fig. 1.4) were used to identify indicators as they produced the lowest aggregation error (9% and 25%) and structural uncertainty was considered through the use of a series of structurally different intermediate models. Small fish without significant economic value, including old wife (*Enoplosus armatus*), footballer sweep (*Neatypus obliquus*), king wrasse (*Coris auricularis*) and bullseyes (*Pempheridae* spp.) were identified as potential indicators of the impacts of extraction of other demersal fish due to

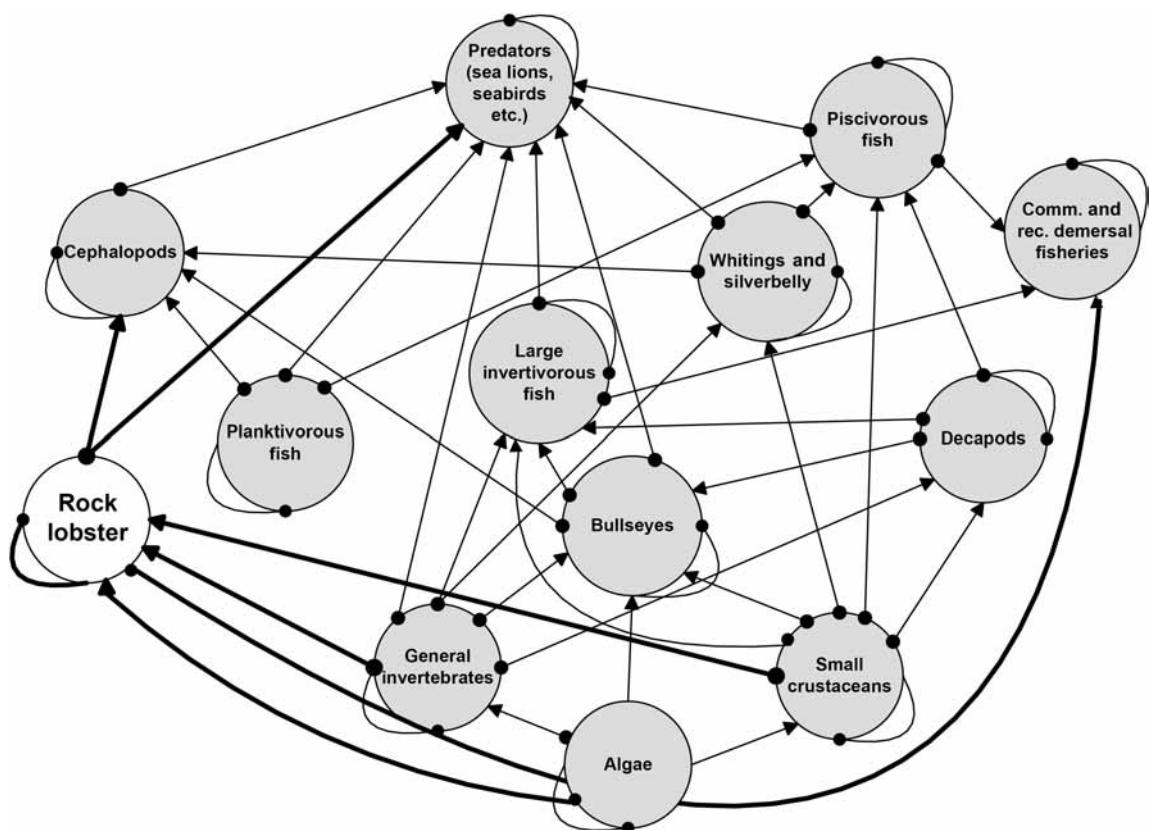


Fig. 1.4 Simplified inshore demersal model of the effects of fishing by *Panulirus cygnus* in Jurien Bay in Western Australia (from Metcalf *et al.*, 2011, with permission).

positive impacts across alternative models. Small crustaceans (amphipods and isopods) displayed positive impacts due to bait input from the rock lobster fishery and were identified as potential indicators of bait effects. Monitoring of these indicators may aid the detection of incremental changes in the present-day ecosystem that could be related to the activities of these fisheries. This study suggests useful methods for the future but no action to introduce these indicators to the fishery management system appears to have been initiated at this time. Equally, these methods are useful for current management purposes, but do not provide a basis for estimating the extent of the historical ecological impacts of these fisheries since their inception (see below).

1.3.2 *Homarus americanus*

Ecosystem structure and foodweb

The confluence of the cold southward flowing Labrador Current and the warm northward flowing Gulf Stream in the shelf area off the north-east USA and Atlantic Canada creates a dramatic latitudinal gradient across LME 7, 8 and 9. The latitudinal contrast is most evident during the summer when SSTs can be as high as 23–26°C in coastal southern New England, while temperatures in the Bay of Fundy some 200 km to the north reach maxima of only 11–12°C (see Plate 1.4). Influenced by the continental climate and prevailing westerly winds, this part of the Northwest Atlantic is strongly seasonal. Strong summer thermoclines become established with notable exceptions such as the Bay of Fundy, which is subject to extreme tidal mixing. Coastal waters freeze during the winter in large areas of the Gulf of Saint Lawrence and in smaller embayments to the south.

The coast of the Northeast USA and Maritime Canada strongly reflect the glacial history of the region. The seabed and shoreline variably consists of glacially scoured bed rock and unconsolidated gravel, sand and mud. The general distribution of bottom sediments has been well mapped, although the local detail may be sparse (Frank *et al.*, 2006, 2007).

Primary production and associated fishery productivity on the relatively broad and shallow shelf area of the north-west Atlantic LMEs 7, 8 and 9 is large and regionally variable (Sherman *et al.*, 1996; Frank *et al.*, 2006, 2007). There have been intensive studies of both the pelagic (Johnson *et al.*, 2011) and demersal biodiversity of these LMEs, demonstrating the rich and structurally complex set of habitats and species that inhabit the area, with high ecological values across the regions. A number of areas have been designated for special protection and management (<http://www.mar.dfo-mpo.gc.ca/e0009691>), and there has been intensive development of indicators for use in EBM (O’Boyle *et al.*, 2005; O’Boyle & Worcester, 2009).

Most fisheries in LME 7, 8 and 9 of the north-west Atlantic are managed as single species, although both the USA and Canada officially embrace and are gradually implementing EBFM. In Canadian waters, the lobster fishery is managed by the Department of Fisheries & Oceans, and is divided into 41 LFAs. The Canadian lobster fishery is mostly limited to <50 m depth, except on the southern Scotian shelf. The near-shore fishery includes the south coast of Newfoundland, the southern Gulf of St. Lawrence, coastal Nova Scotia and New Brunswick. Canada’s offshore fishery on the south-western Scotian Shelf includes Brown’s Bank, Crowell Basin, George’s Basin and the north-eastern slope of Georges Bank (Fig. 2 in Moody Marine Ltd, 2010). Lobsters taken from the relatively small LFA 41 are currently MSC certified. The lobster fishery in the US Management Area 1 (Gulf of Maine) is currently undergoing an assessment to determine if it complies with the MSC standard, scheduled for completion in late 2012.

North-west Atlantic lobster populations have undergone a substantial increase in abundance since the 1980s (Fig. 1.5), apparently as a result of environmental changes, but the relationships of abundance to environmental conditions are not understood. Predation release with decline in groundfish populations at the end of the 20th century is one hypothesis to explain the increase in lobster abundance, but the processes that might explain this have not been demonstrated clearly. Lobster fishery production throughout the north-west

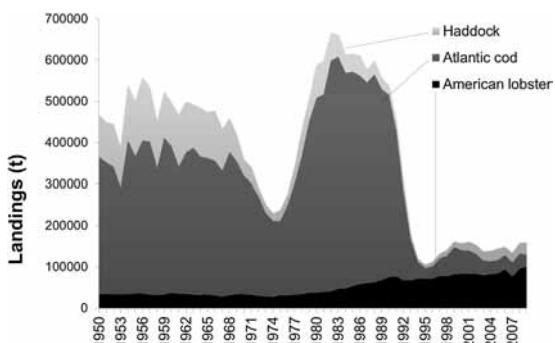


Fig. 1.5 Haddock, Atlantic cod and American lobster caught in Large Marine ecosystems 7, 8, and 9. Data from FAO (2011).

Atlantic remains very high relative to conditions from about 1920–80, despite very high fishing pressure, suggesting that productivity of lobster populations is elevated relative to conditions which prevailed during most of the 20th century. Despite this, the Atlantic States Marine Fisheries Commission has called for a 5-year closure of the fishery on the Southern New England stock, as the stock is considered to have fallen below the main trigger point in this part of its geographic range and needs rebuilding (ASMFC, 2010). Demersal and benthic fishes have long been recognized to be major predators of *H. americanus* (Herrick, 1911). The widespread depletion of groundfish, including cod, in the north-west Atlantic is strongly correlated with the upsurge in American lobster, crab (*Chionoecetes opilio*) and northern shrimp (*Pandalus borealis*) abundance in recent decades (Acheson & Steneck, 1997; Worm & Myers, 2003), suggesting the groundfish predators play a central role in population regulation. Further time series analysis of US National Marine Fisheries Service trawl survey time series in the Gulf of Maine points to a strong inverse correlation between the abundance of the American lobster (kg/tow) and the aggregated abundance of four species of groundfish (Atlantic cod, cusk, longhorn sculpin, monkfish and wolffish), as well as the singular abundance of cod (Boudreau & Worm, 2010). *Homarus americanus* is also reported from stomachs of a more near-shore

assemblage including striped bass (*Morone saxatilis*), shorthorn sculpin, (*Myoxocephalus scorpius*), cunner (*Tautogolabrus adspersus*) and white hake (*Urophycis tenuis*) (Steimle *et al.*, 2000; Nelson *et al.*, 2003).

A series of studies of trophic relationships of lobster has been conducted in the fishery area. Very young shelter-dwelling juveniles may be suspension feeders, and suspension feeding may continue with growth (Lawton & Lavalli, 1995), but suspension feeding was not found to be important in one detailed study (Sainte-Marie & Chabot, 2002). Juveniles and adults generally prey on the same species, but proportions change with growth: a wide variety of prey items has been reported including gastropods, crabs, polychaetes, fish, echinoderms and other benthic invertebrates (Lawton & Lavalli, 1995). Unidentified flesh may be important in the diet, which may come from dead fish, trap bait or live-captured fish (Lawton & Lavalli, 1995; Sainte-Marie & Chabot, 2002). Lobsters may also consume plant material (Lawton & Lavalli, 1995). Diet may vary seasonally, with the moult cycle (higher calcium prey may be sought after the moult) and with area. Earlier reports that lobsters are scavengers, unspecialized feeders or opportunistic omnivores appear unsupported based on recent studies which suggest that lobsters are selective feeders. Crab may be a particularly important part of the diet because of its high protein content, and was found to be a high proportion of the diet, particularly of adults, in one study in eastern Canada (Sainte-Marie & Chabot, 2002). Juvenile lobsters are preyed on by a variety of inshore species including other lobsters, crabs (*Cancer*), sculpins, flounders and cunners, and predation is particularly concentrated on shelter-dwelling juveniles in the period after moulting (Lawton & Lavalli, 1995).

Effects of fishing

Steneck *et al.* (2004) examined the process of ‘fishing down the food web’ in the Gulf of Maine as could be inferred from archaeological evidence, early naturalist observations and the scientific literature. They identified a Phase I as an ecosystem

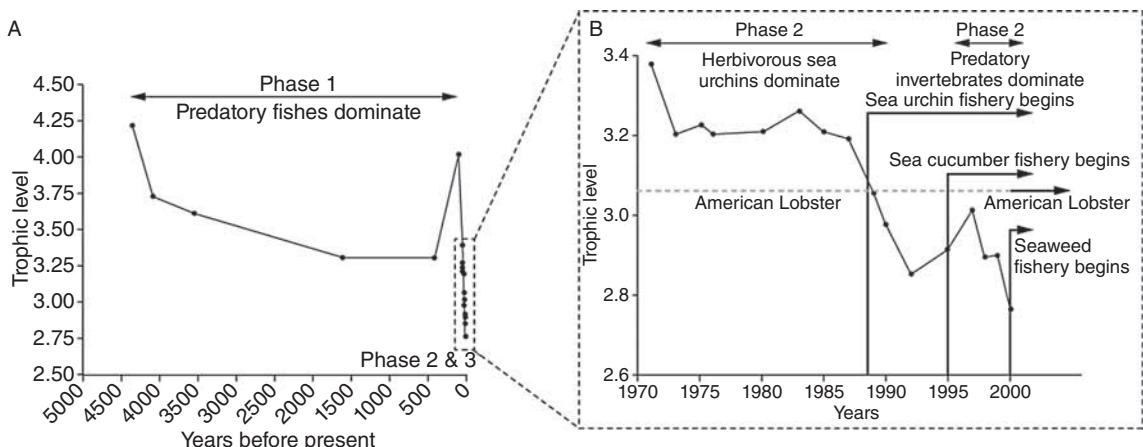


Fig. 1.6 Reconstructing the history of the coastal ecosystem - evidence of phase shifts and trophic dysfunction. Constructed from a paper by Steneck *et al.* (2004). With permission.

dominated by large apex predators, such as fish and marine mammals; Phase II where the ecosystem was dominated by sea urchins; and Phase III dominated by predatory invertebrates such as lobster and crab whose populations have been released from predation by larger (fish) predators (Fig. 1.6). Trophic analysis indicated declining average trophic level of the food web over time. Steneck refers to this serial loss of trophic levels as ‘trophic dysfunction’, pointing out that low diversity food webs like the Gulf of Maine are particularly vulnerable to such trophic cascades, and that greater functional redundancy (more species) within a trophic level confers resistance to trophic cascades.

Much of the coastal ecosystem within the geographic range of the American lobster has been subject to the serial depletion of top marine consumers, a globally classic example of ‘fishing down the food web’ (Pauly *et al.*, 1998; Conti *et al.*, 2012) and the scientific evidence has been building that this has had important consequences for the abundance of the American lobster and other large benthic crustaceans. For further discussion and evidence in relation to this issue see Worm & Myers (2003); Frank *et al.* (2006, 2007); Steneck *et al.* (2004); Boudreau & Worm (2010).

Ecosystem modelling

Gulf of Maine Ecopath model

Zhang & Chen (2007) developed an Ecopath model to evaluate changes in the Gulf of Maine ecosystem over a period of considerable groundfish depletion by harvesting. Their studies showed the Gulf of Maine has undergone a switch from a groundfish-dominated to a crustacean-dominated system, with American lobster and crabs at historic high levels of abundance. Several hypotheses have been developed to explain such a switch, ranging from trophic interactions between groundfish and crustacean species to increased food availability to crustacean species due to discarded baits in the lobster fishery. The study developed a mass-balance ecosystem model separately for the two time periods (1980s and 1990s) using Ecopath with Ecosim (EWE). The model has 24 function groups including lobster, the focal species of the analysis as a mid-level consumer and prey of groundfish. Other important groups in the ecosystem such as zooplankton, phytoplankton and detritus were also included in the model. The input data on abundance and vital rates were obtained from published papers and reports. The trophic structures of the ecosystem in the mid-1980s was found to differ

from that of the mid-1990s, when a decrease in top predator biomass coincided with an increase in the biomass of mid-level consumers (Plate 1.6). Ecosim was also used to predict the response of the lobster population to the recovery of the top predator, Atlantic cod (*Gadus morhua*), in the Gulf of Maine. Although the full-scale recovery of cod and other depleted groundfish is predicted to adversely impact lobster production, it would help restore the spectrum of fisheries available to the fishing industry as well as probably a more naturally resilient ecosystem structure and function of the ecosystem.

The ecosystem model developed in the Zhang & Chen (2007) study, although preliminary, provides us with a new approach to evaluate the trophic interactions of lobsters and other organisms, helps us better understand the ecosystem dynamics, and provides information critical to the development of an EBM strategy for the interdependent lobster and groundfish fisheries. More studies of this type are needed, however, to reduce uncertainties in input data, to evaluate the performance of the model, to better develop ecological indicators and benchmarks, and to better understand the long-term history of shifts in ecosystem structure and function.

Link *et al.* (2011) reviewed current and ongoing ecosystem modelling efforts in the North US shelf LME with emphasis on how they are being used in a living marine resources management context. An external independent peer review of these modelling approaches (Smith, 2011) confirmed that there were a number of modelling approaches underway in, and directly relevant to, LMEs 7, 8 and 9. However, many of these model types and modelling approaches were of limited value for EBFM in the region. The core issues of EBFM relating to reference points and other practical management tools that will provide for appropriate and agreed maintenance of the structure and functions of the ecosystem have yet to be established. While many of the modelling approaches have the basic architecture that will enable them to include lobsters, so far there has been very little progress in the development of ecosystem models that do include lobsters and the lobster fisheries. Further, given the presumed relationships between groundfish popu-

lations and lobster populations, and the associated socio-economic relationships, it could be well argued that any ecosystem modelling that does not include lobsters will fail to meet the basic requirements of EBFM for these LMEs.

1.4 Human role in ecosystem dynamics

1.4.1 Institutional structures

A recent trend to emerge in EBM has been the recognition that in order for this process to be successful the economic and social spheres must be better incorporated (see for example O'Boyle & Worcester, 2009). While some authors have felt that there has been perhaps an overemphasis on the ecological aspect of EBM and the major gaps are now in dealing with the social and economic issues (Rosenberg *et al.*, 2009), there now seems to be a rebalancing being achieved as economic and societal objectives are more frequently mentioned as key components in the successful implementation of EBM (Curtin & Prellezo, 2010). This gap is perhaps best represented by the difficulty that EBFM systems have in creating processes and structures that result in the effective involvement of stakeholders from a wide range of institutions and civil society into the decision-making processes about resource harvesting. Garcia *et al.* (2003) alluded to this perception of imbalance when they noted that humans cannot be looked on as external influences on the ecosystem. They noted that the interdependence between ecosystem well-being and human well-being requires the conservation of habitats, reducing human impacts and the maintenance of ecosystems for current and future populations.

The fishery sector has not been immune to the wide-ranging nature and pressures brought about by globalisation. Aided by technological advances, globalisation has resulted in a greater exploitation of high-value fisheries for export products and the emergence of environmental and social standards that ensure the survival of by-catch species and greater resilience of ecosystems, and promote responsible codes of fishing practice. In Australia,

an increasing number of studies have been conducted on the changing social and economic conditions in rural communities, focused on areas connected with, if not wholly dependent upon, primary industries. However, much of the research has focused on the agriculture sector and on broad-acre agricultural regions. This research gap is also evident in Canada where, as Troughton (1995) observed, ‘Despite their major regional economic significance, there are very few studies of change in forestry, mining, and fishing industries, especially the changing nature of technology and its impacts on employment and communities.’

In a study of the western rock lobster fishery, Huddleston & Tonts (2007) stress the contribution that the western rock lobster fishery makes to the economies of many coastal communities in Western Australia and the important contributions of rock lobster fishers and their families to the social fabric of these communities. In that case, the important contribution and legacy of the fishery to the development of these communities was considered able to continue to be enhanced if fishery stakeholders engage in a more proactive media and communications campaign capitalizing on local and regional media to foster a positive impression of and build up future support for the fishery.

In an attempt to further address this seeming imbalance, one of the first comprehensive studies of industry restructuring in the fisheries sector in Western Australia focused on the linkages and implications of restructuring on the social, economic and cultural facets of coastal communities in Western Australia (Huddleston, 2009). The western rock lobster fishery is the most valuable single species fishery in Western Australia with a sizeable financial and employment contribution to coastal communities along the Western Australian coast. The study presented a snapshot of this fishery at a time when fishery managers were deliberating changes in management arrangements and its effects on coastal communities that historically had depended, and to a great extent still depend, upon rock lobster fishing. It provides empirical evidence that lends support to the view that the pro-market policies promoting competition and entrepreneurialism have resulted in a spatially uneven development and distribution of benefits in regional

Australia. The study emphasizes that while specific localities can deal with the changes brought about by globalisation and policy change, the manner in which these communities deal and cope with these changes depends on, among others, the level of diversification of the local economy, demographic and social structures, and other factors such as the level of resilience and the base of social capital within the community.

1.4.2 Direct effects of management

The lack of compliance with regulations is an obvious threat to the sustainability of any commercial fishery, and compliance programmes (detecting non-compliant activities, at-sea fishery-independent observers, educational programmes and professional development for fishers, etc.) are usually an important aspect of any fisheries management regime. For example, this was addressed early in the development of the western rock lobster fishery. In the 1960s, effort limitations were introduced and it was probably not a coincidence that illegal fishing activity became widespread. Subsequently, undersized animals and egg-bearing lobsters stripped of their brood were being processed and this illegal market spread from the local markets to markets in eastern Australia. As a result, measures were introduced to counteract the problem, specific legislation to restrict processing to licensed establishments, more inspectors, increased fines for offences, convictions recorded against the vessels rather than their skippers, and licenses cancelled after the third offence. These measures helped to make this fishery a highly compliant industry. Even today, much effort goes into ensuring compliance and research into improving the efficiency of compliance (McKinlay & Millington, 2000; McKinlay, 2002). As few as two from every 1000 animals checked by enforcement officers are found to be illegal.

An early assessment by the Department of Fisheries in Western Australia concluded: ‘Overall, the (western rock lobster) fishery is unlikely to cause significant trophic (“food web”) cascade effects, as the protected sub-legal-sized lobsters and breeding stock components form a relatively constant significant proportion of the biomass which remains

from year-to-year, and the catch, particularly in inshore areas, is less than the annual variability in biomass due to natural recruitment cycles.' Nonetheless, the rock lobster-specific ecological risk assessment (completed in 2008) considered that, due to the lack of information, the removal of lobster in deep-water regions might be having some level of impact on the surrounding ecosystem, and this was classed as a moderate risk. Consequently the deep-water areas of the fishery have become a focus of research, with preliminary work, now completed, and continued monitoring and research to underpin management of the Capes Marine Park has been initiated to expand on these preliminary findings (Fletcher & Santoro, 2011). However, since most of the lobster biomass (the sub-legal sizes and ages) actually occurs in the shallow waters, any effects of fishing on the legal-sized parent stock is likely to have a major ecological impact in these shallow water ecosystems (MacArthur *et al.*, 2007). The sub-legal biomass is likely to have been heavily reduced by the cumulative effects of many years of fishing, relative to the natural situation. Although the extent of this reduction has not been estimated it is likely to be similar to the level of reduction of breeding biomass by the fishery relative to the unexploited level, which is targeted by the fishery to be retained at about 25% of unfished biomass – a 75% reduction. This infers that the trophic ecological impacts on other species from reduction of the sub-legal biomass by the fishery could be very substantial, and an important ecological consequence of fishing stocks down to levels as low as 25% of the unexploited lobster biomass.

MacArthur *et al.* (2007) also report that studies have found relative levels of western rock lobster biomass more than 300 times higher, and levels of egg production 100 times higher, inside unfished shallow water sanctuary areas relative to nearby fished areas. It is therefore likely that studies of the deep-water ecological interactions will not give a complete picture of the ecological effects of the fishery on food chains that would have existed prior to the commencement of fishing, or that would have existed under very light fishing pressure. Estimating these impacts requires a comparison of the distribution of the modern-day biomass across the

age spectrum with the estimated biomass and structure that would have existed prior to fishing (see Chapter 6), models of the food chain effects of the historic lobster removals relative to the unfished conditions, and models of the impacts of the current level of lobster harvests in the modern-day ecosystems.

The legislated design of western rock lobster pots, the materials they are made from and the strict control of replacement pots prevent 'ghost fishing' problems for lobsters arising as an issue. A study of human impacts on the marine environments of the Abrolhos Islands estimated that potting might physically impact only small areas of fragile coral habitat at the Abrolhos, where fishing is only allowed for 3.5 months of the year. Generally, throughout the coastal fishery, rock lobster fishing occurs on sand areas around robust limestone reef habitats covered with coralline and macro-algae such as kelp (*Ecklonia* sp.). This type of high-energy coastal habitat is regularly subjected to swell and winter storms and so is considered highly resistant to physical damage from rock lobster potting. The significant recent reductions in fishing effort to protect the level of breeding stock will also have reduced these risks even further.

1.4.3 Indirect effects – top-down forcing by predator removal

Marine food webs throughout the North Atlantic appear to have been altered dramatically by the depletion of large predatory groundfish (Frank *et al.*, 2006, 2007). Frank and co-workers observed that increases in the abundance of mid-level consumers such as forage fish and crustaceans responding to relaxation in levels of predation has been most evident in simpler, less diverse ecosystems where fewer unexploited predator species can play the functional role of those removed. While there have been some limited modelling studies in the Western Australian situation, and 20 species have been identified as known or potential predators on lobsters, there have been no studies of the effects of predator removal directly affecting abundance of *P. cygnus*.

1.4.4 Indirect effects – bottom-up forcing by bait subsidies

While the evidence for top-down forcing as the explanation for the boom in lobster abundance in LME 7, 8, and 9 has been gathering force, bottom-up effects may also play a role, primarily as bait subsidies to the lobster energy budget. Because traps in the Canadian and US fishery have escape vents, small lobsters may enter a trap, consume bait and leave. Herring bait can be detected in stomach analysis. As it is assimilated over time it gives an altered nitrogen stable isotope ratio in lobster tissue compared with that observed in lobsters feeding on a bait-free natural diet.

In the Western Australian LME 44 situation, there have been several studies of the role of bait in the lobster fishery. The conversion ratio of bait to landed lobster biomass in the fishery is about 1:1, across fishing seasons 2007–10, equivalent to an annual input of about 8540 t of bait in these fishing years. Estimates of the bait subsidy to lobsters vary from 13% to 80%, depending on the methods used and sample design of the studies. The most recent studies from inshore habitats where lobsters spend most of the early life and are in rapid growth phase indicate that lobsters may derive up to 30% of their energy supply from bait (Macarthur *et al.*, 2011). This also indicates that this extensive input of bait also has the potential for a significant ecosystem level impact on other species that feed on fish carcasses and the other forms of bait used in this fishery. The bait is primarily fish waste sourced from other countries (comprising 86% of the bait used in the 2009/10 fishery) and from other states of Australia, but also includes pig fat (1.3%) and kangaroo parts (0.2%). Modelling studies suggest that the bait provisioning for the ecosystems and species other than lobsters potentially results in enhanced populations of a wide variety of species, potentially disrupting natural species and ecosystem level structure and function (Metcalf *et al.*, 2011), supporting the earlier studies indicating significant ecosystem disruption by the use of bait in this fishery (Waddington & Meeuwig, 2009). An important impact of this bait subsidy in this ecosystem is likely to be for octopuses, which have been observed to enter the traps and consume bait.

The octopus population is emerging as a subsidiary fishery in the region, and the enhanced octopus populations may also have ecological impacts on other benthic species in the shallow inshore reef ecosystems.

1.4.5 Climate change impacts

This is a development for lobsters and their fisheries that has been recognized over the last 10 years. However, oceanographic aspects have been studied for much longer. It is also important to distinguish between climate dynamics and climate change trends. Aspects of both climate change and climate dynamics include changes in sea level, temperature, salinity, acidity, ocean circulation and consequent medium- to long-term changes in the ecology of species in the marine environment (see also discussion in Chapter 4 and Chapter 8).

In the LME 44 region, Caputi *et al.* (2010) and Caputi *et al.* (2010) reported that climate change is causing an increase in water temperature that is seasonally variable, a weakening of westerly winds in winter, and an increase in the frequency of El Niño events. Rising water temperatures over 35 years are hypothesized to have caused a decrease in size at maturity and size of migrating lobsters from shallow to deep water, increases in abundance of undersized and legal-sized lobsters in deep water relative to shallow water, and shifts in catch from shallow to deep water. The size of migrating lobsters is hypothesized to be related to the water temperature about the time of puerulus settlement (4 years previously). Climate change effects on puerulus settlement, catchability, females moulting from setose to non-setose, timing of moults, and peak catch rates were assessed. As climate change models project that the warming trend will continue, these biological trends may also continue. The changes may have negative (increasing frequency of El Niño events) or positive (increasing water temperature) implications for the fishery, which need to be taken into account in stock assessments and management.

Cheung *et al.* (2011) reported on the development of an approach that applies the projections of global climate change impacts on marine biodiversity, fisheries and socioeconomics to develop

EBFM that is relevant to regional and local scales of management. This approach is being trialled for the West Coast Bioregion in Western Australia. There are no data arising from this project to date.

Projected climate change impacts on natural resource and socio-economic sectors of the northeast USA were examined in Northeast Climate Impacts Assessment (Frumhoff *et al.*, 2007), which featured the American lobster as a case study. The assessment modelled impacts under a range of carbon emissions scenarios projected by the International Panel on Climate Change (IPCC). The study employed three global atmosphere–ocean general circulation models: U.S. National Atmospheric and Oceanic Administration’s Geophysical Fluid Dynamics Laboratory (GFDL) Model CM2.1, the United Kingdom Meteorological Office’s Hadley Centre Climate Model, version 3 (HadCM3) and the National Center for Atmospheric Research’s Parallel Climate Model (PCM). Model output included projections of precipitation, air and seawater temperature, pressure, cloud cover, humidity, along with other climate variables downscaled to sub-regions of interest in the northeast USA. Downscaling of model output to these sub-regions involved coupling the coarse scale climate models with finer-scale regional models of ocean dynamics.

1.5 Single species to ecosystem management – how far have we come?

The essence of the shift from the more traditional single-species management approach to the EBM of fisheries is to manage the targeted species and the impacts of fishing in the context of the broader ecosystem and its condition. This is so that fishing does not directly, inadvertently or indirectly degrade the condition of the ocean ecosystems, and gives both the biodiversity of the oceans and the populations of the fished species the highest level of resilience to both the impacts of fishing itself and other environmental impacts. The EBFM approach also recognizes that there are multiple fisheries that operate in an ecosystem, and that they may interact

with each other in direct and indirect ways, and they may have cumulative impacts on non-target species in the ecosystem. By using objectives and values for ecosystem and fishing in equal part, this creates a coupling between natural and social systems that has been missing from the traditional systems of single-species management and is key attribute of effective forms of EBFM (Essington & Punt, 2011).

It is normal for the fisheries management systems (such as often described in EBFM) to be responsible for designing and delivering many of the management actions, but the key difference between what is now emerging as EBFM and what is considered to be EBM is the full integration of the social and ecological values of the ecosystems into the resource harvesting systems. It turns out that taking a comprehensive approach to EBM in fisheries management involves taking a more precautionary approach to stock management, recognizing that there are many uncertainties that are practically unknowable, and explicitly incorporating non-targeted aspects of the ecosystem into the setting of fishing objectives to ensure that high levels of resilience are maintained in the ocean ecosystems. This benefits the natural systems and also the social systems, as it usually requires a rebuilding of target stocks to higher levels, from which, in most cases, greater harvest can also be taken than is currently the case.

Many of the key issues and steps towards a more effective EBM approach to fisheries management were described by Ward *et al.* (2002), and there have been various subsequent interpretations and proposed developments of this approach. However, the implementation of the various aspects of marine EBM and EBFM is far from uniform or agreed. A complete issue of the journal *Fish and Fisheries* was recently devoted to discussing the topic (Essington & Punt, 2011), and it is clear that there are still a number of disagreements about what the concept of EBFM means in practice and how it represents the broader practice of EBM for marine ecosystems. In lobster fisheries, there are no standard approaches to EBFM that have yet been adopted, although there are a number of research programmes underway studying various elements that will be needed in a complete EBFM (such as

Fletcher *et al.*, 2010). The main stumbling block to adoption of a complete and effective form of EBFM – such as the approach described for Antarctic fisheries by Constable (2011), and demonstrating the features advocated by Rice (2011) – in lobster fisheries is the very low level of current lobster populations, and the complexity and variety of scales of the ecological and social systems that lobster fisheries operate within.

Significant reductions in total fish biomass through high levels of fishing can affect ecosystems, since species of one or more higher trophic levels are effectively removed allowing other lower trophic levels to expand, and eventually become the focus of fishing ('fishing down the food web'; Pauly *et al.*, 1998, 2002). Similarly, the excessive reduction of the biomass or species making up other lower trophic levels can also result in a flow-on effect at higher trophic levels, reducing the food available for predators that would have otherwise preyed on these lower trophic level species. While this effect is perhaps most easily observable with effects on large predators (sharks, billfish, birds, etc.), the trophic consequences of excessive fishing of middle and lower trophic order species also flows to all life stages, including the newly spawned and juvenile individuals, which are themselves preyed upon by small predators. This includes lobsters, which may be best classified as middle order trophic order species, despite their ontogenetic shifts in dietary preference and relatively broad range of food items at specific ages (MacArthur *et al.*, 2007). Such 'trophic cascade' effects are most likely to be observed in ecosystems that do not have highly effective fishery management controls, or where management systems do not retain appropriately high stock biomass levels and avoid the fish-down of stocks of target species to ecologically low levels. Fishery management systems in general do not give any significant priority to maintaining predator abundance at levels that will maintain top down trophic function, or to monitoring or avoiding trophic cascades (Rice, 2011).

1.5.1 *Panulirus cygnus*

All fisheries in Australia's LME 44 region are subject to management plans that embrace the prin-

ciples of EBFM as opposed to single target species management approaches (Smith *et al.*, 2007). For the 21 managed fisheries in the region, 15 have published Stock Assessments and 16 have published Ecological Risk Assessments (Fletcher & Head, 2006). Of those with published Ecological Risk Assessments, one fishery had inadequate spawning stock levels, one had moderate bycatch species impacts, one was assessed as having moderate protected species (marine mammal) interaction, two were assessed as having moderate food chain impacts, and one had moderate habitat impacts.

Australia is committed to fisheries ecosystem management but the use of fisheries ecosystem management is not arranged around the LME boundaries. The defining basis for EBFM as practised in Western Australia is that the scope of issues covered is restricted to those that can be managed by the relevant fisheries management agency (hence the 'F'), as well as those that need management reaction and can be influenced (as opposed to delivered) by the fisheries management agency. In this sense, EBFM can therefore cover either part of a fishery, all the issues affected by an entire fishery, up to managing the full collection of fisheries operating in a region (which would then also deal with their cumulative impacts and the allocation of resource access amongst the individual sectors), but only to the extent that this can be influenced by the fisheries management agency. The level chosen for management intervention will depend upon the scope of the assessment required and the jurisdiction of the agencies involved. However, to implement EBFM fully would not only require the management of all fishing-related activities, but all other activities operating within the region that potentially affect fishing (Fletcher, 2008). This contrasts with the broader ecosystem management approach, which deals explicitly with all issues across an ecosystem or region, and includes the management of all aspects of fishing and fisheries management as an integrated component of EBM (Ward *et al.*, 2002). This broader approach mandates the involvement of a wider range of agencies and stakeholders than the narrow approach of EBFM with its focus on fisheries production, and potentially results in more inclusive processes of

consultation and more robust area-based management arrangements and outcomes.

In Western Australia the Department of Fisheries recognizes the West Coast, South Coast, Gascoyne, Pilbara and Kimberley bioregions. The West Coast Bioregion is approximately equivalent to the boundaries of LME 44. Within the Australian West Coast Bioregion the department has identified the biological resources that are to be managed. These resources include the ecosystems and their constituent habitats, captured species and protected species. The risks associated with each individual ecological asset are examined separately in the EBFM framework using a formal qualitative risk assessment system based on judgements by the fishery managers about the consequences of an event and the likelihood of that event occurring, or more-simple problem assessment procedures (Fletcher *et al.*, 2010).

Fletcher *et al.* (2010) report on a study using the West Coast Bioregion in Western Australia to assess if a regional framework could assist in providing for better natural resource management planning at a regional level and could also meet the legislative responsibilities for managing fisheries and aquatic ecosystems in a more holistic manner for EBFM purposes. They found that the framework that they used was able to meet both of these objectives because a pragmatic, management-focused approach was taken. The potential complexity of EBFM was addressed using a step-wise, risk-based approach to integrate the issues identified and information gathered into a form that could be used by the fisheries management agency. The levels of knowledge needed for each of the issues were matched to the level of risk and the level of precaution adopted by the fisheries management system. Uncertainty in estimating the risks is a significant issue when considering the ecological, social and economic risks but implementing the EBFM approach used by Fletcher *et al.* (2010) made pragmatic decisions about risk and uncertainty, and did not automatically generate the need to collect more ecological, social or economic data or require the development of complex ecosystem models. This EBFM framework also accommodated to some extent the expectations of stakeholders by using a hierarchical approach so

that stakeholder groups could input their issues. However, the EBFM process subsequently consolidated these to be effectively used in specific fishery management planning issues. This approach, being able to determine the relative priority for management of all fishery assets in a region, allowed the framework to provide for an efficient use of government resources to manage the fisheries of the region because expenditure currently directed towards low-risk elements can be redirected towards higher risk elements.

In addition to the developing EBFM framework, all fisheries in Australia's West Coast Bioregion within LME 44 are subject to management plans that are intended to embrace the principles of EBFM as opposed to single target species management approaches. The fishery management plans have components that identify the interactions with the various other fishery resources that either coexist in the area or may have significant interactions. This includes ensuring that impacts of fishing gear on habitats that may be important spawning or nursery grounds for another fished species are restrained or avoided, and that the impacts of introduced pests or industrial sites on habitats that are important for the fisheries are avoided as far as possible.

The form of EBFM being developed in Western Australia is an important first step towards development of an effective framework for the spatial management of all fisheries that occur in a region of the LME scale. The next phase in the development of this fishery management process is to identify mechanisms to further engage with other agencies involved in the management of activities within the marine environment in LME 44 and to determine how their processes link to the EBFM framework to be applied in LME 44. For this to be successful, prior agreement will be required on these aspects to facilitate the process:

- the determination of the spatial structure and distribution of the ecosystems and habitats in the region – there are currently two widely accepted but different regionalizations that are used for different management purposes in the LME
- what constitutes the key areas and elements of the ecosystems – this is currently in develop-

ment by the federal government and disputed by the state-level fisheries managers

- what standards are to be applied in managing the ecosystems and species – there are no national or state-wide standards other than production standards for fished species, and
- what monitoring and reporting systems will be implemented to confirm compliance – there are only limited national or state-wide monitoring systems in place, principally for stocks of fished species.

Eventually this should lead the design and implementation of an effective system of EBM for LME 44 that incorporates the fishery management systems currently being planned and implemented as EBFM.

Other specific improvements in recent years for the *P. cygnus* fishery include the development of a model for the fishery that can include aspects of climate change (Cheung *et al.*, 2011) and the development of a larval advection model to assess the relative contribution of larval production from different areas of the breeding stock to the abundance and distribution of puerulus settlement (Feng *et al.*, 2011).

While Australia and some other nations are beginning to implement aspects of EBFM for all their fisheries, including those for lobsters, there is no doubt that much work remains to be carried out (Essington & Punt, 2011). Pitcher *et al.* (2009) reviewed progress towards the implementation of effective mechanisms for EBFM, and found that more than half of the top fishing nations (including Australia) failed to demonstrate an acceptable level of implementation of the basic principles of EBFM, and did not have appropriate performance assessment indicators in place. The management system for Western Rock Lobster performs only weakly against the Pitcher *et al.* (2009) criteria (see below).

The process of extending the single-species fishery management concepts into the EBM of whole ecosystems using EBFM approaches has proved to be fraught with many difficulties, and there are no documented successes involving lobsters. Much of this is caused by the failure of the concepts of EBM to be fully recognized within the fisheries context (as expressed in EBFM), and is

related to the well-recognized problem of dealing effectively with the complexity of ocean ecosystems within a fishery management system that has arisen historically from managing a single species. This will continue to remain a problem if the ecosystem complexity remains primarily a matter to be addressed in the existing domain of EBFM governance (Rice, 2011) rather than extending the conceptual approach to be more inclusive, and more closely resemble EBM as a whole. Central ecosystem complexities to be resolved include the difficulty that fishery management systems have in meeting the trade-off that must be achieved in providing allocations of stock to meet the demand for harvesting while simultaneously meeting the ecological demands for high stock levels to be retained to provide for other ecosystem services such as an abundance of the fished species for predators and related dependent species, and the retention of the natural biodiversity attributes (such as the natural form of age/size structure) of fished populations to provide for high levels of natural resilience and ecosystem function. These, and a range of similar ecological attributes of populations, are important as management endpoints for a system of marine EBM to be effective, and are important indicators of the success of EBFM in maintaining the resilience of ocean ecosystems and species diversity in the face of many interacting fishery and non-fishery pressures and the highly complex uncertainties within the fisheries management systems themselves (Ward *et al.*, 2002; Rice, 2011).

Rice (2011) identifies the critical importance of extending governance systems and stakeholders beyond the usual fishery and existing EBFM models if the goals and objectives of EBM of the oceans and their resources are to be achieved. The concept proposed by Rice (2011) draws on the principles of EBM and outlines four requirements for EBFM (or EAF as preferred by Rice) if it is to be effective:

- take account of the main extrinsic forces on the dynamics of fished stocks
- be accountable for the full suite and magnitude of the impacts of fishing
- be governed by processes that are comprehensive, inclusive and participatory

- have decision-making integrated across all sectors that impact the same ecosystem and its values.

These requirements for a fishery to implement an effective form of EBFM are also reflected in the elements of a successful EBM framework as outlined by Ward *et al.* (2002) and Pitcher *et al.* (2009). Many of the issues identified by Ward *et al.* (2002), Pitcher *et al.* (2009) and Rice (2011) remain to be substantively addressed in lobster fisheries. This includes issues such as the intense harvest of new recruits, where high fishing mortality rates are annually applied, apparently leaving only very limited biomass to grow through to the older age classes, the extent of which is considered by Ward *et al.* (2002) and Rice (2011) to be an important indicator of the success of the EBM approach.

The western rock lobster fishery for *P. cygnus*, assessed using the scoring criteria applied by Pitcher *et al.* (2009) (which also represent most of the features raised by Rice, 2011) in their global assessment of EBM (Table 1 in Pitcher *et al.*, 2009) does not demonstrate the elements of an effective form of EBM. The weakest aspects of the present-day system of EBFM in this fishery, assessed using the criteria of Pitcher *et al.* (2009) are

- lack of a broad base of stakeholders from outside the fishing sector who are actively engaged and participate in the setting of shared vision, objectives and targets based on intended outcomes for the ecosystems;
- limited understanding of the ecological role of the target species in the ecosystem, and the consequent lack of knowledge about the direct and indirect effects of the fishery on the ecosystem;
- limited understanding of the ecosystem values and the major factors that impact those values in LME 44;
- a limited performance assessment and review system for environmental impacts of the fishery, with only minimal information about this matter placed in the public domain; and
- a minimal education and training system in place for fishers in respect of ecosystem and resource values across LME 44 – there is only

limited set of processes to inform and maintain current awareness about ecosystem issues in the fishery participants, and there is no formal or informal process/programme for updating and up-skilling the fishery participants, or for redeployment of displaced fishers into other fields of activity.

On managing externalities, there is a strong recent focus in this fishery on the relationships between climate change and variability and recruitment, which is important for setting of harvest strategies, although little apparent focus on of climate factors on growth and natural mortality, both likely to be more important features of an effective stock assessment system operating within a competent EBFM context (Rice, 2011). Other fishing pressures that may have had some impacts on LME 44 in the past include the destructive fishing practices of foreign distant water trawling and long lining fleets, but these have been virtually fully eliminated by strong federal government action to prohibit entry without strict licence conditions.

1.5.2 *Homarus americanus*

In contrast to the collapsing American lobster population in the southern part of the species range, abundance of the lobster in the Gulf of Maine and parts of Atlantic Canada have surged to unprecedented levels in the past few decades in the wake of severe groundfish depletion. While other contributing factors cannot be ruled out, the strong correlation between the decline in fish and the increase in lobster has been taken to indicate a cause–effect relationship (Acheson & Steneck, 1997; Worm & Myers, 2003; Boudreau & Worm, 2010; Wahle *et al.*, in press). The need for an EBM framework, incorporating a broad range of species and their interactions with each other and lobsters, and the environment, is therefore obvious. Managing the ecosystem to recover the fish populations will, if the negative causal relationship between fish and lobster abundance is as strong as is postulated, be likely to suppress the population recovery of *H. americanus*. This could have significant consequences for the population and the lobster fishery

in all parts of its range, as well as other ecological consequences.

The focus of management of *H. americanus* has so far been on developing a better understanding of the ecological relationships and the environmental drivers of the population. In many ways, this parallels the research initiatives for *P. cygnus*, and despite the large difference in the sizes of the two populations and the associated fisheries, progress on development of a more integrated and EBM system is similar for both species. Emphasis in US waters has been on securing a workable institutional structure, with the establishment and operations of the state and cooperative federal structures, and on securing protection for sensitive and iconic habitat types, such as deep-water corals. Despite intensive research activities in development of ecosystem-based modelling systems (Link *et al.*, 2011), these have been only developed for fish, and have not included the invertebrates, and so progress towards fully effective forms of EBFM has been slow. As in the *P. cygnus* fishery, key issues revolve around bringing the institutions and values of all relevant stakeholders into the management process, as well as the ecological and environmental drivers. This is to establish an acceptable set of trade-offs among the various competing interests while simultaneously ensuring that the structure and function of the ecosystem itself is retained to provide resilience to changes in climate and trophic interactions in the medium and long term.

Considerable further activity is required to develop an effective EBFM system for both *H. americanus* and *P. cygnus*. In the case of *H. americanus*, the global review of EBM in fisheries (Pitcher *et al.*, 2009) found that while the USA was ranked as ‘good’ (score of >60%) on the overall set of EBM criteria (along with Norway), implementation of EBM was not ranked highly. This is consistent with the explanation that although there is considerable technical capacity and underpinning theory for the development and implementation of EBFM (in both the USA and Canada) as it could be applied to *H. americanus*, uptake of the principles of EBM into the actual management process for these lobster fisheries has been lagging. This also applies in the case of *P. cygnus* in Australia.

1.6 Implications for management and research

1.6.1 Top-down, bottom-up ecology

The relationships among the world’s lobster species and their predators and prey at the different stages of their life cycle is universally considered to be poorly understood, yet is central to the advancement of understanding the ecological effects of lobster fishing (the real footprint of the fishery). The ecological interactions are only weakly understood – from the role of the pelagic 0+ year class as food for other zooplankton and juvenile fish, to the predation of 20+ age class of lobsters on benthic communities in offshore water and their predation by large fish. Knowledge of these relationships is a major impediment to understanding the ecological effects of the major reductions in population biomass as a result of fishing, and is a major impediment to developing an effective system of both EBFM and ultimately EBM for the ecosystems and habitats utilized by the lobsters.

Other important aspects of the lobster trophy-dynamics includes further analysis of the significance of bait input to the ecosystems where lobsters are fished using baited traps/pots. There is evidence that, at least in the *P. cygnus* population, the bait may be contributing significantly to local production, and this may also be having significant broader ecological impacts on other species (MacArthur *et al.*, 2011). It is unclear if this is having a beneficial or detrimental effect on either the lobster populations or their fisheries, or on the associated ecosystems through alteration to food webs and energy flow.

1.6.2 Inclusive governance systems

Probably the major single failing common to all commercial lobster fisheries is the lack of an effective system of governance that contains all the necessary elements to provide for both EBM and the subset that is EBFM. This is both institutionally difficult and, at least initially, may be expensive to implement to secure the required trade-offs between production and the environment. However,

continuing with governance systems that are both dominated and controlled by fisheries management institutions is not likely to be a successful approach to implementing EBM that includes fisheries, and there are no demonstrated successes. In contrast, where there is inclusive governance, of which fisheries management is part but is not the controlling component, there are demonstrated successful examples of EBM and EBFM.

Nonetheless, further research is urgently needed to better analyse and understand the successful elements of the existing EBM models that are being at least moderately successful, such as that of CCAMLR (Constable, 2011). This is research that couples the ecological, biological, social and institutional issues and their effective resolution with outcomes that provide for the long-term security of lobster stocks and other species sharing the same ecosystems, including high levels of population and ecosystem resilience. There are simple rules of thumb to guide assessments of the effectiveness of such governance systems (Ward *et al.*, 2002; Rice, 2011), but studies of how specific aspects of governance systems can be developed and implemented in the various environmental, social and economic contexts of a variety of the world's lobster fisheries remains as a very high priority.

1.6.3 Stock rebuilding strategies

Fished lobster populations worldwide are low, compared with both their own intrinsic benchmarks and those established for other marine species. While it is well understood that being highly fecund, broadcast spawners, and having widespread distributions confers a measure of resilience against the effects of fishing, and most likely avoids species extinction in the short term, these attributes have not prevented other species from coming under severe population pressures from the combined impacts of excessive fishing and environmental change. In the concept of EBM, populations of targeted species fulfil several important functions in addition to providing for continuing harvests, and particularly for maintaining ecosystem structure and function, and providing resilience in the face of the changing climate. Rebuilding lobster populations to higher levels offers the further

benefit of permitting catches to be progressively increased from their currently depressed level (in most places), albeit probably not to the historically highest ever levels of yield. Further, while the global catch of lobster is increasing, this is primarily driven by the increasing yield from the northern populations of *H. americanus*. In this case, the increase in yield is not uniform across all areas of the fishery, and is thought to be confounded with the effects of fishing activities for the finfish species.

It is clear that incrementally increasing the absolute size of lobster populations, even if maintaining the current level of fishing mortality relative to population biomass, is likely to be the most appropriate long-term precautionary approach to increasing overall yield from the world's lobster fisheries. To enable this to happen, new approaches to population rebuilding need to be designed and trialled. This could include, for example, explicit allocation of long-term rebuilding targets within harvest strategies, passive allocation of closed areas for enhancement of breeding biomass, setting escapement limits for age/size classes, setting aside areas for enhancing settlement success, and increasing legal catch size limits to promote increased reproductive success. Irrespective of the specific strategy, these and other likely effective approaches need to be trialled across a number of the world's managed lobster fisheries, lobster species, and ecosystem types.

1.6.4 Environmental drivers of settlement patterns

The environmental factors that affect the distribution and then ultimately the settlement of young lobsters from the planktonic phase, while different for each species and in some cases different among areas, is a major component of uncertainty that affects the management of all lobster species. Further research is needed to build better models of behaviour and distribution of the planktonic stages, to provide for ultimately a better understanding between the abundance and distribution of breeding biomass and the eventual recruitment of mature lobsters into the fishery that have survived the planktonic phase. This is a central and substantial

uncertainty that plagues lobster fishery management at all levels. The continuing studies on the environment and recruitment of *P. cygnus* by Feng *et al.* (2011) and *H. americanus* (Wahle *et al.*, 2004, 2009) are important steps in this direction.

1.6.5 Historical ecosystem structure

The structure and function of the ecosystems, the dominant predator–prey relationships, and the trophodynamics of the unexploited ecosystems are largely unknown in LME 44 in Western Australia, and not well understood in LME 7, 8, 9 in Canada and the USA. While knowledge of these matters is currently embryonic, it is central to developing a long-term understanding of the dynamics of change in these ecosystems that has affected lobster abundance and distribution, and also for developing a better understanding of the drivers and causes of broader ecosystem changes that have been observed. In recovering populations of species that have been heavily fished, such as these two lobster species, it is critical to be able to compare present-day conditions in both their populations and their ecosystems to the conditions of the past. This involves developing models of past conditions and dynamics, and preparing benchmarks against which the modern day conditions can be compared. For each of the lobster species, for an effective use of the EBM approach, estimates of the historic habitat-based distribution, abundances, size structure in the population and patterns of migration would be needed. This knowledge can then be used in ecosystem models with productivity parameters to develop a better understanding of the current condition of the lobster populations relative to their long-term history, and better inform both the likelihood of being able to rebuild both populations and productivity to former levels and management approaches that might be most successful. For example, for *H. americanus*, determining the strength and patterns of top-down population control that has been applied by the fish predators that have now been reduced to low abundances will allow a considerably improved level of resolution to be applied in bio-economic models designed to rebuild fisheries (lobster and finfish) across the region in both a systematic and timely manner. These models should

also be able to predict the recovery of other important population parameters such as the diversity of age and size structures, which is important to rebuilding resilient structures and functions in the lobsters' ecosystem. The alternative is to remain transfixed by the single-species management systems of the past, which search for simple population relationships and drivers, and then proceed to erect complex collections of individual and weakly connected corrective management arrangements that may not achieve the desired outcomes, falling foul of the system complexity.

The LME region 7 (North eastern US shelf) is now considered to have a strong theoretical basis for modelling the complexity, and early results (Link *et al.*, 2011; Smith, 2011) indicate important implications for policy development. These include confirmation of the obvious outcomes that the maximum sustainable yield (MSY) single-species approach to setting harvest limits cannot be used individually for a group of species that have ecological interactions. In short, the sum of the individual MSY is greater than the MSY developed for the combination of species (Smith, 2011). This infers that use of multiple single-species MSY limits for fisheries will result in overharvesting when taking into account the suite of ecological interactions amongst the ecologically related species and the effects of ecosystem dynamics.

1.7 Conclusions

Mahon *et al.* (2010) studied the governance characteristics of LMEs. They reported that LME 44 and LMEs 7, 8 and 9 are among the LMEs considered to have high capacity for good governance in that they are among the least complex LMEs with a highly functional institutional environment and capacity for effective governance. This, coupled with low heterogeneity among countries, will probably reduce the likelihood of conflict. The LMEs considered here (44 in Western Australia and 7, 8 and 9 in Canada and the USA) would probably be most amenable to conventional hierarchical governance through interplay of national/international instruments, supported by strong technical inputs. The countries of these LMEs are also those most

likely to have the enforcement capacity required for this approach. The indication is simply that these are the LMEs where this approach would have the greatest chance of successful governance.

Pitcher *et al.* (2009) made an evaluation of progress in implementing EBM of fisheries in 33 countries. Of the six indicators chosen to measure the readiness to implement EBM only the USA, Norway, New Zealand, South Africa, Australia and Canada had scores suggesting that they were likely to achieve reasonably effective implementation of EBM. Clearly, development of institutional systems

that provide for good governance that is consistent with the principles and practice of EBM can be most easily developed in these countries, but, even there, a lot of challenges remain. In other countries, efforts to implement EBM, and effective forms of EBFM, need to be redoubled, perhaps with institutional reforms and improvements to provide effective forms of governance that are agreed and appropriate to local cultural, social and economic conditions, but still deliver the principles and practice of EBM, and the various models of EBFM that are nested within EBM.

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Chapter 2

Genetics of Wild and Captive Lobster Populations

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Abstract

There has been a significant increase in the number of genetic investigations into lobster biology in recent years. We summarize and evaluate the insights provided by these studies, with emphasis on population structure, reproductive biology, diet, species identification and fisheries-induced evolution. The applications of genetic techniques are far reaching and likely to become increasingly important to aquaculture and fisheries research and management. In particular, applications of species identification and DNA barcoding techniques allow for surveillance of product substitution and contamination. It can also be used to map species distributions, understand food webs, attribute catch to stocks and for mapping the distribution and abundance of planktonic larvae. We conclude by discussing how the development of new genetic technologies is likely to deliver further novel insights about the biology of lobsters and provide important foundations for future fisheries management.

Key Words: population structure; stock assessment; species identification; DNA barcoding; genetic techniques; fisheries management

2.1 Introduction

The last few decades have seen a dramatic increase in the number of genetic studies on lobsters (Fig. 2.1). Typically, these studies involve the use of molecular markers to investigate aspects of the ecology and reproductive biology of populations. Advancements have also been made in the understanding of the phylogenetic relationships among taxa (e.g. Ptacek *et al.*, 2001; Palero *et al.*, 2009a,b).

In this chapter, we review genetic studies carried out on wild and captive lobster populations. These studies fall into four main categories: evaluation of population structure, species identification and dietary analysis, evaluation of reproductive biology and investigations of fisheries induced evolution. Our aims are to report on the work that has been carried out in these areas and to explain the implications of this work to fisheries management and aquaculture.

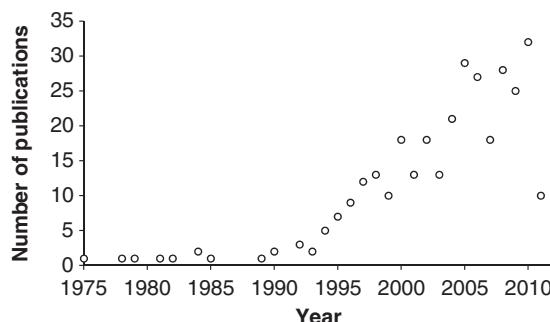


Fig. 2.1 Change in the number of articles indexed on the Web of Science database with key words 'lobster, DNA, Genetic, allozyme and isozyme' between 1975 and May 2011, and screened for topic of ecology and evolution, not physiology and molecular biology.

2.2 Population structure

Natural populations of most species can be subdivided into separate subpopulations or demes in which random mating takes place. When there is subdivision, or population structure, genetic variation (the presence of two or more forms of a gene or alleles) within the species exists at two levels: (1) genetic variation within local populations and (2) genetic variation among local populations. The level of population structure is often represented by the F_{ST} statistic (Wright, 1931), which measures the proportion of the total genetic variation due to differences among subpopulations. F_{ST} varies between 0, when all subpopulations have the same allele frequencies (no divergence), and 1, when all subpopulations are fixed for different alleles (complete divergence).

The existence of population structure within a species suggests there are strong barriers to demographic exchange between populations. This is because even small amounts of genetic exchange between populations (gene flow) are enough to prevent large allele frequency differences establishing. For example, one migrant per generation moving between local populations will prevent different alleles being fixed in each population, and 10 migrants per generation will ensure that allele frequencies are essentially the same (Slatkin, 1987). It should be noted that these numbers are the

effective number of migrants, which in most cases is much smaller than the actual number of migrants. For commercially exploited species, failure to detect underlying population structure is a concern because it may result in overexploitation and depletion of localized subpopulations, with a corresponding loss of genetic variation (Carvalho & Hauser, 1994; Begg *et al.*, 1999).

In marine species the level of population structuring is largely determined by the dispersal capacity of individuals. Species with planktotrophic larvae that spend months in the water column tend to maintain low levels of genetic structure across large geographic scales, while those with short planktotrophic larval phases or that are direct developers usually have much higher levels of subdivision (Waples, 1987; Palumbi, 1994; Johnson & Black, 2006; Lee & Boulding, 2009). While these patterns hold true for many species, the level of structuring is sometimes influenced strongly by other factors. For example, impediments to dispersal created by topographic or oceanographic features can lead to moderate to high levels of population structure in planktonic dispersers (Lavery *et al.*, 1996; Barber *et al.*, 2002; Taylor & Hellberg, 2003). Adaptation to local environments (e.g. low salinity or temperature) can also lead to genetic differences between populations at genes under selection and linked neutral loci, even when there are high levels of dispersal across the species' range (Nielsen *et al.*, 2009).

In spiny lobsters, most species are characterized by an absence of genetic population structure, consistent with their capacity for high dispersal during an extended planktonic larval stage (Ovenden *et al.*, 1992; Silberman *et al.*, 1994; Thompson *et al.*, 1996; Tolley *et al.*, 2005; Inoue *et al.*, 2007; García-Rodríguez & Perez-Enriquez, 2008; Naro-Macié *et al.*, 2011). However, in some species, barriers to dispersal have led to significant differences in allele frequencies between localities. For example, in a survey of allozyme variation along the Baja California Peninsula, Perez-Enriquez *et al.* (2001) found a pattern of genetic differentiation in red spiny lobster (*Panulirus interruptus*) that was consistent with the presence of three subpopulations ($F_{ST} = 0.101$). They hypothesized that the subpopulations, occurring in the southern,

central and northern regions of the peninsula, were a consequence of cyclonic semi-permanent eddies limiting the mixing of larvae between regions. An alternative explanation for the pattern was that it resulted from a phenomenon known as ephemeral genetic patchiness, which will be discussed in the next section.

The retention of larvae by oceanographic processes is also thought to be responsible for the mitochondrial (mt)DNA sequence divergences between populations of spiny lobster (*Palinurus delagoae*) along the South African coastline (Gopal *et al.*, 2006). In the European spiny lobster (*Palinurus elephas*) a combination of both oceanographic processes and geographic formations appear to contribute to genetic differentiation among regions across the species' range. Palero *et al.* (2008) showed significant differences in mtDNA sequence variation between Atlantic and Mediterranean regions, as well as between localities within each region. They attributed divergences between regions to reduced gene flow between populations, while genetic differentiation between localities within the Atlantic region (Brittany and Ireland–Scotland) were explained by the effect of the Gulf Stream and meso-scale processes caused by incoming Atlantic waters were thought to be responsible for genetic differentiation within the Mediterranean. In other examples, genetic structuring within species has been attributed to barriers created by large expanses of ocean or sharp salinity gradients. Analysis of restriction fragment length polymorphism (RFLP) variation in mtDNA by Brasher *et al.* (1992) revealed significant differentiation between populations of *Sagmariasus verreauxi* from southern Australia and New Zealand that were attributed to low larval survivorship while crossing the Tasman Sea. In Caribbean spiny lobster (*Panulirus argus*), Diniz *et al.* (2005) found divergences in mtDNA sequences between populations from the Caribbean Sea and Brazil that they attributed to a barrier imposed by a sharp decline in salinity caused by outflow from the Amazon and Orinoco rivers.

Patterns of population structure in Norway and clawed lobsters are similar to those found in spiny lobsters. The most comprehensive study on Norway lobster found low levels of population structuring

($F_{ST} = 0.018$) across the species' range (Stamatis *et al.*, 2004). Interestingly, this study, which was based on mtDNA sequence variation, found no signs of an Atlantic–Mediterranean divide. Stamatis *et al.* (2004) suggested that this was due to a recent demographic expansion of *Nephrops norvegicus* populations. More recently, a lack of differentiation between Atlantic and Mediterranean populations of *N. norvegicus* was also been found with nuclear DNA markers, providing further support for demographic expansion hypothesis (Stamatis *et al.*, 2006).

Clawed lobsters also show evidence of low levels of population structuring. An allozyme survey by Tracey *et al.* (1975) revealed genetic differences between inshore and offshore populations of American lobster (*Homarus americanus*), but only in one out of the 44 loci examined. Together with data from migration studies, which also suggest limited mixing of inshore and offshore populations, it was suggested that *H. americanus* was subdivided into local populations with little interbreeding between them. These local populations were, nonetheless, genetically very similar. More recently, a survey of microsatellite DNA variation also found little genetic differentiation between *H. americanus* populations, though one population showed much greater differentiation with other sampled populations, possibly due to a massive lobster die-off that occurred prior to the study (Crivello *et al.*, 2005).

Similar patterns of population structure have been observed in the European lobster (*Homarus gammarus*). An allozyme survey by Jørstad *et al.* (2005a) found low levels of genetic differentiation (overall $F_{ST} = 0.016$) across the species' range (Norway to North Africa). In particular, lobsters from three areas including northern Norway, the Netherlands and Aegean Sea in the Mediterranean were genetically different from lobsters from other regions. Low to moderate population structure was also found using RFLP analysis of mtDNA (Trianafyllidis *et al.*, 2005). Given the limited capacity for dispersal across the species' range, the low level of differentiation found in the European lobster has been attributed to all populations being derived from a common refuge after the end of the last ice age (~15,000 years ago). This example emphasizes

a key point made earlier, the absence of population genetic structure does not necessarily mean that all populations are part of a single population in terms of demographic processes because few migrants can homogenize allele frequencies. It can also be hard to disentangle the effects of historical versus contemporary gene flow.

2.2.1 Chaotic genetic patchiness

The term ‘chaotic genetic patchiness’ (Johnson & Black, 1982) is used to described non-patterned, small-scale genetic heterogeneity among marine populations. When this pattern exists, populations a few kilometres apart can be as genetically different as populations separated by distances of hundreds of kilometres. These patterns are also temporally unstable; differences between local populations emerge and disappear across generations (Johnson & Black, 1984; Watts *et al.*, 1990; Hedgecock, 1994b; Larson & Julian, 1999). Chaotic genetic patchiness is common, and is most often observed in marine organisms with planktonic larvae.

Genetic patchiness can arise from natural selection acting after settlement. Alternatively, it can result from temporal genetic variation in the larval pool, combined with patchy settlement (Larson & Julian, 1999). A clear example of how temporal variation of recruits can lead to genetic patchiness has been described in the western rock lobster (*Panulirus cygnus*). In this study, Johnson & Wernham (1999) examined allozyme variation in monthly collections of puerulus at two sites nearly 350km apart. While there were no allele frequency differences between sites in each monthly collection, allele frequencies changed over time. The combination of temporal variation in allele frequencies and contrasting patterns of recruitment resulted in genetically different cohorts at the two sites. In addition, the pattern was ephemeral as it was not repeated in the subsequent 2 years.

Various processes can cause temporal variation in the recruits including natural selection or changes in source population. However, one of the most important contributing factors is believed to be large variance in the reproductive success of individuals owing to sweepstakes-like chances of

matching reproductive activity with oceanographic conditions conducive for larval survival (Hedgecock, 1994a). Several life history characteristics of lobsters, such as high fecundity and planktonic larval stages that suffer high early mortality, suggest sweepstake reproductive success may be common in the group. This has two major implications for management. Firstly, unless clear barriers to dispersal are apparent, evidence of temporal stability of population structuring is needed before concluding the species is genetically subdivided. Secondly, a consequence of large variance in individual reproductive success will be that the effective population size (N_e) will be much lower than the census population size (Hedrick, 2005). Since the magnitude of genetic drift is determined by N_e , the ability of populations to maintain genetic variation may be much lower than it may seem. As we discuss later, there have been several examples where declines in genetic diversity have been documented in commercially exploited marine species even though census population sizes remained very high (many millions).

2.2.2 Post-glaciation demographic expansions

In addition to estimates of genetic diversity, tests for genetic differentiation among localities and the construction of phylogenies, analysis of DNA sequence data can provide valuable insights into the demographic history of populations. Two widely used methods include calculation of the summary statistics D (Tajima, 1989) and F_s (Fu, 1997), which can be used to test for a deviation from predictions based on a constant population size and no selection, and the calculation of mismatch distributions (pairwise nucleotide differences between sequences). The shape of the mismatch distribution varies depending on the type of demographic history. Multimodal distributions suggest a population of constant size, whereas a unimodal distribution suggests a demographic expansion. The timing of population expansions can be estimated using the formula $T = \tau/2\mu$, where T is the time in generations when the population expansion begins, τ is the age of the demographic change in mutational units estimated from the

mismatch distribution and μ is the mutation rate (Rogers & Harpending, 1992).

A consistent finding that has emerged when these analyses have been applied to lobsters is the occurrence of post-glaciation population expansions. Signatures of population expansions have been found in spiny lobsters (Tolley *et al.*, 2005; Gopal *et al.*, 2006; Palero *et al.*, 2008, Naro-Maciel *et al.*, 2011), clawed (Triantafyllidis *et al.*, 2005) and Norway lobsters (Stamatis *et al.*, 2004). They are often attributed to an increase in available habitat as glaciers melted and coastal regions were flooded. In some cases, population expansions may have involved ancestral populations that were fragmented into different glacial refugia, leading to the existence of divergent lineages within species (e.g. *Panulirus argus*, Naro-Maciel *et al.*, 2011). It also seems that some species were affected more than others by these historical events. Palero *et al.* (2008) found that *Palinurus mauritanicus* haplotypes coalesced at an older age than *P. elephas* haplotypes, indicating a smaller effect of the last glacial event compared to *P. elephas*. Since *P. mauritanicus* is found in deeper waters than *P. elephas*, they suggested that sea level and temperature changes would have affected *P. mauritanicus* populations to a lesser extent.

The population expansions that have occurred in lobsters require consideration when interpreting contemporary patterns. Low levels of population structure likely reflect ongoing larval dispersal, but may also be a consequence of demographic history. It follows that, for many species, current levels of genetic exchange between populations may be much lower than suggested by the observed level of structuring (e.g. European lobsters).

2.3 Species identification

Determining an organism's identity is a fundamental step in many aspects of biological investigation and fisheries management. Species identification relies on a taxonomic framework, which historically was developed largely through analysis of morphological characters. Increasingly this approach has been augmented by molecular characters (Yang *et al.*, 2008; Cabezas *et al.*, 2009). The

power of DNA sequence analysis for resolving evolutionary relationships comes from the processes of mutation, genetic drift and selection, which through time leads groups of organisms to differentiate. Unlike most morphological characters, DNA sequences evolve in predictable ways, and an understanding of this process facilitates the resolution of phylogenetic relationships (Hillis *et al.*, 1996). Molecular systematics has made important contributions to resolving taxonomic questions in lobsters and their allies, and to understanding the evolutionary origins of extant species diversity (Ovenden *et al.*, 1997; Ptacek *et al.*, 2001; Groeneweld *et al.*, 2007; Palero *et al.*, 2009a,b; Tsang *et al.*, 2009).

A spin-off of molecular systematic analysis that has particular relevance to understanding lobster biology and management is the concept of DNA barcoding (Hebert *et al.*, 2003a). The principle of DNA barcoding is that most species bear diagnostic DNA sequences, and their identities may be revealed through comparison to reference DNA sequences from known (ideally taxonomically vouchered) specimens (Hebert *et al.*, 2003a). In animals, a single gene, the mitochondrial cytochrome oxidase c subunit 1 (COI or *cox1*), has found wide usage as a standardized tool for distinguishing species (Hebert *et al.*, 2003b). COI is useful for this task because it has a high mutation rate, meaning it exhibits sufficient variation to distinguish species, and also, being a mtDNA gene, it occurs in high copy numbers in most tissues. This means that DNA sequence is readily obtainable even from small and degraded samples. An important advantage that DNA barcoding has over conventional species identification is that it is a near-universal technology, and so long as appropriate reference specimens are available, species can be identified without specialist taxonomic expertise. Furthermore, it is highly accurate. In a sub-phylum analysis including 23 of the 48 crustacean orders and 13 of the 17 decapod families, Costa *et al.* (2007) demonstrated that COI barcodes are highly effective markers for distinguishing decapod crustaceans at a variety of taxonomic levels, including species, where more than 93% were successfully distinguished. Similarly, da Silva *et al.* (2011) also showed that COI reference sequences for 101

non-lobster decapod species from the northern hemisphere identified only 3.6% of cases where species barcodes conflicted with morphological assignments, and some of the conflicts highlighted possible taxonomic ambiguity in those groups. These results are consistent with comparisons of species-level discrimination in a great range of vertebrate and invertebrate taxa indicate that the accuracy of DNA barcoding is usually above 95% (Hebert *et al.*, 2004; Barrett & Hebert, 2005; Ward *et al.*, 2005), and in many cases discrepancies between barcoding and conventional diagnosis have resulted from incomplete taxonomies, or mislabelled samples. A potential limitation of DNA barcoding is its reliance on access to appropriate reference sequences. Costa *et al.* (2007) showed that of the 17,635 described decapods, only 5.45% have COI reference sequences available.

Conventional DNA barcoding involves direct comparison of DNA sequences between a specimen and a reference. However, there are many variants on this approach that still rely on detecting DNA sequence differences between species, but which do not involve direct visualization of DNA sequences. Both conventional DNA barcoding and its variants for species identification have been applied to lobsters in a great range of research and management contexts and in both pre- and post-harvest situations. A profile of these applications and the methodologies most commonly employed is provided in the next section.

2.4 Applications of species identification and DNA barcoding to lobster research and management

2.4.1 DNA surveillance of product substitution and cross-contamination

Product substitution, where a valuable food product is illegally substituted for a less valuable product, is a well-described problem in the seafood industry (Yancy *et al.*, 2008; Rasmussen & Morrissey, 2009; Aranceta-Garza *et al.*, 2011), and DNA analysis of samples from wholesale or retail outlets is widely used to enforce accurate labelling of seafood (Gil, 2007; Rasmussen & Morrissey, 2009). Judging by

the lack of published accounts, product substitution is not as significant a problem in the fresh lobster industry compared with other seafoods. DNA-based surveillance is nevertheless a powerful application, and could readily be adapted for product surveillance in lobsters. The method has been applied to other crustaceans including prawns and shrimps and in at least one case it revealed widespread incorrect labelling (Pascoal *et al.*, 2008; Schiefenhovel & Rehbein, 2010).

Another application of species identification related to foodstuffs is in the detection of crustacean parts in products destined for consumption by individuals allergic to those products. Two per cent of the American population exhibit allergies to crustaceans (Sicherer *et al.*, 2004), and accuracy of labelling with respect to foodstuffs is required by law in many countries. Brzezinski (2005) described a simple and rapid DNA-based test to detect crustacean DNA in complex processed and cooked food products, and where crustacean DNA is detected, to identify the species present in the products, including multiple shrimp, lobster and crab species (see also Pascoal *et al.*, 2008). This method of surveillance has value in enforcing regulations for accuracy of labelling of allergenic contents, especially as testing has shown relatively high levels of mislabelling and cross-contamination with respect to allergenic content in foodstuffs (Vierk *et al.*, 2002).

2.4.2 Identification of wild lobsters

Species identification has a role in both basic biological research such as mapping species distributions and understanding foodwebs, as well as in providing information to management such as attribution of catch to stocks and estimation of broodstock. Although adult lobsters are usually easily distinguished morphologically, there are some instances where species identification is not straightforward because morphological differences are slight or poorly described. Jørstad *et al.* (2007) describe an example from Norway where free-living lobsters may be either native European lobsters (*H. gammarus*) or escaped American lobsters (*H. americanus*) imported for aquaculture. Escaped *H. americanus* present a risk to wild European

lobster populations because they have the potential to introduce disease and also because hybridization between the species has the potential to disrupt adaptive gene complexes. Jørstad *et al.* (2007) used microsatellite DNA analysis to identify wild living American lobsters, and demonstrated that the morphological characters typically used to distinguish the species and to identify hybrids were unreliable.

Whereas adult lobsters are usually large, prominent and relatively sedentary features of benthic communities, their planktonic larvae (phyllosoma) are small and capable of wide dispersal (Chittleborough & Thomas, 1969; Phillips *et al.*, 1979). They are also often morphologically cryptic and difficult to identify (Booth *et al.*, 2005). A particularly valuable application of DNA-based species identification in lobsters concerns mapping the distribution and abundance of planktonic phyllosoma larvae. Typically these pelagic larval stages may last between 3 and 15 months (Phillips *et al.*, 1979; Yeung *et al.*, 2000), during which time they may be transported vast distances by ocean currents and winds before finally settling as a puerulus and then a benthic-dwelling adult in shallow water (Phillips & Melville-Smith, 2006). Concerted effort has been invested in understanding the biophysical processes that determine the productivity of lobster fisheries, and, in particular, the determinants of successful settlement (Palma *et al.*, 1999; Caputi, 2008; Lillis & Snelgrove, 2010). Such research requires an accurate means to identify the larval forms, which typically undergo many moults during their pelagic life cycle. Identification is further complicated by the intermingling of phyllosoma from different species in the deep ocean even when the adult forms occur in allopatry (Konishi *et al.*, 2006).

Several studies have employed DNA markers to identify phyllosoma larvae collected in oceanic waters, and revealed frequent misidentification by users of conventional morphological keys. For example, García-Rodríguez *et al.* (2008) developed a PCR-RFLP assay (see methods later) to distinguish the phyllosoma of three Panulirids on the Pacific coast of Mexico (*Panulirus interruptus*, *P. inflatus* and *P. gracilis*). While the adults of these species are easily distinguished, the diagnostic fea-

tures of the phyllosoma are highly variable. Similar investigations have been conducted by Silberman & Walsh (1992) for *P. argus*, *P. guttatus* and *P. laevicauda* in the north-western Atlantic ocean, by Chow *et al.* (2006) for *P. japonicus*, *P. longipes* and *P. pencillatus* in the northwest Pacific, and by Konishi *et al.* (2006) for *Panulirus echinatus* from the central Atlantic ocean. In all of these examples a parallel investigation of conventional morphological characters was conducted and revealed a high rate of misidentification, which cast doubt over earlier studies reliant on morphological characters to identify species and map their temporal or spatial distribution as well as vertical migration behaviours. One of the benefits of parallel investigations of DNA and morphology is that they permit researchers to determine which morphological characters are truly diagnostic for species, and to recalibrate morphological keys, or to provide the first morphological descriptions of larval forms. For example, Palero *et al.* (2009c) used DNA sequencing methods (mtDNA 16s gene) to link larvae to adult slipper lobsters *S. pygmaeus* for which larval forms had not been described.

2.4.3 Characterizing lobster diets

Conventional approaches to understanding the diet and trophic status of lobsters have relied on analysis of stable isotopes, fatty acids and morphological analysis (Mayfield *et al.*, 2000; Guest *et al.*, 2009). DNA analysis has the potential to be a useful adjunct to these methods because it can provide a higher resolution understanding of the diet and can also resolve diets when morphological characters of the diet are unrecognizable, particularly if they make use of multi-copy genes which are most robust to the digestive process (Deagle *et al.*, 2009, Carreón-Martínez & Heath, 2010). DNA barcoding has been extended to investigations of the diet of both adult and larval lobsters. Interest in the diet of phyllosoma is driven by attempts to rear lobsters in aquaculture, where spiny lobsters have proven very difficult to rear to metamorphosis (Matsuda & Yamakawa, 2000), and also for understanding marine food webs. In an investigation of the diet of *P. japonicus*, *P. longipes* and *P. echinatus*, Suzuki *et al.* (2008) used sequencing of clones of the 18s

ribosomal gene to reveal the presence of multiple species of teleostei in the hepatopancreas of phyllosoma collected in the Pacific ocean, and in another sample they detected cnidaria (scyphozoa) and urochordates (larvacea). They further validated the results with feeding trials that indicated a strong agreement between artificial diets and species identified in the samples. The authors proposed that the changes in diet in wild caught phyllosoma, which reflected observed changes in zooplankton, indicated that they are likely to be opportunistic carnivores whose diets reflect available prey, a result supported by lipid signatures (Jeffs *et al.*, 2004). A more recent approach to characterizing diets of phyllosoma successfully incorporated peptide nucleic acid clamping primers to increase the efficiency of amplifying prey rather than consumer, and revealed the presence of at least 11 prey taxa including teleosts, chaetognaths, cnidaria, ctenophora and molluscs, and included up to 10 different prey types in one specimen (Chow *et al.*, 2011). This investigation still relied on cloning technology however, and therefore was relatively labour intensive. Next-generation DNA sequencing technologies, which avoid the time-consuming cloning steps and generates large numbers of diagnostic DNA sequences promise to revolutionise dietary and food web research (Deagle *et al.*, 2009; Pommpon *et al.*, 2012).

Adult lobsters can be major trophic regulators of benthic communities, and understanding their diet can be key to understanding trophic relationships in these environments (Breen & Mann, 1976). Yet, detailed information on lobster diets is difficult to obtain by conventional morphological analysis. Redd *et al.* (2008) used species-specific PCR analysis to demonstrate a non-lethal and highly accurate approach to detecting the major dietary items in the stomach contents of the southern rock lobster, *Jasus edwardsii*, in south-east Tasmania. Feeding experiments were used to establish the rate of passage of food items through the gut of the lobsters, and demonstrated that dietary items are detectable in faeces within 7 hours of feeding, and may still be detected after 60 hours. Importantly, these samples were obtained from faeces that were sampled non-lethally from the lobsters.

2.4.4 DNA-based methods typically employed for species identification

DNA-based species identification of lobsters and their prey is based on the principle that species bear unique, and therefore diagnostic, DNA sequences. All rely on PCR, an enzyme-driven reaction that may be manipulated to replicate selected fragments of an organism's genome so that the DNA is in sufficient quantities that its sequence may be visualized. An introduction to PCR is provided in most biology textbooks. Once PCR is complete, a range of techniques may be employed to reveal the diagnostic DNA characters. The most widely used of these include direct DNA sequencing, species-specific PCR, PCR-RFLP, and modifications of these methods. The methods differ in a number of respects, including speed at which a result is returned, cost, requirement for development of the method for a new suite of species, infrastructure requirements, and the number of species that may be distinguished. Which method is appropriate for a particular application will vary depending on circumstances. Later we outline the characteristics of these methods and provide examples of their use.

2.4.5 Polymerase chain reaction–restriction fragment length polymorphism

A single DNA fragment is amplified via PCR. This fragment is then restricted (cut) with one or more restriction enzymes. There are dozens of restriction enzymes available and each cuts DNA at specific sequences of typically 3–6 nucleotides. For example the *EcoRI* enzyme will cut DNA whenever it encounters GAATTC, whereas the *HindIII* enzyme will cut DNA when it encounters AAGCTT. Subjecting a sample to one or more restriction enzymes will create fragments of varying size depending on where the recognized sequence occurs along the fragment. Restriction enzymes can be selected that will produce diagnostic DNA fragments for species of interest. The characteristic patterns of DNA fragments may be visualized via gel electrophoresis (Fig. 2.2). An example of PCR-RFLP applied to lobsters is García-Rodríguez *et al.* (2008) for *P. interruptus*, *P. inflatus* and *P. gracilis*.

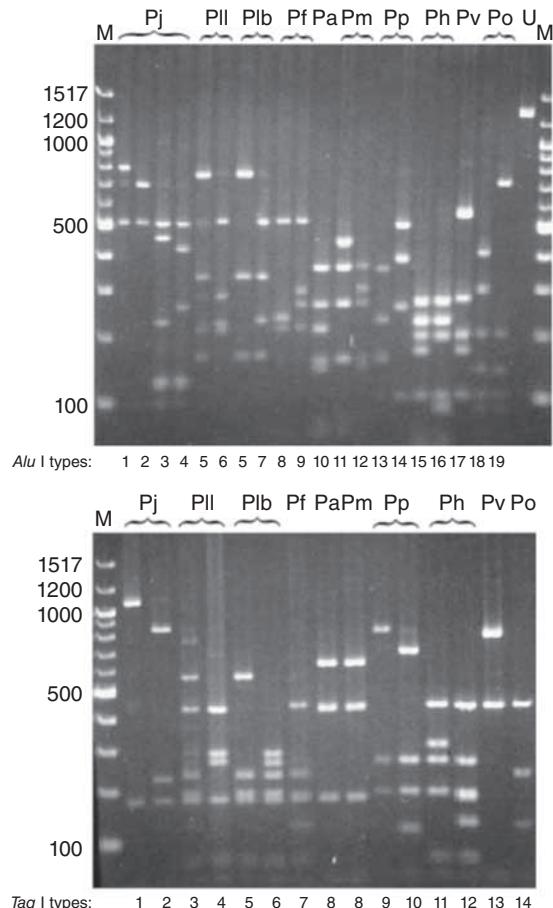


Fig. 2.2 Restriction profiles mitochondrial cytochrome oxidase I (*COI*) gene fragment of 10 spiny lobster species. The top and bottom gels are produced using *Alu*I and *Taq*I restriction enzymes respectively. The sizes of the gene fragments are shown in the left margins. Column M is a 100 bp DNA ladder. Column U is undigested DNA. Abbreviations for spiny lobster (Genus *Panulirus*) species are as follows: Pj *P. japonicus*, PII *P. longipes longipes*, Plb *P. longipes bispinosus*, Pf *P. femoristriga*, Pa *P. 'aka'*, Pm *P. marginatus*, Pp *P. penicillatus*, Ph *P. penicillatus*, Pv *P. versicolor* and Po *P. ornatus*. Reproduced with permission of Springer.

2.4.6 Melt-curve analysis

A DNA fragment is amplified via PCR in the presence of dye that fluoresces when the DNA is in the double-stranded form (dsDNA). The DNA fragment is subsequently cooled so that it forms

dsDNA. The sample is gradually heated, and at a critical temperature the dsDNA will disassociate to become single-stranded DNA (ssDNA). This ‘melting’ temperature is dictated by the sequence of the DNA, and because each species has a unique DNA sequence it will also have a unique melting temperature. Optical systems detect a rapid reduction in fluorescence as the dsDNA becomes ssDNA, and provide accurate estimates of melting temperature for each sample that can then be compared with known references (Berry & Sarre, 2007). This technique has not been applied to spiny lobsters, but has been applied to a variety of invertebrate taxa (Winder *et al.*, 2011). An advantage of this method is that it is relatively inexpensive to conduct, involves less processing than PCR-RFLP, and does not require the purchase of species-specific probes. However, it does require the use of a PCR machine capable of quantitative PCR.

2.4.7 Species-specific polymerase chain reaction

Two main approaches fall into this category. In the first, different-sized DNA fragments are amplified with PCR from each of the candidate species under investigation. This is achieved by the design of unique PCR primers for each of the candidate species. Each species’ PCR primers are situated different distances apart on the target fragment, hence amplify different-sized DNA fragments. The size differences are visualized by separating the DNA fragments with electrophoresis (Fig. 2.3) (García-Rodríguez *et al.*, 2008). The second, more technically advanced method, is based on quantitative PCR technology. Universal primers may be used to amplify a suite of up to five species of interest. A third modified “probe” oligonucleotide is also introduced into the PCR. These probes are designed to be specific to each of the candidate species of interest, and will report the presence of DNA from that species via a unique fluorescent label. Like melt-curve analysis, this second method does not require an electrophoresis step. However, it does require design and purchase of species-specific probes, and a PCR machine capable of quantitative PCR. Probe-based analysis has been applied to the detection of disease in wild and

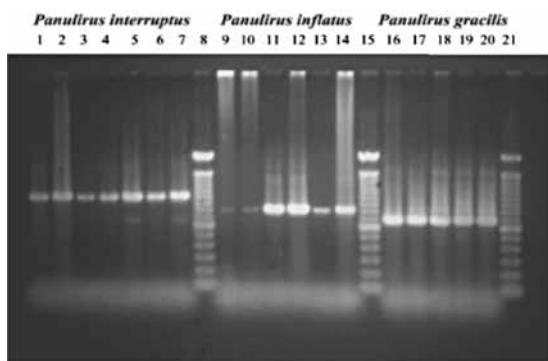


Fig. 2.3 Interspecific differences in the size of PCR products of mitochondrial DNA markers revealed using gel electrophoresis. Each species can be distinguished by a different sized fragment. Lanes 8, 15 and 21 contain a 100-bp DNA ladder (range 100–1000 bp), which is used to estimate the size of the PCR products. Garcia-Rodriguez, F.J. *et al.* Reproduced with permission of NOAA.

captive crustaceans (Martorelli *et al.*, 2010), but equally could be applied to the identification of lobsters.

2.5 Variation in reproductive success

The mating systems of lobsters are highly diverse and often complex (MacDiarmid & Sainte-Marie, 2006), and there are several practical reasons for interest in them. In aquaculture, understanding reproductive behaviours can indicate what operational sex ratios are most appropriate to maintain, and how genetic diversity can best be sustained in captive populations. Selective breeding programs also rely on attributing parentage for the estimation of trait heritabilities. In wild populations, the common practice of size and sex-biased harvest can alter patterns of reproductive success, potentially resulting in both lower productivity through sperm limitation, and changes in genetic diversity. Although observing the reproductive behaviours of lobsters is difficult, particularly in the wild, many aspects can be understood through genetic analysis.

One of the first applications of genetic analysis to understanding lobster mating systems was an allozyme investigation of genotypic frequencies in

the brood of a single *H. americanus* female (Nelson & Hedgecock, 1977). This study revealed genotype frequencies that were inconsistent with parentage by a single male. Recently, more variable DNA microsatellite markers have enabled the precise number of males contributing to clutches to be determined (Streiff *et al.*, 2004; Gosselin *et al.*, 2005). Parentage analysis has revealed great variation between species in the extent of multiple paternity, ranging from zero in the European lobster, *H. gammarus* (Ferguson, 2002), to between 42% and 54% in the Norway lobster, *N. norvegicus* (Streiff *et al.*, 2001). Other lobster groups, including the squat lobsters (Galatheidae), exhibit levels of multiple paternity up to 100% (Bailie *et al.*, 2011). We know of only one investigation of mating systems in spiny lobsters, and it revealed instances of multiple mating by some males (Melville-Smith *et al.*, 2009).

The emergence of molecular parentage analysis in the past two decades has revealed that for many animal groups, observed mating success does not always reflect realized mating success because of cryptic female choice (Burke, 1989; Jones & Ardren, 2003). This has not been extensively studied in lobsters, but the capacity of some lobsters to store sperm for long periods (Waddy & Aiken, 1986) suggests that it is likely. Genetic studies have also revealed mismatches between mating behaviours observed under controlled laboratory conditions and in the wild. For example, multiple paternity was observed in the European lobster in captivity, whereas an extensive field-based study based on microsatellite DNA analysis and genotyping of 1500 offspring from 135 females revealed no instances of multiple paternity (Ferguson, 2002).

These results suggest caution should be employed when generalizing laboratory results to wild populations. They also indicate that lobsters have capacity for flexibility in reproductive behaviours in response to environmental conditions. This is consistent with a field-based study that compared the incidence of multiple paternity in *H. americanus* populations subject with different harvest intensities (Gosselin *et al.*, 2005). In this case the incidence of multiple paternity revealed through microsatellite DNA analysis of fertilized eggs was

Table 2.1 Studies that have used molecular analyses to investigate the mating system of lobsters.

Species	Markers	Mating system revealed	Reference
<i>N. norvegicus</i>	Microsatellite	Multiple paternity	(Streiff <i>et al.</i> , 2004)
<i>H. gammarus</i>	Microsatellite	Monogamy	(Ferguson, 2002)
<i>H. americanus</i>	Allozyme	Multiple paternity	(Nelson & Hedgecock, 1977)
<i>H. americanus</i>	Microsatellite	Multiple paternity	(Jones <i>et al.</i> , 2003)
<i>H. americanus</i>	Microsatellite	Multiple paternity, monogamy	(Gosselin <i>et al.</i> , 2005)
<i>H. americanus</i>	Microsatellite	Monogamy	(Tam & Kornfield, 1996)
<i>P. cygnus</i>	Microsatellite	Monogamy, multiple paternity	(Melville-Smith <i>et al.</i> , 2009)

11–28% in two populations subject to high harvest pressure, whereas no instances of multiple paternity were observed in a single population where harvest pressure was significantly lower. These changes to the mating system are potentially significant in light of field observations in other species showing that the suboptimal density and age structure of lobsters can significantly reduce female reproductive success (Robertson & Butler, 2009).

Another application of genetic parentage analysis to track the survival of re-stocked lobsters (Hedgecock, 1977). Stock enhancement is widely employed for finfish and has been considered for both North American and European clawed lobster fisheries because of declining natural stocks (Addison & Bannister, 1994; Nicosia & Lavalli, 1999; Agnalt *et al.*, 2004; Prodöhl *et al.*, 2007). Jørstad *et al.* (2005b) used microsatellite DNA genotyping to track the fates of wild derived and captivity reared larval lobsters. They showed that wild lobster larvae fared significantly better upon release to the wild than did captive reared larvae. A further examination of the survival of juvenile lobsters to age of 9 months was less conclusive, with very high mortality in both wild and captive lobsters (Jørstad *et al.*, 2009). Genetic tags used in this way are a powerful approach to monitoring re-stocking exercises because they do not suffer problems of tag loss, and can be used for lobsters at all stages of development, not only larger age classes capable of holding physical tags (Addison & Bannister, 1994; Prodöhl *et al.*, 2007).

In summary, molecular parentage analysis has revealed important aspects of the mating systems of lobsters. It has also revealed plasticity in mating

systems that may reflect environmental influences including harvest pressures. Despite these novel insights, relatively few molecular investigations of lobster reproductive behaviour have been published, and they have generally focused on three highly exploited clawed lobster species from the northern hemisphere (*H. americanus*, *H. gammarus*, *N. norvegicus*, Table 2.1). Considering the growing interest in the interactions among harvest pressure, mating systems and breeding success in wild organisms (MacDiarmid & Butler, 1999; MacDiarmid & Sainte-Marie, 2006), and on the evolutionary effects of harvest (Allendorf & Hard, 2009), there are strong grounds for wider application of this technique to lobsters.

2.6 Genetic effects of harvesting

Genetic change in a population as a result of fishing can be caused by selecting for particular heritable life history traits, or by severely reducing the population size to low levels. Under very high exploitation rates it is possible for both of these effects to be operating on a fished population.

2.6.1 Fishing-induced evolution

Managers do not often consider the genetic consequences of exploitation in fished populations, but the need for fishing-induced evolution (FIE) to be incorporated into management thinking is becoming increasingly evident (Allendorf *et al.*, 2008; Jørgensen *et al.*, 2008). The main reasons that evolutionary effects have been largely disregarded and unreported is that they are slow to be become

evident and difficult to prove. The fact that other effects of fishing are far more obvious than fishing-induced change has not helped in promoting a need for genetic effects to be considered.

Fishing has the potential to be more influential in causing evolutionary change in lobsters than many other exploited marine species. The reason for this, is that many lobster fisheries operate at extremely high exploitation rates – for example in some areas and years, the western rock lobster and Canadian *H. americanus* fisheries have recorded exploitation rates of legal sized animals in excess of 75% (Wright *et al.*, 2006) and 85% (Santisteban, 2010), respectively.

Not only are exploitation rates frequently high, but most lobster fisheries have a legal minimum size that provides protection to juveniles of both sexes (e.g. see Table 10.1 in Chapter 10). Many of these fisheries are harvested by methods that minimize injury, such as by potting, and often the pots are fitted with mesh or escape gaps to minimize retention of lobsters below the legal minimum size. Where there is a minimum size in place, lobsters that are brought to the surface are sorted, with those below the legal minimum size being returned to the sea. Since lobsters are robust animals that are capable of being brought up from depth without injury, there is every chance that if handled with reasonable care that they will survive capture. The result is that many lobster fisheries have a very effective knife-edge selection process set at a size usually around that of sexual maturity.

The observed life history change in fished populations that is most frequently considered to have a genetic basis is a decrease in size at maturity over time (e.g. Rijnsdorp, 1993; Barot *et al.*, 2004). Obviously selective fishing pressure could introduce many other less obvious changes, for example changes in growth rates, but any genetic basis for such observations have been less frequently reported.

Detecting genetic change of traits caused by the selection pressure of fishing is difficult because many other factors such as water temperature, population density and food availability can operate in the same or opposing direction to that of fishing selection and can mask changes. Separating evolutionary adaptation from phenotypic plasticity is not

straightforward. Given the reticence of many resource managers to accept the potential for harvest to cause genetic change (Allendorf *et al.*, 2008), it is perhaps not surprising that reported observed changes in traits are most frequently put down to the plasticity of the species being fished, rather than any more lasting long-term change.

While there are very many examples of changes to life history characteristics that have been recorded in exploited fish populations, references in the lobster literature are far less common. Examples from a number of different clawed and spiny lobster species are provided in Table 2.2. No examples of these changes were found in the scyllarid lobster literature, probably because this lobster family mostly tends to support relatively small fisheries and datasets cover shorter time periods than for the other lobster groups. As can be seen from the suggested explanation column in Table 2.2, few of the listed studies considered the reported temporal changes to be due to fishing.

Changes in water temperature and population density-dependent effects over time are quite frequently implicated as the likely cause giving rise to what are most frequently perceived to be phenotypic responses by lobster populations (Table 2.2). This is because many populations show intraspecific differences in size at maturity and growth rates over the distributional range of the stock [e.g. *H. americanus* on the West Coast, USA (Little & Watson, 2005); *Jasus tristani* across different islands in the Tristan da Cunha Island group (Pollock, 1991); *Jasus lalandii* on the West Coast of southern Africa (Beyers & Goosen, 1987); *Palinurus gilchristi* on the East Coast of southern Africa (Groeneveld & Melville-Smith, 1995)]. Authors have therefore seen it as logical to assume that temporal changes in traits such as size at maturity and growth rates have a similar root cause to the spatial differences in these traits.

A specific example of annual changes in size at maturity in different regions of the western rock lobster (*P. cygnus*) fishery over two decades is shown in Fig. 2.4. Regular annual monitoring of size at first maturity in the fishery has taken place by a standardized sampling protocol fishing on the same GPS coordinates [description of methods provided in Melville-Smith & de Lestang (2006)].

Table 2.2 Changes in life history parameters in clawed and spiny lobster species, some of which have been attributed (at least in part) to possible evolutionary change caused by fishing.

Species	Area	Change recorded over time	Suggested explanations	Reference
<i>Jasus lalandii</i>	West Coast, South Africa	Reduced annual growth rate	Environmental perturbation influencing change in productivity of southern Benguela Current	Pollock <i>et al.</i> (1997); Hazell <i>et al.</i> (2002); Brandão <i>et al.</i> (2004)
<i>Panulirus cygnus</i>	Western Australia	Smaller size at maturity	Selective fishing practices; increase in water temperature	Melville-Smith & de Lestang (2006); Caputi <i>et al.</i> (2010)
<i>Panulirus cygnus</i>	Western Australia	Decrease in size of offshore migration	Selective fishing practices; Increase in water temperature	Caputi <i>et al.</i> (2010)
<i>Panulirus marginatus</i>	Hawaii, Northwestern Islands,	Increase in size specific fecundity	Density-dependent response to population changes due to fishing or natural cyclic declines in productivity	DeMartini <i>et al.</i> (1993, 2003)
<i>Panulirus marginatus</i>	Hawaii, Northwestern Islands,	Increase in egg size	Density-dependent response to population changes due to fishing or natural cyclic declines in productivity	DeMartini <i>et al.</i> (1993, 2003)
<i>Panulirus marginatus</i>	Hawaii, Northwestern Islands,	Increase in asymptotic length Decrease in size at maturity	Density-dependent response to population changes due to fishing	Polovina (1989)
<i>Homarus americanus</i>	Long Island Sound, USA	Smaller size at maturity	Density-dependent response to population changes due to fishing or environmental effects	Landers <i>et al.</i> (2001)
<i>Homarus americanus</i>	Bay of Fundy, Atlantic Nova Scotia, Canada	Smaller size at maturity	Increase in water temperature, or density-dependent response due to high recruitment, or response to fishing pressure	Tremblay (pers. comm.)

What is clear from the long-term series is an overall downward trend over time, superimposed by fluctuations occurring at shorter intervals. As with the aforementioned lobster fisheries, there are quite possibly several factors influencing the changes observed in Fig. 2.4. Warm water is known to lead to precocious maturity in this species (Melville-Smith *et al.*, 2010) and has been implicated in the

long-term chain size at maturity (Caputi *et al.*, 2010) FIE has yet to be conclusively established.

Pollock (1995) hypothesized that it is their phenotypic plasticity that enables lobsters to adapt to environmental change, in particular water temperature and food supply, by altering rates of growth, survival and reproduction. In his view, the genetic component determining species-specific size and

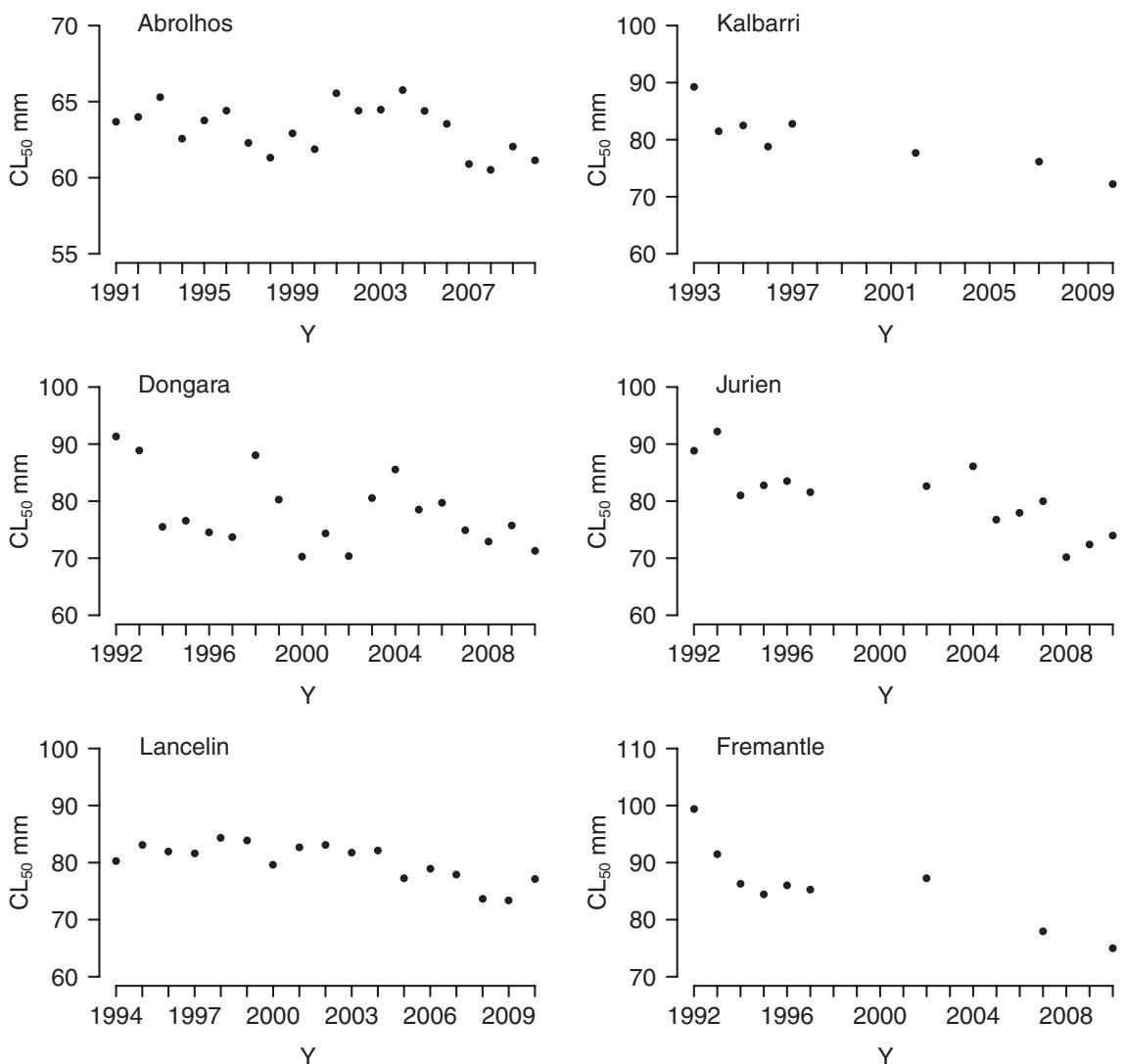


Fig. 2.4 Annual changes in size at first maturity (CL₅₀mm) recorded for *Panulirus cygnus* in six areas of the commercial fishery over approximately two decades (de Lestang unpublished data).

age at maturity is governed by the number of pre-puberty instars, which has been suggested by Hartnoll (1985) to be species specific. Under this scenario, selection pressure would guide a population towards either early maturity through a reduced number of juvenile instars if adult mortality rates were high, or later maturity through increased numbers of juvenile instars in response to high juvenile mortality rates.

Serious attempts to disentangle genetic components responsible for changes in traits from environmental effects have yet to be undertaken for any lobster species. However, this research direction has been increasingly investigated for exploited finfish populations in recent years using reaction norms. A reaction norm is the pattern of phenotypic expression of a given genotype under different environmental conditions (Griffiths *et al.*, 2000)

and the capabilities of the technique are reviewed at length in Dieckmann & Heino (2007). In most of the literature that has been reported to date, maturation as a function of age and size has been used to disentangle evolutionary change from phenotypic plasticity (Heino *et al.*, 2002; Barot *et al.*, 2004), but other traits, e.g. growth (Pardoe *et al.*, 2009), can also be used.

2.6.2 Impacting genetic diversity

In addition to causing selective changes to populations, intensive fishing can lead to declines in genetic diversity (Smith *et al.*, 1991; Hauser *et al.*, 2003; Hutchinson *et al.*, 2003). Loss of genetic diversity can occur even when stocks consist of many millions of individuals, well in excess of the population sizes considered vulnerable to genetic drift (Allendorf & Luikart, 2006). This is because genetic effective population sizes (N_e) can be much lower than the number of individuals in the population (Hutchinson *et al.*, 2003). In marine populations, low N_e can result from high variance in reproductive success caused by a combination of high fecundities and mortalities in the early life stages (Hedgecock, 1994a). Empirical estimates of N_e suggest the difference between N_e and N can be very large. For example, Hauser *et al.* (2003) estimated that N_e in an exploited population of New Zealand snapper was five orders of magnitude smaller than N . Ratios of N_e/N in the range of 10^{-5} to 10^{-3} have also been reported in North Sea cod (Hutchinson *et al.*, 2003), red drum (Turner *et al.*, 2002) and plaice (Hoarau *et al.*, 2005).

Despite heavy exploitation, studies carried out on lobsters so far suggest genetic diversity within populations remain fairly stable. Palero *et al.* (2011) used 10 microsatellite loci to test for signals of a recent genetic bottleneck in European spiny lobster (*Palinurus elephas*), a species experiencing marked declines in mean annual catches along its entire distribution area in recent years. Their results showed fairly constant historical population sizes and suggest that current effective population sizes were in the range from $10^{4.11}$ to $10^{4.67}$. More recently, Kennington *et al.* (2012) found no evidence of a decline in microsatellite or mtDNA variation in the western rock lobster (*Panulirus cygnus*) over a 14-

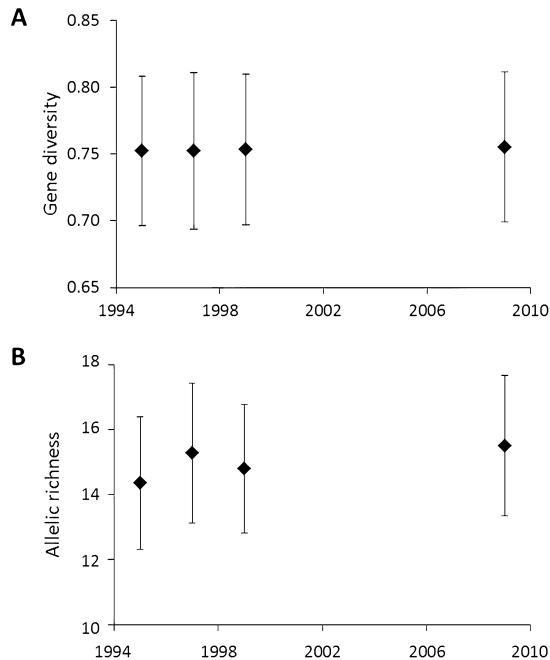


Fig. 2.5 Microsatellite DNA variation in *Panulirus cygnus* collected between 1995 and 2009. (A) Gene diversity; (B) allelic richness (a measure of the number of alleles per locus independent of sample size). Data taken from Kennington *et al.* (2012).

year period (Fig. 2.5). Furthermore, there was no evidence of a recent genetic bottleneck or significant temporal variation in haplotype or allele frequencies. These studies suggest that effective population sizes in lobsters are sufficiently large to prevent the loss of neutral genetic diversity by genetic drift, though, clearly, more studies are needed to determine whether these studies are representative of the group.

2.7 Considerations for aquaculture and stock enhancement

2.7.1 Aquaculture

Large-scale aquaculture of lobster species has yet to become a reality, although there remains considerable interest and advancement in this area, particularly in regard to the production of spiny and

slipper lobster species (Rogers *et al.*, 2010). Aquaculture of clawed lobster has been under consideration since the 1970s (Aiken & Waddy, 1995), but has yet to produce product in volume.

In the longer run, if lobster aquaculture proves to be as successful as it is anticipated to be (Dey, 2011; Phillips & Matsuda, 2011; Vijayakumaran & Radhakrishnan, 2011), selective breeding for desirable commercial traits would need to be considered. In establishing a selective breeding programme it is important to know the heritability (i.e. ratio of phenotypic to genotypic variation) characteristics of the desired traits for the species under consideration. Such work has been undertaken for a number of traits in different crustacean species (Wickins & Lee, 2002) with widely ranging estimates of heritability for single traits – e.g. growth rate heritability ranged from 10% to 72% in the examples quoted. From a positive point of view, this result does provide encouraging scope for improving favourable traits by selective breeding programmes.

Because clawed lobsters have had a long history of being considered for large-scale aquaculture, there have been several investigations into the heritability of particular traits in the *Homarus* genus. Finley & Haley (1983) examined the heritability of intra-specific aggression in juvenile *H. americanus* with a view to selecting for individuals with less aggressive characteristics that would be more tolerant of high-density rearing. Their work showed that genetic variability for aggressive behaviour does exist and that response to selection might be good, albeit slow. Selective breeding has also been successfully used to select for recessive mutations involving *H. americanus* body colour, with the development of red, white and blue colour morphs (Aiken & Waddy, 1995). The benefit of a coloured product would be that it would be easily distinguishable when marketing, from wild product.

In more recent times, Hedgecock & Nelson (2009) have examined the heritability of growth rate and concluded that up to 30% of the variation may be heritable, but that environment plays a very significant role in growth variation amongst juveniles. Genetic mapping of *H. gammarus* being grown under aquaculture conditions in Norway, is underway to develop a genetic databank to use for the selection of brood stock from juveniles that

show good growth, survival and feed conversion ratios (Drengstig *et al.*, 2011). No such work has as yet been reported for spiny and slipper lobster species.

2.7.2 Stock enhancement

Hatcheries for the production of European and American lobster for release, as a way of enhancing the wild capture fisheries, dates back to the second half of the 19th century in both Europe and North America (Aiken & Waddy, 1995). Over different periods, significant quantities of larvae or early juveniles have been released in different countries; for example, the Massachusetts State Lobster Hatchery was releasing half a million stage IV post-larvae each year over a 40-year period from 1951 (Hughes, 1968, quoted by Aiken and Waddy 1995), a hatchery in Norway produced 200,000 juveniles for release in the 1980s (Jørstad & Farestveit, 1999), 49,000 were released between 1983 and 1988 in the United Kingdom (Bannister, 1998) and between 1993 and 1997, 292,000 larvae were released in Ireland.

There was limited consideration of the potential negative genetic implications of enhancement activities in the early years of lobster stock enhancement. In Norway for example, about 40% of juveniles released in the 1980s were the progeny of imported Scottish broodstock (Jørstad & Farestveit, 1999) and in a USA community-based hatchery facility in Maine (which closed in 1992), lobsters with a recessive blue trait were specifically developed for enhancement purposes (Beale *et al.*, 1998). Blue lobsters are rare in the wild in Maine, occurring at a rate of one in three to four million (Beale *et al.*, 1998), and the objective of increasing their proportion in the wild apparently had some success, given that fishermen noticed a higher proportion of blue lobsters in their catches after the facility concentrated on producing mainly those coloured lobsters for release (Sainte Marie, 1998).

More recent knowledge has made fisheries managers aware of the potential hazards of releasing animals that have been raised in artificial hatchery environments. The brood stock used in such programmes is often limited in size and this can cause inbreeding in the hatchery leading to outbreeding

depression in the wild. Inbreeding depression in captive populations can result in either increased homozygosity or reduced heterozygosity (Allendorf & Luikart, 2006). Increased homozygosity can result in increases the occurrence of homozygous genotypes for rare, harmful alleles that are normally hidden in the population of heterozygotes (Busack & Currens, 1995). Reduced heterozygosity can result in decreased performance in situations where heterozygotes perform better than homozygotes (Busack & Currens, 1995). The concern with outbreeding depression is that the hybrid progeny resulting from wild stock mating with hatchery produced stock can have lower performance or fitness than either parent (Allendorf & Luikart, 2006).

The potential adverse genetic effects resulting from stock enhancement programmes has resulted in numerous references to guidelines aimed at minimizing undesirable traits resulting from the hatchery management of the genetics and fitness of hatchery stocks (e.g. Kapuscinski & Jacobson, 1987; Thurstan, 2000). As with many other species, phenotypic differences have been recorded in hatchery stocks compared with those in the wild. Wickins (1986) reported on disproportionately large numbers of hatchery-reared juvenile *H. gammarus* having a distinct crusher claw and instead having two morphologically similar cutter claws. Changing the diet by providing the animals with oyster spat radically reduced the numbers of lobsters without crusher claws and, according to Wickins (1986), produced more active and aggressive individuals with increased feeding opportunities at release than those with just cutter claws.

Genetic differences between hatchery reared individuals and those in the wild are less commonly reported because of the difficulties of distinguishing genetic from environmental effects. Jørstad *et al.* (2005b) raised the larval offspring of females taken from wild and cultured origins in a communal rearing system. At the end of the experiment the numbers of surviving Stage III/IV larvae were identified according to their broodstock group using microsatellite profiling. Survival of the larvae, which was taken as an indicator of larval fitness, showed the offspring of the cultured group to have only about 60% of the survival of wild groups. Jørstad *et al.* (2005b) considered this result

to indicate a genetic component behind the differences in larval fitness in the two groups.

The observed period of survival rates for offspring from three brood sources was extended from larvae of Stage III/IV in Jørstad *et al.*'s (2005b) study, to juveniles of approximately 9 months of age (Jørstad *et al.*, 2009). Results provided evidence that offspring from cultured females have lower, but comparable, survival than offspring from wild females. However, the authors did note the need for further research aimed at examining the reproductive success of cultured individuals and the impact of offspring from this source on future generations of wild lobster populations.

The rearing of spiny and slipper lobster larvae or juveniles for release into wild populations is unlikely to be considered in the foreseeable future, given that most stocks remain reasonably productive, even if landings have fallen compared with earlier years (Booth, 2006; Groeneveld *et al.*, 2006; Phillips & Melville-Smith, 2006; Spanier & Lavalli, 2006). However, one form of enhancement is currently being trialled (Chandrapavan *et al.*, 2010; 2011), whereby slow-growing pale-coloured *Jasus edwardsii* lobsters are being translocated from a deep-water region in the south of Tasmania to shallow water reef on the east coast of the state. The difference in growth rates of lobsters in the two areas are due to density effects, food availability or other unidentified environmental factors (Chandrapavan *et al.*, 2010); the difference in colour between lobsters taken in deep compared with shallow water is considered to be a phenotypic response to diet and/or adaptation to local habitat (Chandrapavan *et al.*, 2011).

There is no detectable genetic subdivision of *J. edwardsii* across its distributional range (Ovenden *et al.*, 1992), and therefore the type of enhancement being trialled in Tasmania would be unlikely to pose any of the potential problems resulting from enhancement through the use of cultured stock, such as has been discussed for clawed lobsters in previous paragraphs.

2.8 Conclusions and future directions

Genetic analysis provides tools to investigate a diverse and expanding number of aspects of lobster

ecology. Some of these contributions, such as the identification of stock structure, complement conventional methods based on field observations (Bowlby *et al.*, 2008). Others, such as the identification of cryptic larval forms, provide unique information. Some aspects, such as molecular parentage analysis provide fundamental biological knowledge, whereas others, such as stock structure analysis, provide information that is essential to the sustainable management of wild fisheries (Stephenson, 1999). Genetic principles and analyses also offer ways to investigate emerging fisheries management themes, such as ecosystem-based management, which requires an understanding of food webs (Fulton *et al.*, 2011), and the evolutionary effects of selective harvest (Allendorf *et al.*, 2008).

Genetic research is a dynamic, rapidly developing discipline and future genetic studies are likely to deliver a range of novel insights, especially with the development of next-generation sequencing technologies, which can generate large amounts of DNA sequence data at relatively low cost (Schuster, 2008). There are three research areas where profound advancements are likely. The first of these is in the improved resolution of stock structure. So far the evaluation of population structure in lobsters has been determined using neutral genetic markers such as microsatellites and mitochondrial DNA. While these markers provide information on demographic parameters such as migration between populations and effective population sizes, they are poor predictors of adaptive genetic variation (genetic variation that affects fitness) and levels of local adaptation (Reed & Frankham, 2001; McKay & Latta, 2002). This reflects a major shortfall because knowledge of local adaptation is essential for defining management units and setting priorities for conservation (Allendorf & Luikart, 2006). The growing availability of molecular markers and reduced costs mean that population genetic studies using tens to hundreds of genetic markers (also known as a population genomics approach) are now possible (Luikart *et al.*, 2003). This increases the likelihood that some marker loci used in a study will fall in or near genes under selection, thereby providing a way to infer the adaptive uniqueness of wild populations. For example, several recent studies on fish have found evidence of selection influencing molecular markers whose patterns of

differentiation are associated with environmental variables (Nielsen *et al.*, 2009; Deagle *et al.*, 2011). These marker loci can be used to identify adaptive differences among populations and populations containing a high proportion of adaptive and unique alleles. Population genomic approaches can also provide increased statistical power for detecting population structure and assigning individuals to populations (Nielsen *et al.*, 2009). For lobsters, this is especially relevant because genetic differences among populations are typically very subtle (see earlier).

A second and related research area that is likely to receive increasing attention is the application of population genomic approaches to investigate FIE. As previously discussed, evidence of FIE in lobsters (as well as most marine fish, Nielsen *et al.*, 2009) comes from non-genetic data and is therefore not conclusive. However, population genomics offers a way to test whether the phenotypic changes observed in exploited populations has a genetic basis. This may be achieved by screening for temporal changes at marker loci using archived material or spatial variation among exploited and non-exploited areas. If the observed phenotypic changes have a genetic basis, the expectation is that some of the markers will be linked to genes controlling variation in the traits undergoing change and therefore show temporal or spatial patterns much different to most other genetic markers (Luikart *et al.*, 2003). Follow-up experimental studies are also needed to confirm the association between the genetic marker and the traits suspected of undergoing FIE. Another approach is to use candidate genes (genes of known function suspected of controlling a particular trait) or markers previously shown to be associated with trait variation to test for changes over time or between exploited and non-exploited areas.

The final area where genetic analyses are likely to deliver significant new insights into lobster biology is in the construction of detailed foodwebs. Globally, fisheries are increasingly adopting the principles of ecosystem-based management (Levin *et al.*, 2009), and tools to monitor the interactions between fisheries and the environment are more in demand (Pauly *et al.*, 2000). Where fisheries selectively harvest species there is the potential to alter flows of energy through ecosystems and to induce

cascades of ecological change. Importantly, such changes may be irreversible if new stable community equilibria are reached. Well-known examples are the creation of urchin barrens in south-eastern Tasmania by heavy fishing of southern rock lobsters in combination with changing water temperature (*Jasus edwardsii*, Ling *et al.*, 2009). Detecting such changes or pre-emptively determining the likely indirect consequences of fishing through the implementation of ecosystem models (e.g. Atlantis, Fulton *et al.*, 2011) requires an understanding of foodwebs. However, because of the complexity and diversity of marine foodwebs they are difficult to generate. As indicated in Section 2.4.3, DNA analyses have attributes that make them well suited to

foodweb analysis, providing much greater taxonomic resolution and capacity for high throughput than conventional methods based on morphological analysis of stomach contents or on isotopic signatures. They also are less reliant on expert taxonomic knowledge and can resolve diets even when no morphological features are evident. The development of next-generation DNA sequencing technologies together with large databases of reference sequences will in the future provide a means to simultaneously exhaustively characterise complex diets from key ecosystem components, including lobsters (Pompanon *et al.*, 2012). This will provide important foundations for ecosystem based management of lobster and other fisheries.

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Chapter 3

Enhancement of Lobster Fisheries to Improve Yield and Value

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Abstract

Enhancement of lobster fisheries has the use of a range of systems over the last 150 years. Attempts to create new fisheries resources by translocating lobsters beyond their natural range have been largely unsuccessful. Although occasional reports of *Homarus americanus* in European waters occurred since the 1990s, no self-producing populations have been documented. The release of hatchery reared *H. americanus* and *H. gammarus* juveniles for recovery of depleted stocks and enhancement of fisheries has had a long history with most recent activity underway in Norway, the UK and Ireland. Research scale enhancement of spiny lobsters has also occurred using juveniles on-grown from wild-sourced puerulus. Success in these operations has relied on understanding processes affecting post-release survival and modifications to the release operations. Enhancements also occur through moving lobsters that are below harvestable size within their natural range. This improves market traits and production by moving lobsters to areas of higher growth. This review explores the performance of lobster enhancement operations through case studies, including one on *Jasus edwardsii*, and also the general principles that underpin enhancement, such as the need for monitoring and evaluation of economic feasibility.

3.1 Introduction

3.1.1 What is enhancement?

Stock enhancement is the release of animals into natural systems to increase the abundance of wild populations. Bell *et al.* (2008) considered that there were three categories of enhancement: restocking, stock enhancement and sea ranching. Restocking is used to rebuild or re-establish populations that are

severely depleted, while stock enhancement is used to increase harvests above that which would be possible with natural recruitment. Sea ranching involves the release of juveniles into unenclosed systems for later harvest, described as ‘put, grow and take’ operations. One of the forms of lobster enhancement discussed in this chapter is translocation, which is a form of sea ranching and involves moving naturally recruited lobsters to different areas, and can occur within and beyond the natural

range. Some authors have used the term ‘translocation’ to refer to exotic species in relation to biological invasions (Occhipinti-Ambrogi & Galil, 2004). However, the term is normally only used in cases where movement is intentional and that approach is applied in this chapter.

Historic translocation outside of range

Enhancement and translocation of crustaceans outside their natural range have been undertaken for centuries, with mixed success (Born *et al.*, 2004). Translocation of lobsters outside their natural range has been through failed attempts with Homarid lobsters from the North Atlantic coasts of Europe, USA and Canada, to the Pacific coast of North America, Japan and Australia (Addison & Bannister 1994, Table 3.1). Although some recaptures of released lobsters have occurred, no recruits have been detected. Likewise, extending the natural range in American lobsters (*Homarus americanus*) to the North American Pacific coast was not successful (Boothroyd & Ennis, 1992). These translocations are typically controversial because of the risk of ecosystem and disease impacts (Addison & Bannister, 1994; Boothroyd & Ennis, 1992; Kuzmin *et al.*, 1996). Problems arising from the translocation of peneaid shrimps in Asia have been used as evidence of the possible outcomes from lobster translocations, where, despite the development of valuable shrimp-farming industries, disease and coastal ecosystem problems have occurred (Kautsky *et al.*, 2000).

Enhancement within range

Restocking of depleted populations has been attempted for depleted populations of European lobsters (*Homarus gammarus*) and American lobsters (*H. americanus*), mainly with the use of hatchery-reared juveniles (Agnalt *et al.*, 1999, 2004; Bannister & Addison, 1998; Burton, 2001; Colburn *et al.*, 2005; Cook, 1995; Davis *et al.*, 2005; Latrouite & Lorec, 1991; van der Meeren, 2005). Success in these operations often also requires changes in management to address the original cause of population decline. Enhancement

operations have also been undertaken for lobster fisheries that are not seriously depleted, but where there is still scope for increased production. This includes stock enhancement with hatchery reared juvenile homarid lobsters and also translocation within range of *Jasus edwardsii*.

3.1.2 The motivation for enhancement

Restocking of depleted populations

Recruitment overfishing, disease or environmental shocks can cause stocks to become depleted to the point where recovery through reduction in fishing mortality can take a prolonged period. Restocking can speed up recovery in these cases and avoid the need for prolonged reduction in catch, which may be socially difficult.

Homarid lobsters are potentially susceptible to recruitment overfishing because of their high market value and biological traits such as relatively low fecundity and variable recruitment. This pressure on the exploited stock combined with the ability to produce juveniles in hatcheries led to them being one of the earlier marine species targeted for restocking (Audouin & Leglise, 1972; Latrouite & Lorec, 1991; Addison & Bannister, 1994; Nicosia & Lavalli, 1999; Svåsand *et al.*, 2004; Schmalenbach *et al.*, 2009; Benavente *et al.*, 2010). Restocking has also been attempted where a dramatic reduction in the population has occurred due to environmental accidents or disasters. After a major oil spill in the coastal waters of Rhode Island, USA, a programme for release of juvenile American lobsters (*H. americanus*) was conducted and monitored (Colburn *et al.*, 2005). However, it was not successful and the population remains collapsed (DeAngelis *et al.*, 2010).

Stock enhancement to increase yield

Stock enhancement has been explored in fisheries that are stable and productive but where there is scope for increase in yield. This has mainly been through hatchery releases of homarid lobsters because of the well-developed larval rearing techniques (Tlusty, 2004), although research has also occurred on hatchery production of spiny lobsters

Table 3.1 Objectives and locations of lobster enhancement operations.

Objective	Species	Country	Status	Reference
Stock recovery and enhancement from hatchery release	<i>Homarus americanus</i>	USA, Canada	First attempted in 1880s, pulse in activity from 1890 to 1917, relatively little activity from 1980 onwards.	Addison & Bannister, 1994, Tlusty, 2004
	<i>Homarus gammarus</i>	Norway, UK, France, Ireland	First attempted in 1870s, renewed interest from 1970 to present. Underway as part of coastal management in some areas.	Latrouite & Lorec, 1991, Bannister & Addison, 1998, Agnalt <i>et al.</i> , 2004, van der Meeran, 2005
Translocation outside of range to establish new fisheries	<i>Homarus americanus</i>	Western North America, Chesapeake Bay, Japan, Norway, UK, Sweden, Denmark	Generally unsuccessful although small numbers and hybrids occur in Northern Europe	Boothroyd & Ennis, 1992, Addison & Bannister, 1994, Stebbing <i>et al.</i> , 2012
	<i>Homarus gammarus</i>	New Zealand, Japan	Unsuccessful	Addison & Bannister, 1994
	<i>Jasus lalandii</i>	Japan, France	Unsuccessful	Addison & Bannister, 1994
Translocation of small lobsters within range to increase productivity	<i>Jasus edwardsii</i>	Australia	Commercial operations underway at small scale.	Green <i>et al.</i> , 2012
	<i>Homarus gammarus</i>	Norway	Commercial operations underway at small scale.	Moksness, 2004
Translocation of adults to restore recruitment	<i>Scyllarides latus</i>	Italy	Research trials only	Bianchini, <i>et al.</i> , 1998
Capture, ongrowing and release of juveniles to increase survival through high mortality bottlenecks	<i>Jasus edwardsii</i>	Australia, New Zealand	Research trials only	Mills <i>et al.</i> , 2006, Oliver <i>et al.</i> , 2006

Panulirus japonicus and *J. edwardsii* for stock enhancement (Barneveld, 1999; Yoshimura, 2000). Hatchery-reared European lobsters (*H. gammarus*) have been released with the explicit objective of boosting rather than merely recovering local populations in Norway, where designated open coastal areas are regulated by law with enhancements regarded as part of the coastal management regime (Agnalt *et al.*, 2004).

Movement of lobsters within range blurs the boundaries between ranching and stock enhancement. It is conducted for a range of reasons including to increase yield and also to reduce cost of harvesting by placing stock closer to port. In northern Europe, it is an old tradition, although not always legal, for fishers to retain undersized lobsters and release them in areas closer to their favourite fishing grounds (Addison & Bannister,

1994). A commercial variation of this currently occurs in the Norwegian licensed sea ranching (Borthen *et al.*, 1998; Moksness, 2004). Translocation has been developed as a management tool to increase the productivity of *J. edwardsii* within a healthy fishery in Tasmania, Australia (Chandrapavan *et al.*, 2010, 2011; Green *et al.*, 2010). These translocations moved slow-growing and low-valued rock lobsters from an underexploited population into faster growth areas to increase production and thus sustainable economic yield.

Introduction outside natural range

Translocations of crustaceans outside their natural range to establish new commercial resources has been successful in some crustacean species, including red king crabs (*Paralithodes camschaticus*), but attempts to extend the range of lobsters has generally failed. These include translocations of the American lobster (*H. americanus*) from the northeast of the USA and Canada to the American Pacific coast (Smith, 1896; Fraser, 1916; Butler, 1964; Ghelardi, 1967; Barber, 1983; Addison & Bannister, 1994) and also beyond the distributional range on the American Atlantic coast, south to Chesapeake Bay and north to Labrador (Boothroyd & Ennis, 1992). European lobsters (*H. gammarus*) were shipped to New Zealand (Anderton, 1911; Thomson & Anderton, 1921), and *Jasus lalandii* translocated from South Africa to France and Japan (Conan, 1986; Wickins & Lee, 2002). In Japan, *H. americanus*, *H. gammarus* and hybrids were produced in research laboratories and released along the north-western coast of Honshu (Kittaka *et al.*, 1983; Addison & Bannister, 1994). Monitoring of the Japanese releases of homarid lobster juveniles revealed a high loss to predators, unless released in cages with shelters (Kittaka, 1985).

Overcoming survival bottlenecks

Like most marine species, lobsters have high mortality among settling post-larvae and early juvenile stages, with these phases considered to be ‘survival bottlenecks’ (Wahle & Steneck, 1991, 1992; Wahle, 2003). Settling post-larvae and shelter-restricted juvenile lobsters are particularly vulnerable if the

appropriate settlement habitat is limited (Johns & Mann 1987), which can be caused by patterns in larval dispersal that carry settling-stage larvae into habitat unsuitable for lobsters (Hudon & Fradette 1993; Hudon, 1994; Incze & Naimie, 2000; Miller *et al.*, 2006). In these cases it is theoretically possible to enhance stocks by improving survival through high mortality bottlenecks.

Understanding changes in survival with size is important where lobster stock enhancement involves the release of hatchery-reared juveniles, as has occurred since the 1870s with homarids (Nicosia & Lavalli, 1999; Cobb & Castro, 2006). Very early in the history of Homarid lobster cultivation the aim was to circumvent survival bottlenecks in juvenile stages (Addison & Bannister, 1994), and provide the local populations annual, stable recruitment through hatchery releases (Gendron, 1998). Recent research has continued to explore the critical size that juveniles need to attain before they are on the ‘safe’ side of the survival bottleneck (Nicosia & Lavalli, 1999; van der Meeren 2000, 2005).

Commercial-scale hatchery production of spiny lobsters is not currently possible, but there may also be opportunities to enhance production of these species through better knowledge of survival bottlenecks. Harvest of *Panulirus cygnus puerulus* from collectors has been shown to have negligible effect on harvests of spiny lobsters (Phillips *et al.*, 2004). This then provides a source of juveniles that can be on-grown to a size where natural mortality is lower. This approach has been applied in *J. edwardsii* which were cultured for a year before release and had substantially improved survival (Gardner *et al.*, 2000; Mills *et al.*, 2005; Gardner *et al.*, 2006a; Mills *et al.*, 2006).

3.2 Monitoring the outcomes of enhancement operations

Responsible stock enhancement is measured against fisheries management goals, rather than aquaculture production goals (Blankenship & Leber 1995; Lorenzen *et al.*, 2010). Several decision frameworks exist for enhancement, but all involve an assessment of whether benefits of enhancement

outweigh any biological and socio-economic costs at a community level rather than the individual firm.

The goals of monitoring should match the goals of enhancement and also account for broader impacts on the environment and the ecosystem. There is also a need to monitor the practical feasibility of operations to ensure that they are technically effective and economically viable (Lorenzen, 2005). Components that require monitoring to assess overall feasibility include survival, changes to growth, and changes to the habitat and ecosystem. Prior to monitoring, careful planning, design and implementation must occur (Lorenzen *et al.*, 2010), and this is where many enhancements have failed. Where the objective is stock recovery, monitoring and evaluation also needs to compare enhancement against natural rebuilding (Meffe, 1992; Hilborn, 1998; Moksness *et al.*, 1998; Wilson *et al.*, 1998).

3.2.1 Growth and reproduction

Density-dependent suppression of growth would be expected to occur as density approaches the carrying capacity of the habitat. This not only reduces productivity but can also reduce survival where animals spend longer periods at smaller, vulnerable size classes (Cooney & Brodeur, 1998; Travis *et al.*, 1998). Growth and reproduction need to be monitored by tracking tagged individuals to evaluate individual demographics, but more importantly if these parameters are included into the stock assessment process then the broader-scale success on the enhancement on the fishery can be modelled and monitored (Lorenzen, 2005; Gardner & van Putten, 2008a,b). In one of the few field-based attempts to assess density-dependent changes in growth of an enhanced lobster population, Chandrapavan *et al.* (2010) found only minor changes even where density was enhanced by around 30% above natural levels in an unfished population.

Changes to growth and reproduction after a translocation may take a number of years to stabilize, which implies monitoring programmes need to be planned for similar periods. In a study of *J. edwardsii*, the southern rock lobster, reproduction changes were monitored for 4 years (Chandrapavan *et al.*, 2010; Green *et al.*, 2010). In the first year,

around 30% of small, pale translocated *J. edwardsii* females that previously had mature setose pleopods moulted into a non-setose state and failed to produce eggs (Green *et al.*, 2010). These lobsters also grew around 1 mm year⁻¹ less than translocated pale lobsters that continued to produce eggs, although still grew 2–6 mm year⁻¹ more than lobsters at their original source site. By the second year all females were producing eggs in the normal seasonal cycle and their larger size resulted in an overall increase in egg production despite the 1-year hiatus in reproduction (Green *et al.*, 2010).

3.2.2 Survival/changes to natural mortality

Enhancement introduces a range of risks to both introduced and resident animals (Schlaepfer *et al.*, 2009), and survival must be measured as part of assessing the viability of the operation. Successful stock enhancement requires a thorough understanding of the ecological processes influenced by stocking in different ecosystems (Støttrup & Sparrevohn, 2007), including biological interactions between the resident and inhabitant fish that may influence productivity (Hilborn 1998). Not surprisingly, the economic feasibility of operations is highly sensitive to survival rates (Gardner & van Putten, 2008a,b), which emphasizes the need for effective measurement of this aspect.

Measuring survival in lobster enhancement operations differs from survival estimation in typical fishery applications because of the change in behaviour and acute predation around the time of release (Oliver *et al.*, 2006; Green & Gardner, 2009). It ideally involves unique ID tagging and recapture of both resident and released individuals (Bannister & Addison, 1998; Mills *et al.*, 2005, 2006). Data can then be used to generate survival estimates with established models such as the Cormack–Jolly–Seber (CJS) method (Cormack, 1964; Jolly, 1965; Seber, 1965) or the robust design method (Kendall, 1999). The maximum likelihood estimation method is now easily applied through program MARK (Lebreton *et al.*, 1992; White & Burnham, 1999). The precision of these survival estimates is a function of the number of tags released and the recapture probability – where

recapture rates are high, reliable survival estimates have been obtained from fewer than 100 tagged lobsters although far higher numbers are usually required (Shepherd *et al.*, 2011). The successful application of survival estimation methods generally occurs in cases where the statistical method is planned before enhancements occur, rather than as a secondary activity that becomes handicapped by inadequate experimental design.

Tag–recapture models contain assumptions which Green & Gardner (2009) described in measuring survival of released lobsters from tag–recapture data as (i) every tagged animal in the population has the same probability of recapture; (ii) every tagged animal has the same probability of surviving; (iii) tags are not lost or missed; (iv) all samples are instantaneous and each release is immediately after sampling; (v) there was no impact of person (tagger) on tag loss; (vi) tag loss was equivalent between released and resident animals; and (vii) season and period at large had no effect on tag loss.

3.2.3 Displacement and integration of released lobsters

One issue of concern for enhancement operations is that resident lobsters may be displaced by released lobsters if space is limited and the carrying capacity is reached, or if there is a territoriality, dominance or aggression (Bannister & Addison, 1998; Hoegh-Guldberg *et al.*, 2008). Likewise, translocated lobsters might be unable to establish residences and home ranges (Hilborn, 1998; Bell *et al.*, 2006, 2008). These issues have been examined using acoustic telemetry technology, which provides fine detail on individual movements and thus foraging behaviour, establishment of home range, location of shelter, aggregation behaviour and habitat use (Zeller, 1997, 1998; Watson *et al.*, 1999; Giacalone *et al.*, 2006; Lindberg *et al.*, 2006; Kawabata *et al.*, 2007; Oliver *et al.*, 2008).

The large size of lobsters, their relatively slow mode of locomotion and non-streamlined bodies mean that tags can be glued directly onto the dorsal surface of the abdominal carapace even down to juvenile stages (Plate. 3.1). Lobsters are also generally far less mobile than finfish and elasmo-

branches and so can be tracked within a triangulated series of monitors such as VRAP telemetry system (<http://www.vemco.com/products/receivers/vps.php>), which consists of underwater acoustic transmitters and receivers.

Where these acoustic tagging methods have been applied to translocated spiny lobsters, there have been no apparent issues of displacement although foraging ranges may be smaller in the released lobsters (Mills *et al.*, 2004).

3.2.4 Habitat and predator change

The risk to ecosystems from the translocation of animals outside their normal range is usually viewed as too great to justify (Ricciardi & Simberloff, 2009a,b), although frameworks have been developed to reduce risk in marine systems to habitat or predator and prey fields (Blankenship & Leber, 1995; Hoegh-Guldberg *et al.*, 2008; Lorenzen *et al.*, 2010).

Monitoring and assessing environmental impacts in the marine system is constrained by the logistical difficulty in working underwater and the dynamic nature of these ecosystems (Rouphael *et al.*, 2011; Smale *et al.*, 2011). Methods include using direct counts or estimates of species within an ecosystem (Jones *et al.*, 2004; Barrett *et al.*, 2009) and bio-indicators as a measure of ecologically relevant changes (Gray, 1979; Smale *et al.*, 2011). Underwater visual census (UVS) is widely employed, although the presence of a diver can disturb larger mobile species such as lobster predators (Watson & Quinn, 1997; Samoilys & Carlos, 2000; Ward-Paige *et al.*, 2010). Likewise, small cryptic prey items can be grossly underestimated, particularly in complex reef systems such as coral reefs (Ackerman & Bellwood, 2000). The advent of towed video and autonomous underwater vehicles has removed some of the restrictions of divers and has been used for deep water lobster research (Waddington *et al.*, 2010), although this also has limitations including the difficulty of *post hoc* identification of species.

Ecological change following enhancement of lobsters within natural range has been assessed in both South Australia and Tasmania, although no significant changes were detected in either predator

or prey abundances (Green *et al.*, 2012). Other studies have shown that reduction in density of lobsters through fishing can have ecological impacts such as release of predation pressure on urchins and also emergence of abalone (Pederson & Johnson, 2006; Pederson *et al.*, 2008). Restoring lobster density to more natural levels through enhancement would thus be expected to compensate for any ecosystem effects of fishing.

3.3 Economic and policy issues

The need for economic research and policy development in translocation operations was emphasized by Bartley & Kapuscinski (2008), who stated that responsible enhancement operations should equitably improve human welfare and be governed by a representative and transparent process. Translocation of lobsters from wild sources presents additional economic and policy challenges to the release of hatchery-reared animals, including the need to manage removals from the wild stock and transfer of genes and disease between areas.

3.3.1 Economic feasibility

The economic feasibility of enhancement is a cost-benefit problem where benefits of increased catch, higher price or lower cost (through higher catch rate) need to exceed costs of enhancement (Thlusty, 2004), plus opportunity costs including foregone yield at the removal site in the case of translocation operations. The initial cost of hatchery production is important and developments that reduce cost at this stage can have a significant effect on the overall feasibility. An example includes low-cost cage growout systems developed for homarid species that enables cost-effective production of larger lobsters with higher post-release survival (Beal *et al.*, 2002).

Lobster enhancement operations take many years for benefits to accrue, so discounted cash flow methods are required to determine feasibility (McCay *et al.*, 2003). This approach was taken to assess feasibility of translocations of *J. edwardsii* by Gardner & van Putten (2008a,b) utilising a length-based bioeconomic model. Translocation was examined with scenarios involving movements

from different slow growth areas to higher growth areas around the state of Tasmania in Australia. Two different methods of translocation were examined, which affected both costs and benefits of the operation. The low-cost system involved the capture of undersize lobsters from slow growth areas through normal fishing operations with these undersize lobsters then moved inshore. This approach had very little marginal cost because fuel, labour and other costs were already sunk in harvesting operations. In the second approach, vessels could be chartered and funded to fish exclusively for the purpose of collecting animals for translocation. Both options appeared economically feasible but the higher cost, chartered option was favoured both in the analysis by Gardner & van Putten (2008b) and also subsequently by the commercial industry. This was because chartering provided greater control over the scale and location of removals.

The most critical result from this analysis was that translocation of lobsters can have large economic benefits with the internal rate of return exceeding 400% in some scenarios examined by Gardner & Van Putten (2008b). Some of the biological traits of lobsters contributed to this outcome, including their ability to be captured and released with low discard mortality, the low rates of movement of *J. edwardsii* in this region, and spatial heterogeneity in growth and recruitment. Not all of the translocation scenarios examined were economically feasible as short distance translocations sometimes led to trivial gains in growth that were outweighed by the costs.

The economically attractive results for *J. edwardsii* translocation are not repeated for most lobster enhancement operations that rely on hatchery production. Most analyses of *Homarus* spp. enhancement operations have shown that the economic yield is low or more typically negative, mainly due to the cost of production and growout of juveniles to a size where reasonable survival is achieved (Bannister & Addison, 1998; Moksness *et al.*, 1998; Thlusty, 2004; Hamasaki & Kitada 2008).

Lorenzen (2005) examined a generalized case of the feasibility and pitfalls of enhancement. His conclusions included that the costs of released animals strongly influence optimal policy, so that high levels of stocking and fishing effort are only feasi-

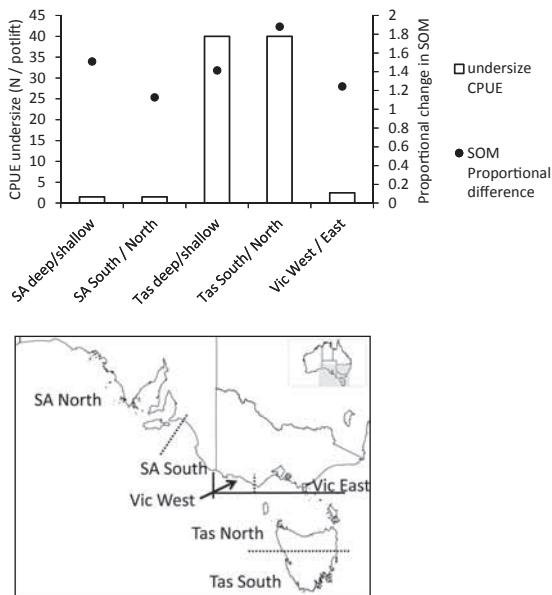


Fig. 3.1 Opportunities for increasing production by rock lobster translocation within range occur where there is both large spatial variation in growth (so that productivity benefits are large) and an abundance of undersize lobsters (so that costs of capture are low). Translocations of *Jasus edwardsii* in Australia appear more feasible in the Tasmanian fishery than in South Australia or Victoria because there is greater capacity to catch large numbers of undersize lobsters at lower marginal cost. In addition, there is large spatial difference in growth, indicated here by the proportional difference in size at onset of maturity (SOM) between either deep or shallow water sites or along the coast (data from Hobday and Ryan 1997, Linnane *et al.*, 2008, 2009, 2010a, 2010b; Gardner *et al.*, 2006b, Gardner and van Putten 2008a).

ble where cost of release is low, relative to gains in yield. In the case of lobster translocation, this situation only occurs where both catch rates at the removal site are exceptionally high and also where there is large variation in growth rate over short distances (Fig. 3.1). Lorenzen (2005), Hilborn (2004) and others have emphasized that analysis of the economic feasibility of enhancement also needs to take account of possible losses in yield through genetic impacts on the wider stock. This problem is an example of the negative externalities that are rarely included in economic assessments of enhancement.

The economic feasibility of enhancement operations would be expected to vary and can be sensi-

tive to prices and costs that change through time. Examining sensitivity across numerous parameters can be complex and tools have been developed to assist these exercises. Most directly applicable to lobster translocations is ‘EnhanceFish’ software (Lorenzen, 2005, <http://www.aquaticresources.org/enhancefish.html>), which provides a bioeconomic model structure that enables sensitivity testing of critical variables. Outcomes tend to be highly influenced by density-dependent biological processes, which are considered to be critical to the biological and thus economic success of enhancement operations (Hilborn, 2004). These processes are important with hatchery releases but appear to be less critical in lobster translocations because supply of animals is constrained by natural recruitment, and field studies of translocated lobsters have detected only trivial density-dependent responses (Chandrapavan *et al.*, 2010). Another software tool ‘Wildlife Introduction Advisor’ has been developed for terrestrial movements and deals with the problem of allocation between end users (Paterson *et al.*, 2008). This has not been applied to lobster translocations but may have potential for assisting with allocation between sectors (e.g. the spatial location of releases to provide equitable access to recreational and commercial fishers).

3.3.2 Optimal management of harvests with enhancement

Lobster enhancements increase the productivity of the stock, so outcomes are similar to an increase in recruitment. In this context, the challenges for optimization of harvests are broadly the same as per normal fisheries where there is a need to balance current harvests (or revenue) against the costs associated with removal of stock, especially the possible loss of future growth and recruitment plus higher marginal costs from reduced catch rates. The fact that enhancement allows productivity to be manipulated with management interventions tends to initiate discussion of management objectives. Put simply, should the extra productivity be managed to increase catches, catch rates, or some combination of the two?

Theory on optimal management of harvesting in wild fisheries is well developed and generally

involves targeting maximum economic yield or ‘wealth-based management’ (e.g. Cunningham *et al.*, 2009). This approach to the management of productivity gains from lobster translocation would typically result in constraining harvests to increase stocks and reduce costs of fishing. More recently, some researchers have argued that the effect of management decisions on labour should be more carefully assessed when attempting to generate societal benefits from fisheries harvests (Bromley, 2009; Béné *et al.*, 2010; Mills *et al.*, 2009). If applied to lobster enhancement operations, this emphasis on job creation would place greater weight on increasing harvests rather than catch rates.

Managing harvests given the common pool nature of the resource is a pervasive issue in fisheries management and especially problematic in enhancement operations. This is because the individuals who gain benefit from harvests are not necessarily the same as those who pay for the enhancement operations. Arnason (2008) examined this problem and found that enhancement operations would tend to release fewer than optimal number of animals (from a societal perspective). Investment into translocation operations described by Gardner & van Putten (2008b) would also be expected to occur below optimal societal levels if left to market processes because the scheme was to be funded by commercial fishers but with benefits split between commercial and recreational fishers. This problem of security of ownership has been addressed through ‘Sea Ranching’ legislation in Norway which was approved in 2000. This law gives the release company exclusive harvesting rights within a release area to decapods, molluscs and sea urchins, both wild and released.

3.3.3 Ownership, policy and risk

Restocking for conservation purposes is usually for public good and thus ownership is not problematic (Mangun 1988). In these cases, costs tend to be borne by government although in theory they could be funded by private firms as part of remediation of development or oil spills (Cosgrove & Hastie 2001; McCay *et al.*, 2003).

Ownership and ‘property rights’ to harvested fish are much discussed in lobster fisheries management and become complex when dealing with enhancements. Macinko & Schumann (2008) examined the transfer of ownership of the southern New England lobster stock from public to private ownership. In that example, the debate over the merit of transfer of ownership is further complicated by releases of hatchery-reared stock. In the case of translocation of *J. edwardsii* in Tasmania, the State Government has stated that ownership of the stock, and thus translocated animals, remains with the State (Gardner & van Putten, 2008b).

Policy for enhancement and translocations have been developed in many jurisdictions and generally relate to managing risk of impact from genetic pollution, ecosystem impacts, and transfer of disease (Borg, 2004). Of these risks, the issue of genetic impacts tends to be treated as the major risk to wild stocks (Sheridan, 1995; Araki & Schmid, 2010). The policy response to this risk has varied between lobster translocation operations. Trans-Atlantic, accidental translocations of *H. americanus* create significant concern due to the potential for hybridization (Jørstad *et al.*, 2007), while, at the other extreme, risk appears to be negligible in translocations of *J. edwardsii* over tens of kilometres (Green & Gardner, 2009).

Policy on translocations also focuses on risks of disease transfer which has occurred in crustacean translocations. The transmission of diseases like Nodavirus in freshwater prawn farming (Kamalam *et al.*, 2008) and crayfish plague (*Aphanomyces astaci*) which affected *Astacus astacus* populations following translocation of *Oncorhynchus mykiss* (Geelen, 1975) shows that this should be a legitimate concern for lobster enhancements. Concern about risk of bacterial disease introduction (gaffkemia) has been expressed with the translocation of *H. americanus* into Europe (Jørstad *et al.*, 2006). Common to each of these cases is that the impact of the translocated pathogen is more severe when introduced to naive populations.

Biodiversity risks are a policy concern for translocations both within and outside natural ranges. For translocations outside the natural range the risk lies in organisms becoming invasive (Mueller & Hellmann 2008; Arbaciauskas *et al.*, 2010), while

translocations within natural ranges carry a risk of change in organism density and thus ecosystem function. Historical translocations that have resulted in invasive species and impacts on biodiversity generally occur through failure to include any value on existing ecosystems in assessing the business case (Cambray, 2003). In cases where lobster translocations result in stock rebuilding, the system has greater naturalness and thus externalities would be considered to be positive.

3.4 Case studies

3.4.1 Clawed lobster restocking

A large-scale restocking programme of *H. gammarus* juveniles into wild populations was initiated in 1990 at Kvitsøy, south-western Norway. Between 18,000 and 29,000, 7–8 months old, magnetic micro-tagged lobster juveniles were released at the archipelago of Kvitsøy every spring from 1990 to 1994. The juveniles are cryptic (Mercer *et al.*, 2001) so are only resighted 4–5 years later (van der Meeren 2005). This cryptic behaviour has prevented measurement of post-release survival in the Norway programme, although survival appeared to be high (50–84% depending upon assumptions) in releases off the Yorkshire coast in the UK (Bannister *et al.*, 1994). In laboratory experiments, there was no difference in survival of hatchery-raised larvae from a geographically separate control population, wild females from the area of the large-scale release study and females previously released as juveniles in that area (Jørstad *et al.*, 2009). European lobster (*H. gammarus*) juveniles released as larger than 15 mm carapace length, integrate into the local populations and subsequently the reproducing stock (Bannister and Addison 1998, Agnalt *et al.*, 2007; Agnalt, 2008; Jørstad *et al.*, 2009).

The large-scale release of juveniles of 11–15 mm in south-western Norway during 1990 resulted in a tag-recovery rate of 8% by 2002 (Agnalt *et al.*, 2004). At the peak of the recaptures, between 1996 and 2000, released lobsters constituted around 50% of landings and the catch per unit effort of lobsters at Kvitsøy became markedly higher than in the surrounding areas.

In the UK, enhancement experiments comprising the release of over 90,000 individuals across several years in four commercial fishing areas off the Yorkshire coast, the Welsh coast on the Irish Sea, the west coast of mainland Scotland and Scapa Flow in Orkney, northern Scotland, produced gross tag-recovery rates ranging from 1% to 4%, although local hot-spot recapture rates close to individual release locations were up to 30% (Addison & Bannister 1994; Cook, 1995; Bannister & Addison, 1998; Burton, 2001). These enhancements had a specific release strategy, involving lobsters grown to 12–15 mm carapace length (CL) so that they were large enough to receive and retain a wire-coded micro-tag, and the animals were released underwater by divers directly onto good lobster habit (Wickins *et al.*, 1986). They were ‘proof of method’ experiments, rather than deliberate attempts to enhance the stocks. Outside of Norway, European restocking programmes did not result in a significant increase in the landings and were continued only at the Orkneys, where they are managed by the local fisheries association.

In all of the European stock enhancement studies, released lobsters survived to produce egg clutches that were similar in size and number to wild females of the same size (Agnalt *et al.*, 2004, 2006). Although the Norwegian enhancements substantially boosted a commercially extinct stock in less than 10 years (Agnalt *et al.*, 1999, 2004), there was no detectable increase in recruitment following this enhancement nor in any of the other European releases. An important conclusion from the European releases was the need for research on strategies for release (Cook, 1995; Knudsen & Tveite, 1999; van der Meeren, 2000, 2003; Burton, 2001). This included establishing the need for normal chelae morphology and carapace through the provision of calciferous shell sand (Beard *et al.*, 1985; Uglem *et al.*, 2006). They were also grown to a large size before release, and released during in early spring when the water temperature and predator activity were low. Releases in Norway occurred in daylight to promote sheltering behaviour and to reduce aggression between individuals (van der Meeren, 2006), while in the UK releases were best conducted at night to avoid predation (Bannister & Addison 1985).

3.4.2 Range extension of American lobster to Europe

Large quantities of wild-caught, market size *H. americanus* have been exported live from north-eastern America to Europe for a century and more. The availability of these animals has led to unintentional escapees and intentional releases on many occasions with small numbers of *H. americanus* captured and confirmed using standard taxonomic techniques from Great Britain (26 lobsters), Ireland, Norway (18 lobsters), Sweden (five lobsters) and Denmark (one lobster) (Jørstad *et al.*, 2006, 2011; Minchin, 2007; van der Meeran *et al.*, 2008; Stebbing *et al.*, 2012). In a few cases the reason for the translocation is known and included intentional release for ‘improvement’ of the fishing ground.

In one small-scale case, *H. americanus* juveniles were raised as a class project at a primary school in Norway around 1990 and were possibly the source for the first positive recordings of the species in the country in 1999 (van der Meeran *et al.*, 2000). Juvenile *H. americanus* and hybrid *H. americanus/H. gammarus* were produced for release in France (Adouine & Leglise, 1972; Latrouite & Lorec, 1991), to enable released lobsters to be distinguished from the native stock when they were recaptured. This programme was closed before the survival of these lobsters could be assessed (Agnalt *et al.*, 1999).

There are several concerns with these attempts to extend the range of *H. americanus* into Europe. The local and the introduced homarid species have similar behaviour and diet needs (Nicosia & Lavalli, 1999) so are expected to compete for resources. *H. americanus*, with potential for larger overall size and larger chelae in relation to the CL, may be dominant in competition for limited resources although aggression appears to be higher in *H. gammarus* (van der Meeran *et al.*, 2008; Skog 2008). Hybridization is also of concern, and although European lobster females preferentially select European lobster males (van der Meeran *et al.*, 2008), one berried *H. americanus* female captured in Norway produced viable hybrid offspring (Stebbing *et al.*, 2012). Transfer of pathogens is a significant concern and is the basis for calls to not only ban translocation but any live trade (Anon., 2011). Outbreaks of gaffkemia have been reported

from holding facilities in Norway, and UK, and had not been documented in wild stocks until recently (Wiik *et al.*, 1987; Jørstad *et al.*, 2011). Epizootic shell disease have been positively documented in a small number of *H. americanus* captured in Norwegian waters, causing fear for dispersal of this disease to Europe (Agnalt *et al.*, 2011).

3.4.3 Improving yield in Southern rock lobster: translocating low quality adults

A form of lobster enhancement has been developed in Australia that involves capturing and translocating *J. edwardsii* within their geographic range. The operation is based on the substantial spatial differences in biology and fleet, especially differences in growth between areas (McGarvey *et al.*, 1999; Gardner *et al.*, 2006b). For example, annual growth increment for females of CL 75 mm can vary from 1–2 mm to more than 20 mm per annum for locations only 200 km apart (Punt & Kennedy, 1997). Wild-sourced lobsters are captured and moved to faster growth areas where they become more productive and also develop a deeper red colour that results in a higher market price (Chandrapavan *et al.*, 2009a).

Translocation within the geographic range does not have many of the problems encountered with other enhancement operations. Genetics and disease transfer risk do not exist because lobsters are moved within distances less than normal larval dispersal. Translocation is combined with a total allowable catch so that the process leads to rebuilding of biomass. This implies that translocation restores populations to more natural levels, which reduces risk of fishery impact on egg production and ecosystem. Ecosystem impacts are especially a concern in the Tasmanian jurisdiction because lobsters are believed to provide predation pressure to limit the expansion of urchin barrens (Pederson & Johnson, 2006; Ling *et al.*, 2009).

These translocation operations have developed to small-scale operations that are funded and managed by the commercial fishing industry with operations in 2012 involving the translocation of 100,000 lobsters per annum. As a consequence of this form of enhancement, the total allowable catch was maintained 5% higher than would have been possible otherwise (Treloggen, 2012). Industry had

been persuaded to invest in these operations on the basis of earlier research showing that these operations were economically viable, mainly because catch rates in source areas were very high at over 30 lobster per trap and gains in growth were substantial (Gardner & Van Putten, 2008a). Smaller experimental trials were run from 2005 to 2008 involving a total of 30,000 lobsters and these demonstrated a range of positive outcomes which were:

- 1 improved market traits of colour and morphology (Chandrapavan *et al.*, 2011)
- 2 increased omega-3 lipid content (Chandrapavan *et al.*, 2009a)
- 3 better survival in live transport (Hawthorn 2009)
- 4 faster growth (Chandrapavan *et al.*, 2010)
- 5 Increased egg production (Green *et al.*, 2010)
- 6 Translocated lobster remained at the release site and had equal survival to residents (Green & Gardner 2009).

Translocated lobsters remained at the release site, had equal survival to residents (Green & Gardner, 2009), and increased egg production (Green *et al.*, 2010).

3.5 Conclusions

Despite a long history of investment and trials, lobster enhancement occurs only in small-scale operations in only a few fisheries so that there is little impact on global lobster production. The

failure of early hatchery operations for clawed lobsters to deliver ongoing increase in production was a history common to enhancement operations of many marine species in the late 1800s and early 1900s. Likewise, the failure of the numerous historical attempts by acclimation societies to extend the range of lobster species was repeated with other marine species, which today we would regard as fortuitous. Hatchery enhancement and range extension operations consistently lacked critical information on juvenile biology and processes affecting recruitment. There also tended to be a lack of monitoring of success or scrutiny of the economic feasibility so that expectations were built without robust support. Enhancement attempts over the last 20 years are characterized by far greater research on factors affecting survival and growth after release plus monitoring and economic evaluation. This has led to some lobster enhancement operations with demonstrated benefits that exceed costs. The success of hatchery releases in Europe is related to the depletion of the wild stock so that current levels of recruitment are low and hatcheries can make a significant impact. Further, research to establish the optimal size at release and culture techniques that assist survival have been critical. The Australian operation based on translocation of undersize lobsters provides an interesting contrast as it involves economically feasible enhancement in a population that has high levels of natural egg production and shows no sign of recruitment overfishing. This demonstrates that there can be opportunities for enhancement of lobsters in healthy fisheries provided that the biology and population impacts of enhancement are well understood.

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Chapter 4

The Impact of Climate Change on Exploited Lobster Stocks

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Abstract

Climate change is predicted to significantly affect the world's oceans, with increases in water temperature, changes in ocean currents, pH levels and winds. This chapter highlights the vulnerability of lobster stocks to climate change due to their long larval life. Western and southern rock lobsters in Australia are influenced by long-term increases in water temperatures which are projected to continue. These increases have influenced the size at maturity and size of migrating western rock lobsters. Climate change has been implicated in the abundance decline and increase in lobster diseases in the southern part of the *Homarus americanus* stock and in the increase in catches in northern regions. Regime shift in the north Pacific has been implicated in changes in abundance of Japanese and Hawaiian spiny lobsters. If the recruitment abundance is vulnerable then monitoring of pre-recruits becomes very important and management strategies need to be sensitive to abundance trends. This chapter highlights the need to downscale climate change models to a spatial and temporal scale relevant to lobster stocks and the uncertainties in the climate change projections and their effect on the ecosystem.

Key Words: climate change; lobster; water temperature; risk assessment; regime shift; catch prediction

4.1 Introduction

Climate change is predicted to significantly impact the world's oceans, leading to increases in water temperature and to changes in the patterns of ocean currents, pH levels, storm fronts and winds (Feely *et al.*, 2004; Herr & Galland, 2009). These environmental factors contribute to the interannual varia-

bility of key parameters for all marine stocks (Cushing, 1982), and as these factors change, so will the population dynamics of these stocks. This chapter will examine the current understanding of the impacts climate change is having, and potentially will have, on commercially exploited lobster stocks in a range of marine environments around the globe.

The long larval phase of lobsters, particularly spiny lobsters, makes them particularly vulnerable to climate variability and hence climate change effects if there are long-term trends on the environmental variables affecting lobster populations. Environmental conditions during this larval phase can affect their advection, growth and survival (Phillips *et al.*, 2000). Many other aspects of the lobster life history of many populations such as the growth, migration, size at maturity and catchability appear to be sensitive to changes in water temperature (Morgan, 1974; Hazell *et al.*, 2001; de Lestang & Melville-Smith, 2006; Caputi *et al.*, 2010; Moland *et al.*, 2011). If these environmental variables that affect different parts of the life history have long-term trends then there could be long-term trends in some of the biological parameters of the lobster stocks that need to be taken into account in the stock assessment and management of these fisheries.

Climate change effects have already been identified in a number of spiny and clawed lobster stocks around the world, generally associated with warming water temperatures. These include the western rock lobster in Australia (Caputi *et al.*, 2010), southern rock lobster stocks in Tasmania, Australia (Pecl *et al.*, 2009), the American lobster (Pearce & Balcom, 2005; Wahle *et al.*, 2009) and *Jasus lalandii* stocks in South Africa (Cockcroft *et al.*, 2008). Regime shift in the North Pacific has been identified as affecting the abundance of Japanese and Hawaiian spiny lobster stocks (Polovina, 2005; Sekiguchi & Inoue, 2010). This chapter examines a number of case studies (three in detail – western and southern rock lobsters in Australia and the American lobster) from different regions and where possible addresses the following issues in assessing climate change effects on lobster fisheries:

- 1 lobster biology and fishery;
- 2 the effect of environmental variability on biological parameters (e.g. distribution, recruitment, size at maturity, growth, disease, catchability) of the lobster stocks;
- 3 the key environmental trends (e.g. decadal shifts, long-term trends) that have occurred in the marine environment that may affect the

fishery e.g. increasing water temperatures, changes in water currents and winds;

- 4 the likely future trends in the environmental variables in the short term (20 years) and long term (>30 years) and their possible effect on fisheries;
- 5 the implications for stock assessment and management; and
- 6 conclusions and future research.

When considering the climate effects on the lobster fisheries it is important to differentiate between the following terms to describe climate trends: climate variability (where there is no particular trend apparent), climate change (a long-term trend indicated) and regime shift (stepwise change in the climate identified). In evaluating climate change trends it is also important to understand the spatial extent where the change is occurring and the rate of change over a specified period. If considering projected changes then the climate model being used and Intergovernmental Panel on Climate Change (IPCC) emission scenario being assumed are also important. Similarly for a climate regime shift, the level of the environmental shift and when that shift has occurred, enable an assessment of the change.

4.2 Case studies

4.2.1 Western rock lobster (*Panulirus cygnus*)

The western rock lobster (*P. cygnus*) fishery of the lower west coast of Western Australia (WA) has an extensive history of research and management being one of the first limited entry fisheries in 1963 (de Lestang *et al.*, 2012). The fishery has a 40-year time series of key research information on spawning stock, puerulus settlement and juvenile abundance, catch and fishing effort, and environmental factors affecting different life history stages. This database makes it one of the best Australian fisheries to study climate change effects.

The western rock lobster has a large geographic range covering 22–34°S with a considerable variation in average sea surface temperatures, 18–23°C

(austral winter) and 20–26°C (austral summer) (Plate 4.1) which is also an advantage in studying climate change effects. The geographical range in water temperatures affects the biological parameters (e.g. size at maturity and migration) of lobsters in the different areas (Melville-Smith & de Lestang, 2006; Caputi *et al.*, 2010). This provides some insights into how long-term changes in water temperature due to climate change may affect the fishery overall.

The fishery has had a long-term average catch of about 11,000 t. However a downturn in puerulus settlement over the 6 years, 2006/07 to 2011/12, resulted in a pro-active management response before these year-classes reach the fishery with a significant reduction in fishing effort (ca. 40–70%) since 2008/09 resulting in a decline in catch to 5,900 t in 2009/10 (de Lestang *et al.*, 2012). The fishery also underwent a major change in management approach moving from an effort-controlled fishery to an individual transferable quota (ITQ) fishery in 2010/11, with a quota of 5,500 being set for the 2010/11 fishing season.

The fishery is influenced by a number of environmental factors such as water temperatures, the strength of the Leeuwin Current and the strength of the westerly winds (Caputi *et al.*, 2001). These key environmental factors can affect the western rock lobster throughout its complex life cycle from spawning; the larval stages over the 9–11 months they spend offshore of the continental shelf (see Figure 10.1 in Chapter 10, Pearce & Phillips, 1988; Caputi & Brown, 1993; Caputi *et al.*, 2001); the level and spatial distribution of the puerulus settlement along the coast; the growth rates of the juveniles (Johnston *et al.*, 2008); the size of the juveniles migrating from shallow (<40 m) to deeper water (40–100 m) and the subsequent catch distribution; the strength of their pre-adult northerly migration (de Lestang *et al.*, 2012); their size at maturity (Melville-Smith & de Lestang, 2006); the moulting of mature females from setose to non-setose condition (de Lestang & Melville-Smith, 2006); and the catchability of lobsters in the pots (Morgan, 1974).

The relationship between annual western rock lobster puerulus settlement and sea level was first demonstrated by Pearce and Phillips (1988), indicating that settlement is much higher in La Niña

years when the Leeuwin Current is flowing strongly than during El Niño Southern Oscillation (ENSO) events. Subsequent work by Caputi *et al.* (1996, 2001) using 30 years of settlement and sea level data confirmed and strengthened this relationship (although the settlements between 2007/08 and 2009/10 were anomalously low suggesting that other factors dominated in these years).

The southerly winds in the austral summer, at the time when the early stage larvae of the rock lobster rise to the water surface, cause an offshore movement in the near-surface waters (the so-called Ekman transport) which carry the larvae out into the open ocean at the start of their 9–11-month migration (Phillips, 1981). In the absence of reliable open-ocean wind and swell data, Caputi *et al.* (2001) used rainfall at a number of coastal sites as a proxy for storm and westerly winds to show that puerulus settlement is enhanced when there have been strong storm-generated westerlies between July and November – the period when the late-stage phyllosoma are returning towards the shelf and transforming into puerulus before settling on the coastal reefs. The current strength during the period of settlement has also been shown to affect the spatial distribution of the settlement along the coast (Caputi, 2008), with increased settlement southwards when the southward-flowing Leeuwin Current is stronger.

Key environmental trends

Some of the key environmental trends that may be affecting the western rock lobster stocks include (i) changing frequency of ENSO events; (ii) more years with weaker Leeuwin Currents; (iii) increase in water temperature off the lower west coast of WA, particularly in austral autumn–winter; (iv) increase in salinity, which includes some large annual fluctuations; and (v) change in frequency and location of storms (and rainfall) affecting the lower west coast of WA.

The increasing frequency of ENSO events since 1990 with eight in 20 years classified as ENSO years compared with 5 years in the previous 20 years has resulted in more years with a weaker Leeuwin Current in recent times (Caputi *et al.*, 2010). However Feng *et al.* (2010) have identified

an increasing trend in the strength of the Leeuwin Current since the early 1990s. The trend in annual values of Fremantle sea level for over 100 years indicate a long-term trend with an average increase of 1.54 mm per year, which corresponds to a warming trend in the global surface temperature rather than reflecting an increase in Leeuwin Current strength (Feng *et al.*, 2004). Two La Niñas that have occurred in the last 11 years (1999/2000 and 2010/11) have been particularly strong, resulting in a strong Leeuwin Current and very warm water temperatures.

Pearce and Feng (2007) have shown that there has been a gradual warming of water temperatures of about 0.02°C per year off the western Australian coast since the 1950s (Plate 4.2), with most of the increase focused on the austral autumn–winter period with little increase apparent in the summer–spring period (Caputi *et al.*, 2009). In addition there has been a change in the frequency and location of storms approaching the lower west coast of WA, which not only affects the rainfall in the south-west of west Australia (Bates *et al.*, 2008) but also results in a weakening of the westerly winds in austral winter, which affects the oceanic conditions. This trend has culminated in one of lowest rainfalls in 100 years being experienced in 2010 in Perth.

Effect of environmental variability on biological parameters

The long-term trend in the frequency of ENSO and its effect on the Leeuwin Current combined with the long-term trend in water temperature and storms off the lower west coast of WA may be having significant implications for climate change effects on the lobster fishery. The change in the frequency and intensity of ENSO events was identified as a significant risk factor for the rock lobster fishery in the early 1990s at a fisheries climate change workshop (Penn, 1992). An ecological risk assessment expert workshop considered the risk to rock lobster productivity from climate change (Department of Fisheries, 2005). They developed an influence diagram describing the risk resulting from possible environmental shifts (Fig. 4.1). The expert workshop gave climate change a low risk rating after

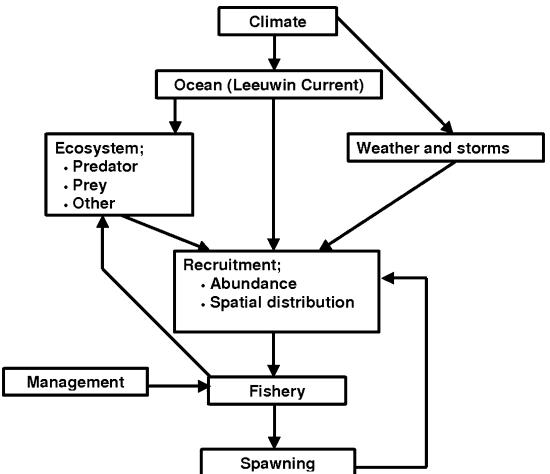


Fig. 4.1 Influence diagram describing the risk resulting from climate change effects on the western rock lobster fishery (Updated from Department of Fisheries Western Australia, 2005)

taking into account that the management would be able to adapt to climate change effects on the fishery.

Caputi *et al.* (2010) identified how climate change may be affecting the western rock lobster fishery. They showed that increasing water temperatures over the last 30–35 years may have resulted in a decrease in size at maturity (Melville-Smith & de Lestang, 2006), a decrease in the size of migrating lobsters from shallow to deep water, an increase in the abundance of undersize and legal size lobsters in deep water relative to shallow water and a subsequent shift in catch to deep water. The size of the migrating lobsters was significantly related to the water temperature about the time of puerulus settlement (4 years previously).

The strength of the pre-adult northerly migration during November–February has been identified as being influenced by the strength of the meridional current at the time of migration (de Lestang *et al.*, 2012). The migration moves further north in years when the southern component of the current is weakest. Water temperature prior to spawning also affects the timing of the spawning period with warm water temperatures associated with an earlier spawning period (de Lestang *et al.*, 2012).

There is currently an extensive research programme under way assessing the factors that may have contributed to the below-average recruitment (*puerulus*) in the last 6 years (2006/07 to 2011/12), including the two lowest recruitments in the 40-year time series. This research is examining both environmental and biological factors. At this stage the historical environmental variables that have explained the variation in *puerulus* settlement do not explain this significant downturn. The egg production at most locations in the fishery is near record levels as a result of the significant effort reductions. The longer the decline continues then the more likely it is that some long-term change in an environmental factor (that may be affecting the spawning or larval phase) may be implicated.

Climate change model projections indicate that the warming trend is likely to continue even after the greenhouse gas concentrations in the atmosphere are stabilized so that these biological trends may continue. The models indicate increases of 1–2°C by the 2030s and 2–3°C by the 2070s (Poloczanska *et al.*, 2007). Some of these changes (such as the increasing frequency of El Niño events) may have negative implications on the western rock lobster fishery but some such as increasing water temperature may have some positive influence on some aspects of their life history.

Implications for stock assessment and management

The climate change trends identified for some fisheries can have significant effects on the stock assessment, which generally have a stationarity assumption of the biological parameters (i.e. assume these parameters are constant). The changes in some of the biological parameters (e.g. size at maturity and migration) of the rock lobster stocks since the 1970s have been included in the population dynamic model of the fishery (de Lestang *et al.*, 2012). The recent series of low *puerulus* settlement that will affect the catches and breeding stock from about 2010/11 have also been factored into the assessment and the management settings of the fishery. Significant effort reductions (40–70%) have been implemented from 2008/09, prior to these low settlements reaching legal size, to

ensure that there is carryover of legal-size lobsters into these low recruitment periods and that the breeding stock is maintained above a threshold level (de Lestang *et al.*, 2012).

Changes in the spatial distribution of stocks also poses some interesting management policy issues to evaluate. Long-term changes in water temperature or strength of the Leeuwin Current that affect larval distribution and lobster migration can cause long-term changes in spatial distribution of stocks. If there are fixed management boundaries used in the management of these stocks such as the three zones in this fishery, then there could be some significant biomass increases in some zones and decreases in others. Does fisheries management maintain the current zone structure and recognize that there could be some long-term ‘winners’ and ‘losers’ in that situation or does it adjust the management to maintain some historical equity in the system? This issue is currently under consideration.

This case study highlights the value of long-term time series in fisheries and environmental data in assessing the effect of climate change and/or other significant environmental or biological perturbations on fisheries. The establishment of a good measure of recruitment, which provides a predictive ability of future catches, is particularly valuable. This monitoring has identified a series of low recruitment that, irrespective of the cause, has required significant adjustment to the management of the fishery. These management changes were initiated in 2008/09, 1–2 years before these poor year classes entered the fishery. Fisheries can be severely overfished when heavy fishing continues as low recruitment levels enter the fishery.

Future research

Once environmental factors affecting fisheries are identified then their historic trends and assessment of future trends help identify the fisheries that may be vulnerable to climate change, positively or negatively. Though global climate models that provide a general direction of environmental trends (Poloczanska *et al.*, 2007) are valuable, the effect on fisheries may require a more specific assessment of the trends at appropriate spatial scales, e.g.

Leeuwin Current and Capes Current. The environmental trends during seasons of the year, e.g. spawning and larval periods, are also important. This highlights the importance of local climate change initiatives in WA examining marine climate change effects off WA and the Indian Ocean Climate Initiative examining storms and rainfall in the lower south-western coast (Bates *et al.*, 2008), which have identified a decrease in the frequency of storms affecting the lower west coast of Australia. The development of the Integrated Marine Observation System (IMOS) in Australia is also a valuable initiative in establishing reference stations providing an understanding of environmental trends (<http://www.imos.org.au>).

This case study has focused on the direct effects of climate change on the western rock lobster. However, there are likely to be some indirect effects such as effect on habitat, prey and predators that also need to be considered. Therefore, when assessing the risk factors of climate change effect on fisheries, the indirect effects need to be considered and included in the long-term monitoring if identified as a significant risk.

4.2.2 Southern rock lobster (*Jasus edwardsii*)

The southern rock lobster is commercially fished in Australia from southern WA, through South Australia (SA), Victoria, Tasmania and southern New South Wales (NSW), although only minor catches are reported in WA and NSW.

It is also an important fishery in New Zealand. In Australia the fishery is independently managed by each state with SA, Victoria and Tasmania using individual transferable quota for management while the other states employ input controls. The average combined catch of the southern rock lobster in Australia and New Zealand is about 5000 t.

Southern and south-eastern Australia are primarily affected by two main current systems. South Australia, western Victoria and western Tasmania are under the influence of the southern extension of the Leeuwin Current, often referred to as the Zeehan Current off western and southern Tasmania. NSW and eastern Tasmania are bathed by the

Eastern Australian Current (EAC), which meets the southern ocean off south-eastern Tasmania (Ridgway & Hill, 2009).

In south-eastern Australia, the rate of ocean warming is ~3.8 times the global average and this area is predicted to establish as the most intense 'hotspot' of ocean warming in the southern hemisphere (Holbrook & Bindoff, 1997; Ridgway, 2007).

Extension of the EAC into waters off south-eastern Tasmania now realizes longer and stronger incursions, which has the effect of transporting both heat (Cai, 2006; Ridgway, 2007), larvae and adults of northern species (Ling *et al.*, 2009; Last *et al.*, 2011) southward to Tasmania. The increased influence of the EAC in eastern Tasmania is demonstrated in the temperature/salinity signature off Maria Island on the east coast of Tasmania over the past 50 years. The south east region has become both warmer and saltier, with mean trends of 2.28°C per century and 0.34 psu per century over the 1944–2002 period recorded at Maria Island, which corresponds to a poleward advance of the EAC extension of ~350 km (Ridgway, 2007; Hill *et al.*, 2008). The EAC is nutrient poor (e.g. often $\leq 1 \mu\text{M}$ nitrate, particularly in summer) compared with the sub-Antarctic water masses that, until recently, dominated the oceanographic signature on the east coast of Tasmania (Harris *et al.*, 1988; Ridgway, 2007). Thus, marine systems in south-east Australia are simultaneously subject to marked increases in temperature and reductions in nutrients and this has led to declines in primary productivity (Thompson *et al.*, 2009). The confluence of the EAC and southern ocean waters forms a sub-tropical front (STF) which moves northward during winter as the EAC recedes and southwards as it strengthens in summer. Clementson *et al.* (1989) found that during seasons of weak EAC and/or strong westerly winds, which pushed southern ocean waters northward from southern Tasmania, the productivity in south-east Tasmania increased by as much as 10 times compared with seasons when the EAC was the dominant water signature.

Jasus edwardsii has one of the longest larval periods of lobsters ranging from 12 to 24 months before recruiting to coastal temperate rocky reefs. These major boundary currents are expected to

influence the distribution of rock lobster larvae as they accumulate offshore and move inshore to settle on coastal rocky reefs. In South Australia, onshore Ekman currents are suggested to influence the settlement of *J. edwardsii* larvae across broad spatial regions (Linnane *et al.*, 2010a). Late-stage lobster larvae were found to prefer the cooler waters adjacent to the STF in eastern Tasmania, and it was suggested that the position of this front during peak larval settlement times resulted in improved settlement in adjacent coastal reef regions (Bruce *et al.*, 2000). A combined bio-hydrodynamic model of south-east Australia indicated that currents favoured a displacement of larvae from the western distribution of the species (i.e. South Australia) to western, southern and eastern regions of Tasmania, the later regions being assisted by westerly winds and the Zeehan Current (Bruce *et al.*, 2007).

The recruitment of pueruli to coastal temperate reefs in eastern Tasmania was correlated negatively to temperature, indicating that the further the EAC current penetrated south during winter and spring, the poorer the recruitment of larvae to the east coast of Tasmania. The warmer waters experienced in the 2000s have resulted in the lowest settlement rates on settlement plates (puerulus collectors) since observations began in the early 1990s and have resulted in a reduction of the total allowable commercial catch (TACC) for the fishery by approximately a third. It is suggested that temperature is an indirect measure of the positioning of the STF. The strengthening EAC has pushed the STF further south, which has resulted in larval settlement on collectors in SE Tasmania showing slight increases during the same time that declines were observed in eastern collectors.

In contrast, collectors in South Australia and western Victoria recorded the highest larval settlement in the mid-2000s. However, these settlements have not resulted in positive recruitment to the fishery, and it is suggested that an exceptionally strong upwelling event in the region in 2007/08 increased the mortality of lobsters prior to recruitment to the fishery. This upwelling resulted in temperatures being well below the average for the annual upwelling that occurs in this region and temperatures remained below the average for an

extended period (Linnane *et al.*, 2010b). It is unlikely that specific temperature declines would have impacted on the lobsters as lobsters are rapidly cooled to lower temperatures during export to overseas markets. However, the duration of the lower temperatures or indirect effects, such as increased predation, may have increased the mortality of lobsters. Similar to Tasmania, the catch rates of lobster in the southern and northern zones of SA and western zone of Victoria have shown substantial declines in recent years resulting in concomitant reductions in their respective TACCs. Upwelling events are predicted to increase globally under climate change predictions (Bakun, 1990), and further research is required to determine the impact of more intense and longer upwelling events on juvenile and pre-recruit lobsters.

Lobster growth rates are temperature dependent (Thomas *et al.*, 2000). In northern regions of the Tasmanian fishery, where water temperatures are the highest, the annual growth rate of lobsters at the legal minimum size limit (i.e. 110 mm and 105 mm carapace length (CL) for males and females, respectively) is approximately four times and 10 times that for males and females found in southern regions respectively (Frusher, 1997). This dramatic difference is a combination of both a doubling of the number of moults each year in northern regions and the impact of maturity. Larger sizes at onset of maturity are recorded in warmer faster growing regions (Linnane *et al.*, 2008). Modelling of future predictions of productivity for the eastern Tasmanian fishery indicates that as predicted water temperatures increase, growth rates of lobsters will increase. This is predicted to have a substantial positive increase in recruitment to the fishery in southern regions of Tasmania where slow growth rates have resulted in a stockpile of lobsters below the legal size limit such that a substantial portion of the stock dies before reaching legal size. Improvements in growth rates will result in more lobsters reaching legal size before dying resulting in an increased legal-sized biomass available for exploitation. Management consideration could also be given to altering the minimum size to take into account the variable growth rate spatially and projected changes due to climate change.

Overall projections for the eastern Tasmanian fishery for 2030 and 2070 using the IPCC A1B (moderate) and A1F1 (high) scenarios indicate that the fishery will see an initial improvement in legal-sized biomass as growth rates increase before an overall decline in productivity of the resource as the increase in growth rates are outweighed by declining larval recruitment. In northern regions of the fishery where growth rates are considered to be at their maximum and projected recruitment declines will appear earlier, the legal-sized biomass should also improve. This is a result of the fleet dynamics model that predicts substantial declines in fishing effort in northern regions as the fishing fleet moves to southern regions of the fishery where recruitment declines appear later and growth rates substantially increase with a concomitant increase in exploitable biomass.

A study into the vulnerability of the East Coast Tasmanian rock lobster fishery also highlighted a number of potential direct and indirect effects on lobster fisheries in addition to recruitment and growth (Pecl *et al.*, 2009). As catchability of lobsters is known to increase with water temperatures (Ziegler *et al.*, 2004), it is likely that as water temperatures increase observed catch rates of lobsters will increase without change in the legal-sized biomass. Potential early declines in legal-sized biomass could therefore be masked by improved catchability of lobsters. Catchability is normally a fixed parameter in many assessment models and careful consideration of this parameter in assessment of fishery stocks is warranted so that increasing temperatures (e.g. due to climate change) on the catchability of lobsters is taken into account and hence does not undermine the sustainability of the resource.

Indirect effects were associated with ecosystem impacts and two examples were presented in Pecl *et al.* (2009). The increasing strength and southern penetration of the EAC has resulted in the establishment of the long-spined sea urchin, *Centrostephanus rodgersii*. This urchin has been responsible for approximately 50% of inshore reefs being converted into ‘urchin barrens’ as the urchins overgraze the previously algae-dominated coastal reefs. Lobsters were observed to be in lower abundances in urchin barrens than adjacent algae-

dominated habitat (Johnson *et al.*, 2005). This could be associated with the lack of algae-associated prey items as Ling (2008) found a 75% decline in diversity and abundance of invertebrate fauna as barrens formed. Anecdotal evidence suggests that habitat-forming algae such as *Macrocystis pyrifera* may have a role in enhancing larval settlement (Frusher, pers. comm.) and this alga has declined by over 95% on the east coast of Tasmania due to a combination of warm and low nutrient waters (Johnson *et al.*, 2011).

Centrostephanus rodgersii requires winter water temperatures above 12°C to complete its larval life and thus self-recruitment is currently limited to northern regions of Tasmania where winter water temperatures are currently above this value. Warming of ocean waters in south-eastern Australia is predicted to see winter temperatures above 12°C for the entire east coast of Tasmania by 2025 and all of Tasmania by 2055 making all shallow (<40 m) coast reefs less favourable for supporting lobster populations.

Octopus (Octopus maorum) are a major predator of southern rock lobster in traps and the number of lobsters killed by octopus is recorded in the mandatory daily logbooks by commercial fishers (Harrington *et al.*, 2006). Positive correlations between the number of lobsters killed by octopus and water temperature were found in all eight lobster assessment regions in Tasmania and these were strongest in eastern regions of Tasmania. In addition to *O. maorum*, another species *O. tetricus* is extending its range into Tasmania as waters warm. Whether the increase in lobster predation by octopus in traps is a result of an increase in the population of octopus as water temperatures increase or whether predation rates on lobsters in traps have increased due to increasing metabolism of octopus is unknown and requires further research. Similarly, whether *O. tetricus* replaces or co-habits with *O. maorum* as it moves further south is unknown.

Range extensions associated with the increasing water temperatures off the east coast of Tasmania have been numerous (Last *et al.*, 2011). The impact of these species and the associated modified ecosystems on lobster abundance and distribution is unknown as research has generally been directed at addressing species-specific issues associated with

assessing the sustainability and optimal harvest of marine resources. In addition to lobsters, several of the range-extending species are known predators of lobsters (e.g. snapper and blue grouper). There is also an increasing catch of the eastern rock lobster *Jasus verreauxi* (now known as *Sagmaria-sus verreauxi*), whose larvae are being brought southwards by the EAC and are therefore predicted to increase as water temperatures and the EAC increase in southern penetration and duration.

For southern rock lobsters, climate change is predicted to present a complex array of differing direct and indirect impacts on lobster abundance and distribution with concomitant impacts on fishers and their communities. Biological responses are predicted to affect growth, natural mortality, reproductive output and recruitment. Fishery assessment impacts will be complicated by changes in catchability, growth, size at maturity and recruitment to the fishery. Ecosystem responses may deliver surprises that have the potential to undermine single-species fishery assessments. Because of the complexity in the differing physical oceanographic conditions in south eastern Australia, responses in one region are unlikely to be comparable across all regions.

4.2.3 American lobster (*Homarus americanus*)

Homarus americanus is an icon of the fishing industry of the north-west Atlantic. It is the most economically valuable single-species fishery in the north-east USA and Atlantic Canada, at an average catch of some 91,005 t between 2001 and 2010. The combined landed value of the fishery in 2010 was about US\$800 million (FAO, 2009; DFO Canada, 2012; NMFS, 2012). Since the 1980s, the lobster catch has surged dramatically, nearing 120,000 t in 2010, and shows little sign of slowing down (Fig. 4.2). This astonishing growth has not been uniform, however. While lobster populations in the northern and middle part of the species range have been growing, those in the southern part have been suffering mass mortalities brought on by stressful warm summer temperatures and disease, leading to the collapse of a once lucrative fishery.

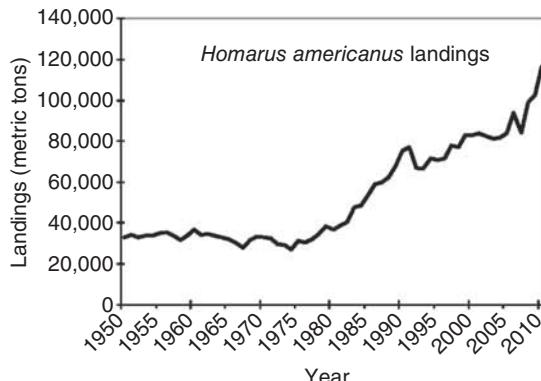


Fig. 4.2 Landings trends of the American lobster fishery, United States and Canada combined, 1950 to 2010 (Data from DFO Canada, 2012; NMFS, 2012)

The potential effects of climate change are therefore of great interest to stakeholders in this fishery.

Projected climate change impacts on natural resource and socio-economic sectors of the northeast USA were examined in the Northeast Climate Impacts Assessment (NECIA, 2006; Frumhoff *et al.*, 2007), which features the American lobster as a case study. The assessment modelled impacts under a range of carbon emissions scenarios projected by the International Panel on Climate Change (IPCC). The study employed three global atmosphere–ocean general circulation models: the U.S. National Atmospheric and Oceanic Administration’s Geophysical Fluid Dynamics Laboratory (GFDL) Model CM2.1, the United Kingdom Meteorological Office’s Hadley Centre Climate Model, version 3 (HadCM3) and the National Center for Atmospheric Research’s Parallel Climate Model (PCM). Model output included projections of precipitation, air and seawater temperature, pressure, cloud cover, humidity, along with other climate variables downscaled to sub-regions of interest in the northeast USA. Downscaling of model output to these sub-regions involved coupling the coarse-scale climate models with finer-scale regional models of ocean dynamics.

The geographic range of the American lobster encompasses one of the steepest latitudinal gradients in sea-surface temperature (SST) on earth

(Plate 4.3) (Longhurst, 1998). Over the distance of a few hundred kilometres, summer maximum temperatures range from the mid-20s centigrade in coastal southern New England, USA, to just over 10°C in the Bay of Fundy, Canada. At the northern limit of its range in Atlantic Canada, the lobster is largely restricted to waters less than 50 m deep. In the middle of its range *H. americanus* is more broadly distributed from the coast to deep-water canyons on the continental shelf break. The southern limit of the species' coastal distribution is Long Island Sound and the northern Mid-Atlantic Bight, USA, but even further south it becomes increasingly restricted to deeper, cooler water out to the edge of the continental shelf off Virginia and North Carolina. Consequently the commercial fishery transitions from a predominantly near-shore one in the north to a predominantly offshore one in the south.

American lobster landings in the USA have nearly tripled over the past three decades, and a wide range of contributing factors has been proposed to explain the rapid increase. They include sharp increases in fishing activity and in the total area fished, enhancements in fishing technology, warming water temperatures, and harvest-driven declines in cod and other fish that prey on lobsters (Fogarty, 1995; Worm & Myers, 2003; Steneck *et al.*, 2011). The recent rapid increase in water temperatures has lagged slightly behind the increase in lobster landings and therefore cannot be the sole explanation. Yet, a comparison of lobster distribution during the relatively cold period 1965 to 1969 with the warmer period 2000 to 2004 suggests the centre of lobster density has shifted northward (Frumhoff *et al.*, 2007).

Effect of environmental variability on biological parameters

Several authoritative texts provide useful discussions of environmental influences on American lobster physiology, growth, development, reproduction, survival and behaviour (Cobb & Phillips, 1980; Factor, 1995; Phillips, 2006). Here we focus on thermal effects on the biology of the American lobster. Ocean acidification has more recently come

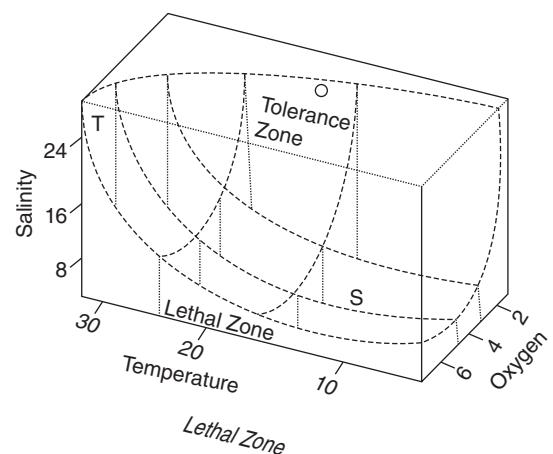


Fig. 4.3 Temperature, oxygen, salinity tolerance envelope of the American lobster *Homarus americanus*. McLeese, D.W. (1956). Reproduced with permission of NRC Research.

to light as an additional consequence of elevated CO₂ emissions (Hoegh-Guldberg *et al.*, 2007). Research on potential impacts to the American lobster is still preliminary (e.g. Ries *et al.*, 2008) and will not be treated here.

Physiological responses

The American lobster generally inhabits waters between 5 and 20°C (Aiken & Waddy, 1986). McLeese (1956) illustrated the interactive effects of temperature, dissolved oxygen and salinity on lobster survivability (Fig. 4.3). In seawater, as long as temperatures remain below about 20°C and oxygen concentrations above 2 mg L⁻¹, the American lobster is comfortably within its physiological limits (Chang, 2004; Powers *et al.*, 2004; Dove *et al.*, 2005). Therefore 20°C has been used as a physiological stress threshold for the American lobster in seawater. Prior acclimation to more extreme conditions can improve subsequent survival.

Larval and postlarval responses to temperature

Seasonality in the temperature cycle influences the timing of the hatch. Eggs begin to hatch when temperatures rise to between 12.2 and 15°C (Ennis, 1995). Thus, the hatch progresses northward during

the summer beginning in June in the south and in August in the north. In the laboratory, development time from hatching to the postlarval instar ranges from 3 weeks at 22°C to 8 weeks at 12°C (MacKenzie, 1988).

Stage III larvae metamorphose to Stage IV post-larvae and begin to seek benthic habitat. Postlarval vertical movements and settlement behaviour are temperature dependent as well (Boudreau *et al.*, 1992; Annis, 2005). This could have important implications for whether postlarvae ultimately settle in suitable benthic habitat. Recent field investigations using postlarval collectors at depths to 80 m, confirm that settlement concentrates above the 12°C thermocline (Wilson, 1999; Wahle *et al.*, 2012). The implication of this is that if temperatures warmed sufficiently above 12°C in future decades, new nursery grounds may become available in locations historically too cold to inhabit.

Growth and maturity

Regional differences in the growth rate of juvenile and adult benthic stages are strongly temperature dependent. The fastest growth rates are found in the southern Gulf of St. Lawrence and southern New England, where summer temperatures rise near or above 20°C, whereas the slower growth rates are found in the colder waters of the northern Gulf of St. Lawrence and the Bay of Fundy. Lobsters in the wild reach harvestable size between 5 and 10 years, depending on ambient temperatures, with year-to-year differences influencing the timing and frequency of the moult (Templeman, 1936; Munro & Therriault, 1983; Comeau & Savoie, 2001, 2002; Wahle & Fogarty, 2006). Lobsters in warmer regions not only grow faster, but they mature at a smaller size than conspecifics living in cooler water. For example, female American lobster mature between 68 and 76 mm CL in the warmer parts of range, but at full 10 mm or so larger in the cooler parts (Estrella & McKiernan, 1989; Comeau & Savoie, 2001).

Movements and migrations

Thermal tolerances strongly influence lobster movements and seasonal migrations, and, hence, seasonal distribution patterns. Behavioural studies

suggest that lobsters move to optimize their thermal environment. In laboratory experiments, adult lobsters that were acclimated at a summer ambient temperature of 15.5°C in the Gulf of Maine avoided temperatures warmer than 19°C and colder than 13°C, and spent most of their time at 16.5°C, slightly warmer than the ambient conditions where they were caught. Lobster activity does not increase monotonically with temperature; instead, lobsters only become active above a threshold of about 10°C (Jury, 1999).

Thus, American lobster movements in bays and estuaries are linked to seasonal temperature change. As waters warm during the spring, lobsters become more active and move into the shallows to the extent they can tolerate reduced salinities (Jury, 1999). At the southern end of the species coastal range, fishermen commonly observe a double migration: a spring influx with warming temperatures, followed by a mid-to-late summer movement into deeper channels, leaving estuaries that exceed 20°C, followed again by a return to the shallows during the autumn as temperatures cool for a period before the winter chill-down and emigration. If average summer temperatures continue to rise, we may witness a northward shift of the double-migration phenomenon.

Key historic and future environmental trends

The coastal and shelf waters of the Northeast USA and Atlantic Canada are strongly connected to the large-scale circulation of the north-west Atlantic (Loder *et al.*, 1998). The south-westerly flow on the shelf is an extension of the Labrador Current system. Augmented by outflow from the St. Lawrence River and smaller river systems, the flow brings cold, relatively fresh water into the region off the shelf, and the surface waters mix with warmer, saltier waters transported northward by the Gulf Stream (Xue *et al.*, 2008). The region is also typified by a strongly continental climate. This leads to a large annual cycle in temperature due to surface heating in the summer and strong cooling in the winter. The winter mixing brings nutrients into the surface waters and leads to high productivity in the spring and summer. The seasonal mixing is augmented by strong tidal mixing in shallow

Table 4.1 Projected increases in bottom water temperature (°C), 2080–4, relative to the historic average (1970–2000). Figures represent the mid-range of the three-model outputs, for each emissions scenario. In the NECIA marine analysis, both the historic and the late century projected time frames vary from other NECIA analyses, reflecting both National Marine Fisheries Service historic data sets and model capabilities (from Frumhoff *et al.*, 2007).

		Northern Mid-Atlantic Bight	Georges Bank	Western Gulf of Maine	Eastern Gulf of Maine
Spring	Lower emissions	1.1	1.1	1.1	1.1
	Higher emissions	3.9	3.3	2.2	2.2
Fall	Lower emissions	1.1	1.1	1.6	1.1
	Higher emissions	2.8	3.3	2.2	2.2

waters along the coasts and on the region's offshore banks.

Both the Gulf Stream and Labrador Current systems are important components of the North Atlantic climate system, and both vary on interannual and interdecadal scales. In general, the variability in these two systems are linked, with high flow along the shelf circulation occurring when the Gulf Stream is further offshore (MERCINA, 2001). Changes in this system have been linked to the North Atlantic Oscillation (NAO), a pattern of variability in the relative strengths of two atmospheric pressure centres over the North Atlantic (Hurrell, 1995). When the NAO is in its positive state, the Gulf Stream tends to be further north and the shelf circulation is diminished (MERCINA, 2001). According to many climate models, positive NAO conditions are expected to dominate over the next century (Osborn, 2004; Bader *et al.*, 2011). The shelf circulation is also sensitive to changes in the supply of freshwater from the continent (especially, the Gulf of St. Lawrence) and outflow from the Arctic (Greene & Pershing, 2007; Greene *et al.*, 2008). Both precipitation at high latitudes and melting in the Arctic are expected to increase under climate change (Bader *et al.*, 2011), potentially counteracting the influence of the expected positive NAO.

During the 20th century, coastal SSTs in the US north east have risen more than 0.5°C (Frumhoff *et al.*, 2007). SSTs were anomalously warm during the 1950s, but this warm period was followed by a cooling spell during the 1960s. Since 1970 average SSTs have risen by 1.1°C (Frumhoff *et al.*, 2007).

Under both high and low CO₂ emissions scenarios, NECIA forecasts of surface and bottom water temperatures suggest a northward shift in thermal conditions favourable to the American lobster (Table 4.1). By late this century SSTs are forecast to rise another 2.2–2.7°C under the lower-emissions scenario, and 3.3–4.4°C under the higher-emissions scenario, rendering many parts of the southern coastal part of the species range uninhabitable during the summer (Frumhoff *et al.*, 2007).

The NECIA analysis of bottom water temperatures for the northeast USA gives the following projection for contrasting emissions scenarios (Table 4.1).

- ‘Under the higher-emissions scenario, bottom temperature increases are projected to be substantially greater along the southernmost part of the Northeast’s coast. By the 2080s, for example, increases in spring bottom temperatures range from 3.8°C in the northern Mid-Atlantic Bight to 2.2°C in the Gulf of Maine.’
- ‘Under the lower-emissions scenario, increases in spring bottom temperatures are more consistent across the region and not as severe: 1.1°C in the northern Mid-Atlantic Bight, Georges Bank, and the Gulf of Maine. Autumn increases are projected to be slightly greater.’

Effects of environmental trends on fishery

While catches have surged in much of the north-eastern USA and Atlantic Canada, at the southern end of the range, harvests peaked in the mid-1990s

and then dropped sharply with localized episodes of high natural mortality. The first was a 1997 die-off in Rhode Island and southern Massachusetts that was linked to the onset of epizootic shell disease, which continues to be prevalent in the population (Wahle *et al.*, 2009). In 1999 lobsters in Long Island Sound experienced a mass mortality related to warm temperatures and hypoxia (Pearce & Balcom, 2005). Although the southern New England lobster catch is a relatively small proportion of the US catch, the collapse of the fishery has created hardships for local lobstermen and their communities.

By contrast, further north, the state of Maine has seen strong and sustained growth in lobster landings of nearly 43,000 metric tons in 2010 (versus about 11,000 metric tons four decades ago) (ASMFC, 2005; Maine DMR, 2011). With lobster recruitment rates high, and other fish stocks depleted, many fishermen in Maine and Atlantic Canada have little alternative than to invest heavily in the lobster fishery. Despite increasing costs of fuel, bait and fluctuations in the price of lobster in an uncertain economy, these record lobster hauls bring a precarious prosperity to lobstermen, their families and associated interests. Precarious, because although landings are high now, there are few other alternative fisheries on which to fall back if the lobster fishery fails. It is worth examining the recent changes in environmental conditions that have led to these contrasting scenarios.

Deteriorating conditions in the south

The scientific consensus points to warm temperatures and hypoxia being key factors contributing to the demise of lobsters in southern New England (Pearce & Balcom, 2005). In the summer of 1999 lobsters in the Sound began dying in alarming numbers. Landings in the states of New York and Connecticut dropped by more than 80% between 1998 and 2002, forcing many lobstermen out of the fishery (Gornitz *et al.*, 2004). Long Island Sound's lobster population has yet to recover. Although the factors playing a role in this die-off have been the subject of debate, warmer water temperatures and hypoxic conditions appear to have set the stage.

Since at least 1979, average August bottom temperatures in Long Island Sound have been rising

and exceeding the 20°C stress threshold with greater frequency (Wilson & Swanson, 2005). During the summer of 1999 August bottom water temperatures exceeded 21°C and in some locations even topped 23.5°C. Elevated temperatures above 20°C continued into October. During that time lobsters in the western Sound were found to be infected with the parasitic paramoeboid, *Neoparamoeba pemaquidensis*.

Other lobster afflictions at the southern end of their geographic range appear to be correlated with chronic exposure to warm temperatures. Symptomatic of long-term exposure to warm temperatures is a condition called calcinosis, involving pathological changes in blood ion balance, pH, protein levels and blood cell counts (Dove *et al.*, 2005). Epizootic shell disease may be temperature related. Smolowitz *et al.* (2005) proposed that elevated temperature could promote shell disease in two ways: (i) by compromising lobsters' ability to remove bacteria through physiological stress and compromised cleaning behaviour, and (ii) favouring the pathogenicity of the bacteria and secondary infections.

Model projections indicate the frequency of extremely warm summers is anticipated to rise (NECIA, 2006). Between 1960 and 1979 August temperatures only crossed the 20°C threshold from 40% to 75% of the time. By model estimates, mid-century August temperatures will breach the threshold virtually every year. According to historical records, lobster larval settlement, juvenile abundance and harvests per unit area of sea bed along Maine's eastern coast have been substantially lower than in western regions (Wahle & Steneck, 1991; Steneck & Wilson, 2001). However, over the past decade, settlement and adult populations along this segment of coast have been increasing dramatically, accounting for most of the recent increases in lobster harvests in US waters (Maine DMR, 2011; R. Wahle, unpublished). However, to date these increases have not been directly linked to change in water temperatures.

Therefore, based on the projected changes in bottom temperature throughout the US segment of the American lobster's range (Table 4.1), the following trends in future lobster distribution are projected by Frumhoff *et al.* (2007):

Northern Mid-Atlantic Bight

- ‘The maximum 20°C stress threshold for lobsters is projected to be consistently exceeded by mid-century in Long Island Sound and other near-shore areas of these waters, resulting in the likely loss of suitable habitat under both high and low emissions scenarios.’
- ‘More frequent episodes of temperatures in the high-stress range (near 26°C) are also likely in the region’s southern coastal waters.’
- ‘Deep waters and submarine canyons, which currently support significant lobster populations, are unlikely to be affected.’

Georges Bank

- ‘Lobsters in these waters are found at the highest densities in submarine canyons where they are unlikely to be exposed to stressfully warm water temperatures.’

Gulf of Maine

- ‘In contrast to the southern part of the region, warming in these colder northern waters may actually boost lobster populations by spurring a longer growing season, more rapid growth, an earlier hatching season, more nursery grounds suitable for larval settlement, and faster planktonic development (which could increase survival and settlement).’
- ‘Some northern parts of the region where thermal conditions have probably limited larval lobster settlement in the past may become more hospitable during this century due to warming.’

Implications for stock assessment and management

The contrasting changes in lobster population dynamics from north to south may require differing management approaches. The most acute management challenge is occurring in the southern part of the species range, where coastal populations have been subject to high rates of natural mortality due to deteriorating summer conditions and disease, leading to a collapsing lobster industry. In 2010 US fishery managers floated an unprecedented proposal to place a moratorium on the southern New England lobster fishery (ASMFC, 2010). The proposal was averted by strong political resistance.

Nonetheless, the industry is still faced with the challenge of consolidating an overcapitalized fishery, and to drastically reduce the one source of mortality they can control, fishing effort (ASMFC, 2010).

Meanwhile, in Maine where lobster populations and harvests are at historic highs, prospects may seem bright to the casual observer, even under the range of climate change scenarios. However, as alternative fish resources have been depleted, Maine fishers are dangerously dependent on this unprecedented lobster production. The situation creates an economic vice referred to by Steneck *et al.* (2011) as the ‘gilded trap’ whereby ‘large financial gain creates a strong reinforcing feedback that deepens the trap.’ Fishers under these circumstances have little incentive to move to alternative sources of income, and become heavily invested in one type of fishery. The economic consequences of a collapsed lobster fishery could be devastating to coastal communities with so few alternative sources of revenue. Multi-species management for ecological and economic diversity is therefore seen as a necessary strategy to buffer coastal economies, and the ecosystems upon which they depend, from catastrophic fluctuations.

Future research

There is a need for future research to address both biological and socio-economic issues associated with climate change, and more broadly, the altered ecosystem in which the American lobster fishery now operates. Several priority research areas emerge:

- It is necessary to make the distinction between adaptation and acclimation in understanding species’ responses to climate change. The former relates to changes at the population level in response to differential selection; the latter refers to phenotypic plasticity at the level of the individual. Novel approaches to evaluate physiological, genomic as well as micro-evolutionary responses to temperature change have been developed with other model organisms, including crustaceans, that could be readily applied to lobsters (e.g. Harvell *et al.*, 2002; Helmuth *et al.*, 2002; Stillman, 2003; Darling *et al.*,

- 2008). Comparative studies of physiological responses across populations under contrasting, naturally occurring, thermal regimes may provide insight into underlying population structure, and in turn help identify populations at risk.
- While research is under way to investigate the shell disease epizootic in southern New England, the link between the disease and environmental conditions remains unclear, and further correlative and experimental work needs to be done.
 - The risks of ocean acidification to the American lobster have only recently come to light, remain poorly understood, and need to be evaluated.
 - Ocean-atmosphere dynamic model development is needed to enable accurate predictions of bottom water temperature, oxygen, and pH levels along coastal zones and their consequences for the American lobster. Recently developed coupled bio-physical models of larval advection for the American lobster should be employed to explore potential effect of these environmental changes on lobster larval settlement (Xue *et al.*, 2008; Incze *et al.*, 2010).
 - Our ability to understand lobster stock–recruit relationships is still constrained by limited knowledge of the sources and magnitude of density-dependent natural mortality before and after larval settlement. Parallel monitoring programmes of critical lobster life stages, water quality and biotic factors continue to be a pressing need.
 - As a key commercial species, there are important socio-economic dimensions to changes in American lobster populations and their ecosystems that need to be evaluated to fully understand the consequences of climate change.

4.3 Other lobster species

4.3.1 Caribbean lobster (*Panulirus argus*)

The Caribbean spiny lobster fishery ranges from the USA to Brazil and is the largest spiny lobster fishery in the world with average landings of 34,600 t over 2000–7 (Muñoz-Nuñez, 2009) with the major countries harvesting lobsters being Bahamas, Brazil, Cuba, Nicaragua and USA.

Regional landings were relatively steady during the 1980s and 1990s at about 30,000 to 40,000 t but have declined to about 20,000 t during the 2000s (Ehrhardt *et al.*, 2010). They identified that besides exploitation effects, changes in the environmental and ecological conditions may be impacting on spiny lobster habitat.

The long planktonic larval life (6–12 months) of the spiny lobster combined with the prevailing ocean currents in the wider Caribbean region means that recruitment in some countries may result from spawning in countries downstream. Stockhausen *et al.* (2000) hypothesized that recruitment in the Florida region may originate from the Caribbean region including Cuba due to the Gulf Stream and the Florida Current.

Ehrhardt *et al.* (2010) highlighted the importance of shallow-water nursery habitat for settling post-larvae as well as a considerable loss of critical coral habitat throughout the Caribbean region since the 1980s, particularly after coral bleaching events in 1990 and 2005. Herrnkind *et al.* (1997) examined the effect of mass sponge die-offs in Florida Keys in 1991–2 on the lobster refuge. They identified a change in pattern of shelter use by the juvenile lobsters with the overall juvenile population declining by about 5%.

The Cuban spiny lobster fishery has experienced dramatic changes in recent years with catches averaging below 5000 t compared with about 11,000 t in the late 1980s. Hurricane Gilbert (1988) has been identified as having a significant impact on juvenile mortality (Cruz *et al.*, 2001) and the recent increase in frequency and intensity of hurricanes in the region may have affected catches. In the Caribbean region the frequency of hurricanes increased three times more during 1995–2005 than previous years, with Cuba showing the highest frequency (Muñoz-Nuñez, 2009). These hurricanes have been shown to have negative impacts on the coastal and marine habitats by breaking coral, sponges and mangrove trees.

4.3.2 Southern African west coast rock lobster (*Jasus lalandii*)

The west coast rock lobster (*J. lalandii*) occurs over a distance of about 100 km from 25°S in Namibia

to 34°S in South Africa. Yields from the Namibian fishery and that of the northern part of the South African fishery declined dramatically since the 1950s (Pollock *et al.*, 2000). The overall catch declined from 16,000 t to less than 5000 t. The Namibian fishery catches falling from about 9000 t until the mid-1960s to 200–300 t in the 1990s. Increases in frequency of oxygen-depleted bottom waters offshore as a result of large increases in productivity was identified as a factor resulting in the depth distribution of lobsters being restricted to shallower waters and affecting recruitment, growth, fecundity and natural mortality.

There has also been a southward shift in the spatial distribution of the west coast rock lobster during the late 1980s/early 1990s (Cockcroft *et al.*, 2008) with a decline in the west coast region and an increase in the southern region including a movement of lobsters into areas not previously associated with high lobster abundance. The change has been gradual and stabilized in the early 2000s. This change has particular implications in the near-shore shallow-water component of the fishery which comprises small vessels using ring-nets. This component is managed by awarding fishing rights based on zone or area of residence. Fishers affected by this change have requested boundary changes of some areas. The offshore component of the fishery consists of large vessels using traps in deep water and fish according to an agreed area schedule.

This range shift has coincided with a decrease in growth rates and increase in lobster ‘walkouts’ (lobsters walking onto the beach and dying in significant numbers) due to low oxygen levels, which suggests an underlying environmental cause (Cockcroft *et al.*, 2008). The decrease in growth rate by about 50% resulted in a decrease in recruitment to the harvestable biomass with catches in the late 1990s declining to half of the 3500–4000 t landed in the 1980s (Pollock *et al.*, 2000). The change may be related to a large-scale environmental perturbation such as the 1990–93 El Niño event, which influenced the productivity of the southern Benguela Current.

This shift has also had ecological implications with the lobsters heavily predating the sea urchin populations, which in turn has had a negative

impact on the lucrative abalone (*Haliotis midae*) fishery. This trophic cascade effect has resulted in a regime shift of the ecosystem with significant increases in sessile invertebrates and macroalgae (Blamey *et al.*, 2010). This issue has been identified as a major risk in an ecological risk assessment of key South African fisheries (Nel *et al.*, 2007). The diet of lobsters that moved into this area is different from those of lobsters in ‘non-invaded’ sites. The shift in lobster distribution has also coincided with an eastward shift in pelagic resources. The cause of these changes and whether they are permanent or part of cycle is uncertain.

4.3.3 Hawaiian lobster (*Panulirus marginatus*)

A climate regime shift in the North Pacific in 1977 and 1989 caused dramatic changes in populations and biological characteristics (Clark *et al.*, 1999; Hare & Mantua, 2000; Polovina, 2005). The ecosystem shift in 1989 is believed to have caused a marked decline in the catch of spiny lobsters (*P. marginatus*) and other marine species in the north-western Hawaiian Islands (Polovina & Haight, 1999; Polovina, 2005). The fishery was closed in 2000 because of uncertainty regarding the population models used to assess the stocks (DeMartini *et al.*, 2003) and remains so to date (http://www.pifsc.noaa.gov/wpacfin/pdf_file/h_vol25.pdf)

4.3.4 Japanese lobster (*Panulirus japonicus*)

There have been some long-term trends in catches in the Japanese lobster fishery which occurs along the south-eastern Japanese coast. Since 1965 there has been a significant decrease in catch in the southern part of the fishery from about 1000 t to about 400 t in 2001 (Inoue & Sekiguchi, 2009). However, in the northern part of the fishery there has been an increase from about 350 to 800 t for the same period.

The north-flowing Kuroshio Current has been identified as having a positive effect on the catch in the northern sector and a negative effect on catches in the southern sector at lags of 2–4 years. Sekiguchi & Inoue (2010) suggest that the current

strength may be influencing the levels of puerulus settlement along the coast. The trend in catches between these two sectors of the fishery varied according to three climate regime shifts that have been identified in the North Pacific during this period: before 1976, 1977–88 and after 1989.

4.3.5 Californian lobster (*Panulirus interruptus*)

Vega-Velázquez (2007) used spectral analysis to identify the periodicity of factors affecting the Californian spiny lobster (*P. interruptus*) abundance along southern California and Baja California. For southern California an increase in abundance was identified in 1976 until the late 1990s and a long-term increasing trend was also evident in the Baja California. The catch in Baja California increased from about 1000 t in the 1970s and 1980s to about 1400 t during the five seasons, 2005–10 (<http://www.msc.org/track-a-fishery/certified/pacific/mexico-baja-california-red-rock-lobster>). These trends were generally attributed a climate regime shift to warmer conditions between the mid-1970s to the late 1990s and were also influenced by changes associated at smaller time periods such as ENSO events. Phillips *et al.* (2000) also showed that catches in the Baja California tended to be higher 4 years after El Niño events that result in high sea levels and strong poleward flow.

4.3.6 Pronghorn spiny lobster (*Panulirus penicillatus*)

Chang *et al.* (2011) used the pronghorn spiny lobster (*P. penicillatus*) off the east coast of Taiwan as an example to evaluate the possible effects of fishing in a changing environment. They used an individual-based model to describe the temperature-dependent life history processes and evaluate the potential impact of increased water temperatures on biological reference points. If temperatures became warmer then there would be an increase in yield-per-recruit and eggs-per-recruit which reduced the risk of overexploitation. This was based on increasing temperature resulting in an increase in stock productivity due to faster growth by shortening the intermoult period, changes in

spawning season and incubation duration. However if the higher temperatures resulted in a large increase in natural mortality, there was an increased risk of overexploitation in the long term. The study suggests that an explicit incorporation of the relationships between environmental variables and biological processes can improve fisheries assessment and management.

4.3.7 European lobster (*Homarus gammarus*)

The European lobster is found along the continental shelf in north-east Atlantic from the warm waters of Morocco to the colder waters near the Arctic Circle (Cobb & Castro, 2006) with annual landings averaging at 2500 t. The main landings occur in the United Kingdom and Ireland. The Norwegian fishery collapsed between 1960 and 1980 to less than 10% of its 1950s level (Agnalt *et al.*, 2007). Major declines have also been reported in Turkey since the 1960s, and Sweden and Denmark since the 1930s and 1940s (Cobb & Castro, 2006). European lobster fisheries have generally been unregulated or minimally regulated by a minimum size or landing of berried females (Cobb & Castro, 2006).

Sheehy & Bannister (2002) identified sea temperatures and onshore winds as the key factors that may affect the European lobster's larval settlement off the north-east coast of England. Because there was no actual monitoring of year-class strength, they used neurolipofuscin in the eyestalk to measure year-class strengths that inferred periods of strong larval settlement in the late 1980s and early 1990s. They suggest that climate change may potentially contribute to greater fluctuations in year-class strength due to increasing instability of the North Atlantic Oscillation that is forced by ENSO events.

The effect of potential future levels of ocean acidification on early larval phase of the European lobster has been examined by Arnold *et al.* (2009). They assessed the effect of CO₂-acidified water at about 1200 ppm, which is the average value expected using IPCC 2007 A1F1 scenarios for 2100. They found no effect on the survival, carapace length or zoeal progression. However, there could be an indirect disruption of calcification and carapace mass in the late zoea larval stages that

may affect the competitive fitness and recruitment success of larval lobsters.

4.3.8 Norway Lobster (*Nephrops norvegicus*)

The Norway lobster is the most important commercial crustacean fishery in Europe with annual catches increasing to about 60 000 t in the mid-1980s and remaining at this level since (<http://www.imr.no/temasider/skalldyr/sjokreps/landings/en>). Peak catches are in the North Sea, west of Scotland and Irish Sea with trawling the most common method. It is widely distributed from north-east Atlantic and the Mediterranean from Iceland and Norway in the north to Morocco and Greece to the south in depths of 20–800 m (Bell *et al.*, 2006).

The stock is dependent on particular types of seabed sediment so it has a highly discontinuous geographical distribution with at least 30 populations in European waters (Bell *et al.*, 2006). Larval retention mechanisms such as gyres near the location of hatching appear to be an important feature of a number of the populations. The larval duration (3–7 weeks) is inversely related to water temperature (Dickey-Collas *et al.*, 2000) and thus may be vulnerable to changes in water temperatures due to climate change. Stocks to the north of the English Channel are stable or fluctuate without long-term trends (Bell *et al.*, 2006). The stocks in the Normandy and Jersey fishery have been certified as sustainable under the Marine Stewardship Council standards (<http://www.msc.org/track-a-fishery/certified/north-east-atlantic/normandy-and-jersey-lobster>). However stocks around the Iberian peninsula which are towards the southern range of the stock have had dramatic declines in recruitment since 1980 that may be driven by climate.

4.4 Discussion

4.4.1 Climate change effect type

This chapter has summarized some significant climate change effects on a number of lobster stocks including the western and southern rock lob-

sters in Australia, American lobster, Japanese and South African lobster stocks. When assessing these climate change effects on stocks it is important to clearly identify the type of change that has been observed. There may be some short-term environmental trends that are not subject to climate change effects, or regime shifts that occur over decades that may be reversible, or there may be long-term climate change trends that have occurred over many years with the trends expected to continue in the future under climate change models. The western and southern rock lobster populations in Australia as well as the American lobster appear to be influenced by long-term changes in water temperatures and hence the changes observed could be classified as long-term climate changes, particularly as water temperature increases are projected to continue. The changes to the Japanese and Hawaiian spiny lobster stocks have been identified as being part of a regime shift in the North Pacific and hence may not be a long-term effect. Similarly the changes in abundance of the Californian spiny lobster have been attributed to regime shift.

If the lobster stock covers a large geographic area then it is also important to identify the spatial distribution of the climate change effect as it is unlikely to affect the whole fishery in a uniform manner. The edge of the spatial distribution may be more vulnerable to any climate change effect as a small change in an environmental variable may push it outside the optimal range of the stock. The environmental change may also result in increased abundance or open up new areas for the stock. The negative climate change effects on the American lobster were first identified on the southern range of its distribution. There has been a corresponding increase in the northern stocks of this fishery. Whereas there was a significant increase in abundance of *J. lalandii* in a southern region of South Africa not previously associated with high lobster abundance which was associated with a decline in the northern stocks near Namibia.

4.4.2 Sensitivity to environmental effects

The long larval phase of lobsters, particularly spiny lobsters, that are generally influenced by environmental conditions make them particularly

vulnerable to climate variability and hence climate change if there are long-term trends on the environmental variables affecting the populations. Current strength and direction during this larval phase can affect their advection and hence their survival. Many other aspects of the lobster life history of many populations such as growth, migration, size at maturity, catchability appear to be sensitive to changes in water temperature (Morgan, 1974; Ennis, 1995; Jury, 1999; Caputi *et al.*, 2010). There may also be interactive effects of temperature with other variables such as dissolved oxygen, and salinity on lobster survivability (McLeese, 1956, Fig. 4.3). If these and other environmental variables that affect different parts of the life history have long-term trends then the lobster stocks will be vulnerable to climate change effects. While there is no evidence of current levels of ocean acidity affecting lobster populations, experimental testing of levels projected to occur in 2100 have identified some potential indirect effects on the European lobster.

The sensitivity of some biological parameters to long-term changes due to climate change effects may be assessed by examining the differences in biological parameters over the latitudinal range that may be due to an environmental variable such as water temperature that varies latitudinally. If there are spatial differences in the biological parameters and there is a long-term trend in the environmental variable affecting the parameters then it may be likely that there is some long-term trend in the biological parameters. Understanding the spatial variation latitudinally was an important aspect of the climate change evaluation of the three major case studies presented. Understanding the water temperature effect over the latitudinal range of western and southern rock lobsters has provided the basis for interpreting the effect of long-term temperature increases on the stocks. This approach provides some valuable insights into how long-term changes in water temperature due to climate change may affect the stock in the different geographic areas of the fishery. At the very least the approach provides a risk assessment process to identify potential biological parameters that may be influenced by climate change effects.

4.4.3 Climate change effects

The key climate change effects observed can affect their overall abundance, the spatial distribution and some biological parameters (Table 4.2). There have been some significant long-term declines in catch of a number of lobster stocks around the world such as the Caribbean lobster in Cuba and USA, South African lobster, European and American clawed lobster stocks, and for some stocks climate change effects have been identified as contributing factors. In many cases these abundance declines are part of the climate changes effects on the spatial distribution with some positive as well as negative effects being observed on spatial stock abundance. This may be the case in the American lobster fishery with a downturn in the southern part of the stock but an increase in catches in northern USA and some Canadian stocks. Frumhoff *et al.* (2007) and Wahle *et al.* (2009) identified the effect of warm water anomaly at the southern extreme of the species range on the health of the lobsters with a number of diseases being identified. The Japanese lobster stocks had a decrease in catch in the southern part of the stock with an increase in the northern part. The South African lobster stocks have also experienced a change in the spatial distribution with a decline in the northern part of the stock and an increase in the southern region.

When assessing climate change effects on fish stocks the focus is usually on the change in abundance and distribution as this information is of most interest to fishers and managers and is generally available on an annual basis over the long term. However, changes in other biological parameters such as growth, size at maturity and natural mortality are probably equally likely to occur, but monitoring of these parameters over the long term is less likely to be available than changes in abundance. The western rock lobster provides an example of long-term monitoring of the commercial catch at sea that has resulted in the detection of long-term changes in some biological characteristics such as size of migrating lobsters and size at maturity. These changes have been identified as being mainly due to changes in water temperature. It is also likely that there will be a trend in some growth

Table 4.2 Description of major climate changes observed and their effect on lobster populations.

Species	Environmental change observed	Effect on lobsters	References
Western rock lobster	Increases in water temperature	Decreases in size of migrating lobsters; decreases in size of maturity; decrease in growth; increase in catchability	Caputi <i>et al.</i> (2010); Melville-Smith & de Lestang (2006)
Southern rock lobster	Increase in strength of Eastern Australian Current and water temperature, lower productivity	Lower puerulus settlement (Tasmania); Increase in growth and larger size at maturity (northern Tasmania); increase in catchability; creation of urchin 'barrens' causes decline in lobster abundance; increase in octopus predation of lobsters	Pecl <i>et al.</i> (2009)
American lobster	Increases in water temperature overall and hypoxia in southern range	Increases in abundance (north-east USA and Canada); decreases in abundance and increased frequency of diseases (southern range)	NECIA (2006); Frumhoff <i>et al.</i> (2007)
Southern African west coast rock lobster	Increased frequency of oxygen-depleted waters	Distributional range shift south; Increases in lobster 'walkouts'; decrease in growth	Cockcroft <i>et al.</i> (2008)
Japanese lobster	Regime shift in north Pacific affecting the Kuroshio Current	Distributional range shift north	Inoue & Sekiguchi (2009); Sekiguchi & Inoue (2010)
Hawaiian Lobster	Regime shift in North Pacific	Decline in abundance	Polovina (2005)
Californian lobster	Regime shift to warmer waters 1976 to late 1990s	Increase abundance 1976 to late 1990s (southern California)	Vega-Velázquez (2007)
Caribbean lobster	Increases in frequency & intensity of hurricanes having negative impact habitats	Decline in lobster abundance (Cuba)	Muñoz-Nuñez (2009); Ehrhardt <i>et al.</i> (2010)
Norway lobster	Increasing instability of North Atlantic Oscillation	Abundance decline (Iberian coast)	Bell <i>et al.</i> (2006b)
European lobster		Increases in abundance fluctuations (north-east England)	Sheehy & Bannister (2002)

parameters that may be influenced by the changes in water temperature and the changes in the size of maturity.

While the main focus of climate effects on a fishery are the direct effects such as changes in abundance and distribution, it is important to also understand the indirect effects on the wider ecosystem. Pecl *et al.* (2009) noted some indirect ecosystem effects including the range extension of the sea

urchin in eastern Tasmania which has been responsible for approximately 50% of inshore reefs being converted into 'urchin barrens' as the urchins overgraze the previously algae-dominated coastal reefs. This, in turn, reduced lobster abundance in urchin barrens compared with adjacent algal dominated habitat. The interaction between lobsters, sea urchins and abalone was also highlighted in South Africa with the increase in lobster abundance

heavily predating sea urchin populations, which had a negative impact on the abalone fishery. Pecl *et al.* (2009) warned that ecosystem responses may deliver surprises that have the potential to undermine single-species fishery assessments. Again this highlights the importance of monitoring as many ecosystem responses will not be predictable.

Most of the climate change effects on lobster fisheries presented have generally focused on changes that are under way or have occurred historically. The American lobster study (Frumhoff *et al.*, 2007) and southern rock lobster study in Tasmania (Pecl *et al.*, 2009) have examined model climate change projections and their likely effect on lobster populations.

4.4.4 Implications for stock assessment

One of the key assumptions in most stock assessment models is that many key parameters, such as recruitment, growth, mortality, size at maturity and size of migration, are stable. When assessing future management options, the forward projections are generally undertaken assuming average recruitment levels. While many models allow for some inter-annual or seasonal variability in these biological parameters, they usually do not incorporate any long-term trends. The present study highlights the importance of questioning those assumptions if the fishery is being modelled over many years when climate change effects have occurred in the region of the fishery.

At the very least, a risk assessment of the sensitivity of the biological parameters to environmental variability and the likelihood to long-term climate change needs to be undertaken. The sensitivity of the model projections to the potential climate change effects needs to be undertaken. For example, Clark *et al.* (1999) identified the need to apply temporal trends in growth and fishery selectivity in the assessment model to overcome the effect of decadal changes in the growth of Pacific halibut as a result of the 1977 climate regime shift in the North Pacific. The stock assessment of the western rock lobster fishery in WA has been revised to assess the impact of the climate change trends on the stock such as size of migration and size at maturity as well as taking into account the current

decrease in the recruitment into the forward projections (de Lestang *et al.*, 2012). The stock assessment model of the southern rock lobster fishery of eastern Tasmanian fishery was also used to assess the projections for 2030 and 2070 using IPCC scenarios to evaluate the effects on the fishery of projected changes in growth rates and recruitment (Pecl *et al.*, 2009).

4.4.5 Implications for management

A long-term decline in abundance is probably the key management risk affecting fisheries. A common factor in the collapse of fish stocks is the combination of a series of low recruitment that may be due to environmental effects and continued heavy fishing pressure. This combination of high exploitation on poor year classes can result in a severe decline in the spawning stock and hence recruitment overfishing. The likelihood of an extended series of low recruitment is increased if the fishery is vulnerable to climate change effects. Under this scenario, management needs to be able to adjust the fishing effort or catch quota so that it is sustainable for the lower recruitment being experienced. This requires close monitoring of the annual recruitment, preferably as pre-recruits such as puerulus or juvenile, so that appropriate management strategies can be put in place when or even before the low abundance year classes reach legal size.

The management of the fishery also needs to be sufficiently flexible to take into account temporal shifts in spatial distribution and other biological parameters such as growth, catchability and size at maturity. Polovina (2005) examined the relative merits of constant and variable harvest strategies for fish populations in ecosystems that have shifted suddenly. Chang *et al.* (2011) evaluated the effects of temperature-dependent changes on the biological reference points using the pronghorn spiny lobster of Taiwan and identified some potential positive and negative effects of climate change on the management of the stocks. However, irrespective of the type of changes occurring in the fishery, stock assessment and management need to take the changes into account.

Any changes in the spatial distribution of the abundance of lobsters will differentially affect

fishers operating in different zones of the fishery. Management would then need to examine policies to recognize the effect of the new spatial distribution on fishers in different zones. This has been identified as an issue in the western rock lobster fishery of WA where migration of lobsters at a smaller size has resulted in a change in relative abundance between two zones of the fishery (Caputi *et al.*, 2010). The change in the spatial distribution of the South African lobster stocks has also resulted in some fishers requesting boundary changes.

4.4.6 Risk assessment approach to assess vulnerability

The climate change effects on the southern rock lobster in Tasmania (Pecl *et al.*, 2009) were assessed in a formal risk assessment. They examined the existing environmental, biological and fishery information as well as forward projections using an existing stock assessment model and two climate change scenarios. The study also identified a range of potential actions to minimize the threat of climate change on the fishery. These actions included long-term monitoring of lobster populations, incorporating changes in recruitment into the stock assessment projection modelling, and communicating issues of climate change to stakeholders. It was noted that the industry had the ability to undertake active management of the stock in the short term which suggested that it has the capacity to respond to long-term trends such as climate change provided responses to stock are monitored.

An ecological risk assessment of the southern rock lobster fishery in Victoria, Australia, identified climate change effects on lobster habitat as an extreme risk with the next highest risk ranked as moderate which highlights the importance of climate change in that fishery's risk profile (Jenkins *et al.*, 2005). An assessment of the sensitivity to climate change of 35 wild capture fish stocks in south-eastern Australia resulted in the southern rock lobster being ranked third highest after two abalone stocks (Pecl *et al.*, 2011). This assessment was based on 12 sensitivity attributes. The range shift in the rock lobster fishery in South Africa and its interaction with the sea urchin and abalone pop-

ulations was identified as a major risk issue in an ecological risk assessment of key South African fisheries (Nel *et al.*, 2007).

The American lobster fishery is most at risk of adverse climate change effects, where summer temperatures have historically approached thermal physiological thresholds. Coastal areas in the southern part of the species' historic coastal distribution, such as Long Island Sound and Buzzards Bay, Massachusetts, as well as pockets in the middle of the range, such as the shallow waters of Northumberland Strait in the southern Gulf of St. Lawrence, are likely to experience an increasing frequency of summers exceeding the 20°C thermal threshold for lobsters. The coastal Gulf of Maine, Bay of Fundy and Northern Gulf of St. Lawrence and deep, offshore lobster grounds are less likely to be adversely affected by projected warming, and it is possible change may positively affect recruitment and growth in some areas. The net effect over the next century may be a northward shift in the species coastal range. It is not unreasonable to speculate that lobster populations will be receding from coastal southern New England and expanding into the northern Gulf of St. Lawrence and Newfoundland.

4.5 Conclusions and future research

This review has highlighted the vulnerability of some lobster stocks to climate change due to the relatively long larval life of some species which makes them susceptible to environmental factors such as ocean currents and water temperature. It has identified a number of lobster stocks where climate change effects have been documented such as the western and southern rock lobsters in Australia, American lobster, Japanese, Hawaiian and South African lobster stocks. Therefore, at the very least a risk assessment of the vulnerability of the lobster stocks should be conducted to assess what aspects of the life history may be vulnerable and its effect on the sustainability of the stock. If the recruitment abundance is vulnerable to climate change then particular attention is required to the monitoring of the year-class strength. If the monitoring of pre-recruits can be obtained then this

provides an early-warning system for management and industry. If a series of low recruitments are obtained the management strategy needs to be sensitive to the variations in year-class strength as the combination of continued heavy fishing on a number of poor year classes can result in the collapse of the stock.

Most of the climate change effects on lobster fisheries presented have generally focused on changes that have occurred historically. While

some studies on the American lobster and southern rock lobster have presented some likely projected climate change trends for the region that the fishery operates in, there is a need to downscale climate change models to a spatial and temporal scale that is relevant to lobster stocks. These studies have also highlighted the uncertainties in the climate change projections and their effect on the ecosystem that further highlights the importance of long-term monitoring for vulnerable stocks.

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Chapter 5

Systems to Maximize Economic Benefits in Lobster Fisheries

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Abstract

Management plans and policy for lobster fisheries usually specify the objective of creating economic benefit from harvests, which is best supported by collection of economic data to evaluate management decisions. The economic benefit from several lobster harvests worldwide is measured as ‘sustainable economic yield’, which is the long-run, sustainable revenue from harvests minus the costs of harvesting. Maximum economic yield (MEY) is increasingly being considered as a formal target for lobster fisheries including in Australian and New Zealand fisheries for *Panulirus cygnus*, *Panulirus ornatus* and *Jasus edwardsii*. Bioeconomic models that combine stock, cost and price information are now being used in lobster fisheries including *Panulirus interruptus*, *Panulirus argus*, *P. cygnus*, *J. edwardsii* and *Homarus americanus* to evaluate regulations such as catch limits, season length, gear limits, and gear type. Economics theory has also been influential in the evolution of management systems used to constrain catch, in particular through the increased use of market-based and rights-based systems (Individual Transferable Effort, Individual Transferable Quota and Territorial Use Rights in Fisheries). These aim to provide incentives and mechanisms for transfer of catch to more efficient operators and reward for conservative stock management that protects future harvests. Economic methods can be used to resolve resource sharing issues in lobster fisheries with most research dealing with recreational and commercial interactions.

Key Words: bioeconomic modelling; maximum economic yield; fishery economics; harvest strategy; resource sharing

5.1 Introduction

Management of lobster fisheries has historically focused on biological outcomes because of the fundamental need to ensure harvests are sustainable. However, economic approaches, methods and goals are increasingly used as management attempts

to increase the benefits from fisheries, rather than merely maintaining sustainable harvests.

Management approaches in lobster fisheries vary widely, although most involve input control components such as gear and vessel constraints. Individual output controls are now used in many fisheries, with this change primarily motivated by

economic theory. This approach is intended to promote improved resource management through allocation of access rights and is well developed in some lobster fisheries of the Pacific and Atlantic Oceans. Occasionally, lobster fisheries have formally included economics within their management framework through the use of reference points that target maximum economic yield in addition to biologic limit reference points (LRPs).

Fisheries economics contributes to dealing with issues of resource sharing and allocation among heterogeneous users. These different user groups include not only the recreational and commercial harvest sectors but also the non-extractive users who are increasingly catered for through recreational activities within marine protected areas (MPAs).

Economics also contributes to resolving some of the emerging and complex problems facing many lobster fisheries. These include managing harvests with growing uncertainty from climate change effects and consideration of complex spatial issues in many fisheries.

As a review chapter on lobster management systems and the role of economics, several fisheries are used as examples to highlight particular analysis or management tools. These examples are not intended to be complete case studies or literature reviews on any one fishery, nor even to cover the world's most valuable fisheries, but rather to highlight the similarities and diversities of particular management tools. As such, the summary attempts to highlight a variety of examples over a wide geographic range of lobster fisheries and the broad application and relevance of the alternative management options discussed.

5.2 Economic concepts used in lobster fishery management

5.2.1 Net economic benefits

Net economic benefit provides a formal measure of the economic yield of fisheries and is simply the total benefit from fisheries less the costs of harvesting, including opportunity costs such as unpaid labour. Deriving benefits to commercial fishermen

and fishing-dependent communities from lobster fisheries is central to the reason that these fisheries are researched and managed. This desire to provide economic benefits is almost invariably included in the objectives of fishery management legislation, which then affects the intent of lobster fishery management plans. However, although this objective is widespread, there is much variation in management attempts to achieve economic benefit or how economic performance is measured and assessed.

In calling for greater effort to manage for net economic benefits in commercial fisheries, Kompas *et al.* (2011) considered that this results from efficiency across three levels:

- 1 fishery level – total catch and/or effort are restricted to the point that maximizes net economic returns over time;
- 2 vessel level – revenues are maximized and harvesting costs minimized for a given quantity of catch; and
- 3 management level – management services are provided effectively and at least cost for the required level of management.

An economically efficient commercial fishery needs to be well structured across all these levels, which is a significant challenge for any fishery management system. It requires consideration of the economic effects across the suite of rules and regulations that provide the fishery operating environment, including management of the size of the harvest, the rules on size limits and seasons, and the size and number of operators. These possible effects can be considered with the use of bioeconomic models, which integrate resource biology and ecology with the economics of fisher behaviour. Bioeconomic models can also consider space, time and uncertainty dimensions.

Lobster stocks not only support commercial fisheries but also recreational and indigenous fisheries. Economics has value in management of such fisheries because it provides a method for making decisions in relation to non-market values. For example, quantifying the utility of recreational fishing can be used to determine the optimal (most efficient) allocation of catch between commercial and recreational sectors.

5.2.2 Economic targets and performance measures

Effective fisheries management requires the establishment of targets that can be used to assess the current status and progress towards intended outcomes. These targets can relate to any number of aspects of the fishery such as measures of the stock, ecosystem, social outcomes and economics. Despite the importance of economic benefits, explicit economic targets for managing lobster fisheries are uncommon. One example is in Australian Commonwealth Fisheries (Anon., 2007a), which include the Torres Strait tropical lobster *P. ornatus* fishery (most other Australian lobster fisheries are managed separately within state jurisdictions). Fisheries harvest systems in this jurisdiction are intended to target levels of exploitable biomass that result in maximum economic yield (MEY; Anon., 2007a; Kompas *et al.*, 2011). In the case of the Torres Strait *P. ornatus* fishery, the harvest control rule consists of a constant exploitation rate ($F_{TARG} = 0.15$) that is intended to approximate the level that produces MEY (Flood *et al.*, 2011). MEY is the theoretically ‘optimal’ sustainable yield (i.e. quantity of lobsters that can be harvested in a given period, usually a season or a year) since it is the yield that can be harvested during each period of time that maximizes the long-run net economic benefits of the fishery. This approach is also being pursued in the *Panulirus interruptus* fishery off Baja California, Mexico, and the *Panulirus cygnus* of Western Australia, where changes to the harvest strategy involve consideration of MEY (Vega-Velázquez 2010a,b, 2011; Anon., 2011).

In other lobster fisheries, economic analysis has been used to assess management strategies that were less explicitly targeting MEY, but nonetheless directed to this general outcome. For example, the Tasmanian *J. edwardsii* fishery has a target for a fishery-wide catch per unit effort (CPUE) by 2020, which approximates a stock rebuilding pathway to MEY (Gardner *et al.*, 2011). Many New Zealand *J. edwardsii* fisheries have harvest strategies with a target CPUE (Bentley *et al.*, 2003; Breen, 2009; Miller & Breen, 2010). In two of these fisheries (CRA7 and CRA8), the industry had competing objectives of high catch and rapid stock rebuilding

– in this case, the implications for economic yield helped compare different options (Holland *et al.*, 2005).

The performance of lobster fisheries against targets is usually through performance measures of catch rate, biomass or egg production. As per economic targets, the economic performance of lobster fisheries is rarely reported, beyond merely the change in gross value of product. Rare examples where economic performance is tracked include fisheries for both eastern rock lobster *Sagmariasus verreauxi* off New South Wales (NSW), Australia, and southern rock lobsters *J. edwardsii* off Tasmania, Australia, which are both managed by individual transferable quota (ITQ) systems. In these fisheries the total allowable annual catch is split among smaller shares, and percentage shares are traded in a market. The value that quota owners place on these units is thus revealed through market trades and is used as a proxy for economic yield in both these fisheries (Phillips *et al.*, 2010; Gardner *et al.*, 2011; NSW TAC Committee, 2011). The market value of the shares is only a proxy for economic yield and not a direct measure, because the value can change with factors unrelated to the lobster stock, such as the availability of business loans and functioning of the market. Nonetheless, market price of shares is easy to obtain and can be insightful (Lindner *et al.*, 1992; Hundloe, 2000). In the NSW *S. verreauxi* fishery, ITQ unit prices almost tripled between 2004/05 and 2008/09, which was taken to imply that net economic benefit had been improving as a consequence of a lower total allowable catch. Specifically, the reduction in catch led to stock rebuilding, so that catch rates increased and less effort was required to take the catch. This drove the market price of the quota units upwards, because less effort implies lower cost of fishing.

Perhaps the most comprehensive reporting of economic indicators in a lobster fishery is in the two *J. edwardsii* jurisdictions in South Australia (Northern and Southern Zones). These assessments include changes in employment, contribution to gross state product and economic yield. In these lobster fisheries, economic yield of the fishery is determined through a survey process where costs and revenues are obtained directly from the fleet

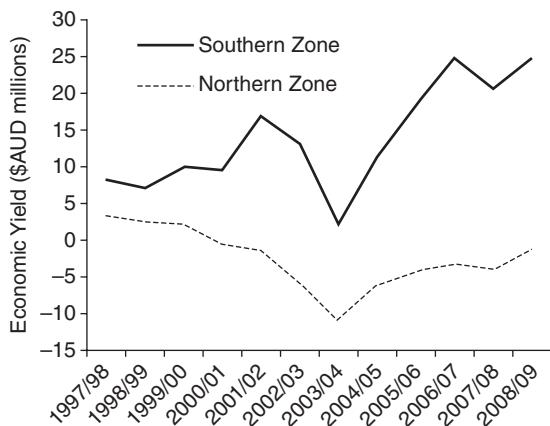


Fig. 5.1 Economic yield as estimated from regular economic assessments in the two Australian *Jasus edwardsii* fisheries (Source: EconSearch, 2010a,b).

(EconSearch, 2010a,b). This can provide a different perspective on fishery performance to that based on traditional performance measures such as aggregate catch or catch rate (i.e. average catch per unit effort). In the Northern Zone fishery, economic yield for the fleet has been negative for the last 9 years, which provides a strong motivation for management change; the management response was to lower total catch so that stocks and catch rate increased, leading to a reduction in the cost of harvesting (Linnane *et al.*, 2010b; Fig. 5.1).

Managing for economic yield is not only about the target but also the pathway to that point and dealing with uncertainty and change in the fishery. The management decision pathway can be examined through a methodology known as management strategy evaluation (MSE), which involves assessing the consequences of a suite of management options to identify trade-offs in performance. MSE models form part of an adaptive management cycle using simulations. Application of MSE does not seek to prescribe an optimal strategy, but rather provide the decision maker with information on the implications of each option. MSE is often used to conduct a retrospective analysis whereby critical decision points and key assumptions are identified. This process has been successfully applied in New Zealand *J. edwardsii* fisheries so that biological and socioeconomic objectives have been achieved (Holland, 2010). MSE has not been applied widely

in lobster fisheries elsewhere, and Holland (2010) makes the point that it is distinct but complementary to bioeconomic modelling so that more collaboration between economists and fishery scientists is likely to be the most useful approach for guiding management decisions.

5.2.3 Bioeconomic modelling

Bioeconomic modelling of lobster fisheries generally involves combining biological and fleet information with cost and revenue information. The effect of the tonnage harvested on revenue is straightforward but two aspects of the interaction between stock and economic outcomes are especially important for understanding the effect of catch on economic yield (Fig. 5.2). The first is the ‘stock externality’, which describes the reduction in cost of harvesting lobsters when the stock is more abundant and thus catch rates are higher (Holland, 2011). The second is the ‘marginal stock effect’, which describes the decrease in sustainable production (and thus revenue) that can occur with growth- and recruitment overfishing.

Lobster fisheries have many traits that can be modelled to examine opportunities for change in management. Individual lobsters are easy to measure and then release with low discard mortality, which means that the size of the individuals harvested can be adjusted to manage economic yield per recruit (Acheson & Reidman, 1982; Botsford & Hobbs, 1986). Price can vary with size, season and physical traits such as colour, which enables economic gains to be made through variation in the timing of harvest (Cheng & Townsend, 1993; Melville-Smith *et al.*, 2003; Chandrapavan *et al.*, 2009; Hamon *et al.*, 2009).

The cost component of lobster fisheries is also well suited for economic analysis, especially in trap-based fisheries where traps are standardized by regulations. With standardized effort units, costs can be readily estimated by surveys and scaled with effort. Substantial opportunities appear to exist to increase economic yield in many lobster fisheries through management of traps (especially if soak time is regulated). For example, Gates (2000) estimated that the cost of harvesting in an *H. americanus* fishery could be reduced by 25% through more efficient use of traps. Trap constraints have been

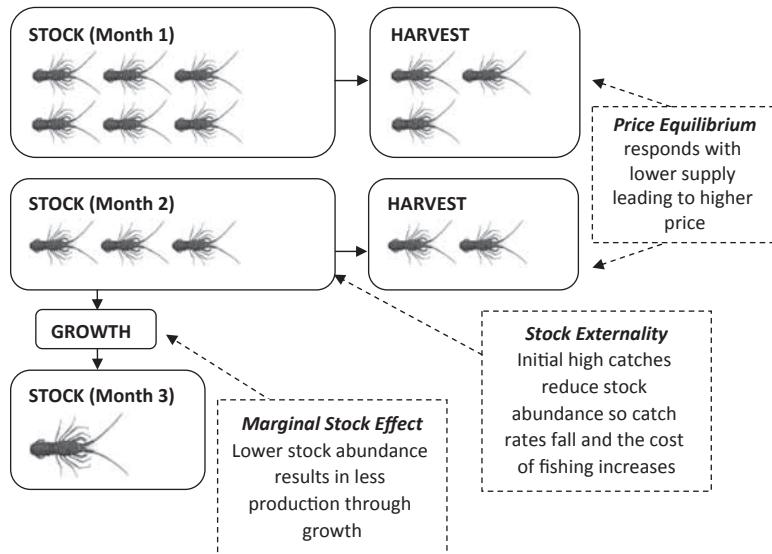


Fig. 5.2 Processes that can increase economic yield from lobster fisheries despite lower catches. Price equilibrium responds to supply which can dampen reduction in revenue at lower catches. Lower catches result in higher stock abundance which reduces the cost of fishing per lobster (stock externality). Productivity of the stock can be increased at higher abundance through growth and recruitment effects (marginal stock effect; note that density dependent growth and mortality can create a negative marginal stock effect at high biomass levels). A fourth process not illustrated is the potential for price to increase through time so that stock gains in value if caught later (capital growth).

successfully introduced to the Maine *H. americanus* fishery (Brewer, 2010), although this was not a simple exercise with initial attempts to limit total number of traps actually leading to an increase in trap sets and thus cost of fishing due to unexpected social responses, a common problem in input-controlled fisheries (Acheson, 2001).

Modelling of fisheries where multiple gear types are used is more complex because both revenue and cost varies by gear type. This issue was important in a bioeconomic analysis of the *Panulirus argus* fishery on the Yucatan Peninsula shelf where traps, artificial habitats ('casitas'), diving with scuba, diving with hookah and gillnets were used during the adult migration (Seijo *et al.*, 2001). Significant differences were reported for profits from using alternative fishing methods and gears which were related to different selectivities and costs (Seijo *et al.*, 2001). The proportion of catch taken by different gear types has evolved in this fishery, with a greater proportion now harvested from casitas (Salas *et al.*, 2008; Zapata-Araujo *et al.*, 2008); however, the problem of incorporating different

gear types complicates the development of bioeconomic models in the region (Chavez, 2001).

In Florida, several studies have estimated the MEY for *P. argus* using a surplus production approach that assumed an exponential catch function (Larkin *et al.*, 2002; Milon *et al.*, 2001). This functional form matched the observed historic catch and effort data and showed that higher levels of effort do not increase total catch. When this information was combined with the estimated fixed cost and cost per unit of effort from data obtained through surveys, the bioeconomic MEY solution suggested a significant decline in effort (at least 50%) would be necessary to maximize resource rents (i.e. the share of profits that are assumed generated by the value of the natural stock). This model was also used to estimate the expected market value of the right to use each trap for comparison with the reported transfer prices (Milon *et al.*, 1998).

In the West Central Atlantic, dynamic age-structured bioeconomic models have been used to estimate the effect of alternative management strategies of spiny lobster fisheries of Brazil (Caddy & Seijo,

2005) and Cuba (Puga *et al.*, 2005). Recent changes to management policy for the *P. interruptus* fishery in Baja California, Mexico, also included the use of reference points with bioeconomic model input (Chavez & Gorostieta, 2010; Vega-Velázquez *et al.*, 2011).

While empirical bioeconomic models can identify opportunities to increase economic yield, the management system implemented in the fishery can have a profound effect on fishery outcomes. As such, it is useful to consider the variety of management tools used in lobster fisheries from an economic perspective. The suite of management approaches used today are summarized in the following section.

5.3 Lobster fishery management systems

5.3.1 Limited entry

As with any common property resource, open access will continue to attract new users for as long as the private net benefits to these users remain positive. This behaviour has characterized the development of the majority of fisheries worldwide; as economic theory predicts, profitable fisheries attract entrants, and fisheries are most profitable when there are fewer harvesters enjoying high catch rates. Lobster fisheries are no exception.

In the case of commercial lobster fisheries, fishing effort has increased in profitable fisheries. In both of the primary US commercial lobster fisheries, American lobster, *H. americanus*, and Caribbean spiny lobster, *Panulirus argus*, the number of participants increased dramatically for 15–20 years in the late 20th century (approximately mid-1970s through the mid-1990s). The increase in the number of participants corresponded with an increase in annual landings until the mid-1990s for the American lobster while annual landings for the Caribbean spiny lobster remained relatively constant. Despite differences in the number of participants, the vessel-level conditions in the fishery were the same: too many vessels chasing too few lobsters. Limited entry to the fisheries was considered the solution to this undesirable trend by fisheries managers.

Limited entry at its most basic is simply prohibiting new users and is typically implemented at the vessel level. Constraint on the total number of vessels able to operate is the most straightforward management tool for limiting the number of participants and, as such, is applied in nearly every lobster fishery today. In most cases, the total number of permits is capped but they are transferable, so new individuals may be allowed to enter the fishery as others exit.

While many lobster fisheries have implemented limited entry regulations, limiting one component of fishing effort (i.e. number of vessels, permits, individuals, etc.) is rarely successful in limiting overall catch. This is because there are many aspects to fishing that determine vessel-level efficiency and thus overall catch. Factors that determine catch at the trip level (excluding weather, changes in the ecosystem and macroeconomic conditions) include vessel size, number of crew, fishing location, season, gear and trip length. This range of factors generally allows fishers to compensate for constraints on any one aspect of fishing operations by expansion in other areas (Ye & Dennis, 2009a) although in theory, a limit on a totally non-substitutable input could be used to generate 100% of the potential rent.

If fishing effort is not effectively constrained, fisheries operating under limited entry may perform no better than open-access fisheries; fisheries that are managed to restrict entry but otherwise leave fishing effort unconstrained are referred to as ‘regulated open access fisheries’. In such fisheries, participants continue to race for the resource by increasing other aspects of fishing effort. This increased deployment of other aspects of the fishing operations as operators compete involves inefficient extra investment in equipment or ‘capital stuffing’. In lobster fisheries, restricting the number of vessels or individuals should not be expected to improve the profitability of the fishery if other aspects of fishing effort are not also managed.

5.3.2 Effort limitation

Effort limitation or input control systems consist of four elements (although each of these elements is not always applied). These are (i) control on the

number and type of gear, (ii) constraints on the time and space that this gear can be applied, (iii) a system for managing increases in the effectiveness of effort through time as improvements to fishing methods are made, such as through technology, and (iv) systems for managing transferability of effort between operators. In theory, effective application of these elements can allow managers to move the fishery from one operating at open access (where excess effort has dissipated all resource rents) towards a level of effort that approximates maximum economic yield (Morgan *et al.*, 2009a). Economic studies of lobster fisheries consistently demonstrate substantial economic benefits from reducing fishing effort, especially with effort limitation systems (Bell & Fullenbaum, 1973; Campbell & Hall, 1988; Ley-Cooper & Chavez, 2010).

Many aspects of trap design can be regulated in effort-limited lobster fisheries with the objective of controlling efficiency, including maximum dimension, diameter of the opening, controls on the number of 'shorts' or juvenile lobsters used as attractants (e.g. *P. argus* in Florida), distance between slats and the use of escape gaps or rings (Schoeman *et al.*, 2002). Aside from controlling effort, these regulations also enable the escape of bycatch and juvenile lobsters. However, regulation of gear also tends to have undesirable economic outcomes because it increases the cost of fishing by reducing catch rates and increasing trap construction costs. It also prevents innovation in trap design that could otherwise reduce costs of fishing.

Aside from trap design, the basic effort control in many lobster fisheries is a cap on the amount of gear available, which is applicable not only in trap fisheries but also other capture measures for lobsters such as trammel nets, which are used for several fisheries including *Palinurus elephas* in the Mediterranean Sea and *Panulirus homarus* in the western Indian Ocean (Goni *et al.*, 2003; Al-Marzouqi *et al.*, 2007).

The harvesting capacity of the fleet is not only a function of the design and amount of gear but also the frequency or duration that gear is deployed through the year. Consequently, effort limitation systems are typically supplemented by seasonal and geographic harvest restrictions (closed seasons and or areas). Economic efficiency is increased

where controls are placed on the total amount of gear available to the fleet rather than the days fished because closed seasons tend to create pulses in supply and often, as a result, lower prices. Closed seasons and restrictions on vessels (trips or gear) also imply that capital invested in vessels and processing facilities is not being used to its full capacity (potential), which is inefficient but may be justified to protect spawners and or juveniles.

There are a plethora of other factors aside from gear design, quantity and temporal limits that affect production and harvesting capacity. In lobster fisheries these include the knowledge and experience of fishers, changes in technology (from synthetic rope to electronics like GPS), the geographic range covered by the stock (local or shared stocks; issues related to enforcement), and the intensity with which the traps are managed at the vessel level (e.g. number of trap 'pulls' or soak times) to name a few. Many of these factors contribute to a process termed 'effort creep', where the effectiveness of effort increases through time. Effort creep can be a serious problem for input-controlled lobster fisheries.

One approach to reduce active effort and to compensate for effort creep is to decrease the total number of traps allowed in the fishery, that is, establish a total allowable effort level (either at the vessel level or fleet level). The ability to trade or transfer effort between individuals in lobster fisheries would be an improvement in the program from an economic perspective because it promotes fleet rationalization since the traps or pots can shift to more efficient operators, which reflects a better use of capital. Transferability allows for the creation of a market for effort such that the traps have an asset value linked to future catch flows. This linkage between fishers wealth in fishing assets and future health of the fishery is one of the aspects that is promoted for output or quota systems (discussed below) because it rewards resource stewardship (Wilen, 2006).

There are several examples of tradable (transferable) effort limited lobster fisheries worldwide or individual transferable effort (ITE) programmes. One early example is the Florida lobster *P. argus* fishery, where such a system was introduced to improve economic yield from the fishery rather than for biological reasons. This was required

because trap numbers had increased through open access nearly 10-fold from the mid-1970s to the early 1990s so that catch rates fell and profitability of individual operators declined. The initial steps in resolving the problem of declining catch rates and corresponding increase in average cost was to cap the number of traps and then reduce trap numbers to prevent crowding of gear. Capping the number of traps was accomplished by requiring labelling of each trap with a unique number (Plate 5.1). Following capping, individuals holdings were reduced by 10% in each of the first three seasons through a process termed 'active reductions'. This reduced the number of traps in the fishery, but the process was not popular and was temporarily suspended. Active (across-the-board) reductions in pot numbers were resumed in 1998, but at a lower level of 4%, and accompanied by 'passive reductions' whereby 10% of traps were removed upon transfer between operators. The switch from active reductions to a passive programme is inefficient at reducing effort (since reductions only happen if people trade and so will lengthen the time to reach MEY; Milon *et al.*, 2001), but preferred by industry members. By 2011, the number of traps had been reduced by approximately 40% and the passive reductions are planned to continue until the number of traps falls another 20%.

The management approach used in Florida was broadly repeated with *H. americanus* in one area of the north-eastern USA in 2003 and in the Western Australian fishery for *Panulirus cygnus*, which was managed with an ITE system until changing to output management in 2011. In the Western Australian ITE system a fixed and limited number of units were allocated to fishers. These 'units' were initially the entitlement to use a trap so their number was originally equivalent to the number of traps. The units and traps were later separated so that so changes in the total number of traps in the fishery could be achieved by adjusting the ratio of fishery access units to physical traps that could be deployed. This enabled reductions in the total number of traps in the fishery and promoted fleet rationalization through the transfer of units between operators (Anon, 2005).

Although the ITE system for *P. cygnus* had capacity to increase economic yield from the

fishery, several problems were encountered in the application of the system which contributed to the system being discontinued in 2011 in favour of ITQs. As per the Florida fishery, reductions in trap limits in the ITE system were unpopular so it was politically difficult to set the trap-unit ratio at an optimal level for economic yield. A bioeconomic analysis of the fishery indicated that a large reduction in effort of around 40% of 2007/08 levels was required to maximize economic yield (Reid, 2009). Even if this change in effort had been made, the resistance to effort reduction was a recurrent problem due to the need to respond to effort creep in ITE systems. Effort creep was also symptom of poor deployment of capital or 'capital stuffing', which remained a problem as fishers continued to compete against each other for catch.

Catch in these examples of ITE systems responded to stock availability rather than market demand with peaks in landings around periods of highest stock availability. This included the season opening, peaks in catchability and with stronger recruitment. This supply driven pattern in fishing created gluts and famines in supply with little incentive to maximize the value of the catch (Reid, 2009). In the case of the *P. cygnus* fishery, a large portion of the catch was sold into lower priced domestic markets rather than premium live export markets in Asia. The increase in catch in years of high recruitment resulted in large fluctuations in catch and thus revenue between years, which created difficult conditions for businesses during subsequent recruitment troughs. Termination of the ITE system in the *P. cygnus* fishery and the shift to ITQ management in 2011 led to fishers reducing catch by around 40% at the start of the season when the price was low and also targeting higher value size classes (Hoskings, 2011).

The Florida ITE system also illustrates a problem common to many lobster fisheries that attempt to utilize transferrable rights systems to facilitate the movement of harvest to more efficient operators. This transfer market had an informal market structure, as opposed to a formalized online market where past transactions are visible; hence it required interested buyers and sellers to seek out one another. The undeveloped and informal nature of this market affected trading in the Florida fishery and was com-

pounded by distinct cultural and geographic participants (Shivlani & Milon, 2000; MacLauchlin *et al.*, 2009). In addition, the unfamiliarity with asset values and need to invest in a search for a trading partner with comparable units to trade has hampered the operation of this market. van Putten *et al.* (2011) showed that a market for trade in *J. edwardsii* harvest rights became increasingly dominated by a smaller number of larger individuals through time, which creates asymmetry of information and compounds the problem of an informal market structure.

One important control common to most lobster fisheries is the use of size limits which are especially effective because of the ability to handle, measure and release lobsters unharmed. Although size limits are usually established for biological reasons, they can also be used to manage economic yield. Chavez & Gorostieta (2010) used bioeconomic modelling to show that higher minimum legal sizes could be used to improve economic yield of the *Panulirus interruptus* fishery in Baja California, Mexico because the productivity of the stock was suppressed by growth overfishing.

5.3.3 Quota management

The regulation of total catch has received much attention in fisheries economic research. Systems that constrain catch to a level where economic yield is maximized usually involve a total allowable catch (TAC) limit that balances the benefit of a higher catch (higher revenues) against the benefit of a higher catch rate (lower costs). Catch setting in quota systems thus involves adjusting the TAC along a pathway that targets sustainable economic yield rather than merely stock sustainability. Output controls such as TACs also can allow for the removal or relaxation of input control regulations that would otherwise force costs higher, such as trap limits, closed seasons or even size limits. However, TACs alone cannot prevent harvesters (even if they are limited in number) from competing at sea for catch. This is equivalent to the regulated open access problem discussed with respect to limited entry management systems.

In lobster fisheries with TACs where the quota is split into tradable shares (i.e. quota management

systems or ITQs), harvest is expected to shift to more efficient operators that can pay more for the shares. This process of fleet rationalization is expected to reduce total capital inputs and labour costs in the fishery and thus raise economic yield. For example, ITQs were successfully used in the *J. edwardsii* fishery in Tasmania, Australia, to reduce the fleet and number of active fishers from 340 to 209 over a period of a little more than 10 years (Gardner *et al.*, 2011). The fact that ITQs are traded in markets also means these have value that is linked to discounted future cash flows. Many authors have discussed the effect of this asset value on stewardship of fishery resources, although this does not always occur (e.g. Emery *et al.*, 2012).

Aside from the expected increase in efficiency of the fishery through rationalization, quota management systems can theoretically generate several other benefits. They provide a robust system for controlling catch that can be practically difficult with effort controls – this allows residual stock to build and support higher catch rates, effectively lowering the cost of fishing (formally termed the ‘stock effect’). Under ITQ programmes, fishers compete to a lesser extent for catch so capital stuffing is reduced and capital can be better utilized across longer open seasons. As with simple quotas, ITQ programmes can also allow for the removal or relaxation of input controls and thus simplify management and enforcement. Lobster prices often increase with quota systems because fishers are better able to target effort to periods or product categories that receive higher price (Chandrapavan *et al.*, 2009). The potential for benefiting from size or seasonal premiums is greatest for stocks that sell into global markets where any supply effect on price is diluted by competing producers.

Successful application of ITQ management in terms of increased economic yield has occurred in the fishery for eastern rock lobster *S. verreauxi* off NSW, Australia. This small fishery adopted a TAC in 1994 and ITQ management in 2000. Stocks have steadily rebuilt, the catch rate doubled between 2000/02 and 2007/08, the fleet has contracted with 38% fewer shareholders and input controls are steadily being removed. The capitalized value of catch shares almost tripled between 2004/05 and

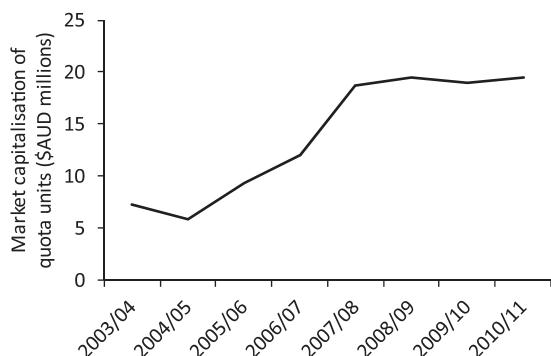


Fig. 5.3 The value of tradable ITQ catch shares from the Australian fishery for eastern rock lobster *Sagmariasus verreauxi* over time. Market capitalization is the total number of shares multiplied by the average market price (Source: NSW TAC Committee, 2011).

2007/08 (Fig. 5.3; Liggins *et al.*, 2009; NSW TAC Committee, 2011).

A substantial test of the economic theory of ITQ-managed lobster fisheries is the willingness of fishers to lower the TAC to either target long-run higher economic yield or to respond to a short-term decline in stock productivity. This is essentially a test of resource stewardship (Parslow, 2010). Voluntary reductions have been taken in the New Zealand CRA4 *J. edwardsii* fishery in response to stock declines using an agreed upon formal management procedure (Butterworth & Punt, 1999; Breen *et al.*, 2009). Similar procedures have been applied successfully in other New Zealand lobster fishery zones with substantial growth of stock and quota unit values in some cases (Holland *et al.*, 2005; Breen, 2009; Holland, 2010).

ITQ systems have been less successful in promoting resource stewardship in Australian *J. edwardsii* fisheries. Catch rates declined between 2005 and 2010 in both South Australian zones, both Victorian zones and the Tasmanian fishery as a consequence of low recruitment and high TACs. TAC reductions were proposed by fisheries managers and researchers that were supported by the majority of industry members in some cases, although in most cases there was resistance to TACs that would reverse stock declines. As a consequence, catch rates reached record lows in most

areas by 2010 (Linnane *et al.*, 2010a). In the case of the South Australian southern zone and the Tasmanian fishery, the early years of ITQ management had been successful in terms of biomass rebuilding and growth of asset values with these measures at least doubling between 1995 and 2005 (Gardner *et al.*, 2011; Linnane *et al.*, 2011). This experience of financial benefit from constraining TACs made the resistance to TAC cuts during periods of low recruitment even more surprising.

The different histories of the New Zealand and Australian *J. edwardsii* fisheries indicate some of the factors that affect outcomes of ITQ systems. Formal management procedures to define an agreed response to stock declines were lacking in Australia but proved successful in New Zealand. This effectively concedes that fishers will continue to focus on short-term revenue in ITQ systems rather than asset values (linked to future cash flows) so the implementation of an ITQ system alone is inadequate to provide good stock management (Bradshaw, 2004). The catch shares in Victoria and Tasmania also lacked exclusivity, so fishers were reluctant to reduce the TAC in an attempt to rebuild stocks because of the risk that rebuilding could be undone by expansion of recreational catch or MPAs (Lyle *et al.*, 2005; Hobday *et al.*, 2005).

Aside from stewardship in TAC setting, other aspects of ITQs have generally increased economic yield in Australian lobster fisheries. Most underwent fleet rationalization through sale of catch shares to more efficient operators (Hamon *et al.*, 2009; van Putten & Gardner, 2010). Input controls have been relaxed in all Australian ITQ fisheries, including the Western Australian *P. cygnus* fishery, which adopted ITQ management in 2011 (Morgan *et al.*, 2009b; Anon. 2011). Relaxation of input controls in Australian lobster fisheries with ITQ management has reduced costs and has also allowed shifts in the seasonal timing of catch to command higher prices (Hamon *et al.*, 2009; Hoskings, 2011), although price remains highly leveraged to external factors such as exchange rates (Hurn & McDonald, 1997; Hoskings, 2011). There remains considerable scope to further reduce input controls in most lobster ITQ fisheries with the retention of many input components such as seasonal closures and

size limits. Barkai & Bergh (1992) showed that substantial lowering of the minimum legal size combined with conservative TACs gave excellent biological and economic outcomes in the South African west coast *Jasus lalandii* fishery. This example of better integration of input controls with ITQ systems would be expected to hold for most ITQ lobster fisheries yet size limits have rarely been reviewed in lobster fisheries after ITQ management was introduced.

Aside from the difficulty in setting TACs that target economic yield, ITQ systems in lobster fisheries have additional challenges in resolving economic problems. One issue is that these systems tend to promote a shift away from owner-operators to lease-reliant fishers where allowed (van Putten & Gardner, 2010). This issue is typically cast as a social problem (Pinkerton & Edwards, 2009) but it can also affect economic outcomes through the politics of decision making with lease-reliant fishers receiving little benefit from rising catch rates (as higher catch rates tend to inflate the lease price). Market price can also be reduced through information asymmetry, especially when processing facilities are able to control market share through quota ownership – a problem that has been resolved in some cases by a cap on ownership for individuals (van Putten *et al.*, 2011). Lastly, there are also concerns about the community benefits from the pursuit of economic yield from fisheries that can, for example, result in changes in the geographic distribution of the fishery (Knapp, 2011).

Bromley (2009) initiated a debate on ITQ systems in general, with criticisms of several traits of ITQs including the initial allocation process and the lack of rent capture by the community. His first concern, that ownership of community assets is permanently transferred at no cost, can be resolved by either auctioning or selling the initial allocations as per the giant crab *Pseudocarcinus gigas* fishery in Tasmania, Australia (Gardner & Mackinnon, 2002). Limited duration allocations were also proposed and they have been discussed in the Baja California *P. interruptus* fishery (Costello & Kaffine, 2008) and the New England *H. americanus* fishery (Macinko & Schumann, 2008). However, restricting the duration of the right can

have negative implications for planning and investment that are part of the intended benefits of rationalization (Harte *et al.*, 2009). Bromley's (2009) other main concern, that the community gets little benefit from economic rents obtained through ITQ systems (other than employment and economic impact effects; Harte *et al.*, 2009), has been at least partially resolved in some cases. For example, the Fishery Management Strategy for the NSW *S. verreauxi* fishery includes a 'Community Contribution' royalty of 6% of the gross value of catch (Anon, 2007b), which is effectively a Georgist tax¹ on access to a community asset; however, this tool is not available in all nations (e.g. US fisheries). In 2009/10 this equated to around 19% of the total rent as revealed by the value of quota lease payments (NSW TAC Committee, 2011).

5.3.4 Territorial use rights

Rights of access to particular fishing areas or territories (i.e. individual transferable grounds, ITG; Seijo, 1993) or territorial use rights in fisheries (TURFs) involves the allocation of fishing areas to private firms, cooperatives, sectors or individual fishermen. Such systems have been used in lobster fisheries including the spiny lobster (*P. argus*) fishery of Punta Allen, Mexico. The important element of this system from an economic perspective is the reduced competition between operators relative to ITQ systems because, at the extreme, individual fishers have sole access to individual lobsters. As a consequence, there is incentive for more efficient use of capital, better fishing to market demand within years and to carry stock across years for smoothing of business cash flow.

The Mexican Caribbean fishery is based on fishing rights and concessions allocated to fishermen organized into 19 cooperatives. There are an estimated 2400 fishermen harvesting spiny lobsters in small-scale boats using four alternative fishing techniques, each with distinct economic and biological implications: (i) artificial habitats called

¹Georgist taxes arise from an economic philosophy that people own what they create, but that things found in nature, such as fishery stocks, belong equally to all.

'Cuban casitas' using hand nets or 'jamo'; (ii) traps; (iii) set nets deployed during the winter migration; and (iv) scuba diving in natural habitats and harvesting lobsters from traps without lifting them. Management via cooperatives began in 1947 when the State granted cooperatives the exclusive property rights to harvest a number of high value species, including lobsters. Currently there is a limited entry policy with no licenses being issued to new fishermen's cooperatives. As with most other lobster fisheries, there is a closed season, minimum size restriction and prohibition on the harvest of gravid (egg-bearing) females. As a co-managed fishery, the community has implemented additional local rules and community enforcement mechanisms.

In the Punta Allen fishery, one fishing cooperative has co-managed the resource with a history of sound decision making (Seijo, 1993; Solares-Leal & Alvarez-Gil, 2005). One of the main characteristics distinguishing this lobster fishery from others in the region is the initially informal (but legal) allocation of property rights that cooperative members have achieved by dividing the lobster fishing grounds into 150 lots (campos) ranging in size from 0.5 to 3.0 km².

Some of the factors that determined the relative success of the Punta Allen spiny lobster fishery are the following (Seijo *et al.*, 1989; Seijo, 2007; Sosa *et al.*, 2008):

- 1 the isolation of the Punta Allen fishing village, which encouraged a self-help approach to community development;
- 2 an institutional framework which allocated exclusive property rights to fishermen's cooperatives;
- 3 the initial informal allocation of property rights by distributing them in lots among cooperative members;
- 4 community organization and good leadership which has maintained order and stability;
- 5 effective self-enforcement of internal rules, with avoidance of free rider behaviour;
- 6 the use of artificial habitats that enhance biological and fishery productivity;
- 7 the use of habitat and species-friendly fishing gears; and

- 8 the training and technical assistance in inputs purchasing processes, quality control and product marketing.

5.4 Resource sharing and allocation of lobster stocks

5.4.1 Recreational and commercial sectors

In many lobster fisheries, commercial or artisanal harvests preceded recreational harvests. In such cases, the sequential development of sectors has resulted in a management system that does not jointly consider all users simultaneously. Recreational anglers, as citizen owners of the common good natural resource, may feel entitled to access and this *de facto* harvest right can cause problems (stock constraints) when recreational fishing effort grows. Hence maximizing the economic value of the resource, or attempting to operate at optimum yield, requires a system for both constraining total effort and for shifting allocations between sectors. In the South Australian *J. edwardsii* fishery, two objectives have been defined for this reallocation: (i) 'optimum utilization', so that the resource is allocated in a way that achieves the best use for the community at large; and (ii) 'equitable distribution' so that the resources are to be allocated in a way that distributes the benefits of use fairly amongst users (PIRSA, 2009). In practice these can be opposing, and the current allocation relies on a fixed catch share.

There are two broad alternative approaches to developing inter-sectoral reallocation mechanisms – the administrative approach and the market approach (Reid, 2010). For effective functioning of any reallocation system there must be an initial allocation to each sector and an agreed unit for transfers between sectors (Pearse, 2006). Allocations, in this context, can be considered on the input or output side (i.e. numbers of traps or weight of catch landed, respectively) and are relatively straightforward for user groups that employ the same metrics (i.e. number of traps, weight of harvest). A complicating factor in many lobster fisheries when considering all user groups is that

gear and management controls often differ between groups. In such cases, the marginal analysis required to theoretically optimize allocations from an economics perspective is complicated.

The administrative approach to reallocation between sectors involves intervention by managers to achieve a more optimal outcome. Reid (2010) proposed that this could be applied in lobster fisheries with a buy-out of lobster traps from the commercial sector to increase recreational opportunities. Managers need to weigh the net benefits of different allocations to all users (e.g. commercial trap fishermen, commercial divers, recreational divers, etc.). Such an analysis would compare the marginal value of changing the allocations. Put simply, if an extra lobster is caught, which sector would derive most benefit and thus should receive the allocation?

The difficulty in applying administrative methods for resource allocation (i.e. lack of fisher support) has led to proposals for market-based mechanisms. An example is market-based trade in shares between sectors. The argument for the use of market mechanisms is based on the premise that allocation via a government process results in inferior economic utilization of the resource. One market-based solution is to promote the joint commercial and recreational sectors. Some commercial *P. argus* fishers in Florida have attempted to capitalize on the recreational demand by taking customers onboard as a tourist experience. The tourists receive fresh lobster, which they helped to harvest, and the fishermen received a higher price for the same lobster. Another more integrated market system for recreational allocation has been proposed by Sutinen & Johnston (2003) where recreational management organizations trade in the catch share market on behalf of recreational fishers.

Measuring the marginal benefit of recreational fishing is more complicated than for commercial fishers and this contributes to the emphasis of the cost components in most analyses of recreational lobster fishing economics (Frijlink & Lyle, 2010). The benefit from commercial fishing is simply quantified by the revenue received, but the benefit of recreational fisheries is enjoyment (or rarely subsistence), which is encompassed in the term ‘utility’. The utility of recreational fishers has the

trait of ‘diminishing marginal utility’, where most value or enjoyment comes from the first lobster and this benefit diminishes with each subsequent lobster in a given period of time. Further, recreational benefit is often not constant with size, with larger or ‘trophy’ lobster being more highly valued than would be suggested by their weight alone.

Although most of the economic research and debate around recreational catch deals with allocation between sectors, the setting of the total recreational catch can be approached in the same manner as total allowable catch limits in the commercial sector. As per commercial fisheries, maximizing the net benefit from recreational fishing involves balancing higher catches (utility) against declines in catch rate (cost). In theory it is possible to target maximum sustainable utility (net of costs), although this is not implemented formally in recreationally lobster fisheries. The concept is applied at a simple level where managers attempt to increase utility of the recreational sector by allowing (or encouraging) more people to participate but to harvest fewer lobsters each (Yamazaki *et al.*, 2011). Unsuccessful recreational fishing trips have low utility so managing for high catch rate or ‘strike rate’ is important in the recreational sector as per the commercial sector. Managers should, however, be aware of incentives to increase recreational values that also serve to reallocate harvest away from the commercial if that was not the intent. For example, in the Florida fishery, managers have established a 2-day recreational sport season that is immediately prior to the opening of the commercial season; any increases in harvests by the recreational sector (such as through increasing popularity) come at the expense of lower commercial harvests in the season that opens soon after. This reallocation reduces economic incentives for commercial fishers to support catch constraints on their sector.

5.4.2 Customary harvests

Non-commercial fishing occurs not only for recreation but also for the subsistence benefit of obtaining food. Subsistence and artisanal lobster harvesting occurs throughout the Pacific, and the desire to protect this form of harvesting has been used in some cases as argument against promotion

of larger scale commercial harvesting (Skewes, 1990). Different motivations for harvest compound the political difficulty in economically optimal resource allocation between sectors. The South African *J. lalandii* (rock lobster) fisheries are quota managed but substantial additional allocations were made for subsistence harvesting. Rock lobsters are a valuable species so the boundary between subsistence and commercial fishing was blurred and the change dramatically affected stock management (Plaganyi & Butterworth, 2008; Boyd & Adriaans, 2002).

Customary harvests are considered in the allocation of catch across sectors in many jurisdictions. Each Australian lobster fishery includes consideration of customary Aboriginal catch in management, although in most cases the catch is too small to influence discussions on resource sharing or TAC setting. For example, customary harvests in Western Australia and NSW were each less than a tonne in 2009 (Reid, 2010; NSW TAC Committee, 2011). In both these cases the small customary harvest is a right and therefore is noted in allocation discussion but is exempt from management of total catch. Customary Maori harvests in New Zealand are more substantial and management of this harvest occurs within a co-management system (Yandle, 2006). Customary rights and allocations generally take precedence over other harvesting sectors and thus come under less economic consideration in relation to constraint of catch.

5.4.3 Non-extractive users

Marine animals have non-extractive value, which has been measured in Norway by the value that the community placed on the recovery of collapsed lobster stocks (Ojea & Loureiro, 2010). A direct, non-extractive benefit that exists from lobsters is the benefit or enjoyment that recreational user groups (e.g. recreational SCUBA divers and snorkelers) gain from viewing lobsters, which has been quantified for dive charter tourists viewing *P. argus* in the Turks and Caicos Islands (Rudd, 2001).

Resource allocation to these groups is often used as justification for MPAs to provide opportunities for people to view natural densities of exploited

species. Accounting for this allocation of stock to MPAs by reducing catch by harvest sectors is important for management because displaced catch will otherwise increase harvest rates in open areas, leading to depletion of the stock and long-run economic loss (Buxton *et al.*, 2004; Hobday *et al.*, 2005). Some authors have speculated that spillover of recruits from MPAs would compensate for loss of yield, although this is not possible if the fishery is managed to MEY targets in which case a net loss must occur (Polacheck 1990; DeMartini 1993; Guenette & Pitcher 1999; Sladek Nowlis 2000; Hilborn *et al.*, 2006).

Optimizing the allocation between extractive and non-extractive users is difficult to resolve. Arnason (2009) explored the use of a market approach through tradable ITQs but showed that these fail because quotas for conservation and for extraction constitute two fundamentally different goods.

5.4.4 Dividing catches between nations

Lobster stocks are often shared across jurisdictions including between nations. This is most commonly through larval source and sink dynamics that imply the need for a collaborative approach to management of egg production. Issues of dividing catches between jurisdictions are complex in many lobster fisheries such as the European fisheries for *P. elephas* (Bonaviri *et al.*, 2005) or the western central Atlantic fisheries for *P. argus* with source-sink dynamics and harvesting occurring across Cuba, Brazil, Bahamas, Honduras, USA, Nicaragua, Mexico and Belize (Cochrane *et al.*, 2004; Ehrhardt, 2005; Chavez, 2009).

There are four spatial aspects that complicate the targeting of economic yield in the management of the spiny lobster fisheries of the West Central Atlantic: (i) it is a transboundary resource, (ii) it is characterized by a metapopulation with source-sink configurations, (iii) gears and fishing methods are heterogeneous with differing effects on population structure, and (iv) the heterogeneity in management strategies, regulations (including differing legal sizes and trade restrictions) and enforcement (Cochrane *et al.*, 2001).

Resource sharing becomes more complicated, and political, when harvestable size lobsters walk between jurisdictions, as occurs in the Torres Strait tropical rock lobster *P. ornatus* fishery during annual migrations. Resource-sharing arrangements in this case occur between Australia and Papua New Guinea through the Torres Strait Treaty, which was ratified in 1985 (Ye *et al.*, 2008; Ye & Dennis, 2009b). Within this fishery there are further allocation issues between dive and trawl sectors and between indigenous and non-indigenous harvesting, which can require bilateral agreements to be harmonized. The economic implications of the alternative allocation options have begun to be examined recently to assist in resolving these complex issues.

5.4.5 Managing conflicting objectives

Many resource industries are managed within constraints intended to meet social objectives even though these constraints can reduce efficiency and result in foregone economic yield. The intent is often to promote aspects of regional development, including employment and community networks. Examples include mining industries that promote regional work forces rather than ‘fly-in-fly-out’ labour, despite increased costs (Cheshire, 2010) or spreading of water allocations between irrigation regions to share benefits even if this outcome is less efficient than concentration of irrigation schemes (Mainuddin *et al.*, 2007).

Lobster fishery management policy usually includes reference to social outcomes in addition to economic and environmental. For example, the US Magnuson–Stevens Act includes a National Standard that management measures shall consider efficiency but not have economic allocation as its sole purpose. Although the desire for social outcomes from lobster fisheries is widespread at the governance level, there have been few formal attempts to place formal social constraints around management of lobster fisheries. In one example, the Tasmanian *J. edwardsii* fishery management plan included a LRP of 220 vessels (from an initial 340 vessels) and ownership limits of 200 catch shares (from a

total of 10,507) at the commencement of ITQ management in 1998. This was intended to prevent contraction of the fleet away from regional areas (Frusher *et al.*, 2003) but subsequent contraction of the fleet through trading of catch shares caused this limit to be breached in 2007. At this time it would have been possible to restore the size of the fleet through regulations that reduced economic efficiency (such as longer closed seasons or a reduced maximum trap holding per vessel) but ultimately this social LRP was simply discarded (Gardner *et al.*, 2011).

Lobster fisheries sometimes involve constraints on individual ownership to prevent a concentration of ownership. This can assist in preventing asymmetry of market power, but also contributes to the perceived social benefit of having ownership spread across many individuals. This social benefit includes preserving the small-scale nature of the fishery and helping sustain coastal fishing communities. In the Florida *P. argus* fishery, these management goals have been extended by granting exceptions to transfer penalties and fees to family members. While such regulations around ownership are well intended, they can be difficult to enforce. In addition, limiting concentration is challenging if there are strong familial relationships within a community.

A criticism of targeting maximum economic yield with ITQs is that the rents generated from these community assets can readily flow out of the region, for example in cases where owners of catch shares live overseas. This situation has occurred in *J. edwardsii* fisheries where interstate pension funds have purchased ITQ catch shares and has resulted in active fishers boycotting lease markets. Macinko & Bromley (2002) argue for greater recognition of the economic flow-on effects of fishing industries and this is captured in the South Australian lobster fishery economic assessments (Econ-Search, 2010a, b) where state and regional economic impact is estimated through input–output analysis. The fate of economic rents from fisheries is important in this discussion – community benefit can occur where rents are fed back into regional investment or are captured and used effectively by Government, but benefit is less apparent when rents

flow out of the community to remote owners of the catch shares.

5.5 Developing issues in lobster fishery economics

Despite the significant amount of research that has been conducted on lobster fisheries, there remain a few topics with economic implications that are likely to be investigated in the future. These topics include the need to further explore issues about the design of rights based management systems, to consider fisheries within a broader ecosystem context, the implications of marine protected areas (MPAs), and the need to consider the potential effect of climate change. Each of these is discussed briefly below.

5.5.1 Rights-based management systems

Issues in rights-based management that are not fully resolved include:

- 1 how the rights are conferred and upheld,
- 2 who has access to own the lobster resource rights,
- 3 implications of formal versus informal markets for rights as they relate to the characteristics of the participants,
- 4 which component of the population structure (if any, minimum and/or maximum size restrictions) or portion of the fishery stock TAC may be used,
- 5 how is it to be caught (fishing methods and gears used), and
- 6 when is fishing authorized to take place.

Each of these aspects require further research in lobster fishery economics because the most common approach to rights-based fishing in ITQs fails to optimize the value of harvests because of these factors. For example, Holland (2011) modelled ITQ management of the Maine lobster fishery and concluded that the loss through competition for catch within season would account for around 30% of the potential economic yield (through congestion of gear and stock externality).

One important aspect of the rights-based management systems mentioned above is the need to specify the traits of the property rights granted or assigned by the lobster fisheries management authority. Namely the

- 1 exclusivity of the rights conferred;
- 2 durability (duration) of the rights conferred;
- 3 security or quality of the title conferred by the rights;
- 4 transferability of the rights;
- 5 divisibility of the rights assigned; and
- 6 flexibility associated with the use of the rights.

Each of these aspects of the access right of fishers affects the outcomes of management. One especially critical and topical aspect in lobster fisheries around the world is the exclusivity of rights, which affects the willingness of stakeholders to conserve stocks for later gains. The exclusivity of rights is reduced in cases where harvests are transferred to other sectors, for example between recreational and commercial or between fishing and MPAs.

Some additional questions to be answered in the future include: How can the property rights systems used in lobster fisheries improve the incentives for stewardship, conservation and sustained profitability? What sorts of distributional implications are there in each of the rights-based lobster fisheries reported in this chapter? What sorts of operational requirements do the different types of property rights documented here demand in terms of research, enforcement, administration and actual lobster fishing operation, and who is responsible for paying for these activities?

5.5.2 Multiple species and ecosystem interactions

The efficient use of any stock is complicated when there are significant interactions with other species, such as when bycatch from lobster fishing contributes to the value of the fishing operation (Brock *et al.*, 2007) or where fishers use capital across multiple fisheries, such as lobster, scallop and scallop (Moreno-Baez *et al.*, 2012). Bioeconomic models are ideally suited to identify the effects on fisheries performance from shared inputs (such as

gear and vessels) and outputs (such as where bycatch is dependent on targeting of lobster). In addition to the aim of an efficient commercial harvest, bioeconomic approaches can also evaluate other values, including ecological services and recreation (Eggert, 1998).

The potential ecosystem impacts associated with fisheries include the consideration of predator and prey species (e.g. Kar & Chakraborty, 2010). The majority of bioeconomic research to date on predator–prey species has involved cases where both species are targets of commercial operations. For example, Ryan *et al.* (2010) use a bioeconomic model of the *H. americanus* and herring fisheries in the Gulf of Maine where herring was the primary bait for lobster traps and herring supply can limit lobster harvest. These fisheries are linked to the extent that economic or environmental changes in one can affect outcomes in the other; finding an efficient management approach for these linked fisheries requires an integrated bioeconomic model. There are also good examples of research using bioeconomic models to explore the ecological interactions associated with managing fisheries (e.g. Brown *et al.*, 2005) that could be applied to lobster fisheries.

Broader ecosystem interactions of lobster fisheries can be explored using models such as Atlantis and Ecosim. This approach was taken with *Panulirus polyphagus* and other *Panulirus* species trawled off the south-east Indian coast to provide insight into the interactions of species within the habitat (Antony *et al.*, 2010). Although these models were developed for examining ecosystem interactions, recent developments include economic components. For example, Fulton (2011) examined the climate change effects on the south eastern Australian marine ecosystem which included economic components of the *J. edwardsii* fishery.

5.5.3 Marine protected areas

MPAs are utilized in coastal management for a range of objectives including enhanced recreational diving opportunities and as research sites for monitoring unfished populations. These non-extractive uses have economic value so the allocation of the

resource between non-extractive and extractive uses is conceptually similar to the allocation issues between recreational and commercial fisheries.

In terms of fishery impacts from MPAs, Hilborn *et al.* (2006) looked at the effect of MPAs on fishery harvests when they were *combined* with existing management. In the general case, displaced catch from MPAs results in lower catch (lower revenue) and lower catch rates (higher costs), which implies a loss of economic yield. This general outcome does not occur in cases where the lobster stock is severely overfished because the displaced catch is not taken elsewhere, as seen in field studies of *P. elephas* (Hilborn *et al.*, 2006; Goni *et al.*, 2010). Modelling of the effect of MPAs on quota-regulated *J. edwardsii* fisheries is consistent with the general model and shows that displaced catch from MPAs reduces overall biomass and egg production unless there is a proportional reduction in the allowable catch (Buxton *et al.*, 2004; Hobday *et al.*, 2005). Economic loss from MPAs can also occur even when catch (revenue) is constant, as seen in the need for greater travel distance to fishing grounds remaining open for fishing *P. argus* in Nicaragua (Daw, 2008). Economic loss in lobster fisheries from MPAs, either through increase in cost of fishing or loss of revenue through reduction in quotas, has implications for rights-based management. This is because the reduced economic yield weakens the exclusivity and security traits considered important by FAO for these systems (2000).

Lobster fisheries are typically spatially heterogeneous in terms of biology and fleet and in these situations the placement of MPAs can significantly affect stock outcomes (Anderson, 2002a). Crowder *et al.* (2000) analysed the general case and concluded that locating MPAs without an understanding of spatial processes such as source–sink dynamics carries a significant risk of damaging rather than enhancing fisheries. This conclusion was also drawn from analysis of the effect of MPAs on *P. argus* recruitment in the Bahamas (Stockhausen *et al.*, 2000) and in a *J. edwardsii* fishery with spatially heterogeneous growth (Haddon *et al.*, 2003). Seijo & Caddy (2008) used spatial dynamic simulations that included distance-related factors and bioeconomic considerations to investigate how

proximity of a reproductive source to the fleet's port affects population viability and economic performance in conjunction with area closures. This approach could be considered in future bioeconomic modelling and analysis of alternative area closure strategies for managing lobster metapopulations with known source–sink dynamics.

In recent years, numerous theoretical studies have attempted to determine general economic outcomes of MPAs. This is a complex literature with both negative and positive economic outcomes from MPAs depending on biological, economic and management parameters (Ami *et al.*, 2005). MPAs that allow a restricted set of operations, for example excluding trawl, often increase the economic yield of remaining fisheries (Beattie *et al.*, 2002). In cases where the catch is unconstrained and exploitation rates high, the MPA can reduce total harvest so that exploitation rate is reduced. In this case the MPA can deliver economic benefit depending on the transfer rates between open and closed areas (Sumaila, 1998; Anderson, 2002b; Kar & Matsuda, 2008). Hannesson (1998, 2002) discussed the general economic effect of marine reserves as a spatial management strategy and was unable to demonstrate an economic benefit. However this conclusion may not hold where management costs are substantial and these are reduced as a consequence of MPAs (Armstrong & Reithe, 2001).

5.5.4 Climate change

Lobster fisheries usually require adaptive harvesting and management due to inter-annual variability in productivity. This approach will be increasingly important in managing climate change effects on lobster stocks which include changes in the distribution and productivity of fisheries, such as the recent decline in recruitment of *P. cygnus* and *J. edwardsii* (Fig. 5.4; Pecl *et al.*, 2009; Caputi *et al.*, 2010). Climate change can effect production of lobster fisheries in many ways, such as changes in reproduction, recruitment, growth and productivity of ecosystems (Anderson & Seijo, 2010). Effects through ecosystem linkages is naturally complex, for example the climate change-linked increase in *J. lalandii* abundance off the South African west coast fishery is leading to reduction of abalone har-

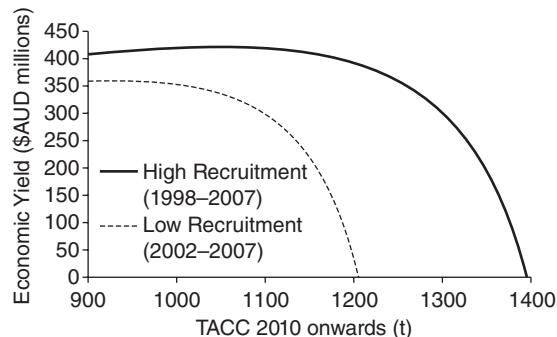


Fig. 5.4 Economic yield of the *Jasus edwardsii* fishery (net present value; millions of dollars) in Tasmania, Australia as a function of the total allowable commercial catch (TACC) from 2010 onwards. Results are shown for two different observed recruitment time series. Climate change is predicted to lower average recruitment (Pecl *et al.*, 2009), represented here by the 2002–7 5-year series which had lower average recruitment than the longer 10-year data series from 1998 to 2007. Lower recruitment reduces overall economic yield and also shifts the peak of the curve to the left, showing that maximum economic yield occurs at a lower TAC (Source: Gardner *et al.*, 2011).

vests through interaction with urchins (Plaganyi *et al.*, 2011). Climate change effects are difficult to predict even on the harvests of single species because biological and ecological processes can counteract, such as increase in growth, decline in recruitment and increase in mortality projected for the *Panulirus penicillatus* fishery off the eastern coast of Taiwan (Chang *et al.*, 2011). An analysis of the *J. edwardsii* fishery off eastern Tasmania, Australia, indicated both increase and decrease in economic yield was possible depending on the time scale investigated (Pecl *et al.*, 2009). Likewise, both increase and decrease in employment, economic yield and flow-on income effects were projected for the Australian Torres Strait *P. ornatus* fishery (Plaganyi *et al.*, 2011).

The uncertainty of climate change will impose new challenges on bioeconomic modelling, which is usually based on historical information. It has also been shown to reduce the ability of fishers to make informed decisions in a *J. edwardsii* fishery that incorporates co-management (Nursey-Bray

et al., 2012). Data to determine effects of previous climate changes in the best of cases cover some decades and would not be an appropriate guide for future expectations. To estimate such risks, we can use quantitative methods like Monte Carlo analysis to calculate the probabilities of exceeding LRP_s with alternative management strategies (Seijo & Caddy, 2000). They are useful to estimate the probabilities of exceeding economic LRP_s of performance indicators as a result of economic and/or environmental uncertainties arising over time. An additional option for acknowledging the associated uncertainties in the decision-making process of managing lobster fisheries is the application of decision theory for systematic choice under uncertainty considering different risk attitude criteria, with and without mathematical probabilities.

5.6 Conclusions

Lobster stocks are a valuable resource to many fishing communities globally. The historical focus on management of these resources has been to ensure biological sustainability. This objective has generally been successful and now the greater challenge of ensuring fishery sustainability and optimizing fishing harvests remains. Fisheries economics is increasingly being used in lobster fisheries both to assist with the year to year management decision of setting catch limits, and also the creation of management structures that promote efficient harvesting of the resource. This process of utilizing economics in lobster fisheries is an important development because most fisheries legislation lists the generation of economic benefit as an objective, but the process is rarely fully developed in lobster fisheries.

Very few lobster fisheries record and report economic information as part of their routine assessment process, which contrasts with the considerable detail provided on stock levels in most fisheries. This requires attention because it represents a failure to deliver information on the objective of most fisheries legislation to manage for economic benefit. Information that provides a guide to the economic performance of fisheries is readily avail-

able in fisheries with tradeable access or catch shares and easier to access relative to stock data. This includes catch share values, total market capitalization of catch shares (number of units multiplied by the market price of a single unit), lease price and economic rent (lease price multiplied by the tonnage of the total harvest is a proxy for this). Reporting, analysing and discussing economic information on fisheries that responds to profit (such as catch share value) will help change the way that lobster fisheries are viewed, placing greater emphasis on economic yield rather than tonnage of catch.

Progress has been made in developing bioeconomic models for several lobster fisheries but only a small subset of these are used within the formal management system to target defined outcomes for the fishery. In almost all cases where bioeconomic models have been constructed for lobster fisheries, a large performance gap has been identified between current management and optimal performance for the fishery. The lessons here are that investment in bioeconomic modelling of lobster fisheries is worthwhile and that fisheries are rarely managed efficiently in the absence of economic analysis. As in the corporate world, good decisions require economic information and analysis.

Management systems for several lobster fisheries worldwide are based on economic theory and there have been substantial changes, with the most obvious being the adoption of incentive- or rights-based management systems (ITQ systems in particular). This has increased economic yield in many lobster fisheries through transfer of catch to more efficient operators and through targeting MEY in TAC setting. Despite these gains, ITQ systems and lobster management systems in general have many unresolved economic problems. Competition between operators for stock remains and affects harvesting patterns within seasons that reduce economic yield. Also, the stewardship that theoretically should result from ownership of a catch-share asset is not always apparent, especially when short-term leasing is allowed and the results of bioeconomic models are not available to guide catch setting. As a result, extensive input controls are retained in lobster fisheries although they are often inefficient. These

range from well-recognized inefficient controls like trap limits to size limits; substantial gains in economic yield are available if input controls are relaxed in favour of constraints on total catch.

Economic approaches can improve decision making and so are especially useful in confronting the challenges of modern lobster fishery management. It appears likely that there will be greater use of economics in allocating catch to different gears, different sectors and between jurisdictions. Many developing issues in fisheries are highly complex and require approaches such as bioeconomic (and ecosystem) modelling to predict the likely outcomes. This includes analysing the establishment of MPAs which can result in counterintuitive outcomes of reduced economic yield and ecosystem function across the wider fishery. Likewise, understanding the impact of climate change on lobster fishing communities requires an understanding of economic linkages.

Technology will undoubtedly change the way in which markets operate in lobster fisheries in the future. Market trading systems remain very simple in most lobster fisheries so there is scope for better electronic systems to support trades between fishers and processors, and also in the sale and lease markets for ITQ or ITE units. Food-producing firms in agriculture increasingly use financial systems to track profitability across the supply chain on a daily basis to promote adaption and incremental improvements in their performance. This would presumably have great opportunity in lobster fisheries, where daily changes in catch rate and price make it difficult for fishers to make optimal decisions through the fishing season. Greater use of electronic trading and financial systems not only helps individual lobster fishing firms but also fisheries managers because it would enable the monitoring of useful economic indicators of fishery health at low cost.

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Chapter 6

Lobster Ecolabelling

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Abstract

Both small- and industrial-scale lobster fisheries were among the first wild-catch fisheries to have been certified and ecolabelled. This chapter reviews the basic principles of ecolabelling as it applies to lobster fisheries and aquaculture, and describes the global trends in the certification of farmed and wild-catch spiny and clawed lobsters. We describe the four extant lobster fisheries certified by the Marine Stewardship Council (MSC), and discuss issues raised by the MSC assessment process. We discuss the motivations of the different actors with an interest in lobster ecolabelling, and provide an example set of criteria to guide a benchmarking assessment (relative comparison) of the performance of a selected set of aquaculture ecolabelling systems. Our analysis revealed that among the systems we considered there are at least five major weaknesses that need corrective attention to provide for more robust assessment and ecolabelling systems for lobsters – a lack of consistency, limited transparency, lack of explicit standards, imprecise technical specifications and limited capacity for verification. We found that the costs and benefits from ecolabelling are strongly differentiated across the scales, and particularly with respect to the environmental and social benefits derived from the certification assessment process and outcomes. The lack of global consistency and accuracy across certification schemes, and the dynamics of the certification marketplace, have important but different consequences across the scales, leading to different and often unrealistic expectations from both fishers/producers and consumers. Without correction, this will lead to eventual decay in the value of ecolabelling systems for all seafoods.

Key Words: lobsters; *Panulirus cygnus*; *Homarus americanus*; *Homarus gammarus*; *Panulirus interruptus*; marketing; certification; benchmarking; costs and benefits

6.1 Introduction

The global catch of spiny (Palinuridae) and clawed (Nephropidae) lobsters [as reported by FAO: FishstatJ. (2011)] has steadily increased over the past

10 years, reaching about 250,000 t/year by 2009 (Fig. 6.1). This production is dominated by just three species (*Homarus americanus*, *Nephrops norvegicus*, *Panulirus argus*) which jointly comprise more than 80% by weight of the globally

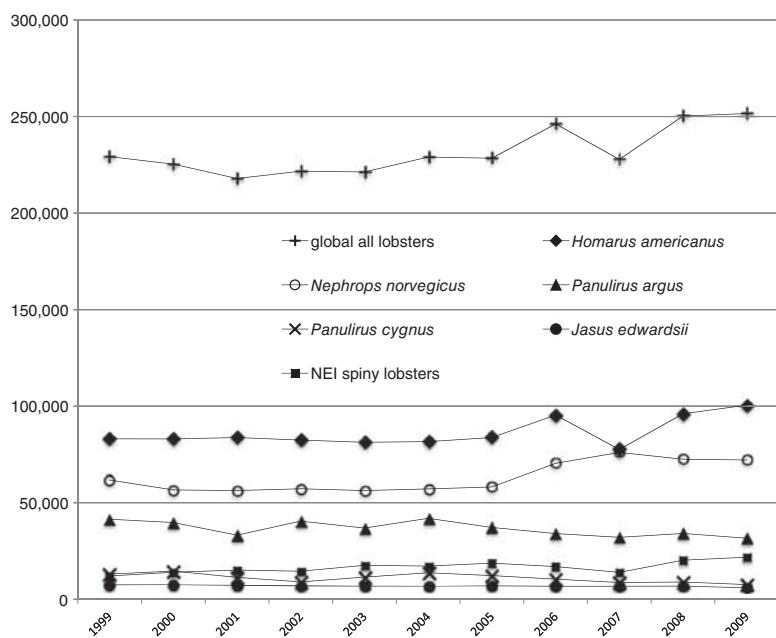


Fig. 6.1 FAO-reported annual global catch (tonnes) of the main species of spiny and clawed (Nephropidae, Palinuridae) lobsters from 1999 to 2009 (FishstatJ, 2011).

Table 6.1 FAO-reported catch (tonnes) and the reporting country of ‘not elsewhere included’ (NEI) spiny lobsters, 1999 to 2009 (FishstatJ, 2011).

	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
Indonesia	3244	3596	4490	4758	5348	5439	6648	5254	4705	9896	11,500
Nigeria	1245	1939	1699	193	1904	1943	2456	2881	1610	2265	3147
Mexico	1328	2052	1727	1923	2044	1757	1746	1823	1601	2056	1816
Malaysia	1079	1065	1508	2039	2087	1566	1812	1010	885	1088	725
Pakistan	1077	807	756	802	749	716	576	601	591	603	511
Somalia	520	410	530	480	500	500	400	500	500	500	500
Australia	520	359	274	330	1211	1471	1061	768	675	655	444
Madagascar	338	329	359	400	436	450	500	550	380	450	432
Zanzibar	306	68	30	64	81	65	218	463	395	393	
USA	287	361	324	306	306	378	351	406	304	338	323
Sierra Leone	51	56	30	43	40	122	75	100	55	234	230
Philippines	249	250	309	328	236	161	145	148	181	177	211
Fiji, Republic of	220	200	224	110	1	277	330	385	219	190	200
Morocco	38	32	39	163	108	171	123	131	292	254	195
Congo, Republic of	9	10	50	90	123	138	130	103	92	101	134
Ghana		39	342	97	28	127	49	3	5	25	128
Panama	485	612	845	687	624	684	1053	837	320	199	113

reported catches over this past decade. In addition to the apparent increase in global catches of these three major reported commercially caught species, there is also a large and increasing catch of spiny lobsters that are not identified to species level in the FAO data, probably comprising a mix of the mostly Palinurid species, from the tropical coun-

tries. Foremost among these are the commercial and subsistence fisheries of Indonesia, Nigeria and Mexico. These nations reported a combined ‘not elsewhere included’ (NEI) catch of 16,463 t in 2009, comprising more than 75% of the total reported NEI catch of spiny lobsters from the global fisheries in that year (Table 6.1).

The true global catch of lobsters may well be considerably more than disclosed in the reported statistics because, as is well known, the subsistence and locally traded catch of lobsters in many tropical and developing countries is only weakly accounted for in catch statistics (Pitcher, 1993). The catch data for both individual and NEI species from those countries in the FAO data (39,093 t in 2009) are therefore likely to be a significant underestimate of the true situation. If the true catch of lobsters is double the FAO-reported catch in the tropical and developing countries, the total catch of lobsters from developing countries was likely (in 2009) to be between 15% and 27% of the global catch depending on the level of under-reporting.

Ecolabelling of seafood products has emerged over the last 10 years as an essential part of the marketing strategies for a number of the commercially marketed lobster products, and this trend will probably continue to grow in importance as consumers become more aware of ocean issues and become more discriminating about the products they purchase. What started as a trickle of interest in wild-caught lobsters ecolabelled by the Marine

Stewardship Council (MSC) (<http://www.msc.org>) programme has turned to a stream of major wholesalers, retailers and providers giving preference to ecolabelled products from various certification schemes. The MSC programme has certified five lobster fisheries, with a further four under assessment. These nine fisheries caught 44,875 t of lobster in 2009 (Table 6.2), representing 18% of the global FAO-reported 2009 catch of all spiny and clawed lobsters and 22% of the catch of the top three species.

Ecolabelling is part of a family of certification procedures that serve to inform purchasers about the extent to which a product complies with guidelines and requirements relating to the way in which that product has been produced. These guidelines and requirements may be expected or imposed, they may be voluntary or mandatory, and they may be superficial or rigorously detailed. Ecolabelling is a form of certification that relates specifically to the ecology and environmental impacts of a product, and is also known as eco-certification. Ecolabelling may be a component in much broader systems of certification that cover a range of consumer

Table 6.2 Certification status of spiny and clawed lobster (Nephropidae, Palinuridae) fisheries within the MSC certification system (from FishstatJ, 2011; www.msc.org).

Species	Fishery	FAO location	2009 reported catch (tonnes)	Certification status (MSC, 2011)
<i>Homarus americanus</i>	Maine lobster (trap)	Area 21, Atlantic North-west	33,000	in assessment
	Eastern Canada offshore (trap)	Area 21, Atlantic North-west	692	certified
<i>Homarus gammarus</i>	North-east England lobster (pot)	Area 27, Atlantic Northeast	518	in assessment
	Normandy and Jersey (trap/pot)	Area 27, Atlantic North-east	290	certified
<i>Panulirus cygnus</i>	SSMO Shetland inshore brown and velvet crab, lobster and scallop (creel/pot)	Area 27, Atlantic North-east	21	in assessment
	Western Australia rock lobster (pot)	Area 57, Indian Ocean Eastern	7634	certified
<i>Panulirus interruptus</i>	Baja California red rock lobster (trap)	Area 77, Pacific Eastern Central	1816	certified
<i>Panulirus tristani</i>	Tristan da Cunha rock lobster (trap)	Area 47, Atlantic Southeast	435	certified
<i>Panulirus argus</i>	Sian Ka'an Banco Chinchorro Biosphere Reserves spiny lobster (hand)	Area 31, Atlantic Western Central	469	in assessment

concerns, such as provenance and traceability of products, food hygiene, social issues and fair trade (Liu, 2010). The extent to which ecolabels are effective in providing assurance to the purchasers about ecological and environmental issues is the subject of this chapter. We consider here what is meant by ecolabelling for lobsters, how it is applied, how it relates to the broader procedures of certification, what the attributes are of an ecolabelling programme, what constitutes an effective ecolabel, and we summarize the experience of ecolabelling of lobster products in the context of where ecolabelling as a global concept is headed.

Ecolabelling has been in place for many years for a range of product types, including products in sectors as diverse as building materials, furniture, energy consumption and food [such as the Blue Angel scheme in Europe (Muller, 2002)]. Recently, there has been an increasing trend for ecolabelling to become incorporated in the vertical integration of food production, and absorbed within the 'private' certification schemes, which are ecolabelling schemes that are developed and applied by non-government entities (Washington & Ababouch, 2011). This development is a response by large companies and conglomerates to rationalize sources and supply lines, secure better control over production systems, establish focused procurement strategies, and control the costs and supply of products. In seafood, the development of private certification schemes and ecolabels is growing rapidly as a mechanism for meeting consumer demand for ethical products with a known provenance. A key driver for the rise of private certification and ecolabels is the perception that government regulatory systems are lacking in objectivity and weak in some countries, and that some may fail to provide for the level of environmental sustainability and responsible fisheries management that meets expectations of both local communities and the consumers in developed countries (Gutierrez *et al.*, 2011; Pérez-Ramírez *et al.*, 2012a).

Recognizing the growth of private certification schemes, governments are now moving to explore cooperative arrangements, with private certification systems as a means of securing rapid change and independent verification of sustainability (Washington & Ababouch, 2011). For example,

France, New Zealand and Iceland have all announced in recent years that they will be adopting a national approach to fisheries certification and are providing support for national programmes of certification for their products (Anon, 2011; Iceland Responsible Fisheries, 2011).

6.1.1 What is ecolabelling?

Certification

Ecolabelling is a form of product certification. In the seafood industry, there are many types of certification, but all are designed to provide assurance to buyers (either re-sellers or consumers) that claims that may be made by a producer about their product are verifiable and accurate. Certification assures a purchaser that the products are produced and handled in the manner that is either required under law or in the manner specified by the producer, by the re-seller or by a specific assurance programme promoted by an industry, government or non-government organization.

An ecolabelling certification system can provide assurance to each link on the product supply chain, so the first purchaser of wild-caught or farmed lobsters (such as a seafood processor or wholesaler) can pass on the labelled product and be confident that claims made about the product are correct and verified. Certification can take many forms and may focus on either broad- or fine-scale aspects of seafood products and their production, such as the handling and food hygiene of a product as well as ecological sustainability. However, certification may not always result in an ecolabel applied to individual products. Some purchasers may not require individually labelled product because, for example, they do not operate in markets where retailers require individual labels, or they sell only parts of the lobster. In these cases, a purchaser may only require a certified product to be able to correctly assure customers that the lobster or lobster product has been produced in compliance with specified rules or guidelines that protect the environment. Ultimately, the product type and marketing conditions dictate to each producer which type of certification and ecolabel they should choose, and how robust their declaration of sustainability

must be to convince buyers of the legality and sustainability of the products being marketed.

The principal driver for certification is consumer awareness and demand – the ‘engine room’ for ecolabelling (Ward & Phillips, 2008). This is translated by retailers, wholesalers and providores into their own market niches, where they can create market advantage or maintain parity with other products. While this sometimes involves differential pricing, this is not always a feature of an ecolabelled product or certification system (Mathew, 2011; Pérez-Ramírez *et al.*, 2012a). The demand for ecolabelled products by consumers may, at least in part, be seen as confirmation and more rigorous reassurance that the products they are purchasing are indeed produced sustainably, as consumers may have assumed or have been led to believe in the past. The need for consumer reassurance on this has been created by the many examples that have become public knowledge about poor management practices, including fishing and farming systems that conduct their operations for short-term gain at the expense of long-term productivity and ecological health. A principal benefit of ecolabelled lobsters is therefore likely to be the retention or enhancement of market access as the buying patterns of consumers become more sensitive to ocean issues and the ecological sustainability of seafood production, and this is reflected in procurement policies and purchasing decisions of major retailers, wholesalers and food distribution conglomerates such as Wal-Mart and Aeon (see Leadbitter, 2008). A further key benefit for wild-catch lobster seafood products is that by becoming ecolabelled they can be seen to be verifiably part of an industry-wide commitment to ecological sustainability, and so winning a better market image and increased standing in national and international government and non-government circles as a pro-active industry.

Labels – types and applications

Certification and ecolabelling has become big business. Consumer awareness of many environmental issues has driven the rapid rise of certification in products as diverse as agricultural products, health, tourism, education, forests and now seafood. With

the rise in popularity of certification and ecolabelling in seafood has come a plethora of individual schemes and labels that provide a great diversity of types and quality of verification assurance for seafood consumers. The different schemes also compete with each other for labelling and sign-up of products, offering different levels of certification, targeting different aspects of the environmental issues, and importantly offering different levels of costs and ease of verification.

Some schemes are simple, cheap and can be secured by correspondence with only minimal site evidence or product inspections required, and will provide verification of compliance with simple criteria. Other schemes have technically complex sets of criteria that must be satisfied, and intensive and expensive site and product verification procedures that may take years to achieve. Few schemes provide the full details of their standards and how certifiers make the decisions about whether or not a product meets those standards. Producers wishing to enter into a certification system face daunting variety and complexity in choosing a scheme, particularly for farmed lobsters, where there are many certification systems but few with global recognition or applicability (Ward & Phillips, 2010).

Certification schemes for seafood are beginning to resolve themselves into seven broad functional groups – schemes that focus on wild-catch products, farmed products, business to business, business to consumer, global, regional and local areas. Some schemes have significant functional overlaps, and hence would classify into a number of these groups even though they have one specific focus. The established seafood schemes have been reviewed and their characteristics discussed several times in recent years (Ward & Phillips 2008; Parkes *et al.*, 2010; Washington & Ababouch, 2011). Many schemes claim to adhere to one or more of the international organizations that provide guidelines and principles for carrying out ecolabelling and certification, such as ISEAL, a voluntary alliance of several certification organizations that provide guidance on their common approach to social and environmental standards (<http://www.isealalliance.org>). However, there are few public domain reports and assessments of the quality of the various schemes in relation to the international frameworks,

and no agreed sets of definitions on key terms (such as ‘sustainability’) or agreed procedures for the assessment of the rigour of verification that might be able to underpin such assessments. Some schemes even fail to meet the most basic standards as established by the FAO (FAO, 2009; Parkes *et al.*, 2010; Washington & Ababouch, 2011).

The technical complexity (and cost) of an ecolabelling scheme is not a good guide to the quality, the impact or the relevance of the certification (Ward, 2008a,b). Schemes that have highly technical criteria may not always have relevance to specific markets, and so consumers will not necessarily respond to the availability of a certified or ecolabelled product. Put simply, some marketplaces are not sensitive to an ecolabel because the issues that the product has been verified to comply with are not the issues of concern for the consumers in that market. For example, the first lobster fishery to be certified under the MSC programme was Australia’s western rock lobster fishery (in 2000), but, since its inception, lobsters from this fishery have not been marketed in Australia with the MSC ecolabel and, until recently, there has been very limited consumer awareness of the MSC label in respect of this product. Australian consumers broadly have the view that the government regulations work well to ensure that the lobster fisheries are ecologically sustainable, and so the issues addressed by the MSC criteria are of little relevance in the Australian marketplace for lobsters. A primary driver for the western rock lobster to become MSC certified in 2000 was the increasing sensitivity of the export market sector to issues of ecological sustainability, and, specifically, the potential market benefits that MSC certification could have for this lobster in European markets (Rogers *et al.*, 2003).

Ecolabelling schemes are available worldwide for lobster products, both wild-capture and farmed lobster products. Recent reviews of seafood ecolabelling and certification systems have identified a diversity of certification schemes that could apply to lobsters with a wide variety of objectives, complexities and effectiveness (Ward & Phillips, 2008, 2010; Washington & Ababouch, 2011). Some are of global coverage, such as Friend of the Sea (FOS), Marine Stewardship Council and the Aquaculture Certification Council. Others focus mainly

on local products and are linked to local markets, such as the OceanWise Canada programme in Vancouver, the Australian Conservation Foundation’s Sustainable Seafood programme on the east coast of Australia, the Gulf of Maine Research Institute ecolabel for seafood from the Gulf of Maine, in the New England region of the USA. Local certification schemes appeal mainly to local consumers, and may not provide any traction for a producer in export markets. Meanwhile, global certification schemes, irrespective of the quality of their standard or assessment procedures, are always likely to be more attractive for products exported to markets in other countries or places distant from the source of capture or production. Nonetheless, even though they may be mainly of local relevance, local certification schemes may also apply a high standard and have high quality assessment and verification procedures, and being local or global infers little about the robustness or relevance of the standard being applied. Being a generic and globally applicable certification programme requires a number of trade-offs to ensure that the programme can be available to most fisheries or products, whereas a local programme can be focused on issues of local concern and provide a good match to the interests of local consumers and marketplaces.

The success of the early private certification systems has led to the inevitable unregulated growth of competing certification systems. This competition has been based on four central features:

- 1 price – cheaper for producers to acquire certifications and ecolabels;
- 2 product – alternative and customized formulation of sustainability objectives to suit specific markets and customer demand;
- 3 regional differentiation – customizing of assessments to suit local conditions and consumer interests; and
- 4 buyer preference – specific customized certifications to meet the needs of major buyers.

In order to develop and maintain market niche and advantage, many major businesses are now using their own sustainability terms and specifications for products to be accepted into their stores. Some of these businesses also accept the major schemes (such as MSC) but increasingly the store-

level gateway is being widened as businesses realize that there is a major shortfall in the supply of certified seafood, and that this situation is likely to persist. The softening of the early stringent requirements of some stores for seafood certification by the MSC is a natural response to the interaction of limited product supply with strong consumer popularity in some markets. Many retailers now, for example, implement procurement policies that include a wide range of assurances for consumers about seafood sustainability, and include, but are not restricted to, products certified by the major ecolabels. To ensure that there is 'due diligence' that backs up any specific or inferred assurances for consumers about sustainability, some retailers also use in-house assessments of the basic sustainability parameters (such as catch history), and they may supplement this with business-to-business arrangements with a specialist seafood assessment/certification entity (such as the Sustainable Fisheries Partnership: <http://www.sustainablefish.org>). Business-to-business programmes provide (usually) confidential advice to wholesalers and retailers based on proprietary criteria and decision systems that are not made fully available for public scrutiny. In this sense, the sustainability standard is not revealed in full, and where businesses make claims about their lobster products, customers must therefore rely on the consumer protection laws and the consequent standards of evidence that apply in their jurisdiction to protect their interests.

The two dominant global ecolabelling schemes for wild-caught products, MSC and FOS, appear to have certified about 20% of the global wild catch of lobsters. Certified lobster production data are not available for FOS, but only two small New Zealand fisheries for lobsters appear to be listed as FOS-certified products (FOS, 2011). However, the MSC programme has about 18% of the global lobster catch, including 22% of the top three commercially caught species, within its assessment and certification system (Table 6.2). The MSC would therefore appear to have only limited penetration into the world markets for lobsters, even though it is recognized as the most technically complete certification system and has a long history in assessment of wild-catch lobsters (Ward & Phillips, 2010). Nonetheless, the benefits of even this limited level of

ecolabelling may actually flow beyond the labelled products themselves, influencing consumer's perceptions of other lobster products, and other fisheries that operate and are managed in the same way. In this sense, the drivers and the rewards for certification and ecolabelling can be very broad and diverse, intrinsically linked to existing markets, market opportunities and to non-market benefits (Rogers *et al.*, 2003). These benefits however may not flow to fishers or producers in an equitable manner, and indeed fishers/producers may not be the primary beneficiary from ecolabelling of their products.

In the planning for MSC assessment of the fishery for *H. americanus* in Maine (USA) there has been considerable resistance from producers because of the cost and commitments associated with the MSC assessment. Among other issues, there is a perception that the MSC programme is expensive, may not present the best aspects of the lobster fishery to North America consumers, and once assessed and certified the fishery would be always locked in to keeping the certification along with the additional bureaucracy and costs (Goyert *et al.*, 2010). The MSC consideration of this fishery still remains incomplete, after nearly 4 years in assessment, and is currently scheduled for completion in August 2012. For many of these reasons, other fisheries have announced they will allow their MSC certification to lapse (Urch, 2012), perhaps signalling the beginning of a major shake-out in the business of providing ecolabelling services to seafood producers.

Chain of custody – provenance, substitution

A central aspect of the concept of ecolabelling is maintenance of the chain or product custody for certified/ecolabelled products. This is essential in order to ensure that there is no product substitution – the false inclusion (co-mingling) of non-ecolabelled product with labelled product. Comingling could be attractive to producers to avoid paying the cost of the verification process or to simply profit from an ecolabel that has been applied to a product produced from a related fishery or area. There is evidence for at least one example where the chain of custody for an MSC-certified fish

product has failed. A study of the mitochondrial DNA of fish purchased in retail stores demonstrated that 8% of the MSC-certified Chilean seabass was not the certified species, and 15% of the fish that were the certified species did not come from the certified fishery (Marko *et al.*, 2011). In this case, the MSC ecolabel is rendered as inaccurate and significantly misleading for consumers.

Piggybacking of an uncertified product on a related product that is certified, known also as ‘free-riding’, is also a popular strategy. This involves development of marketing strategies by altering the marketing names of products (when names are unprotected) in order to make them similar to the names of certified similar products from nearby regions or fisheries. Free-riding can also involve aggregation of products into groups of products, such as by regions, to convey the impression to consumers that if one product is certified then the other products in that group are also likely to be sustainable.

Establishing and maintaining a chain of custody is both important to producers for protection of their product integrity and also a key aspect in the marketing identity of their products. Issues of provenance are also of increasing importance in a number of markets for a range of reasons beyond sustainability, such as product handling and food safety. All eco-certification schemes involve an element of chain of custody, and, like the criteria and verification process itself, this can be complex and costly, or simple and cheap (and possibly minimally effective). Irrespective, consumers and buyers alike are increasingly demanding provenance and chain of custody certification as an independent component of procurement. This focus on provenance is driven substantively by concerns over food safety and handling both at the sources and in the supply chain, and for many resellers, ecolabelling is just one further aspect to be included into their customer assurance programmes.

6.1.2 Global context

The rise of private certification systems has prompted the government sector in a number of countries to consider how to deal with this aspect of global trade (Sainsbury, 2010; Washington & Aba-

bouch, 2011). Among other issues, many of the private certifications, including the major ones, are considered by some to be misleading consumers through the vague claims they make for sustainability and their weak processes for ensuring compliance, leading to a significant risk that unsustainable products are being sold to consumers in the guise of ecolabelled products (Food & Water Europe, 2011). At the very least, there is only minimal evidence that the private certification systems are resulting, either directly or indirectly, in significant improvements in ecological aspects of sustainability (Ward, 2008a; Cambridge *et al.*, 2011; Washington & Ababouch, 2011). This raises the question of appropriate return on investment – if the public funds expended on the support, design, development and implementation of these various ecolabelling schemes had been committed instead to direct investment by national governments into improvement programmes for the well-known problems of fisheries systems, then it is possible that considerably greater ecological outcomes would have been achieved over the past decade.

Despite the increasing popularity of ecolabelling, there are concerns that the use of this form of eco-certification disadvantages the fisheries for seafood in developing countries. The main arguments relate to the standards being applied in the ecolabel, the procedures used in order to certify compliance with the requirements of an ecolabel, and the cost of securing and maintaining compliance relative to the benefits available to producers (Mathew, 2011; Molyneaux, 2011; Pérez-Ramírez *et al.*, 2012a). To counter some of this criticism, the MSC programme has adopted risk-based procedures to assess fisheries, and is trialling various forms of alternative cost-effective approaches to assessment (Oloruntuyi, 2010). While some of these have merit, they tend to focus explicitly on stock assessment issues, and deploy various surrogate measures that may not provide appropriate levels of accuracy. Although this can be addressed to some extent using conservative limits and precautionary approaches, they maintain the certification focus on issues of sustainability that are not always relevant to the many small-scale and local community fisheries of developing countries. This is perceived to be a process that is attempting

to force developing countries to adopt both the assessment systems and the standards that apply to large-scale industrial fisheries, to the detriment of traditional fishers and local communities (Ponte, 2008; Molyneaux, 2011).

As a result of these and other similar issues, there continues to be an ongoing debate about the relevance of the current suite of ecolabelling programmes and related voluntary certification approaches for the interests and needs of producers in developing countries, where about half the world's seafood is traded (Mathew, 2009; Oloruntuyi, 2010; Molyneaux, 2011; O'Riordan, 2011).

National systems of regulation of seafood production may be considered as a minimum set of substantive standards set at performance levels which ensure that most production systems within their jurisdiction comply, and preferably all comply. This applies pressure to the few producers that may be employing the worst practices to improve or face national government level punitive actions. While there is a big range of standards being implemented by the various certification systems, at least some of them exceed government standards in a number of countries, and the popularity of these programmes points to the weaknesses in government standards. As a form of regulatory response to this situation, where private certification systems may be seen to be raising the performance bar but doing so with varying levels of effectiveness, there is international pressure to develop a set of global governance processes within which ecolabels and certification systems for both public and private certifications would operate. One important aspect of this is benchmarking – the development of a system that would enable a direct comparison of the different public and private certification systems for ecolabelling seafood (both wild catch and aquaculture) using common typology and metrics for assessing their relevance and effectiveness (Washington & Ababouch, 2011).

The FAO has provided a basic framework for both wild-catch and aquaculture system sustainability, and these guidelines are the most useful starting point for national systems (FAO, 2009, 2011a). However, the lack of established mechanisms for assessing the extent to which the private and national sustainability systems comply with the

FAO guidance has held back the adoption of the various private systems into national governance. To some extent this could be overcome with the establishment of a system for benchmarking of the wild-capture and aquaculture seafood eco-certification systems, allowing the private and national sustainability systems to be placed in the context of global benchmarks for the extant systems. The design and implementation of such a global benchmarking of national and private certification systems is a natural role for FAO, following the current FAO initiatives for wild-caught seafood (FAO, 2011b), and development of these needs to continue in the near future to permit a rationalization of the burgeoning global eco-certification of seafood to be set in the context of global benchmarks.

An international system for benchmarking of seafood eco-certification systems would not be simply an adoption/extension of one of the existing private systems, as this would create a further emergent set of complexities and risks. In any case, this would be inadequate as many of the existing systems are based mainly on process assessment and do not effectively assess outcomes, nor assess sustainability issues in developing countries. However, systems benchmarking is a well-understood practice in many sectors (such as agriculture), and adoption by the global seafood sector within the FAO context, building on the existing approach to conformity assessment (FAO, 2011b), would be a relatively achievable step that would serve to align the current array of diverse ecolabelling systems within a single international framework that combines wild-catch and farmed products and could be agreed by national jurisdictions from both developed and developing countries.

6.2 Ecolabelling objectives

6.2.1 Consumers

Ecolabelling systems respond to the consumer and industry awareness of the issues. From the consumer perspective, the ecolabel should give them confidence that ecological and environmental issues that either do or could affect the lobster

products are kept within acceptable limits. Consumers understand that fishing and farming of lobsters has environmental and ecological impacts, but that these impacts should be kept to a minimum and acceptable level, and meet basic standards for animal handling. It is therefore expected that an ecolabel that is promoted as including all issues of sustainability will indeed cover the areas of concern. This is usually the domain of the ‘early adopters’: consumers who are the most sensitive and the most demanding that standards do comply with their interests. The interests and standards of the early adopters serve to set the framework, and provide the guidance for programmes that are developing to provide consumer assurance about seafood sustainability.

Consumer expectations normally will revolve around the basic elements of the architecture of certification, and they will need to be assured that

- 1 there is a certification standard that is properly constructed and expressed to reflect relevant issues, and that this standard is clearly and simply expressed so that what the ecolabel represents is clear to consumers;
- 2 the standard is applied to all certified products with equity and probity, without partisan exceptions, so that the opportunity to ‘game’ that standard is minimal, and that securing an ecolabel does depend on achieving the standard and is not related to degree of standing, influence or political affiliations of actors in the fishery or management system;
- 3 there are procedures in place to verify compliance of the products with the standard, and that these procedures are comprehensive and balanced, are technically robust, and are fully independent of the fishery and any funding or political influence; and
- 4 the complete certification process is transparent and publicly accessible.

6.2.2 Retailers and wholesalers

Merchants, restaurants, food service organizations, seafood processors and food packaging at all levels in the chain from producer to consumer have a direct interest in ecolabelling, principally from the

commercial perspective. As consumer awareness and demand rises for increased assurance that seafood is produced in a sustainable and ethical manner, wholesalers and retailers need to ensure that they maintain their market share and meet that demand. However, in the process of meeting demand for ecolabelled products, these re-sellers must carefully manage the expectations of their customers to match the supply of product that is available for sale, and keep this in balance with the other factors influencing consumer purchasing decisions. Objectives for the resellers are therefore typically related to aspects such as

- 1 relevance and clarity of message: the image and advantages portrayed by the ecolabel must be a good match to the interests and demand of their consumer profile, to develop and maintain a customer base for ecolabelled products;
- 2 ease of marketing: there must be a simple message that relates to a strong topic of public concern, there must be good technical backing for the existence of the issue and the effectiveness of the ecolabel in leveraging producers to improve fishing practices in respect of the identified issue, and information for consumers must be readily available in credible but non-technical language;
- 3 quality of product: ecolabelled seafood must be at least as good a product (in terms of freshness, presentation, packaging, taste and food hygiene/safety) as any competing but non-ecolabelled products; consumers are unlikely to purchase inferior quality products simply because they are ecolabelled;
- 4 availability of product in unique form: for development and maintenance of a customer base, resellers need ecolabelled product that establishes a market niche, offers a diversity of product lines, and can provide and maintain a good flow of product.

The rise of private certification systems that are unique to individual major retail chains is a natural response to these commercial objectives. Private certification under the control of a re-seller serves to establish a more secure footing for the presentation of ecolabelled products to consumers that follows the usual business models used to market

other commodities, and allows for a more consistent and controlled source of products for resale that have an established history and set of known characteristics that can be marketed in a unique manner.

In response to consumer pressure, more stringent voluntary codes of practice are also being developed by various retailer groups as one further, more manageable mechanism, to implement and demonstrate better seafood sustainability practices. For example, the Sustainable Seafood Coalition is a consortium of major UK retailers that has recently announced an intention to develop and adhere to codes of practice for the sourcing of more sustainable products. The consortium intends to fill what it perceives as legislative gaps through the use of voluntary codes on the use of bycatch species (to minimize waste) and the use of self-declared environmental labels (<http://www.clientearth.org/sustainable-seafood-coalition>).

6.2.3 Fishing and aquaculture industry

The commercial seafood industry has a diverse range of expectations it is seeking to achieve by securing ecolabels for its products. These potentially include

- 1 assist to open up new markets;
- 2 secure existing markets that are projecting that they will preference ecolabelled products in the future;
- 3 seek price advantage for their products;
- 4 internally benchmark across a diversity of operators/producers;
- 5 maintain high standing with national governments; and
- 6 secure funding for research or community development projects that might otherwise not get supported by government or NGO funding sources.

Fishers and producers do not always consider that these benefits will be achieved by ecolabelling, or be achieved at a level that will offset the additional costs and resources need to support the assessments and the ongoing surveillances (Goyert *et al.*, 2010). Even when these benefits are likely to be secured, there is uncertainty about the distribution of these benefits (Goyert *et al.*, 2010).

As ecolabelling of seafood is now entering a phase of rapid growth of alternative and competing systems, many more ecolabelled products from various schemes are entering markets. Faced with the need to secure certification for many products, minimizing the costs of achieving a certification balanced against what benefits the certification will deliver has become a driving force for producers. The availability of systems that offer certification and ecolabels in a cost-effective manner has reinforced the diversity, and while potentially raising issues about the quality and objectives of such schemes, this also makes certification available to a greater range of fisheries and aquaculture producers than would be the case if only the larger and more expensive schemes were in operation.

6.2.4 Non-government organizations

Non-government organizations (NGOs) are the dominant force in the delivery of ecolabelling and certification of seafood. While there are some certification systems that appear to be supported by governments (such as in Japan and in Europe), the major global certifiers have been established as independent NGOs. This includes ecolabelling programmes such as the MSC, which is a registered charity (<http://www.msc.org>) formed after an initial alliance between Unilever and WWF, as well as business-to-business certifiers such as the Sustainable Fisheries Partnership, which arose from an association with the Trust for Environmental Innovation, and is now an independent non-profit entity (<http://www.sustainablefish.org>).

In general, most of the NGO interest in ecolabelling has been funded by various global philanthropic foundations and trusts, many of which are principally interested in human development, food security, environmental quality and the associated environmental concerns. In seafood, these interests are therefore focused around ensuring that fish stocks are maintained or recovered so that they provide for a strong and continuing flow of seafood, and around maintaining the environmental health of the ocean ecosystems. The environmental NGOs (eNGO) engage in ecolabelling and certification activities at a range of levels, depending on their sphere of influence and available capacity. Their

activities related to market-based incentives may include

- 1 participating in assessment and certification activities, making submissions and advocating for specific outcomes and conditions;
- 2 mounting public campaigns against certification of specific products;
- 3 securing funding and providing support for assessments and certification of specific products;
- 4 preparing and publicizing their own assessments in the form of report cards and league tables;
- 5 facilitating coalitions of eNGOs to coordinate opposition or support for the certification of specific products and improve ocean conditions.

Greenpeace operates a report card system that ranks major retailers against a set of criteria that assesses sustainability procurement policies, engagement in seafood sustainability projects, the labelling and traceability of stocked products, and the extent of marketing of species on the Greenpeace red list of products. The details of the criteria or the assessment procedures are not disclosed. Greenpeace uses direct pressure from consumers to force change in retailer product lines. For example, Greenpeace claim their campaign forced a revision of procurement policy and practices in Costco, a major North American retail chain (<http://www.greenpeace.org/usa/en/campaigns/oceans/seafood/>).

Seafood Watch, based at the Monterey Bay Aquarium, operates a widely accepted NGO assessment and report card system for fishery products, and the recommendations developed and publicized by this system are widely used by both re-sellers and by other NGOs in their own programmes (<http://www.montereybayaquarium.org/cr/seafoodwatch.aspx>).

WWF operates programmes that support both industrial-scale and small-scale fisheries for MSC pre-assessment, assessment and certification (<http://wwf.panda.org/>). In this case, WWF engagement leads to both costs and benefits for the producers. The engagement of WWF into the MSC assessment process in a number of fisheries as a benefactor

prevents the full engagement of WWF in the assessment process as an independent environmental stakeholder, hence depriving assessments of an independent NGO input, a key attribute of the MSC process. The WWF funding for MSC assessments also sends strong signals to small-scale fisheries about the expected pathway they should follow in terms of management models that are acceptable, and the types of issues and costs they should expect to encounter if they choose to proceed to either MSC or other forms of ecolabelling for their products.

Perhaps the most significant problem relating to WWF direct support for MSC assessments is that this sends signals to other NGOs and funders about the strength of the relationship between the MSC programme and the WWF. This potentially inhibits an engagement of seafood producers with wider spread of potential funders (including governments and alternative NGO funding sources) because it could be perceived that such support may indirectly provide support for the MSC programme and WWF itself, a form of cross-subsidization that is usually carefully avoided in the NGO sector. Restricting avenues of funding support in such a way principally disadvantages small-scale fisheries in developing countries, and is an unintended consequence of WWF funding for fisheries to engage in the MSC programme. Similar issues have been raised about the involvement of WWF with the Aquaculture Stewardship Council, an initiative for ecolabelling of aquaculture products modelled on the MSC (Standing, 2011).

6.2.5 Governments

The rising popularity and global spread of private certification systems and ecolabels has identified gaps where national government regulatory programmes are either not fully effective or are specifically not addressed because they are outside their mandate. While the extent of this mismatch is yet to be quantitatively established (Washington & Ababouch, 2011), the rapid rise in levels of public acceptability of the many diverse private schemes has prompted governments to consider supplementing their regulatory requirements with experiences drawn from some of the private systems. In

Australia, for example, the national government's fishery sustainability assessment system (implemented within the national Environment Protection and Biodiversity Conservation Act 1999) has been inspired by the structure of the MSC Principles and Criteria, although assessments are conducted within government agencies based on public submissions and some limited expert evidence without the system of third-party verification that is used by the MSC (SOE, 2011). Other governments, who consider that their national regulatory system is strong and does deliver sustainability at the level of the best private systems (such as New Zealand) are beginning to invest heavily in subsidizing selected private certification systems to assess seafood in their entire national jurisdiction. The apparent support for private certifications by governments can also be interpreted as a mechanism of initial assessment to determine the actual extent of compliance of the major seafoods from the relevant jurisdiction. Clearly, the private certification sector provides a lead to market opinion and this has flow-on consequences for national governments, irrespective of the content.

Some governments appear to consider private certifications as more of a threat than an opportunity, serving to mainly demonstrate weaknesses and gaps in the national regulatory systems. As a result of this widespread concern, and to address concern about the potential for misleading information to be provided to consumers from ineffective ecolabelling systems, the FAO is proposing to develop a system of benchmarking for seafood certification programmes – an evaluation methodology to enable an assessment of the relative quality of different certification/ecolabelling schemes (Washington & Ababouch 2011).

6.2.6 Developing countries

Fisheries in developing countries are considered to provide two-thirds of the world's fish production, half of the world's traded seafood and support for the livelihoods of 95% of the world's fishers (Oloruntuyi, 2010). Communities and fish producers in these countries have an altogether different view of ecolabelling and certification from those held by producers and consumers in developed countries,

principally because ecolabelling is a commercial incentive applied to seafoods traded within and between developed countries (Molyneaux, 2011; Pérez-Ramírez *et al.*, 2012a). It is significant that the main evidence for a price increment associated with MSC-ecolabelled seafood has been derived from the market for pollock, the world's most valuable commercial seafood product, and traded almost exclusively in developed countries (Roheim *et al.*, 2011). Nonetheless, the design of this study conducted in UK supermarkets has been disputed, and the extent to which the apparent price premium is generically applicable and transmitted to the producers has also been questioned (Sackton, 2012).

The motivation, objectives and approach to certification in developing countries are different because they relate principally to local issues and because the costs of securing certification are usually substantial and disproportionate to the price achieved by export products from the developing countries. These views reflect a number of different circumstances that prevail in many developing countries, relative to the fishing sector in developed countries, and arising from the closer coupling between fishing for seafood and the social and cultural environment of the fishers themselves. These differences include

- 1 commercial fishing of pelagic or shoreline reef species by artisanal scale fishing gear and vessels for small local markets, or for regional fish processing centres;
- 2 fishing by family-operated local small-scale commercial enterprises for supply of seafood to local community markets, local tourism ventures and for cashless trade within a local community;
- 3 fishing for customary purposes such as to provide food for formal family or village purposes and ceremonies, for exchange with other communities or to provide gifts to visiting dignitaries; and
- 4 endorsement that modern fishing practices comply with long held traditional practices and maintain cultural links with tradition and customs.

The objectives and aspirations for certification of fisheries in developing countries therefore should

include these various links to culture and custom. Further, given the leverage imposed by developed nations on the seafood resources of developing countries (through aid, trade and economic development opportunities), developing country fishers may also be at risk of exploitation, and equity and transparency of benefit distribution can become an issue of concern (Andreve Diaz, 2009; Washington & Ababouch, 2011).

In developing countries, certification systems focused on sustainable seafood may therefore also need to encompass objectives in the social and cultural aspects of fishing, as well as issues like fair trade. The MSC certification of the *P. interruptus* lobster fishery in Mexico is considered to have reaffirmed the important role of the fishing cooperatives in providing for co-management, strong organization of the local fishers and achievement of community-based objectives (Pérez-Ramírez *et al.*, 2012b). In addition to the high cost of assessments and maintaining ongoing certification, none of the major global ecolabelling or certification systems includes these aspects to any extent. It is for these reasons that some developing countries claim that ecolabelling is biased against their interests, forcing a developed nation model of sustainable fishing onto their social and governance systems without regard for consequences (Ponte, 2008; Johnson & Prime, 2009; Molyneaux, 2011). As a direct result, locally based alternative labelling schemes are being developed to better match the needs and capacity of local fishers, such as the labelling scheme of the Seychelles Hook and Line Fishermen Association (Lagarde & Pommeret, 2010).

6.3 Comparative performance assessment

The global spread of apparently competing major certification and ecolabelling systems has proceeded without any specific forms of benchmarking. Although there have been a number of recent evaluations of ecolabelling systems [such as Environmental Law Institute (ELI), 2008] questions remain about the standardization of such assessments, and their capacity to fully interpret the char-

acteristics of the respective systems given their global spread and wide variety of approaches. In this section we present a set of performance criteria specifically derived for aquaculture certification/ecolabelling systems, consistent with the generic guidelines for evaluating ecolabelling performance (Ward, 2008b; ELI, 2008). We use these criteria to present a worked example for performance assessment of aquaculture ecolabels, following from our earlier work on these same criteria (Ward *et al.*, 2011). Here we apply the criteria to evaluate a set of aquaculture ecolabels, but the approach and the principle underpinning the assessment applies equally to performance assessment of wild-catch ecolabel systems.

6.3.1 Criteria

The tension between the concept of sustainability and the existence of well-recognized impacts of seafood production limits the design of ecolabel schemes. In designing ecolabelling schemes, planners need to always achieve a balance between being too aggressive in the direction of constraining all environmental impacts, and the need to secure enough labelled product to enable the scheme to become a business success. Indeed, the rush to certify product and secure the ecolabelling business has been a prominent feature of a number of the dominant seafood schemes, and issues have surfaced related to the relaxation of standards for this purpose (Ward, 2008a).

Irrespective of this issue, a performance assessment of ecological sustainability in seafood production systems must respond to both a breadth of the issues and the stringency of the standards. Ecolabelling systems therefore should be assessed on their comprehensiveness and their stringency in terms of sustainability, on the quality and technical rigor of their verification processes, and on the levels of transparency of their evaluation process.

Consistent with the perspective of ELI (2008), 'eco-certification' is seen by consumers to be the primary focus of ecolabels, and this depends most critically on assessment of the impacts of the full scope of ecological impacts of the production and processing of the seafood products. Other aspects

of consumer concern (such as the human health benefits, and trade distortions that may be invoked by the selective use of ecolabels) may be better assessed and reported through mechanisms other than market-based incentives, or the use of specific labels such as those of FairTrade. While the FAO has clearly identified these additional matters as possibly important issues associated with seafood production, they cannot be considered equivalently with ecological impacts, and may be best dealt with in other labelling, or governance, systems (Washington & Ababouch, 2011). Among many important issues that affect seafood production in an era of increasing globalization of trade in commodities, an important principle to be applied in constructing the criteria is that the production and processing of seafood products should not be conducted in a manner that exports or substantially externalizes the ecological impacts to any other region, ecosystem or seafood product.

The balance and inherent bias of the internal decision structure of an ecolabel scheme is also an important attribute to be assessed. There are many contextual matters that need to be in place for a fully acceptable seafood ecolabelling system (aspects such as strong stakeholder engagement systems), but good performance in such matters should not substitute for weak performance in the core consumer-held issues of ecological impacts. In the MSC wild-catch ecolabelling system for example, this is partly addressed by requiring that a satisfactory level of performance is independently achieved in each of the MSC's three primary principles (a strong level of achievement in one principle cannot substitute for a weak level of performance in either of the other principles).

To properly represent these matters in an unbiased decision structure, the standards embodied in ecolabels should robustly include ecological issues and related impacts, with reference benchmarks set at high levels of ecological protection, and ensure that the ecological performance of seafood products in this respect are not 'diluted' by performance in other issues. In this respect, the structure of the decisions about the ecological impacts and their assessment of performance are considered here to be critical and defining elements of the overall robustness of seafood ecolabelling.

For this reason, in evaluating here the likely robustness of a sample of the extant aquaculture ecolabels and initiatives, we consider that any system that permits averaging or equalization systems that include a mix of critical and non-critical performance indicators (without an appropriate weighting system) will not meet the basic design standard required of a robust aquaculture ecolabelling initiative. Importantly, the 'stringency' of the ecological standards to be applied by an ecolabel should not be traded-off for the broader success/penetration of an ecolabel into the marketplace of such labels (ELI, 2008). To do this would inevitably lead to the propagation of lower standards of ecological impacts, and hinder the application of genuinely protective levels of ecological impacts throughout an industry or region. Nonetheless, initiatives without stringent international 'sustainability' standards may have other desirable aspects, and provided that the objectives and constraints are clear and explicit, and that product claims and inferences from the ecolabel are not misleading, these initiatives may also have important roles in promoting incremental improvement in a specific industries/products.

Creating stringent standards risks creation of an omnibus standard that fits all situations but at a level of specification that is too high to be actually applied in a compliance/verification system (such as that of a third-party certification). This may lead to a situation where there is a high level of subjectivity and flexibility in the standard being applied, which also threatens the credibility of the ecolabel (Ward, 2008a). Overall, and although FAO guidelines are mainly focused on process and not outcomes and hence do not require the setting of any specific level of 'stringency' in any of the performance standards (FAO, 2009), without the use of stringent and universal standards for ecological protection, the robustness of an ecolabel will be questioned, and ultimately will become ineffective in the marketplace. The specification of that standard will usually need to have regional and possibly local derivatives that are coherent with the overarching standard with deviations explicitly applied by reference to local conditions.

This situation is confounded by the different findings of various certification and ecolabelling

systems for the same products. Not only are there different interpretations of sustainability as it applies to specific types of seafood (Washington & Ababouch, 2011), but reviews of this diversity confound the issues by expecting that sustainability has a single ‘correct’ interpretation. Parkes *et al.* (2010) assert that different schemes lack ‘accuracy’ because they arrive at different conclusions about the sustainability of a product, inferring that the lack of up-to-date and comprehensive information, and a lack adequate peer review, have led to differing outcomes. However, it is entirely unsurprising that, in the absence of universal benchmarks within accepted and unbiased decision models, ecolabelling schemes promoted by different organizations will reach different conclusions based on the different decision structures in their assessments, and different weighting used in their assessment processes. It is important to use current and high-quality data and information to assess the sustainability of seafood products. But even using the exact same methodology, the same data and information base, and high quality science support, different stakeholders have reached different outcomes on many occasions, as measured by the number of robust objections to the outcomes of MSC assessments. The lack of ‘accuracy’ (Parkes *et al.*, 2010) is probably more correctly considered to be a lack of consistency across schemes, and this is in large part a natural reflection of diversity of views and objectives held in the broader community (beyond the fishing sector) that is central to the concept of sustainability. Any system designed to evaluate ecolabelling schemes in an unbiased manner must be able to accept the diverse base of stakeholder values and expectations and incorporate such diversity into the evaluation framework operating within effective decision models.

The evaluation of Parkes *et al.* (2010) further confounds the diversity by establishing an *a priori* divide between what they consider ‘certification’ schemes and the ‘recommendation’ schemes. Parkes *et al.* (2010) find that the recommendation schemes lack ‘precision’ in the sense of not having fine-scale resolution of products or issues, are not able to provide for chain of custody over products and make decisions ‘in-house’. With the rapid growth of certification and ecolabelling that is currently

under way, these same issues now affect many certification systems, and, conversely, some of the ‘recommendation’ schemes are more rigorous than a number of ‘certification’ schemes. All schemes of both types erected by Parkes *et al.* (2010) rely heavily on expert judgement – even the MSC scheme, which claims a scientific and numeric basis, is drawn from a crude grading scale applied by expert judgement. It is counter-productive to artificially create a divide among the various valid interpretations and diversity of sustainability, the breadth of which represents the breadth of consumer concerns.

To be consistent with the generic approach to robust ecolabelling, any aquaculture ecolabelling initiative should effectively demonstrate these four core attributes.

- 1 The scope and coverage of the initiative should be clear, explicit and cover all the important aspects of the production and process of the products being endorsed by the label. This should be comprehensive so that a product carrying the label reflects a high level of ecological protection amongst all the relevant issues associated with production and processing of the labelled product.
- 2 There needs to be substantive and transparent governance structure. Certification systems give decision-making powers to a variety of bodies, ranging from boards of directors to dispute resolution panels, the presence of which enhances the rigor of governance provided the operations of the system are transparent and readily available in the public domain.
- 3 The sustainability standard that the product is expected to comply with in order to be awarded an ecolabel should be expressed clearly and resolved effectively into a set of performance criteria against which the product can be measured. The decision structure needs to be clear, and with any explicit and implicit criteria weightings clearly described.
- 4 Consumers must be able to be assured that the ecolabelling programme is governed and implemented in an equitable and fair manner, including verification of compliance, so that there are no major biases internal to the programme that

might favour a specific product or product class, and that no producer stands to be unfairly promoted or penalized.

In the example analysis of aquaculture systems presented here, our aims are to

- 1 construct a set of evaluation criteria that reflect the issues and concerns that broadly relate to the ecological impacts of aquaculture that are likely to be of concern to producers, consumers generally and local communities where products are grown and processed; and
- 2 apply the criteria to a selected set of aquaculture certification initiatives to determine if they appropriately cover the issues and can provide unbiased assessments of the ecological impacts of aquaculture operations and products.

6.3.2 Assessing performance

Establishing a system and the criteria to conduct a comparative evaluation of ecolabelling schemes has proved to be very challenging. Difficulties outlined by Washington & Ababouch (2011) include establishing international agreement on what is meant by ‘sustainability’, and the need for timely reviews and assessments to ensure that comparisons remain relevant and timely. However, while these and many similar matters can be considered as ‘blockages’, they are also among the key requirements of a system for evaluation and comparative assessment of ecolabelling schemes, and a well-designed benchmarking programme should be able to provide a process for effectively resolving and reporting on these aspects of performance assessment.

Here, to reflect the core areas that define a robust aquaculture ecolabel, we have constructed a benchmarking system that uses two sets of criteria for evaluation of ecolabelling schemes:

- 1 Ecological performance: 12 criteria within five classes to evaluate the extent to which aquaculture ecolabelling/endorsement schemes appropriately represent the desirable characteristics of a successful seafood ecolabelling scheme (from Ward, 2008b) (Appendix Table A1); and
- 2 Standard stringency: 10 criteria to enable a consistent relative evaluation of the stringency of

sustainability standards encoded within the schemes (Appendix Table A2).

These two sets of criteria were applied to a sample set of the extant aquaculture ecolabelling initiatives to provide a consistent relative evaluation. We chose the initiatives based on the extent of publicly available data and information in the areas of each criterion, and to reflect a range of their intended scales from global to local. Our intention here was to assess the extent of compliance with our criteria, to reveal any gaps that are common to all or many initiatives. The extent of publicly available information is also an important aspect of an ecolabelling initiative, and so the extent of our evaluation here provides some level of indication about the extent to which an interested consumer could pursue the details of specific ecolabelled products and the robustness that underpins the issuance of the ecolabel for that product.

To encompass the diversity issues (such as those highlighted by the Parkes *et al.* (2010) analysis), we included ‘comprehensiveness’ within our criteria so that an artificial distinction was not created between schemes that are certification/ecolabels and those that make public recommendations. Both types are prominent in marketplaces, and they all represent some aspect of the breadth of consumer concerns, and they all have the potential to influence purchasing decisions. While there are important differences (for example, some certification schemes have high levels of transparency in stakeholder engagement not displayed by some of the recommendation schemes), they all rely heavily on expert judgement, and the best of the recommendation schemes are better than many certification schemes in some of these matters.

Using our criteria for ecological performance and stringency of standard we graded at least one indicator for each criterion (Table 6.3 and Table 6.4). Our evaluation of these selected set of schemes against the aquaculture criteria we established (Appendix) demonstrate that there is a significant gradient of performance across the schemes (Plate 6.1). The scoring revealed a major difference among the schemes on the Independence criterion of the ecological set of criteria. The Independence criterion was established to assess the extent to

Table 6.3 Scheme scores against the criteria for ecological performance (%).

	Ecological criteria (12 performance indicators)					
	meaningful	consistent	independent	transparent	public	Total score
GAA	100	56	33	67	67	67
WWF	100	56	50	67	67	69
EUREPGAP	89	56	100	83	67	78
Naturland	89	56	100	67	33	69
MAC	89	56	100	67	50	72
SFW	100	78	100	83	50	83
median	94	56	100	67	58	71

Table 6.4 Scheme scores against the criteria for standard stringency (%).

	Standard stringency (10 performance indicators)										
	Scope	Outcomes	Compre-hensive	Balance	Clear	Effective	Technical	Achievable	Verifiable	Maintained	Total score
GAA	100	100	67	100	67	67	33	67	33	100	73
WWF	100	100	67	33	33	67	33	100	33	100	67
EUREPGAP	100	100	67	100	33	33	33	67	33	100	67
Naturland	67	100	67	33	33	33	33	67	33	100	57
MAC	67	67	67	33	33	33	33	67	33	67	50
SFW	100	100	67	100	67	67	33	67	67	33	70
median	100	100	67	67	33	50	33	67	33	100	67

which standard owners demonstrate a high level of independence from the certification system or from any financial benefits associated with successful certification outcomes, without which consumers may perceive a scheme as biased. Schemes that cannot be independent of sectorial interests may lack objectivity and will probably have a limited life in consumers' eyes. Both GAA and WWF support schemes that appear to demonstrate limited independence. WWF has recently established the Aquaculture Stewardship Council (ASC) to develop standards and oversee certification, which may help to overcome some of this issue, although there remains a strong set of linkages (<http://www.worldwildlife.org/what/globalmarkets/aquaculture/council-faqs.html#13>). If the Aquaculture Stewardship Council follows the model of the MSC, then WWF will become similarly conflicted. In addition to its role as primary initial sponsor and now overtly supporting the MSC as an effective certification

system for marine capture fisheries, WWF currently acts as client and environmental stakeholder in a number of MSC certification assessments, a situation that is inherently conflicted and in some cases leaves the assessment without any form of genuinely independent environmental stakeholders to engage in the fishery assessment process. In the MSC model of assessment, this potentially leaves the assessment process as primarily informed by evidence provided by the client and the fishery being assessed. By following the MSC model, the ASC may also not be able to always ensure an adequate level of independence between standard owner and certification system.

Common weaknesses in ecological performance at the scheme level included

- 1 Consistency (three indicators): *a certification or endorsement has the same meaning across the range of products and ventures.* The SFW scheme

- appears to be the most consistent scheme we evaluated, providing the most consistent and explicit methodology for assessment of aquaculture products and ventures, and appears to provide for a moderate level of consistency across the various products it endorses. The other schemes are considerably weaker in this respect, and appear to be unable to provide consumers with a consistent message about ecological sustainability and stringency of their standard.
- 2 Transparency** (two indicators): *the identity of the key institutions (such as the standard owner, board members, technical advisors, independent auditors, and financial backers), the governance arrangements, and detailed assessment reports are freely available in the public domain.* The SFW and EUREPGAP schemes performed well on this criterion, but the remaining four schemes appeared to be much weaker in this respect.

Common weaknesses in the standard stringency criteria included:

- 1 Clear:** *the standard is explicit, expressed in simple and clear terms, and precise about achievement and reference benchmarks, to ensure that the standard that the ecolabel is intended to represent is clear and accessible to all parties.* The GAA and SFW schemes scored moderately on this criterion, but the other schemes were weak.
- 2 Technical clarity:** *the expected performance and achievements that are required from a facility/product in respect of the standard is expressed in quantitative technical terms, so that performance can be assessed in an objective manner.* All the schemes we evaluated here scored weakly on this criterion.
- 3 Verifiable, practical:** *the verification of compliance with the standard is carried out by an expert and independent third-party system, with practical systems and benchmarks expressed in practical terms.* The SFW scheme scored best against this criterion, but none of the schemes were strong in this respect.

Across all the schemes we evaluated, a number of specific improvements were needed, which we

expect could be developed using some of these approaches.

- 1 Comprehensiveness:** issues here could be corrected by conduct of a vertical analysis of issues, from global to regional, relative to the certification objectives/claims and effective benchmarks for environment protection.
- 2 Balance:** conduct focus groups across stakeholders to examine overall decision structure, particularly the explicit/implicit weighting of indicators contributing to certification decision.
- 3 Technical:** within each indicator, conduct an analysis of explicit/implicit weighting of benchmarks, and the implications of thresholds, treatment of uncertainty, burden of proof, and default conditions on certification decisions.
- 4 Verifiable:** develop standard operating procedures for monitoring/reporting on each indicator, with a focus on benchmarks and thresholds.

The diversity of performance across the aquaculture schemes we considered here, separate from product/market niche, detracts from the value of ecolabelling systems in general, and will eventually downgrade the utility of ecolabels as a force in the purchasing decisions of consumers. The diversity of labels and the cost and quality of their recommendations and endorsements are already recognized as issues, and are having impacts in the marketplace. In some countries the consumertraction of ecolabels has faded as the marketplace is swamped with competing labels (O’Riordan, 2011), and without clear improvements in governance and consistency, it seems likely that seafood ecolabels as a significant contributor to consumer purchasing decisions for seafood will continue to decline in effectiveness. A number of fisheries certified by the MSC have recently withdrawn from the programme, including the majority of companies from the first large fishery group to be MSC certified – the Alaskan Salmon fisheries. These withdrawals have arisen because of the failure of the MSC ecolabel to meet the marketing expectations and provide for sufficient increase in benefits to justify the substantial cost of MSC assessments and ongoing surveillances (Urch, 2012).

6.4 Ecolabelled lobsters

In this section, we report and discuss the ecolabelling situation of four wild-caught lobster species that have been assessed by the MSC process and awarded ecolabels. These species have been chosen for discussion here because they represent a significant volume of the world's spiny and clawed lobsters that are traded, and there is a history of ecolabelling with assessments that are available in the public domain.

6.4.1 *Panulirus cygnus* (Australia)

Fishery background

The western rock lobster (*Panulirus cygnus*) is endemic to Western Australia, found in temperate to subtropical waters off the west coast ranging from Cape Range (21°46'S, 114°10'E) in the north to Albany (35°05'S, 118°02'E) in the south. It is a large and long-lived lobster, with a maximum weight in excess of 5 kg and a potential lifespan of 20–30 years. The centre of the species range is the waters (to 200 m depths) along the mid-west coast (Geraldton to Perth) where the greatest abundances of the adult lobsters occur. The species is commercially fished in waters across the area stretching from Shark Bay (24°30'S) in the north to Cape Leeuwin (34°24'S) in the south.

The life cycle of *P. cygnus* includes a long (~9–11 months) oceanic larval phase during which natural mortality can be high. Natural mortality rates of larval phases have been estimated at about 80% per annum, reducing to about 50% per annum by age 6 years in the mature adults (Phillips *et al.*, 2003). Adults mate annually between July and December and females carry the spermatophores until eggs are spawned between August and January. Depending upon the female's size and age, 100,000 to 1 million eggs are spawned. Hatching of eggs occurs in summer (mostly December–January) on the outer continental shelf. The larvae disperse up to at least 1500 km offshore in the south-eastern Indian Ocean. The larvae then return to near the continental shelf edge, facilitated by favourable currents, from about July onwards and metamorphose into the final 'puerulus' post-larval stage

which swims onshore and settles in shallow reefs in less than 30 m of water (Kailola *et al.*, 1993; Phillips & Pearce, 1997). The settled pueruli develop into juveniles and live on coastal reefs for 3–6 years before becoming available to the fishery (Phillips *et al.*, 1991).

Female *P. cygnus* are sexually mature at approximately 5–6 years of age, when their carapace length (CL) is about 90–95 mm, but this varies with location and growth rate along the coast. Generally, pueruli settle at approximately 8 mm CL, and 1 year after settlement the juveniles are about 2.5 cm in CL. Three-year-old juvenile lobsters usually have a CL of 3.9–5.5 cm, 4-year-olds are about 5.6–6.8 cm, and 5-year-old and older animals are greater than 6.9 cm in CL.

Panulirus cygnus is omnivorous and nocturnal, with a diet that changes according to moult stage, season, size and habitat. Post-moult lobsters prefer epiphytic coralline algae (e.g. *Corallina* species, *Metagonolithon* species) and intermoult forms prefer molluscs. Adults eat similar but larger food than that of juveniles – epiphytic coralline algae, molluscs, small crustaceans, polychaete worms and sipunculids. Predators include, but are not limited to, various species of fish, sharks and octopus, and the Australian Sea Lion (MacArthur *et al.*, 2007).

Until 2009/10 the fishery was managed by a total allowable effort (TAE) system and associated input controls. The main control mechanism was the number of units (pots) for the fishery, together with a proportional usage rate and the number of days allowed to fish within an approved season, which created the TAE in pot lifts (i.e. number of pots in the fishery multiplied by the usage rate and the number of days in the season). This was known as the individually transferable effort (ITE) management system, and was used as a basis for maintaining catches within total allowable catch limits. The number of pots allowed in the fishery was set at 69,000 in the early 1990s, and since 1993/94 a usage rate of 82% has been maintained. In 2005/06 and 2007/08 further reductions in the usage rate were introduced in two of the three management zones. Significant further reductions in fishing effort were introduced in 2008/09 and 2009/10 to achieve a nominal catch limit that reflected the low puerulus settlement of previous years and conse-

quent reduced abundance of maturing lobsters entering the fishery.

Subsequently, management has moved from the ITE system to an output (quota) management system. The shift to quota allocation was made because it was found to be difficult to control the achievement of total allowable catch in real time and with sufficient accuracy using the complex and cumbersome ITE system to ensure equity between fishing regions and individual fishers. In the 2010/11 fishing season, a total allowable commercial catch (TACC) of 5500 tonnes was set, individual catch limits per pot were introduced, the legal minimum CL was maintained at 7.7 cm, the legal maximum size for females was retained, and a number of new space and time closures were introduced. In addition, for the first time, the available quota was explicitly allocated to the three fishing sectors: commercial 95% and recreational 5% of the TAC, and 1 tonne to customary fishers. A new plan of management for the fishery is currently in development to reflect these major recent changes in the management system.

Since 2006/07, the levels of puerulus recruitment into all three zones of the western rock lobster fishery have been well below long-term averages, even though egg production is considered to have been at or above limit reference points (<http://www.fish.wa.gov.au/Species/Rock-Lobster/Lobster-Management/Pages/Puerulus-Settlement-Index.aspx>). This reduction in recruitment has yet to impact catches and catch rates, but the expectation that it will do so has provoked a major reduction in TACC, and the transition from being an input controlled fishery (managing effort) to output controlled (managing catch). The halving of the allowable catch levels is a response to the ongoing low recruitment levels designed to maintain breeding biomass in the future. These changes, in turn, have led to a major reduction in the number of fishers operating in the fishery. Fishing mortality is high on new lobster recruits entering the fishery. The commercial catch is made up almost entirely of newly recruited lobsters, mainly of ages 4–6 years. The annual fishery exploitation rate on these lobsters has been estimated to range from 0.92 to 2.30 for different regions of the fishery (Wright *et al.*, 2006).

The commercial fishery for western rock lobster is a ‘potting’ fishery. This activity occurs from inshore regions in shallow waters out to the edge of the continental shelf (~200 m depth) with the only allowable method of capture being the use of pots of either a batten design made of wood slats or plastic, or beehive pots made of cane. The pots are fitted with escape gaps to permit most lobsters smaller than legal size to escape from the pots before they are pulled. Baited pots are released (set) from boats either near reefs where the lobsters usually live or in regions (usually with a sandy bottom) thought to be on migration paths. The pots are normally left overnight to attract the nocturnally active lobsters to the baits. A 48-hour soak time (a pot that is left for 48 hours from the time that it is set, to the time that it is pulled), can produce an average 20% increase in the catch rate in deep water (>37 m) compared with pots with a 24-hour soak time.

Bait used in the pots is primarily whole blue mackerel (*Scomber australasicus*) and fish heads from a variety of species, imported from other countries and elsewhere in Australia. Less than 4% of the bait used is derived from local (Western Australia) sources. In the 2009–10 fishing season, 4576 t of bait was used in the pots, for a catch of 5899 t of lobster (DoF, 2011).

Sea Lion Excluder Devices (SLEDs) have been fitted to the pots since 1 December 2012 in some areas of the fishery to prevent young sea lions from entering the pots, becoming trapped and drowning. SLEDs are required to be used in pots set in areas of the fishery where there is a high risk of encountering young sea lions.

Certification issues

The fishery was first assessed and certified by MSC in 2000, and recertified in 2006 and again in 2011. The reassessment in 2011 identified a number of ongoing issues in the fishery that had not been resolved. As a result, the 2011 certification was conditionally awarded subject to several specific requirements for the fishery to complete (SCS, 2011a).

The 2011 assessment found that the fishery has a robust stock assessment model that is used within

an effective management system to effectively constrain the fishery within catch levels that maintain appropriate limit and target reference points. Nonetheless, the details of several aspects of the system have yet to be finalized because of the recent change from the ITE to a quota management system. The MSC assessment considered the stock size to be acceptable, above the target reference point of 25% of the egg production levels that were recorded in the early 1980s, a time in the fishery that was considered to have been in good condition and safely yielding an average catch of 11,400 t per annum. The assessment reported particular concern about the use of estimates of egg production without robust fishery-independent estimates of breeding biomass or established relationships between egg production, puerulus settlement or juvenile abundance. Also of concern in the assessment was the unclear and dynamic nature of the management system, with a number of key aspects of the process remaining to be established and systematically implemented. It seems unclear, beyond the halving of permitted catch levels, how the management system will respond to the effect of the declining levels of puerulus settlement currently being experienced in the fishery (SCS, 2011a).

Environmental impacts of the fishery are limited, with only minor issues of bycatch and limited habitat impacts of the baited pots. The provision of a bait subsidy in the ecosystem (0.8–1.4 times the biomass of harvested lobsters) is identified as an issue that may have much broader, but unknown, ecological consequences. The physical impacts of the use of pots are considered to be minor. Other issues in the fishery relate to

- 1 a lack of comprehensive stakeholder consultation and participation processes;
- 2 limited understanding of the trophic and population impacts of the removal of almost all lobsters from the ecosystem before they have reached one-third of their maximum age;
- 3 the ecological effects of maintaining lobster abundances at less than 25% of their unfished levels of reproductive output and the consequent potentially large ecological impact of depressed biomass of juvenile lobsters compared to the unfished conditions; and

- 4 a limited understanding of the role of large/old lobsters in egg production and in the ecological functioning of the ecosystems.

The very high fishing mortality focused on the new fishery recruits near the age at first maturity limits the extent to which size structure in the catch or the fishery independent surveys can be used to infer changes in the lobster population, and, although plans are being developed, there are currently no significant areas permanently closed to fishing that could provide data on natural mortality rates or other natural history parameters across the age classes in the population. These issues were not evaluated in the 2011 MSC assessment, even though the assessment indicators require the ‘ecological role of the stock’ to be assessed as part of the setting of target reference points for the fishery.

Other environmental issues that remain to be evaluated include the unknown fate of non-retained lobsters (legal sized but egg-carrying females and undersize lobsters of both sexes) when they are released – there are no fate and mortality data on discarded animals that may be consumed by predators (such as sea lions, sharks or large fish) entrained on the fishing vessels. The substantial numbers of day-time release of non-retained animals (with limited cover from predators) estimated at about 10% of the catch, is likely to be a significant risk, and an additional source of undocumented mortality and uncertainty. The documented increased rate of effort/pot in recent years may therefore have increased levels of undocumented mortality on the lobster population even though there may be no increase in retained catch. Equally, the extent of catch high-grading operating under the new quota management arrangements in the fishery remains to be determined, and could be an important additional factor in new recruit mortality.

The MSC 2011 certification of the fishery for the reassessment found that there were three weaknesses that warranted application of a specific condition, requiring development of actions to enable the fishery to maintain its MSC certification. These conditions cover both aspects of the stock management and the environmental impacts of the fishery.

The conditions required for management control of the fishery revolve around having a set of well-

defined decision rules that control harvest in response to observed conditions and models of the stock, including such aspects as levels of puerulus settlement and breeding stock size. In particular, the lack of a systematic process for making decisions about the controls in the fishery, including the setting of total catch limits, has proved to be an ongoing issue.

Three major conditions were set for this fishery by the 2011 MSC assessment (SCS, 2011a):

- 1 establish control rules that are ‘well defined’;
- 2 explain how the information that is currently collected is used to inform/assess the formal control rules; and
- 3 provide evidence that ‘sufficient reliable information on the spatial extent of the fishery has been collected to identify the nature of the impacts of the fishery on different habitat types. In order to do so the client shall provide information on the spatial extent of both the key habitats and the associated fishing effort’ (SCS 2011a).

6.4.2 *Homarus americanus* (Canada)

Fishery background

The offshore lobster (*H. americanus*) fishery of Atlantic Canada is undertaken in deep waters of the Scotian Shelf from 50 nautical miles out to the limit of Canada’s 200 nM Exclusive Economic Zone (EEZ) within a statistical zone known as Lobster Fishing Area (LFA) 41, and principally in waters of 100–320 m depths. The fishery was first certified as complying with the MSC standard in 2010.

These lobsters are generally most abundant, and support the most productive fisheries, in coastal waters, embayments and basins that receive a regular supply of pelagic larvae (Wahle *et al.*, 2004, Incze *et al.*, 2006). Typically, the lobsters settle on cobble/boulder substrates that are their preferred habitat (Wahle & Steneck, 1991, 1992; Wahle & Incze, 1997). This habitat provides shelter for the juvenile lobsters for 3–4 years, after which they move into other habitats either along the coast or into deeper waters for feeding and reproduction. While this is the pattern for coastal lobsters where most studies have been undertaken, little is known

about settlement and benthic ecology of juvenile through to adult stages in offshore waters, where shelter may be less readily available. A more detailed review of the biology and ecology of this species can be found in Chapter 8 of this volume.

Lobsters in the LFA 41 area are most likely to be have been derived from the inshore shallower waters, although tagging studies have documented migration over large distances (hundreds of kilometres) and moving from offshore into shallower coastal waters and the reverse (Pezzack *et al.*, 1992). The source of larvae for the offshore lobsters is unclear, and larval studies indicate a high level of advection and exchange across the broader Nova Scotia and Gulf of Maine region, suggesting that recruitment may be derived from a mixture of local and distant parent stock within a large meta-population (Moody Marine, 2010).

The lobsters typically grow slowly, potentially to a very large maximum size – specimens of 10–20 kg captured many years ago can be found in several North American museums (Moody Marine, 2010) and in Nova Scotia where they do not mature until about 8 years of age or more. They have a 1- or 2-year reproductive cycle, and low individual fecundity. The lobsters in this fishery are estimated to require 8 or more years to reach the LFA 41 legal minimum size of 82.5 mm CL (DFO, 2000). They moult annually up to 120 mm CL, decreasing to once every 3–4 years at 150 mm CL, and once every 8–15 years above 170–180 mm CL (Pezzack & Duggan, 1990). Female lobsters in the south-west Nova Scotia area first reach maturity at 90–120 mm CL, and average fecundity ranges from 5–10,000 eggs at first maturity to 130–150,000 eggs at 200 mm CL.

The present-day fishery certified by the MSC is operated by a single commercial enterprise with two vessels, fishing to a quota for lobster of 720 t annually. The fishery began in July 1971 as an alternative fishery for swordfish longline fishermen who had lost their market because of newly established maximum acceptable levels of mercury in food products. At that time, the lobster fishery initially focused on the known lobster grounds of southern Georges Bank but quickly spread to the eastern and south-western portion of nearby Browns Bank. Catches in the deep-water areas rose to 678 t by 1976 (Moody Marine, 2010).

The fishery is conducted using rectangular wire coated lobster traps set in strings of 120–150 joined by a ground line, with traps set about 25 m apart. Traps are constructed in panels connected by biodegradable clips and all traps are fitted with escape vents for small lobsters. The two currently operating vessels, of 30–45 m in length, set about 30 strings at a time each of about 3 km, with a 4–5-day soak time. The vessels are equipped with salt water holding tanks, and can each carry up to about 20 t of live lobsters.

The fishery is managed by

- 1 harvest restrictions – the TAC has been unchanged at 720 t since 1986;
- 2 voluntary restriction on fishing season for market and quality reasons, and to allow the lobsters to moult and grow;
- 3 a minimum size limit;
- 4 escape panel(s) on all traps;
- 5 prohibition on landing berried and v-notched females;
- 6 mandatory satellite vessel monitoring equipment (VMS) on all vessels;
- 7 on-board observers at discretion of the government management agency;
- 8 100% dockside monitoring to weigh all lobsters landed;
- 9 random at-sea boarding by Fishery Officers;
- 10 aerial surveillance; and
- 11 mandatory completion of an Offshore Lobster Monitoring Document.

The compliance record in the offshore lobster fishery is reported to have been excellent (Moody Marine, 2010). Nonetheless, in the event of breaches, sanctions in the form of heavy fines and forfeiture of catch are provided for in the relevant Canadian legislation, and these regulations seem to have been effective in deterring non-compliance with licence conditions and fishery regulations.

The catch in the fishery comprises a significant proportion of lobsters up to 170–180 mm CL, which are large animals relative to maximum recorded size, and is indicative of a low level of exploitation. In the inshore fishery (LFA 34) large lobsters were caught at the start of the fishery (a century ago), but decreased rapidly as fishing effort increased (Pezzack & Duggan, 1995). The high relative abundance of large lobsters in LFA 41 is particularly important given that the minimum legal minimum size is 82.5 mm CL, well below the size of first maturity.

The level of fishing mortality (F) is low, and the size distribution satisfies the criteria of a healthy lobster population. However, there are no direct estimates of fishing mortality, and no forecast capability, but most key indicators for abundance, fishing pressure, egg production and recruitment are stable or increasing in a desirable direction (Moody Marine, 2010). There appears to have been only slight changes in stock status since the 1980s. It has been concluded that the current TAC of 720 t in place since 1985 has had little or no negative impact on the lobster stock in LFA41 and at present appears to be a sustainable harvest strategy (Moody Marine, 2010).

Bycatch in the fishery appears to be limited, about 50kg per trip in total, although it is spread across a wide range of fish and invertebrate species (Moody Marine, 2010). The ecological impacts of this are unknown. Interactions with whales has been raised by stakeholders as an issue, and whales have been observed entangled in fishing gear, although the source of this gear is not known.

Certification issues

This fishery is exploiting part of a widespread metapopulation of lobsters that has had strong levels of recruitment over the past decades, and is exploited by other lobster fisheries that have not been certified by the MSC [although the Maine Lobster fishery (USA) is currently undergoing MSC assessment]. There is no unified stock assessment across the whole population, and the setting of permissible catch appears to be driven solely by the historic catch levels. Indeed, the TAC could be considered to be a fixed annual biomass rule with no basis in sustainability other than an acceptable and ongoing history of catch. As a result of the lack of a stock assessment system, this fishery relies on empirical indicators for guidance about setting of both future catches and the identification of any specific problems in the stock. The fishery has been criticized (Moody Marine, 2010) for failing to have a well-constructed set of indicators, trigger points

and planned responses in the event that recruitment fails, or there are other potential issues with the stock such as a changing size structure in the catch, irrespective of whether such changes are the direct result of fishing.

Four major conditions were set by the MSC assessors in certifying this fishery (Moody Marine, 2010):

- 1 Discards and bycatch – better monitoring, reporting and analysis of data on both discarded lobsters and non-target species.** In order to be able to take proper account of the extent of discarding (in stock assessments) and of the catch of non-target species (in determining the population-level significance of the type and level of bycatch) the fishery has been required to develop a formal system for monitoring and assessment of the bycatch.
- 2 Indicators, reference values, uncertainty and decision rules – a more formalized stock assessment system.** There is a lack of formalized quantitative reference values that make proper allowance for uncertainty and are used in conjunction with clear decision-making rules. As a result, appropriate limit and precautionary reference points, or proxy measures with similar intent or outcome, were required to be implemented and used to inform fully documented decision-making rules. These were expected to be able to take into account stock biology, exploitation history and major uncertainties in the data and any specific functional relationships.
- 3 Ecosystem Impacts, protected, endangered or threatened species – improved information base required, particularly for mortalities.** While the interaction with important species such as whales was considered to be very limited, the lack of a reliable knowledge based was considered to be a significant weakness, and a more formalized system for recording interactions and mortalities was required, linked to fishing licence approvals and crew training.
- 4 Management system and strategies – improved objectives for resource and environment impacts assessment and management.** The management system for the fishery was required to

develop specific objectives and a performance assessment system for the lobster resource and for the ecosystems where the fishery operates, with special reference to the interaction of the fishery with whales.

6.4.3 *Homarus gammarus* (France, UK)

Fishery background

The Normandy and Jersey wild-catch trap fishery for the European lobster *Homarus gammarus* was certified by MSC in June 2011. This fishery operates in the Granville Bay area and associated territorial waters of Basse Normandie (France) and Jersey (UK). The fishery that has been certified by the MSC is operated by about 50 vessels from Basse Normandie and about 60–75 vessels from Jersey. The numbers of vessels involved in the fishery cannot be determined accurately because many fish only on a part-time basis, but all are small vessels of mostly less than about 12 m overall length. Each vessel requires a licence to fish their specific territorial waters and a separate licence to fish the Granville Bay shared management zone. Co-management of the fishery takes place within the framework of the Granville Bay Treaty (between the UK and France), which allows for shared access to French and Jersey waters in Granville Bay, with shared management of the marine resources (MEP, 2011).

The fishery uses two types of baited traps – inkwell pots, which are a round or square pot made from mesh with an opening at the top, and parlour pots, which are rectangular pot made from mesh with two internal chambers. The pots are deployed in strings of 12–50, typically relying on a heavier pot at each end to keep the string in place. Both types of pot target both lobster and brown crab (*Cancer pagurus*) in a mixed fishery. Basse Normandie vessels may have a maximum of 1000 pots, while Jersey vessels may have up to 1500, although most vessels have fewer than these maximum permitted numbers.

Homarus gammarus is abundant around the coast of Western Europe from Norway to North Africa, although it is most abundant around the coasts of the North Sea, the UK and northern

France. It has been depleted by fishing in many areas throughout its range, but is still found in the areas where there is a lot of suitable habitat such as rocky reefs – as in the Granville Bay area.

The ecology and the trophic relationships of *H. gammarus* are moderately well understood, although data are lacking for the specific area of this fishery. For example, the newly settled juvenile stage has rarely been found in the wild, but it is assumed that it inhabits small crevices and is a generalist feeder like the adult. Adults (particularly males) are antagonistic to each other, suggesting that density-dependent processes might be important, at least in the adult population. The adult lobsters favour habitat with large amounts of physical structure, as found amongst the rocky reefs of Granville Bay. The ecology and biology of this species is discussed in more detail in Chapter 8 of this volume.

The fishery is input-managed by control on number of pots and limited vessel entry. Estimates of fishing effort are different between the French and UK components of the fishery and the dispersed and part-time nature of a lot of the vessels in the fishery mean that the data on effort is both limited and not likely to be accurate. While the number of licensed pots (of both types) is available, there are only limited estimates of latent effort (pots licensed but not used), and metrics of annual pot lifts have only been documented for the Jersey component of the fishery, and since 2007. These data are further complicated by being unable to distinguish between effort targeted at the lobster and effort targeted at other species of crustaceans taken in the same traps. Distinguishing this effort is important because of the different dynamics of the market drivers for the different species, and hence the incentives to target different species in different years. Across the French component of the fishery, for the purposes of management the effort is documented as the gross metric of vessel fishing months. There also appears to be no data on discards of the target species.

The French and UK management systems are somewhat different, although key management rules are agreed as (MEP, 2011):

- 1 fixed number of Granville Bay licences;
- 2 limit on the pots per vessel;

- 3 minimum landing size (87 mm CL);
- 4 escape gaps are required in parlour pots so that they do not retain undersized animals;
- 5 parlour pots are banned in an area in the Granville Bay Treaty zone to reduce effort and avoid ghost fishing;
- 6 all pots must be tagged with boat registration and year—only a limited number of replacement tags are available for lost pots.

In Basse Normandie, the following additional management measures are in place:

- 1 the number of parlour pots each vessel can have is half the total (there are no restrictions on the ratio of inkwell to parlour pots in Jersey);
- 2 five areas ('cantonnements') are closed to lobster and all other forms of professional and recreational fishing apart from line fishing;
- 3 no parlour pots are permitted in Basse Normandie territorial waters;
- 4 pot tags in Basse Normandie are renewable every year instead of every 2 years, with different colours for parlour and inkwell pots. Jersey has recently changed from annual to biennial tagging for logistical reasons.

The catch of lobster from this diverse fishery has been difficult to estimate. The catch from the French component is landed at a wide variety of places and different types of purchasers, and is acknowledged as being difficult to estimate. The declared catch estimates of about 80–100 t annually are probably a significant underestimate although the trends in time may be reliable (MEP, 2011). The catch from the Jersey component of about 140–160 t annually is probably more reliable, since all landings are required to be logged, and there is a compliance system in place. There is a recreational fishery that operates in the same area, but catches are largely unknown, and estimated to be of the order of 2 t annually (MEP, 2011).

No data appear to be available on bycatch, although the area is well known for its high levels of biodiversity, and there are a number of rare and protected species that frequent the area of the fishery, including marine mammals (MEP, 2011), which are the subject of at least some level of

interaction in most other lobster trap fisheries. Key lobster fishing sites are also protected as Ramsar sites, indicating their acknowledged ecological value for birds, and suggesting the need for data on actual and potential interactions with the fishery.

The bait used in the fishery is from wild-capture fisheries, mainly four species of fish sourced as bycatch from the trawling industry and purchased as fishery waste that would otherwise be discarded. While this is an important aspect of efficiency – use of fishery wastes – the MSC assessment for this lobster did not assess the significance of the impact of the fisheries that this waste is sourced from. The further important element of use of bait is the subsidy provided to the local ecosystem foodweb from the input of large quantities of bait, which has become an important issue in other baited-trap lobster fisheries (Saila *et al.*, 2002; Waddington *et al.*, 2008).

Certification issues

The stock is assessed using CPUE data of various forms, and by using the empirical analysis of trends over time to provide evidence that the stock is stable. However, the catch sampling shows that the population is truncated at the minimum legal size, indicating a high fishing mortality imposed at the minimum legal size, and suggesting that the fishery is heavily reliant on new recruits as they enter the fishery. This is further supported by the size distributions of lobsters in closed areas, which show a mode of about 105 mm CL, whereas the fishery catch and fishery independent sampling outside the closed area found almost no lobsters at or above the modal size of lobsters found in the closed areas, which is most likely to be a reasonable estimate of the modal size of lobsters in an unfished population. There is no formal system for stock assessment in this fishery, and the sustainability of the stock and the ongoing fishery is assessed and managed using the empirical indicators derived from trends in catch per unit effort (CPUE), as mentioned above. The MSC assessment for the fishery relied on an assessment of the vulnerability of the species to fishing, as provided for in the risk-based MSC framework.

Four conditions have been applied to the MSC assessment:

- 1 Expand the population structure.
The fishery was identified as being weak on stock assessment criteria, and was assessed using a risk-based framework. Under the more formal MSC approach to certification, this fishery would not have been able to be certified, as it failed to achieve a passing score on the MSC principle for stock assessment. The fishery was considered to need to work to reduce the current high level of exploitation rate and dependence on recruits. As a result, the fishery has been required to develop a credible plan of action within 5 years that will result eventually in an increase in the size/age classes in the population, progressing towards a more normal population structure reflective of that of an unfished population. This has been required to promote resilience and precaution in the fishery, representing a prudent response to the possible impacts of changes in the environment and stock situation that are as yet unpredicted and unknown, specifically in the circumstances where there is no formal stock assessment system.
- 2 Develop reference points.
The current situation is that there are no formal reference points, only a minimal data and information system across the fishery that might support reference point assessments, and no pre-agreed sets of actions that would be implemented by each group of fishery managers in the event that one of the reference points was breached. The fishery was considered to need to better define harvest control rules so that it is agreed that fishing effort will be reduced as a pre-defined reference point is approached. The fishery has therefore now been required to develop both reference points for target and limit conditions of stock in the fishery, and to develop agreed harvest control measures should those reference points be breached.
- 3 Improve data on retained species.
The fishery has been required to collect better data on the catch of one associated species – the velvet swimming crab. This species is taken in the fishery by the same gear, and is retained for sale, but there are some concerns about the lack of data on this species, and the possible effect

of the lobster targeted fishery on the populations of this crab species.

4 Develop a research plan.

The fishery is required to develop a research programme that provides relevant support for the fishery.

6.4.4 *Panulirus interruptus* (Mexico)

Fishery background

The wild-catch trap fishery for this species (known as the California or Red Spiny Lobster) operates in the Pacific Ocean waters of Baja California, Mexico. The Mexican fishery was first certified by the MSC in 2004 and is the first small-scale, community-based fishery certified as complying with the MSC standard. The fishery was successfully recertified to the MSC standard in May 2011 (www.msc.org; SCS, 2011b).

The California Spiny Lobster (*Panulirus interruptus*) is a temperate to subtropical species, distributed from Southern California (USA) south to the Baja California Peninsula tip in Mexico. The most frequently used common name is California spiny lobster, also used by FAO (Holthuis, 1991), but other common names such as the California lobster and red lobster are used locally. In Mexico, the species is known as the Red lobster *Langosta roja* (Vega-Velázquez, 2006). No genetic differences in the population have been detected using mitochondrial DNA analysis of animals along the Pacific coast of Baja California, suggesting that there is a single population in the north Eastern Pacific (García-Rodríguez & Pérez-Enriquez, 2006). The notion that there is a single population is also suggested from the larval distribution (Johnson, 1960; Pringle, 1986) and adult abundances (Vega-Velázquez, 2006), with the main part of the population centrally located on the peninsula.

The species is distributed in rocky areas, and occurs from the low intertidal zone to waters of about 100 m depths. Female lobsters have only one brood each year, and breeding occurs in spring first in the northern parts of the range, followed progressively by the animals in the southern waters (Vega-Velázquez, 1991). Breeding and hatching occurs mainly in shallow (<20 m) depths, after which

animals return to the deeper waters (Ayala *et al.*, 1988).

The phyllosoma spend about 8 months at sea, passing through 11 moults, then transforming into the puerulus followed by the juvenile stage. Juvenile lobsters settle from the water column in shallow reef and sand areas, where they prefer dense cover of the seagrass *Phyllospadix torreyi* (Zosteraceae) (surf grass) in waters down to 4 m depth (Castaneda-Fernandez de Lara *et al.*, 2005a). Here, the juvenile lobsters will usually spend their first 2 years. Adult lobsters are omnivorous, consuming algae, snails, mussels, sea urchins, clams and fish, and while they are commonly found in the rocky habitats they will also search sandy habitats for their food. This lobster is preyed upon by a wide variety of fish, sharks, eels and octopus (Barsky, 2001).

The fishery operates in four main areas where the lobsters normally occur in sufficient abundance and can be readily trapped. The greatest density of the stock is distributed between Cedros Island and Punta Abreojos in Mexico, within a 5-km band along the shore. Most of this area is part of the Vizcaíno Biosphere Reserve, except Cedros Island (SCS, 2011b). Rights to fish the stock were first exclusively allocated to fishermen's cooperatives in 1936–38, by assigning a group of species (lobster, abalone and others) within a specified fishing territory for each organization (Vega-Velázquez *et al.*, 1997). A unique scheme of limited entry originated from this system, and this now allows for control of effort and adherence to basic regulations (Vega-Velázquez *et al.*, 1997, 2000). Currently, there are about 25 cooperatives that have control of the fishing grounds (see Chapter 10 of this volume).

The fishery is managed through limited access rights, regulatory measures to protect reproduction and recruitment such as protection of ovigerous females, and specific mechanisms for coordination and co-management. Regulations in the fishery result from a coordinated effort from all stakeholders to discuss issues and concerns at the state level and reach agreements about rules to be applied. The regulations have remained basically unchanged from 1960 to 1990, but subsequently have undergone a number of modifications. The main regulations include a closed season, a minimum legal size (82.5 mm CL), and a prohibition on the catching of

egg-bearing females. In addition, there are restrictions on fishing gear and concession of fishing rights in specific areas or zones. Since 1993, the latitudinal variations in the reproductive cycle of *P. interruptus* along the Mexican coast have allowed the fishery to be managed through phased closures in the four zones. Catches have increased from 400 t in 1960–61 to about 1000–1500 t during the 1970s and 1980s. The maximum catch of was taken in the 2000–1 season, and since then has broadly stabilized at about 1500 t (Fig. 10.9).

The current biomass ($B = 14,120$ t) in the last five seasons (up to 2009–10) has been estimated to be 50% larger than BMSY (9402 t); fishing mortality (F) has been estimated at 0.10, half the FMSY (0.20); and effort (f) has been estimated as 2,218,377 trap-hauls, about 38% of the FMSY (5,785,700 trap-hauls) (Vega-Velázquez *et al.*, 2010). The fishery appears therefore to be in good compliance with its internal rules, which have adopted the precautionary approach of ensuring that B remains above BMSY (termed the Optimum Level). However, it is somewhat unclear whether this is treated as a limit reference point or a target to be achieved, and the formal set of responses if either of these limits are breached are somewhat unclear. Irrespective, the stock is currently considered to be clearly above BMSY.

The current biomass of *P. interruptus* in the US fishery is estimated to be between 11% and 16% of the 1880's historical baseline for this stock. As a result of this low population level there appears to be an increased level of variability in the modern population, a probable reduced level of resilience and an increased risk of recruitment overfishing (McArdle, 2008). The present-day ecological impacts of this low population biomass and present levels of lobster catch are unknown; however, McArdle (2008) considers that the evidence indicates that since fishing commenced the species has crossed a population threshold and now behaves as an opportunistic species in the face of frequent intense disturbances (fishing) rather than a periodic species responding to occasional large-scale (environmental) disturbances. It is unclear of this also affects the stock in Mexican waters.

The high value of the Mexican fishery, and the need to maintain strict controls over effort to meet

the stock management objectives discussed above, have led to the development of an inspection and surveillance system inside the fishing area to eliminate illegal fishing. The system is recognized as a Community Surveillance Committee, and has legal standing. The Surveillance Committee also assists with the enforcement and compliance with the legal minimal size rules, working with the cooperatives during the landing process. Where non-compliance by a fisher is detected, economic sanctions or fishing activity suspensions may be applied including the potential exclusion of membership from the cooperative.

To provide information and advice for stock assessment and discussion purposes, monitoring in the fishery consists of

- 1 monthly catch and effort information;
- 2 monthly sampling programme of the size and sex structure of all catch from one fishing vessel during the season;
- 3 monthly sampling programme for the size and sex structure of a proportion of all commercial catch;
- 4 sampling programme that analyses the reproductive stages of lobster during the closed season; and
- 5 market prices during the fishing season.

Certification issues

The MSC certification of the fishery identified a number of specific deficiencies that needed corrective actions (SCS, 2011b). These corrections were most numerous in the MSC Principle 2, inferring that knowledge about the fishery was weakest in aspects of environmental impacts. The corrective action required for MSC Principle 1 focused on improving the stock assessment process, and including improved estimates of the post-harvest release mortality for the sub-legal lobsters, the catch of which appears to be substantial but not well documented.

The habitat impacts of the traps are likely to be minimal. Bycatch from some parts of the fishery is substantial, constituting 12% of the total catch and at least 40 taxa of crustaceans, molluscs, fish, sharks and rays, and one cormorant species (Shester,

2008). One study of the fishery found that 86% of the total catch of lobsters are lobsters below legal size, and are discarded (Shester, 2008). This pattern of bycatch infers that the fishery is not highly selective relative to other lobster trap fisheries, although probably also reflects the high diversity of habitat and invertebrate biodiversity in the region. A key issue identified was the bycatch of cormorants (8% of the bycatch) in at least one specific area of the fishery (Shester, 2008). The impact of this rate of bycatch (with complete mortality – no cormorants are released alive) on the population of the cormorant is considered to be an important issue for the fishery to address. Also, related to bycatch, the MSC assessment identified the lack of an overall bycatch documentation and analysis system as a priority for the fishery to address.

The other main environmental impact issue identified in this fishery is the use of bait. There are two aspects to the environmental issue of bait in lobster fisheries. First, the use of bait derived from fisheries (or other sources) that may not be harvested in a sustainable manner, hence transferring ecological impacts from the lobster fishery itself to other fisheries, and possibly to local fisheries for less-valued food species that nonetheless may be important for local human consumption. Second, the ecological impacts of provision of a large amount of biological wastes into the ecosystem that may provide an attraction and major energy subsidy for scavengers and other species that might otherwise not be a major feature of the local ecosystem, hence disrupting the natural food webs and trophic relationships of the fished areas. These two aspects may be a significant issue in this fishery as about 2.3–3.5 kg of bait is used per kilogram of landed lobster catch, which is equal to a total use of 4500 to 5000 t of bait in the fishery each season (SCS, 2011b). The bait appears to be mainly oily fish such as sardines, mackerel and bonito that are purchased elsewhere in Mexico, but this is supplemented with substantial numbers of fish sourced from local unregulated fisheries (Shester, 2008).

Bait used in the traps in this fishery is also probably an important food source for the lobsters. Studies on other species of *Panulirus* and on *Homarus* have suggested that up to one-third of lobster production may be derived from the energy

subsidy provided by bait used in a trap/pot fishery (Saila *et al.*, 2002; Waddington *et al.*, 2008).

Product traceability is a central aspect of any certification process, and is often a vexed issue in small-scale community fisheries. In this fishery, the lobsters are landed by fishers from each cooperative at designated processing plants that are limited to specific cooperatives. Control of product acceptance by the cooperatives and the limited range of boats in the fishery provide for a high level of traceability, allowing the certification system to maintain a chain of custody over products that are caught in compliance with the MSC criteria, and limiting the risk of co-mingling of certified product with non-complying lobsters.

Specific requirements imposed on the fishery in the 2011 MSC certification are

- 1 development of an improved stock assessment system, with a peer review;
- 2 assessment of the post-release mortality of the sub-legal sized lobsters, and incorporation into the stock assessment system;
- 3 documentation of the source of bait, and evidence that it is secured from sustainable fisheries;
- 4 development of a system for monitoring and reporting the bycatch species, and assessment of the main species for sustainability.

6.5 Conclusions

Ecolabelling of lobsters now has a significant history (>15 years), beginning with the efforts to design the MSC programme and simultaneously secure an ecolabel for Australia's western rock lobster in the late 1990s. Subsequently a number of other lobster fisheries and ecolabelling programmes have addressed similar issues, principally how to build and maintain sustainability in its various guises, and how to convince fishers, consumers and markets more generally of the veracity of this concept for lobster fisheries.

While the various ecolabelling programmes and fisheries each have unique features, and the respective certification assessments involve a focus on a somewhat different set of sustainability issues,

there are a number of generic themes that can be drawn from this history. Here, we consider these themes in turn, and point to the underlying issues so that future certification and ecolabelling initiatives may be more effective both in building more sustainable wild-catch fisheries for lobsters and provide for more consistency in assessments, and hence build higher levels of consumer acceptability of lobster products in the marketplace.

6.5.1 Management issues

The great diversity of ecolabelling systems that have recently emerged and are being applied worldwide, with varying levels of efficiency and effectiveness, result from the global diversity of the perceptions of sustainability and the consequent requirements of consumers and producers. The diversity of such interests has fuelled the growth of the various types of certification systems, each responding to specific sets of issues. It is evident that sustainability and eco-certification covers a wide variety of issues and interests for consumers and producers, and it is highly unlikely that any single generic sustainability assessment system will prevail and generate significant effective market-based incentives. In the same way that a single system of fishery management cannot be applied worldwide, so a single ecolabelling model also cannot be relevant to all seafood production. As a result, for those ecolabelling systems that choose to be global, it is clear that a much broader engagement with a wider diversity of stakeholders and a more flexible set of standards and processes are required if these systems are to be effective and persist.

While a single fisheries management model, such as that promulgated within the MSC scheme, can be applied to high-value and high-volume fisheries, it is less clear if such an approach can be accepted by the many smaller fisheries, especially those that are not wholly dependent on trade with developed countries. Fisheries management models, such as that underpinning the MSC approach, that seek to optimize economic production as the primary goal have been unable to secure the broad-based support of some NGOs and communities that have additional objectives, such as community

development or recovery of the health of ocean ecosystems. After more than a decade of activity, the limited penetration of the MSC programme into global lobster fisheries demonstrates that the reliance of an ecolabel on a single underpinning decision model drawn from a specific approach to fishery management will continue to be a challenge for bringing the majority of the global production of lobsters into effective forms of eco-certification. Twelve fisheries have, for various reasons, withdrawn from the MSC programme in recent years (www.msc.org). Strong signals of resistance to such expensive and comprehensive private ecolabels are now becoming evident, with major fisheries allowing their MSC certification to lapse, to be replaced with more cost-effective certification systems that are focused on a different set of issues (Urch, 2012).

As the business of ecolabelling of seafood becomes more rationalized, and perhaps more mainstreamed into national government activities, it will be necessary for the private certification criteria and assessment systems to be considerably broadened beyond those represented in today's schemes. This will need to also involve a much broader range of stakeholders than just fishers and seafood producers, and to be based on a different stream of objectives and information metrics that bring into the assessment systems the key aspects now currently largely absent – social and community benefits and direct and indirect ecosystem/ecological impacts of intensive fishing. For broader acceptance and effectiveness, ecolabelling and certification systems of the future will therefore need to admit a broader range of system values (including for example the value of maintaining diversity and resilience in ocean ecosystems; and the value of local fishing activities for social, economic and cultural reasons), various alternative views about objectives and criteria, and different constructs and process models about how ocean ecosystems operate, particularly to maintain higher levels of population-level resilience to non-fishing impacts (such as the effects of changing levels of ocean acidity). It is clear that modern concepts of maximum economic yield from lobster (and other) fisheries do not provide for high levels of resilience to be maintained in ocean ecosystems, and future

ecolabelling systems that recognize the need for ecosystem rebuilding will need to provide for genuine eco-certification rather than simply recognizing and rewarding forms of industry best practice.

Global governance of the burgeoning set of private seafood ecolabelling systems is currently weak. The FAO has a mandate to lead the development and application of appropriate systems that can assist national governments in such matters, such as conformity assessment FAO (2011b), and there is an active discussion about the specific role that FAO could play (Washington & Ababouch 2011). However, in addition to process standards, it is clear that there will need to be different outcome standards applied in different national circumstances. Such standards could be nested within globally agreed constructs for seafood sustainability, and will need to be supported by coherent information systems that will inform consumers of the issues of sustainability in an objective manner. If ecolabelling of seafood (wild-catch and aquaculture) is to persist in a meaningful way, a coherent global system of governance is required, embodying agreed constructs of ocean health and outcome-based metrics/benchmarks appropriate to the circumstances of different regions and local communities. While there are different business enterprises and approaches underpinning the production of wild-catch and farmed seafood, this is not a major issue for consumers, and ecolabelling of products of the future will need to provide for a single nested system that provides unbiased consumer assurance that draws together the relevant sustainability issues from both wild catch and aquaculture.

The need for global standards and systems for ecolabelling is now more urgent than ever, as global trade of seafood products across national boundaries becomes more dominant. Without common standards, and agreed regional variations, for the global oceans, the free market and minimal governance structures currently in place for seafood certification and ecolabelling may well create perverse outcomes. The externalization of the impacts of fishing across national borders is already an issue, and unregulated proliferation of ecolabels that provide marketing support for products of low eco-

logical sustainability may lead to greater threats to ocean ecosystems and fish stocks rather than a reduction in threats. Put simply, in a global business environment that is essentially unregulated and without conformity standards, competition among private ecolabels will breed diversity that importing and exporting countries have little influence over. Consumers are then likely to suffer under ‘the race to the bottom’ as eco-certification systems compete on price and market-share for the certification business, and develop ecolabels that trade-off a high quality certification system and standard of ocean health against cost-effectiveness to secure advantage in the business of certification. In this global environment, a greater number of private ecolabels and certification systems will mean a greater threat to ocean ecosystems and fish resources, not the converse.

6.5.2 Stock issues

The fishable stocks of lobsters where they have been measured are uniformly low to very low – some either approach or fall below the generic 10% B_0 standard for collapsed fisheries (Worm *et al.*, 2009) when fishing would normally be expected to be closed. While seafood production can continue from such low population levels in the short term, the inference of this is that at such low population levels there are very fine margins for error in setting of constraints on fishing effort, no matter whether the fishery is input or output controlled. In the modern-day setting of multiple pressures on lobster populations from a range of non-fishing pressures, including growing effects of changing ocean temperatures and acidity, and greater variability in ocean currents, the level of precaution built into management of lobster stocks needs to be increased. For example, while recruitment collapse may not be able to be avoided when it is driven by environmental factors, better planning and management by increasing the levels of precaution can provide a pathway for more stable fishing yields and less intense stakeholder disruption through episodes of major recruitment failure.

Each lobster fishery has different requirements, but, typically, increasing and maintaining diversity in geographic distribution of the natural lobster

population, increasing age structure in the population towards that of a more natural (unfished) structure, increasing the range of sizes/ages in the catch (above maturity) and adopting explicit risk-spreading practices such as providing for a diverse range of small closed fishing zones to maintain a spatial spread of breeding biomass, egg production and potential recruits, all can contribute to increased levels of precaution in lobster fishery management. These also can contribute substantially to rebuilding of present-day stocks across the range of the fishery, and have other significant benefits such as reducing the overall cost of managing the fishery. Certification and ecolabelling systems that do not recognize and explicitly set benchmarks for such risk-management practices into their assessments of sustainability are not providing the fishing industry, managers or consumers with a strong foundation for judgements about sustainability. Future eco-certification systems will need to redress this important gap.

Certification and ecolabelling systems that rely solely on the use of simple empirical indicators (e.g. evidence of sustained catch histories) are not adequate to provide reasonable assurance that a fishery is sustainable. Modern constructs of sustainability require continued vigilance with provision of early-warning systems that alert managers to conditions in the stock that may lead to ill-advised shifts in biomass levels. Early warning is necessary to provide for sustainable fishing because, among many others, there is major inertia in developing agreed forms of management responses, and taking decisions to reduce or reallocate fishing effort can take years to implement in both large and small fisheries. Without early warning of impending issues, using empirical indicators such as catch history, or mean size of animals in the catch, as the basis for setting harvest strategies is highly risky as a management approach in fisheries of all sizes.

6.5.3 Environmental impacts

Low stock sizes not only have major effects on fishery yields and risks of failure but also have substantial impacts on other species in the ocean ecosystems that prey on lobsters or are preyed upon by lobsters. These ecologically dependent species

are all influenced by low stock sizes, with impacts linked to extent of exclusivity displayed by the dependent species. These trophic linkages relate to both diversity and to abundance in lobster populations, and are related to all life stages, not just those of importance for harvest. So for example, lobsters are typically very abundant in their early planktonic and juvenile life stages, where they are preyed upon by many predators – mainly other small pelagic or benthic species. These life stages typically comprise greater than 70% of the total biomass of a lobster population (Fig. 6.2), and can be substantially affected by low fishable stock sizes. The predators on these life stages (such as other small zooplankton, benthic molluscs, juvenile fish) are likely to be trophically linked to many further larger species as prey, and in this manner, low stock sizes in fished lobster populations can have major potential for impacts in other trophically related species. This trophic-cascade of potential impacts is very poorly understood in lobster fisheries (McArdle, 2008; SCS, 2011b), as in other fisheries, but can be managed through risk-reducing management strategies that are designed specifically to reduce the risk of significant trophic impacts of fishing on dependent species.

The main purpose for reducing these risks to other species is to contribute to increased ecological resilience of the ecosystems, which indirectly assists to maintain lobsters in their natural role in ecosystems, including their natural productivity. Regime shifts are considered to threaten the natural abundances of many species, and maintaining resilience in the ecosystems within which lobsters live is increasingly being accepted as a key management target for lobster fisheries. In other fishing systems, such as in the Antarctic, where maintenance of ecosystem resilience and provision for trophically dependent species is explicitly set at a high priority, minimum target stock sizes for fished species have been set at levels of 75% B_0 , to provide for fishing yields that are likely to impose only minor stresses on ecosystems and dependent species (Constable, 2011). Clearly lobster fisheries do not presently approach this level of stock risk reduction, and certification and ecolabelling systems of the future will need to establish a robust and consistent approach to this problem of how to make informed

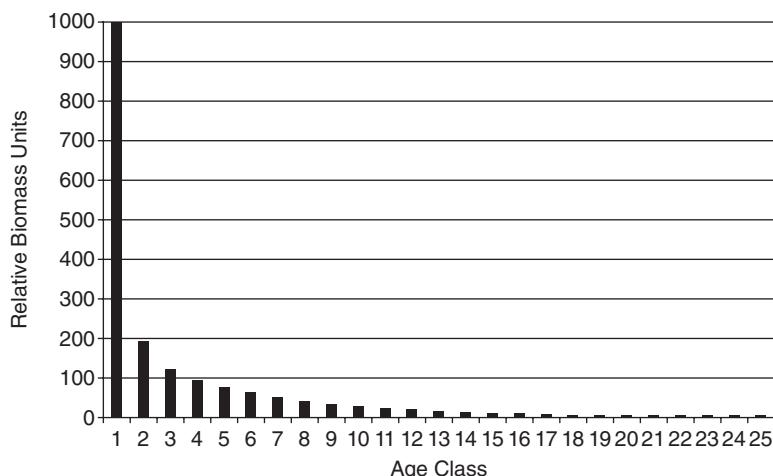


Fig. 6.2 Modelled population structure for Australia's western rock lobster, *Panulirus cygnus*, derived from density dependent natural mortality rates estimated by Phillips *et al.* (2003) for juvenile life stages, and a mid-range estimate of the maximum age for this species. The age class represents the year following settlement from the planktonic phase.

judgements about the level of resilience risk that is currently within, and should be the target, for, lobster fisheries.

The irony of this situation is that while lobster fisheries at very low stock sizes are today considered to be sustainable by many certification/ecolabelling programmes, increasing stock size to reduce trophic risks and increase ecological resilience (as described above) would also permit a greatly reduced risk from other impacts such as recruitment failure. Also, with increasing stock sizes, fishery yields can be increased compared to current yields. This double-payoff (Ward, 2004) can provide greater resilience, reducing both ecological and fishing risks, and in many cases will permit increased yields to be taken with greater long-term security. This can be easily incorporated into management systems as a formal target allocation of biomass for annual stock rebuilding (at even very small percentages), to gradually increase stock sizes until they attain target levels that are more consistent with ecosystems that are ecologically and fishery resilient. An important role for eco-certification systems and ecolabelling of the future will therefore be to establish appropriate metrics that recognize high minimum stock sizes as an important aspect of ensuring resilience in the fished stocks, including acceptable rates of incremental rebuilding increases in stock size.

The cumulative impacts from fishing on the global ocean ecosystems appear to have been grossly underestimated, especially within the context of the risks of accelerating climate change (Rogers & Laffoley, 2011). Equally, uptake and implementation of ecosystem-based management of fisheries has been very limited, with few national jurisdictions demonstrating an adequate level of implementation (Pitcher *et al.*, 2009). The contribution of lobster fisheries to the cumulative regional (and global) impacts imposed by fishing has also been largely ignored by all the present-day ecolabelling systems, and the assessments generally consider the local environmental impacts of lobster fisheries to be minor. A recent review of the environmental impacts of the MSC programme (Cambridge *et al.*, 2011) reports that, over the history of assessments conducted in the programme, only three environmental outcomes have been improved from a fail to a passing score as a result of a condition imposed by the MSC certification process (one reduction in bycatch, and two reductions in risk to threatened species), and none of these involve a certified lobster fishery. The review identified a number of improvements in environmental information, monitoring systems and assessments of environmental risks, but found very little actual environmental impact of the certified lobster fisheries and very little improvement in environmental

outcomes created by the MSC certification. As a result, the MSC programme appears to be responsible for only minor improvements in the environmental performance of lobster (and other) fisheries that already are considered to have only low levels of environmental impacts. The disparity between the global assessments of fishing impacts and the local scale of eco-certification assessments highlights the inadequacy of the eco-certification standards, which maintain a close focus on the direct rather than also involving the indirect and cumulative impacts of fishing which have to be also taken into account when considering the broader impacts of fishing on ocean ecosystems.

6.5.4 Developing countries

Based on the FAO catch data (FishstatJ, 2011), we estimate that between 15% and 27% of the global lobster catch was taken in tropical and developing countries in 2009 (from the reported 39,000 to a plausible 78,000 t). This level of catch clearly has important social, economic and possibly environmental consequences in these countries. The vast majority of this catch is likely to be taken in small-scale fisheries and in subsistence fisheries, but, in aggregate, is of both local and national importance. A significant proportion of this production is traded with developed countries as a mechanism to generate hard currency, but this provides only a limited commercial incentive for such fisheries to engage or pay for ecolabelling programmes. In addition, fishers in these countries have a number of other objectives for engaging in ecolabelling and certification, and are interested in a range of non-market benefits. As a result, the current forms of ecolabelling and certification are not attractive for most of the lobster fisheries in these developing countries, particularly without major external funding support (Pérez-Ramírez *et al.*, 2012a). In these circumstances, the cost for achieving an eco-certification becomes a significant barrier, and cost is widely considered to be a significant impediment preventing fisheries in the developing world from being able to achieve certification (Mathew, 2011). Further, the applicability of the MSC form of ecolabelling, based on models of fishery management

mostly applicable to large-scale industrial fisheries, has been also widely challenged. It has been asserted that MSC ecolabelling is inherently biased against the small-scale and multi-species tropical fisheries that are typical of the developing countries (Mathew, 2011) and that it promotes the globalization of seafood as a commodity (Pérez-Ramírez *et al.*, 2012a), and this may not always be in the best interest of developing countries.

Pérez-Ramírez *et al.* (2012a) found that international reputation, image and community standing were attributes of ecolabelled fisheries to which fishers were attracted, and that securing independent endorsement of their fishing practices was attractive for these and a variety of other reasons even where products are not extensively commercially traded. The inference of the ‘pass/fail’ model, and the focus on threshold scores and performance measures as employed in many certification and ecolabelling systems, is a particular issue for all current and potential ecolabelled fisheries (Tlusty, 2012). The application of ‘pass/fail’, for example as implemented within the MSC programme, has resulted in status in market terms being awarded to lobster fisheries that have highly developed stock assessment systems and harvest strategies in place (such as Australia’s western rock lobster fishery) that is equivalent to the status of fisheries with no robust form of stock assessment or harvest strategy (such as the Normandy and Jersey wild-catch trap lobster fishery). In consumer and marketing terms, these two fisheries are equal in sustainability value, since both carry the MSC ecolabel on their products. The actual disparity between the standard applied in such cases creates internal pressure for increased standards of conformity to be used in assessments, and a dissatisfaction with the ecolabel within the better performing fishery and consequent pressure for relaxation of the standard.

To assist with such issues, and to try to better meet the needs of developing countries, ecolabelling and certification systems of the future could be better designed around forms of progressive compliance, such as the now commonplace ‘star’ system, with defined steps of progression within specific regional programmes designed to address

both regional and global issues. With an appropriate set of performance indicators, set to reflect the real issues of developing countries, there would appear to be no reason why ecolabelling and certification systems would not be better accepted, more widely implemented, and more effective in creating improvements in fishery systems. Such a system could be appropriately designed and supervised within the regional FAO mechanisms, with implementation by national governments in partnership with NGOs, and appropriate technical procedures for independent third-party verification against defined and high quality standards for each 'star' level.

6.5.5 Successful certification and ecolabelling of lobsters

To persist and be successful in influencing improved seafood sustainability practices, certification/ecolabelling initiatives of the future will need to be fully transparent, publicly providing the specific details of the standard against which each product is being assessed; the principles and criteria and the methodology of verification; and the application of a robust and independent third party verification process, including the identity, experience and standing of the assessors and certifiers. To enable producers to provide assurance that their products have been produced in ways that are both legal and meet a high environmental standard, successful ecolabelling and certification systems will also probably need to be regionalized, to recognize the different local conditions and standards under which producers must operate. None of the major seafood ecolabels currently have established activities that meet all these needs of the future.

Internal assessment/certification systems (including business-to-business systems) are highly valuable and important for industry development, as a self-assessment tool to secure progressive improvement and internal consistency within an industry or a region, and for industry-wide benchmarking purposes. However, industry self-assessment and compliance with government minimum standards, while both a necessary part of modern fishing and aquaculture practices, are not sufficient to either ensure the modern concepts of sustainability are

attained or to convince consumers and markets that this is being actually achieved. Nonetheless, business-to-business systems are likely to continue to expand, providing 'due diligence' verification services to wholesalers, retailers, providores and restaurants to meet the expectations of customers that their supply of seafood meets a basic standard for ecological sustainability and provenance. This may also expand to provide services to cooperatives and fishery managers as there is an increased mainstreaming of standards into national government and regulations.

As the number and diversity of private certification systems grows, so too will the imperative for national governments to embed the standards represented by these systems into minimum national standards to be enforced by regulation. Achieving an international set of benchmarks for such minimum national standards for both wild-catch and aquaculture products will be a key element of the next phase of ecolabelling in the seafood industry. These global benchmarks will need to move beyond process and provide for the independent verification of outcomes. While governments have traditionally set minimum acceptable standards, with the globalization of trade and ecolabelling, national governments are now also moving to establish international standing in food safety and sustainability of seafood products. Without global independent third-party verification systems, the application and achievement of government minimum standards, no matter how stringent they may appear, will be no more successful than the plethora of weakly designed certification and eco-labelling systems that currently dominate the seafood market.

As the number of lobster products that have some form of eco-certification and ecolabelling continue to grow, price differentials and unique market access for these products will gradually diminish. We expect that, as this begins to become more evident (O'Riordan, 2011), the labelling systems will move out of the hands of the NGO system and into the domain of governments and fishers themselves. Irrespective, it is clear that the issues about environmental impacts, management of the stocks, the social and cultural values, and the transparency of benefits of fishing are unlikely to

completely fade away. We anticipate that many of the performance benchmarks being now established by the labelling systems will become more established in normal practice of fishers and governments worldwide. Equally, we expect that these standards will be further developed to apply regionally and nationally, and while they may differ around the globe, they will better match the local circumstances in the coupled social-ecological system within which lobsters are fished, providing more equitable access to, and benefits from, higher ecological standards for lobster fisheries. It seems highly unlikely that eco-certification of seafood will be successful and persist in the medium to long term unless the central attributes of successful fisheries (Gutierrez *et al.*, 2011) become more properly reflected within new standards of global relevance. Key attributes of successful fisheries that have formal consultation mechanisms built into their management systems (as for example occurs in the majority of smaller fisheries, and expected for all fisheries within the MSC ecolabelling standard) have been found (Gutierrez *et al.*, 2011) to include

- 1 strong local leadership;
- 2 individual or community quotas;
- 3 social cohesion;
- 4 protected areas;
- 5 enforcement mechanisms;
- 6 long-term management policies; and
- 7 life history of the resource (benthic and demersal resources are more successfully managed than pelagic and multiple species resources).

But possibly most important of all, in expanding the conceptual models underpinning ecolabelling and seafood certification, the application of a single universal standard for sustainability used by present-day ecolabelling systems should probably be balanced against the need to provide for a

seafood sustainability system that encompasses production of almost all of the lobster and other seafood products. Thus, the present-day approach of certifying a modest component of the world's seafood in 'pass/fail' systems to demonstrably meet a high level of sustainability will need to be traded off against the goal of entraining most of the global seafood production into a broader construct of continuous improvement sustainability systems. Some of these seafood products may perhaps embody a somewhat lower level of sustainability performance but all of which will be entrained on pathways of incremental development. This itself is an objective worthy of investment by the global actors, even those such as the MSC that are presently bound to singular expressions of the sustainability standard, and the FAO which is making only slow progress on development of a framework for effective global governance of ecolabelling and certification of seafood sustainability that meets the expectations of the national governments as well as better outcomes for the producers, the oceans and the dependent human communities.

Appendix

Example Aquaculture Criteria and Grades: ecological performance and sustainability stringency

The criteria used here (Table A1) to evaluate the extent to which aquaculture ecolabelling/endorsement schemes are derived from a broader analysis of the desirable characteristics of successful seafood ecolabelling schemes (see Ward 2008b). A more detailed set of criteria are also presented to enable an equivalent evaluation of the stringency of sustainability standards encoded within the schemes (Table A2).

Table A1 Criteria and performance indicators to evaluate the ecological performance of an aquaculture ecolabelling or endorsement scheme. Grades are assigned as H (high level of compliance with the evaluation indicator), M (medium level of compliance) and L (low level of compliance).

Scheme Criterion	Performance indicator	Intent	GAA ¹	WWF ²	EUREPGAP ³	Naturland ⁴	MAC ⁵	SFW ⁶
A. Meaningful endorsement	1. Objectives of the incentive program are clear and meaningful	Objectives properly constructed, clearly reflect scope of environmental issues endorsed	H: Objectives clear, reasonably matched to the issues endorsed	H: Objectives clear, reasonably matched to the issues endorsed	H: Objectives clear, reasonably matched to the issues endorsed	H: Objectives clear, reasonably matched to the issues endorsed	H: Objectives clear, reasonably matched to the issues endorsed	H: Objectives clear, reasonably matched to the issues endorsed
	2. Standard is clear and meaningful	Standard is unambiguous, has a declared scope and a clear relationship with the environmental issues being assessed	H: Standard covers the main issues relevant to shrimp aquaculture	H: Standard covers the main issues relevant to tilapia aquaculture	M: Standard does not properly cover effluent management or biodiversity issues	M: Standard does not properly cover effluent management or biodiversity issues	M: Standard treats some issues superficially, e.g. effluent management, site impacts, groundwater	H: Standard covers the main regional issues relevant to aquaculture
	3. The standard is written for all relevant ventures/ products that will carry the endorsement	Standard applies to all relevant aspects of operations that are the subject of the endorsement	H: Standard relates to the majority of ventures and products	H: Standard relates to the majority of ventures and products	H: Standard relates to the majority of ventures and products	H: Standard relates to the majority of ventures and products	H: Standard relates to the majority of ventures and products	H: Standard relates to the majority of ventures and products
	4. Explicit and consistent methodology for verification	Verification procedures are explicit, efficient and effective; compliance is clear; endorsement is consistent	M: Standard has potentially different levels of verification stringency	M: Standard has potentially different levels of verification stringency	M: Standard has potentially different levels of verification stringency	M: Standard has potentially different levels of verification stringency	M: Standard has potentially different levels of verification stringency	H: Standard applied by single expert judgement system, with consistent verification

5.	Robust information and data support the verification	Verification uses credible data and information; information gaps and uncertainty are treated in a precautionary manner	L: Limited quantitative measures, lack of guidance about uncertainty	L: Limited quantitative measures, lack of guidance about uncertainty	L: Limited quantitative measures, lack of guidance about uncertainty	L: Limited quantitative measures, lack of guidance about uncertainty	M: uncertainty is treated explicitly but limited guidance in verification process	M: quantitative measures, lack of guidance about uncertainty
6.	Standard is balanced, and has a high level of technical merit	Standard has balanced decision elements, reflected in the technical basis of the standard	M: Balanced, but not a strong technical base	M: Balanced, but not a strong technical base	M: Lacks off-site impacts and environment interactions	M: Broad standard, but most indicators are not technical	M: Balanced, but not a strong technical base	M: quantitative measures, lack of guidance about uncertainty
C. Independence	7. Compliance of the venture/product with the standard is verified by independent third-party certification	Independence ensures minimal potential for motivational bias in the verification process	L: Relationship appears close, and potentially pecuniary	L: Compliance verification remains unknown	H: Appears a high level of independence in compliance verification	H: Appears a high level of independence in compliance verification	H: Appears a high level of independence in compliance verification	H: quantitative measures, lack of guidance about uncertainty
8.	Standard-owner and any related organizations are financially independent of seafood products, no conflicts of interest	Standard owner has no cross-links with seafood organizations, nor derives benefits from the sale of endorsed seafood	L: Mixed interests in the standard owner, potential pecuniary conflicts	H: the standard owner is independent	H: the standard owner is independent			
D. Transparency	9. The institutional and governance structure backing the scheme is public domain information	Identity, institutional arrangements and governance are freely available	M: partly public domain, but limited in research, funding, and industry relationships	M: the verification system remains unknown	H: structures are complicated but public domain	H: structures are complicated but public domain	H: structures are public domain	H: structures are public domain

Table A1 continued

Scheme Criterion	Performance indicator	Intent	GAA ¹	WWF ²	EUREPGAP ³	Naturland ⁴	MAC ⁵	SFW ⁶
	10. Assessments to determine compliance with the standard are public domain	Assessments and reports freely available to the public	M: the availability of assessment reports is limited	L*M: no public release of reports	M: no detailed assessment reports	L: no public release of assessment reports	L: no public release of assessment reports	M: summary reports are public domain
E. Public input	11. The public is notified widely of the engagement of a venture with the assessment, and outcomes widely publicized	Ensures that there is a broad awareness of the assessment process, and the opportunity for public involvement	M: engagement is unclear	L*M: no provision for public advice of engagement	M: engagement is unclear; outcomes are public	L: no public advice or engagement in compliance assessments	M: engagement is unclear; outcomes are public	L: no public notification of engagement; outcomes are public
	12. Stakeholder input is actively sought from all sectors into the verification process for the purpose of ensuring that community norms are maintained	Ensures that any interpretations, judgments or decisions made in the verification process can be set in the context of community norms and acceptability	M: stakeholders are active in standard or setting, but it is unclear if stakeholders are also involved with individual assessments	L*M: no provision for public advice or engagement in compliance assessments	M: stakeholders active in standard setting, but unclear if stakeholders are involved with assessments	L: no provision for public advice or engagement in compliance assessments	M: limited provision for stakeholder input or engagement in compliance assessments	L: no provision for public advice or engagement in compliance assessments

¹ GAA: Global Aquaculture Alliance – standard evaluated here is the GAA standard for shrimp aquaculture version 9/09 (<http://www.gaaalliance.org/bap/standards.php>).

²WWF: WWF Aquaculture Dialogues – standard evaluated here is the standard for Tilapia aquaculture (the shrimp aquaculture standard remains in draft form only) (<http://www.worldwildlife.org/what/globalmarkets/aquaculture/sustainability-standards-tilapia.html>).

*WWF have announced that certification will be conducted under the auspices of GLOBALGAP, but this has yet to be implemented and we are unable to evaluate the effectiveness. For this evaluation the grades have been assigned to be equal to those of EUREPGAP where the certification procedure would constitute the main component of the grade. This is shown in the table in the format X*Y, where X is the grade as at early 2010, and Y is the grade that would be assigned if the EUREPGAP process was applied to the standard.

³EUREPGAP: a GLOBALGAP scheme – standard evaluated here is the aquaculture base and shrimp module V1.0-1 Apr09 GLOBALGAP (EUREPGAP) aquaculture standard (http://www.globalgap.org/cms/front_content.php?idart=378&idcat=48&lang=1&client=1).

⁴Naturland – Association for Organic Agriculture: standard evaluated here is the Naturland Standards for Organic Aquaculture, version 11/2009, focusing on the shrimp supplement (http://www.naturland.de/organic_aquaculture_standards.html).

⁵MAC Marine Aquarium Council: standard evaluated here is Mariculture and Aquaculture Management International Performance Standard for the Marine Aquarium Trade, Final Issue 1 January 2008 (http://www.aquariumcouncil.org/Product_Services.aspx?tab=p1).

⁶SFW SeafoodWatch, Monterey Bay Aquarium. standard evaluated here is the Aquaculture Evaluation Recommendation Criteria, version May 9, 2006 (http://www.montereybayaquarium.org/crc_seafoodwatch/sfw_aboutsw.aspx).

Table A2 Criteria and performance indicators to evaluate the stringency of the sustainability standard applied by an aquaculture ecoclabelling or endorsement scheme. Grades are assigned as H (high level of compliance with the evaluation indicator), M (medium level of compliance) and L (low level of compliance).

Standard Criterion	Performance Indicator	Intent	GAA	WWF	EUREPGAP	Naturland	MAC	SFW
1. Scope and focus of the standard	Standard covers all relevant impacts and issues; requires evidence of performance that reflects the importance of issues	Standard covers all relevant ecological issues of sustainability; standard does not emphasize marginal or biased issues	H: but neglects some ecological and hydrodynamic interactions	M: weak on issues of site contamination, native biodiversity and effluent management	M: weak on issues of site contamination, native biodiversity and effluent management	M: weak on issues of site contamination, native biodiversity and effluent management	H: the standard deals with a wide range of the important issues relevant to each region	
2. Outcomes and processes	Standard covers both the processes and outcomes of the management systems	Standard covers both the process of management and the outcomes demonstrably achieved	H: covers outcomes and a number of the important processes	H: Standard is strong on process and somewhat weaker on outcomes	H: Standard is strong on process and somewhat weaker on outcomes	M: Standard is strong on process and weak on outcomes	H: covers outcomes and a number of the important processes	
3. Comprehensive and achievable verification	The standard is comprehensive and written so that a robust verification of compliance is feasible and achievable	Standard is sufficiently detailed that the verification procedure can determine if there is compliance	M: for some indicators robust	M: for some indicators robust	M: for some indicators robust	M: for some indicators robust	M: the standard is generally comprehensive with clear guidance for verification of compliance	M: for some indicators robust

Table A2 *continued*

Standard Criterion	Performance Indicator	Intent	GAA	WWF	EUREPGAP	Naturland	MAC	SFW
4. Balance	The weighting of specific indicators in the final certification decision is balanced	Explicit and implicit weighting of indicators and decision structures is consistent with the ecolabel claims	H: mix of 'must pass' and scoring provides an appropriate balance	L: appears to be limited balance across the 61 indicators	H: suitable balance to the indicators	L: no guidance to interpret threshold situations	L: appears to be limited balance across the indicators	H: appears and appropriate balance of indicators and decision elements
5. Explicit and Precise	The standard is explicit, expressed in simple and clear terms, and precise about achievement and reference benchmarks	Ensures that the standard is clear and accessible to all parties	M: only some of the indicators are numeric, but otherwise the standard is reasonably clear	L: indicators are mostly qualitative, many have only limited guidance on interpretation	L: indicators are mostly qualitative, many have only limited guidance on interpretation	L: indicators are mostly qualitative, many have only limited guidance on interpretation	L: indicators are mostly qualitative, many have only limited guidance on interpretation	M: most of the indicators are quantitative, and otherwise the standard is reasonably clearly expressed
6. Universal, normative, effective	The reference benchmarks are effective in mitigating ecological impacts	Ensures that the benchmarks are universal and protective, not flexible or optional	M: indicators use benchmarks not widely protective	M: limited use of protective benchmarks	L: benchmarks are mostly subjective and potentially flexible	L: benchmarks are mostly subjective and potentially flexible	L: benchmarks are mostly subjective and potentially flexible	M: benchmarks are mostly normative and generally effective
7. Technical Clarity	Achievement required from a facility/product is expressed in quantitative technical terms	Ensures that verification of achievement of the standard can be carried out in an objective manner	L: limited quantitative basis for indicators and little guidance for certifiers	L: heavy emphasis on planning systems; few numeric control points for certifiers	L: limited quantitative basis for indicators and little guidance for certifiers	L: limited quantitative basis for indicators and little guidance for certifiers	L: limited quantitative basis for indicators and little guidance for certifiers	L: limited quantitative basis for indicators and little guidance for certifiers

8. Achievable	Reference benchmarks are set at best performance; capacity for interim certification is explicit	Provides for best practice and continuous improvement	M: simple standards are applied, and there appears to be limited guidance available for improvement	H: specific pathways for continuous improvement are identified within the certification process	M: lack of quantitative benchmarks is an impediment to robust verification
9. Verifiable, practical	Verification of compliance is expert and independent 3rd party system, with practical systems and benchmarks	Ensures that the verification is an effective, objective and achievable quantitative system	L: verification seems to be mainly subjective	L: there is no information about the verification process in the public domain	L: few control points are numeric, and there is little guidance for dealing with uncertainty
10. Maintenance of the standard	There is a specified and accessible system for updating the standard and maintaining its currency and relevance to the issues that are within the scope of the ecolabel	Ensures that the standard continues to be relevant to current issues in sustainability and in the technology improvements in facility operations and monitoring systems	H: incremental upgrades of the standard have been placed in the public domain, and subject to stakeholder comment	H: there is a strong system for updating and maintenance of the standard	M: the process for updating the standard is unclear

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Chapter 7

Essential Habitats for *Panulirus* Spiny Lobsters

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Abstract

The shallow distribution of *Panulirus* spiny lobsters makes them especially vulnerable to overexploitation and their coastal habitats to the synergistic effects of multiple environmental and anthropogenic stressors. In order to incorporate measures to protect habitats of these lobsters into fisheries management regimes, knowledge is required about the life history strategies and the patterns of habitat use by different benthic life stages. This knowledge is substantial for a few species but insufficient for most other species. Also, little is known about the interspecific trade-offs that promote the coexistence of *Panulirus* species at different spatial scales. This chapter reviews the main features of essential habitats for *Panulirus* lobsters and the trade-offs involving habitat resource use between coexisting species. Also addressed are the multiple stressors that are resulting in loss/degradation of *Panulirus* habitats and some measures that may potentially mitigate these effects, including the controversial issue of habitat enhancement to alleviate demographic bottlenecks.

Key Words: essential habitat; habitat loss and degradation; habitat management; habitat specialist; life history strategy; ontogenetic shifter; *Panulirus*; species coexistence; spiny lobsters

7.1 Introduction

Spiny lobsters (Family Palinuridae) are conspicuous, often abundant members of many benthic marine communities and a valuable fishing resource in all the places in which they occur (Phillips & Melville-Smith, 2006). The life cycle of spiny lobsters consists of two major phases: a lengthy planktonic larval phase that develops in oceanic water,

and a benthic phase that begins when the natant post-larvae (pueruli) settle onto some benthic habitat. This life history transition connects oceanic and benthic habitats. Benthic spiny lobsters are quite mobile but cannot build their own shelters; therefore, they depend on structured habitats for protection and survival. The most diverse genus of the family is *Panulirus*, with 24 recognized taxa (species/subspecies) (Table 7.1) that are distributed

Table 7.1 Distribution and adult habitats of recognized *Panulirus* species/subspecies in the first ('clear water') and the second ('turbid water') major phylogenetic lineages (adapted from Phillips *et al.*, 1980; George, 2006; Chan, 2010), and their possible life history strategies based on available information on patterns of habitat use by different life history stages.

Species	Distribution	Adult habitat	Life history strategy
First major lineage (clear water)			
<i>Panulirus argus</i> (Latreille, 1804)	W Atlantic	Coral + rock	OS
<i>P. brunneiflagellum</i> Sekiguchi & George, 2005	Ogasawara Islands	Volcanic rock	?
<i>P. cygnus</i> George, 1962	W Australia	Limestone reef	OS
<i>P. echinatus</i> Smith, 1869	Atlantic islands, NE Brazil	Volcanic rock	HS
<i>P. femoristriga</i> (von Martens, 1872)	W Pacific	Coral + rock	?
<i>P. guttatus</i> (Latreille, 1804)	Caribbean	Coral reef	HS
<i>P. interruptus</i> (Randall, 1840)	California, Baja California	Rock	OS
<i>P. japonicus</i> (von Siebold, 1824)	Japan to E China	Mudstone	OS?
<i>P. longipes longipes</i> (A. Milne Edwards, 1868)	Indian Ocean	Coral + rock	?
<i>P. longipes bispinosus</i> Borradaile, 1899	New Caledonia	Coral + rock	?
<i>P. marginatus</i> (Quoy & Gaimard, 1825)	Hawaii	Reef	HS?
<i>P. pascuensis</i> Reed, 1954	Easter and Pitcairn Islands	Volcanic rock	HS?
<i>P. penicillatus</i> (Olivier, 1791)	Indo-W Pacific to E. Pacific	Coral + rock	HS
<i>P. versicolor</i> (Latreille, 1804)	Indo-W Pacific	Coral + rock	HS
Second major lineage (turbid water)			
<i>P. gracilis</i> Streets, 1871	Central E Pacific	Rock + gravel-sand	OS?
<i>P. homarus homarus</i> (Linnaeus, 1758)	Indo-W Pacific	Rock + sand	?
<i>P. homarus megasculptus</i> Pesta, 1915	Arabian Sea	Rock + sand	?
<i>P. homarus rubellus</i> Berry, 1974	SW Indian Ocean	Rock + sand	HS?
<i>P. inflatus</i> (Bouvier, 1895)	Mexican Pacific	Rock	HS
<i>P. laevicauda</i> (Latreille, 1817)	SW Atlantic	Rock + fine shell	?
<i>P. ornatus</i> (Fabricius, 1798)	Indo-W Pacific	Rock + silt	OS
<i>P. polyphagus</i> (Herbst, 1793)	Indo-W Pacific	Rock + mud	?
<i>P. regius</i> de Brito Capello, 1864	W Africa	Rock + silt	?
<i>P. stimpsoni</i> Holthuis, 1963	S China Sea	Rock + silt	?

HS, habitat specialist; OS, ontogenetic shifter.

across the tropical and subtropical belt of all the world's oceans (i.e., between 35°N and 35°S) wherever suitable habitat is available, to maximum depths of about 100 m (Phillips *et al.*, 1980; George, 2006; Chan, 2010). The shallow distribution of *Panulirus* lobsters makes them especially vulnerable to overfishing, but the persistence of benthic

populations depends to a great extent on the spatial distribution, degree of structure, and condition of the benthic habitats in which they live. In this chapter, we provide a review of the essential habitats for different *Panulirus* lobsters with different life histories, the microhabitats ("shelters" or "dens") used by these lobsters in different habitats

to take refuge from predators and to modulate harsh external conditions, the factors that affect shelter selection, and the potential trade-offs that allow sympatric species of *Panulirus* to coexist at regional or local spatial scales. We also address the synergistic effects of environmental and anthropogenic stressors that are resulting in ever-increasing rates of loss or degradation of the coastal habitats of *Panulirus* lobsters and some management measures that could help mitigate such habitat loss or degradation.

There is considerable knowledge on the habitats used by the sub-adult and adult stages of *Panulirus* lobsters because these are typically the life history stages that support the fisheries. This knowledge has provided an important tool to study the phylogenetic relationships among the species/subspecies that form the two major lineages recognized in this genus. Thus, for species in the first major lineage, the typical coastal habitats of the adult lobsters are rocky or coral substrates washed by clear, non-turbid “oceanic” water without significant riverine inputs. For species in the second major lineage, the coastal rocky habitats of adult lobsters are often washed by turbid waters of low salinity, laden with fine terrigenous sediments flowing from small or large rivers, or are located on open beaches where coarser, sandy sediments are frequently stirred up by the surf so that these lobsters are tolerant of, but not necessarily dependent upon, turbid or low-salinity conditions (George & Main, 1967; George, 2006) (Table 7.1). However, because successive life history stages of a species may have different optimal habitats, a definition of the habitat of an animal species should consider the behavior of that animal and two important dimensions: space and time (Southwood, 1977; Pittman & McAlpine, 2001). For example, Caddy (2008) defined the habitat of any life stage of a species as “that critical sub-area within the overall species range where abiotic/biotic features give this life history stage some protection from predation and the opportunity for foraging and other life history activities.” Another important consideration is that most benthic habitats are distributed in patches forming complex seascapes (Hanski & Simberloff, 1997; Boström *et al.*, 2006), wherein focal patches (e.g., vegetation) can be viewed as “islands” embedded

in a matrix (e.g., sand) that may affect animal movements and survival depending on relative isolation (Boström *et al.*, 2011).

Within a complex seascapes, one habitat may be sufficient for a species to complete its life cycle and that would comprise its essential habitat, but other species may require different habitats to satisfy the changing need of individuals, so that the essential habitat of these species may comprise nursery, adult, and spawning habitats (Pittman & McAlpine, 2001; Krumme, 2009). Thus, based on the patterns of habitat use by the juvenile and adult life stages, most species can be categorized into one of three life history strategies: (i) *ontogenetic shifters*: species in which post-larvae tend to settle in habitats and locations different from those used by adults and undergo ontogenetic transitions to the adult life stage habitat; (ii) *habitat generalists*: species in which the post-larvae can stay, or move among, numerous habitats and are not site attached, and to the extent that ontogenetic shifts occur, they do not follow a well-defined pattern and/or are minor compared with ontogenetic shifters; and (iii) *habitat specialists*: species in which post-larvae settle into the same location they will remain throughout their benthic life (Adams *et al.*, 2006; Adams & Ebersole, 2009).

Knowing which habitats are essential for which species has important implications for fisheries management and conservation (Pittman & McAlpine, 2001), but as life history strategies are not phylogenetically constrained, species-specific data are required to determine which species fall into which life history categories (Adams & Ebersole, 2009). Sufficient information about settlement locations, habitat use, movement ranges, and potential connectivity between juvenile and adult habitats exists only for a few *Panulirus* species, some of which clearly fall into the categories of ontogenetic shifters or habitat specialists, but the amount of information is more limited for many other species (Table 7.1). Although we acknowledge that the genus may also comprise habitat generalists, we only consider those species tentatively ascribed to the categories of ontogenetic shifters and habitat specialists as a first approach into the essential habitats for different *Panulirus* lobsters.

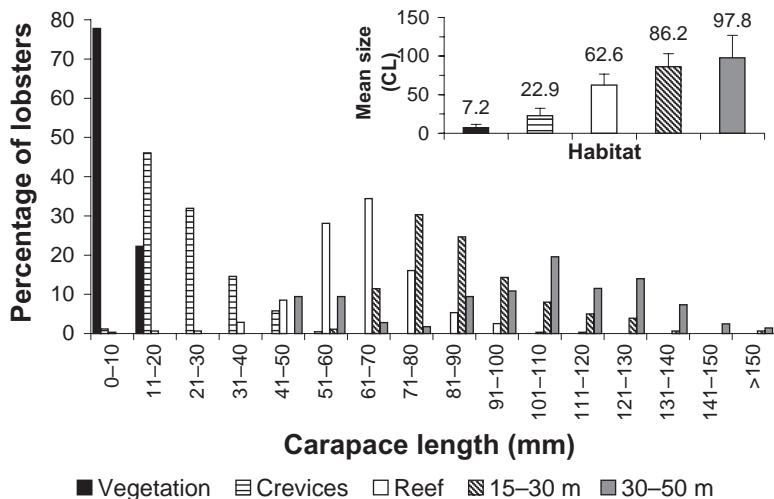


Fig. 7.1 Size distribution of *Panulirus argus* lobsters across the continental shelf of Puerto Morelos, Mexico, from the shallow nursery habitats (vegetation) to the deeper adult habitats (30–50 m). The mean size (\pm standard deviation) of lobsters in each habitat is indicated in the upper right inset (composite data from Lozano-Álvarez *et al.*, 1991a, 1993, 2007; Briones-Fourzán & Lozano-Álvarez, 2001a).

7.2 Essential habitats for ontogenetic shifters

For a species to be considered an ontogenetic shifter the post-larvae must settle into habitats distinct from those used by adults and the individuals must undergo further ontogenetic movements to non-juvenile habitats. There can be some overlap in the habitats used by juveniles and adults, but the general direction of ontogenetic movement should be towards the adult habitat (Dahlgren *et al.*, 2006; Haywood & Kenyon, 2009). Based on these criteria, species of *Panulirus* that may be considered as ontogenetic shifters are *P. argus*, *P. cygnus*, *P. interruptus*, *P. ornatus* and, with some doubt, *P. japonicus* and *P. gracilis* (Table 7.1). The documentation of actual ontogenetic movements via the use of external tags (e.g., Phillips, 1983; Gregory & Labisky, 1986; Lozano-Álvarez *et al.*, 1991b) or stable isotope analyses (e.g., Behringer & Butler, 2006a; Waddington *et al.*, 2008) provides better evidence of connectivity between nursery and adult habitats than the mere progression of size classes between habitats (Gillanders *et al.*, 2003). For example, *P. argus* is undoubtedly an ontogenetic shifter, but the spatial extent and degree of separation of the benthic habitats used by the different life stages (marine vegetation–crevices–coral reefs–deep reefs) may influence the pattern of progres-

sion of size classes. Thus, across the continental shelf of Puerto Morelos (Mexico), small juveniles of *P. argus* <20 mm carapace length (CL) dwell in vegetated areas of the shallow (<5 m in depth) and rather narrow (<2 km) reef lagoon, but there is great overlap in the size range of individuals occupying natural crevices over the reef lagoon (6–50 mm CL), the coral reef habitat (9–100 mm CL), and the deeper habitats over the continental shelf (51–160 mm CL at depths of 15–30 m, 41–180 mm CL at depths of 30–50 m) (Fig. 7.1). Regardless, the mean size of lobsters consistently increases over this range of habitats (Fig. 7.1). In contrast, in a small marine park in Cozumel Island (Mexico), where the insular shelf is extremely narrow, large juveniles and adults (30–204 mm CL) co-occur inside a shallow enclosed seawater lagoon (0–3 m in depth) connected to the sea through an underwater tunnel as well as in the adjacent open sea area to a depth of ~15 m, and the mean size of lobsters does not differ between both habitats (Fig. 7.2).

7.2.1 Nursery and juvenile habitats

Nursery habitats, relative to other habitats, must support greater contributions to adult recruitment from any combination of four factors: density, growth, and survival of juveniles, and movement to adult habitats (i.e., connectivity) (Beck *et al.*,

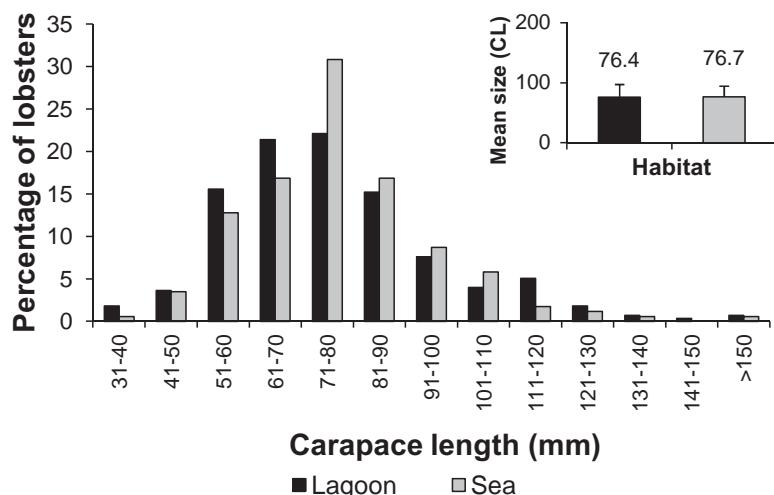


Fig. 7.2 Size distribution of *Panulirus argus* lobsters across the narrow insular shelf of Cozumel Island, Mexico, from a shallow (<2 m), enclosed marine lagoon connected to the sea by an underwater tunnel ('lagoon'), to offshore depths of ~15 m ('sea'). The mean size (\pm standard deviation) of lobsters in each habitat is indicated in the upper right inset (data from Lozano-Alvarez *et al.*, 2003a).

2001; Adams *et al.*, 2006; Krumme, 2009). However, because settlers of many species depend on a mosaic of contiguous habitat types rather than upon a single habitat type, all habitats that result in a contribution of individuals to the adult population can be considered to have a nursery function. These include *essential nursery habitats*, which make a greater than average contribution to adult populations on a per unit area basis (Beck *et al.*, 2001; Heck *et al.*, 2003), and *effective juvenile habitats*, which contribute a greater proportion of individuals to the adult population than the mean level contributed by all habitats used by juveniles regardless of area coverage (Dahlgren *et al.*, 2006; Adams *et al.*, 2006). The pueruli of some *Panulirus* species settle on shallow hard grounds and occupy small holes proportional to their body dimensions in the substrate, although they tend to prefer holes beneath, or surrounded by, macroalgae or seagrass (e.g., *P. cygnus*: Jernakoff, 1990; *P. ornatus*: Dennis *et al.*, 1997; *P. japonicus*: Yoshimura & Yamakawa, 1988; Yoshimura *et al.*, 1994). In other species, the pueruli settle directly in coastal marine vegetation of some sort (e.g., seagrass meadows, macroalgal beds, mangrove edges). In the Florida Keys (USA), hard bottoms covered with bushy red macroalgae (the *Laurencia* spp. complex) appear to be essential nursery habitats for *P. argus* (Behringer *et al.*, 2009), but seagrass meadows, which cover more

area than macroalgae-dominated hard bottoms (Bertelsen *et al.*, 2009), probably represent effective juvenile habitats. In general, the nursery function of vegetated habitats does not depend on a specific plant type or species assemblage but on the structural complexity provided by the vegetation, which increases the provision of food resources and the amount of cover for the early benthic stages ("small juveniles") (Beck *et al.*, 2001). For example, using tethering experiments, Acosta & Butler (1999) found that recently settled individuals of *P. argus* suffered much higher predation on coral reefs than on inshore vegetated habitats.

The pueruli of *P. cygnus* and *P. argus* probably use a combination of chemical, sound, and pressure cues during onshore transport and selection of settlement habitat (e.g., Phillips & Macmillan, 1987; Goldstein & Butler, 2009) and, upon arriving to the coastal areas, they might also be able to follow mass-dependent conspecific cues into vegetated habitats (Zito-Livingston & Childress, 2009). Settled individuals then move to suitable post-settlement microhabitats within these habitats. Thus, where the presence of extensive hard bottoms favors the occurrence at high abundance of erect red macroalgae, small juveniles of *P. argus* use the intricate branches of these algae as microhabitats (e.g., *Laurencia* in Florida, USA, and Cuba: Marx & Herrnkind, 1985; Herrnkind & Butler, 1986;

Butler *et al.*, 1997; Cruz *et al.*, 2007b; *Neogoniolithon* in Turks and Caicos: Bos *et al.*, 2003; *Amansia* in Brazil: Igarashi, 2010). But in places where extensive soft bottoms favor the development of seagrasses, which are structurally simple plants, the presence of many kinds of macroalgae that grow interspersed with the seagrasses increases the complexity of seagrass habitats (Stoner & Lewis, 1985; Cruz-Palacios & van Tussenbroek, 2005; Enríquez & Pantoja-Reyes, 2005), providing microhabitats for small juvenile lobsters. For example, in low-energy seagrass habitats dominated by *Thalassia testudinum*, small juveniles of *P. argus* can find suitable microhabitats in the folds of low-lying, convoluted macroalgae (e.g., *Ulva fasciata* in Cuba: Serpa-Madrigal & Areces, 1995; *Lobophora variegata* in Puerto Morelos, Mexico: Briones-Fourzán & Lozano-Álvarez, 2001a). In Baja California (Mexico), small juveniles of *P. interruptus* mostly use the base of the blades of seagrasses (*Phyllospadix* spp.) as microhabitats despite the local abundance of complex macroalgae. In habitat choice experiments, they showed preference for the complex macroalgae *Gelidium* over *Phyllospadix* and other macroalgal types, but when synthetic plants of similar architecture were supplied with different plant odor cues, they significantly preferred the synthetic plants with *Phyllospadix* odors (Castañeda-Fernández de Lara *et al.*, 2005a). Other microhabitats used by small juveniles that settle in vegetated habitats are the vegetation–substrate interface and the sediment itself, into which they may partially bury (e.g., *P. argus*: Calinski & Lyons, 1983; *P. ornatus*: Dennis & Pitcher, 2001; *P. interruptus*: Castañeda-Fernández de Lara *et al.*, 2005a).

However, suitability of nursery habitats is not necessarily predicted by characteristics of the vegetation; rather, nurseries persist where competent post-larvae are concentrated by circulation features and settlement occurs selectively (Stoner, 2003). For example, some locations in the Bahamas and in Mexico receive an abundant supply of pueruli of *P. argus*, but the paucity of nursery habitat in these locations results in a low abundance of adults (Lipcius *et al.*, 1997; Briones-Fourzán, 1994; Briones-Fourzán *et al.*, 2008a). By concurrently measuring the influx of pueruli and the abundance

of juveniles of *P. argus* in some locations of the Bahamas and Florida Bay, Eggleston & Lipcius (1999) found that far more pueruli arrived at the Bahamas locations but many more juveniles occurred in the Florida locations, and attributed this difference to a greater amount of settlement habitat (*Laurencia*) in Florida. In laboratory choice experiments conducted in Florida, Goldstein & Butler (2009) found that competent pueruli of *P. argus* significantly chose seawater containing odors of the red macroalgae *Laurencia* over artificial seawater, but did not show preference for seawater containing odors from seagrass over artificial seawater, while Butler & Herrnkind (1991) found that exposure to *Laurencia* extracts accelerated the molting of pueruli into first-stage juveniles. However, because the amount of area covered by *Laurencia* (or other bushy macroalgae) is highly variable at local and regional scales, many pueruli likely end up settling in seagrass meadows. Thus, at local scales in Florida, there appears not to be a correlation between abundance of settlement habitat and abundance of juvenile lobsters (Butler & Herrnkind, 1992, 1997; Field & Butler, 1994; Bertelsen *et al.*, 2009).

At some point during the first year post-settlement, juvenile lobsters undergo their first ontogenetic habitat shift. These “large juveniles” cease to find protection among the vegetation and seek structured “crevice dens” within or adjacent to the nursery habitats to find protection from predators, but also to modulate harsh environmental conditions such as intense sunlight, high-energy waves, and strong currents (Sih, 1980; Spanier & Zimmer-Faust, 1988; Gristina *et al.*, 2009). Therefore, rather than responding to a particular type of crevice den, the juveniles respond to the sheltering quality of these dens, be they biogenic (e.g., large sponges, the bases of octocorals, small coral heads, urchin aggregations, bryozoan colonies, empty conch shells, hollow kelp holdfasts, prop roots of coastal mangroves) or abiotic (solution holes, rocky outcrops and ledges, limestone reefs, patch reefs, mud reefs, loose rocks), including man-made objects deployed on the bottom (used tires, construction blocks, scrap metal, and many types of artificial shelters) (e.g., Davis, 1971; Pitcher *et al.*, 1992; Smith & Herrnkind, 1992; Lozano-Álvarez

et al., 1994, 2003; Acosta & Butler, 1997; Butler & Herrnkind, 1997; Dennis *et al.*, 1997; Briones-Fourzán & Lozano-Álvarez, 2001b; Mai & Hovel, 2007; Bertelsen *et al.*, 2009).

The particular time (and size) at which juveniles make this habitat shift depends on complex interactions between availability and size of crevice dens, conspecific density, and predation risk (Eggleston *et al.*, 1990; Eggleston & Lipcius, 1992; Childress & Herrnkind, 2001a; Briones-Fourzán *et al.*, 2007). In Japan, small juveniles of *P. japonicus* often change between small individual holes in vertical reef faces within a 1 m² area and large juveniles move more between larger holes. However, because the amount of holes in the reef faces decreases with increasing hole size, by the time the juveniles reach approximately 35–40 mm CL they move entirely off the reef faces into caves, ledges and spaces under large boulders in which they tend to aggregate (Yoshimura & Yamakawa, 1988; Yoshimura *et al.*, 1994; Norman *et al.*, 1994; Norman & Morikawa, 1996). Mortality of juveniles can be very high where appropriate crevice dens are scarce or sparsely distributed (Smith & Herrnkind, 1992). For example, in the Puerto Morelos reef lagoon, where crevice dens are extremely scarce, the average density of small juveniles of *P. argus* in vegetated habitats was 205 individuals ha⁻¹, while that of crevice-dwelling juveniles was 11 individuals ha⁻¹ (Briones-Fourzán & Lozano-Álvarez, 2001a,b). However, in the absence of crevice dens, even modest increases in algal biomass can significantly enhance the survival of juveniles of *P. argus* (Lipcius *et al.*, 1998). Thus, in Puerto Morelos, juveniles shifted from dwelling in vegetation to crevice dens at a smaller size in more poorly vegetated sites than in more lushly vegetated sites (Lozano-Álvarez *et al.*, 2009). In California (USA), survival of juveniles of *P. interruptus* in crevice dens was higher in the presence of an understorey of stipitate kelps (*Pterygophora californica*) than where these kelps were absent (Mai & Hovel, 2007). Still, that the first benthic habitat shift is a critical time in the life history of spiny lobsters is clearly indicated by their high mortality rates during their first year post-settlement (e.g., *P. argus*: 96–99%, Herrnkind & Butler, 1994; Cruz *et al.*, 2007b; Behringer

et al., 2009; *P. cygnus*: 80–96%, Phillips *et al.*, 2003).

Ontogenetic shifters typically exhibit complex behavioral changes during transitions from settlement through to the adult habitat (Adams & Ebersole, 2009). Thus, upon their first benthic habitat shift, many *Panulirus* lobsters become gregarious and show a strong tendency to share dens with conspecifics (e.g., *P. interruptus*: Lindberg, 1955; *P. cygnus*: Cobb, 1981; *P. argus*: Herrnkind *et al.*, 1975; Childress & Herrnkind, 1996; *P. ornatus*: Trendall & Bell, 1989; *P. japonicus*: Norman *et al.*, 1994). This social behavior is mediated by conspecific chemical communication (Zimmer-Faust *et al.*, 1985; Ratchford & Eggleston, 1998). For an individual seeking shelter, following conspecific scents into a den both reduces its time of exposure (Childress & Herrnkind, 2001a,b) and allows it to assess the quality of the den (Nevitt *et al.*, 2000), while congregating in dens can increase per capita survival through either a “dilution effect” or “group defense behavior” (Zimmer-Faust *et al.*, 1985; Eggleston *et al.*, 1990; Herrnkind *et al.*, 2001; Briones-Fourzán *et al.*, 2007; Childress, 2007). Therefore, the availability of dens that provide the potential for gregariousness can have a profound influence on the local population dynamics of *Panulirus* lobsters (Zimmer-Faust & Spanier, 1987; Eggleston *et al.*, 1990; Eggleston & Lipcius, 1992; Mintz *et al.*, 1994; Childress & Herrnkind, 1997; Herrnkind *et al.*, 1997; Briones-Fourzán & Lozano-Álvarez, 2001b; Mai & Hovel, 2007).

7.2.2 Adult and breeding habitats

When ontogenetic shifters approach or reach sexual maturity, they move again towards adult habitats and, in some cases, undergo extensive migrations towards breeding grounds. For example, in Western Australia, sub-adults of *P. cygnus* undergo a pre-breeding migration from shallow inshore limestone reefs to deeper habitats (>40 m) offshore, where breeding takes place. Many individuals move northwards over quite deep bottoms (140 m), but some move back inshore to suitable habitat in depths of 40–100 m (Phillips, 1983). At these depths, however, habitats dominated by sponges generally contain low numbers of relatively large

lobsters, while habitats dominated by the brown alga *Ecklonia* generally contain higher numbers of relatively smaller lobsters (Bellchambers *et al.*, 2010). In the warmer waters surrounding the Abrolhos Islands, where the benthic habitats comprise coral reefs, *P. cygnus* lobsters start reproducing at smaller sizes than at other locations (Melville-Smith & de Lestang, 2006).

In Torres Strait (between Australia and Papua New Guinea), smaller individuals of *P. ornatus* (age classes 1+ and 2+) actually dwell in deeper reef habitats (14–32 m) than larger individuals (2+ and 3+), which occupy the shallow reefs (1–15 m) (Pitcher *et al.*, 1992; Skewes *et al.*, 1997). The large individuals remain in the shallow reefs for several months, but between August and September of each year, virtually all females and most of the males leave the reefs and migrate for hundreds of kilometers across the Gulf of Papua towards their breeding grounds near Yule Island (Moore & MacFarlane, 1984). Here, breeding takes place in the coastal reefs but the females move offshore to release the larvae and then move back inshore again. These lobsters do not return to their former habitats. In contrast, across the eastern coast of Queensland (Australia), breeding of *P. ornatus* takes place in the local offshore reefs without the lobsters engaging in mass migrations (Bell *et al.*, 1987).

Across the Caribbean region, sub-adults of *P. argus* migrate from juvenile habitats into the coral reef habitat and the bulk of adults dwell in fore-reef areas and offshore reefs to depths in excess of 50 m (Lozano-Álvarez *et al.*, 1993; Acosta & Robertson, 2003). Breeding occurs in the reefs but the females move to deeper areas where currents are stronger to release the larvae (Cruz *et al.*, 1986; Herrnkind & Lipcius, 1989; Lozano-Álvarez *et al.*, 1993). Individuals of *P. argus* do not undergo breeding migrations. However, in some locations thousands of individuals undergo spectacular mass migrations forming single-file queues after the arrival of the first cold fronts in late autumn or early winter causes a sudden drop in temperature and an increase in turbidity (Kanciruk & Herrnkind, 1978). The queues move day and night over open low-relief areas, occasionally stopping to rest when they encounter isolated patch reefs and ledges that often

become packed with lobsters (see review in Herrnkind *et al.*, 2001).

Because a large body size confers an additional refuge against predators (Werner & Gilliam, 1984), large adults of *Panulirus* often dwell singly and may even defend their dens aggressively against conspecifics (e.g., *P. interruptus*: Lindberg, 1955; *P. cygnus*: Chittleborough, 1974; *P. argus*: Herrnkind *et al.*, 1975; Herrnkind & Lipcius, 1989). Large adults can also move extensively between deep and shallow habitats, possibly to forage, so that in some locations they can be found in virtually all the habitats used by the juveniles (Lozano-Álvarez *et al.*, 1991a; Acosta & Robertson, 2003). For example, in a shallow enclosed marine lagoon in Cozumel island (Mexico), very large adults of *P. argus* (>150 mm CL) were often observed walking in the open even during the day (Lozano-Álvarez *et al.*, 2003a).

7.2.3 Foraging habitats

Panulirus lobsters are opportunistic omnivores that forage at night. Although their foraging range tends to increase as they grow, the actual extent and duration of their foraging activities, and the composition of their diet, greatly depend on the types of habitat surrounding their dens. In Baja California, large juveniles of *P. interruptus* consume more amphipods and gastropods in one bay (Bahía Tortugas), but more isopods and coralline algae in another bay with different physiographic and hydrographic conditions (Bahía Sebastián Vizcaíno) (Castañeda-Fernández de Lara *et al.*, 2005b), whereas the adults, which forage over more extended areas, consume more mollusks than crustaceans (Díaz-Arredondo & Guzmán del Prío, 1995). In Western Australia, small juveniles of *P. cygnus* forage over small areas close to their dens, usually within a radius of 20 m but sometimes up to 50 m, moving at rates of 1–18 m min⁻¹ depending on the degree of exposure of the bottoms they traverse, often following circuitous routes (Chittleborough, 1974; Jernakoff, 1987). Large juveniles cover greater distances, between 72.5 and 585 m per night, and forage for most of the night over seagrass, sand, and macroalgal patches close to the limestone reefs where they reside (Joll &

Phillips, 1984; Cobb, 1981; Phillips *et al.*, 1984; Edgar, 1990; Jernakoff *et al.*, 1987; MacArthur *et al.*, 2008). However, they consume proportionally more small mollusks when they forage over seagrass patches (typically in more shallow and protected waters) and proportionally more sponges, colonial ascidians, and coralline algae when they forage over macroalgae/sand patches (typically in deeper, more exposed waters) (MacArthur *et al.*, 2011). Upon moving to the deep habitats, sub-adults of *P. cygnus* can walk at maximum rates of 622 m day⁻¹ (Phillips, 1983), and lobsters that dwell in deep habitats consume more crustaceans than coralline algae or mollusks (Waddington *et al.*, 2008).

Similarly, small juveniles of *P. argus* (<20 mm CL) forage over distances of <1 m from their shelters (Childress & Herrnkind, 1994; Butler & Herrnkind, 1997), large juveniles (30–62 mm CL) forage over tens of meters, leaving their dens 2–30 times per night, usually for short periods at a time (Acosta & Butler, 1997; Briones-Fourzán & Lozano-Álvarez, 2001b; Weiss *et al.*, 2008), and sub-adults/adults (>70 mm CL) can forage for extended periods of time, sometimes walking for hundreds of meters, usually returning to the same area and sometimes to the same den before dawn (Herrnkind *et al.*, 1975; Lozano-Álvarez *et al.*, 2003b, 2009). In Alacranes Reef (Mexico), an isolated oceanic reef in the Gulf of Mexico, the highest densities of *P. argus* lobsters occurred in those areas where the reef patches were both more complex (Ríos-Lara *et al.*, 2007) and nearer to seagrass/macroalgal meadows (Bello *et al.*, 2005), suggesting that the spatial distribution of lobsters in this isolated reef reflects the proximity of abundant shelter to rich food resources. Stable isotope analyses of juvenile *P. argus* dwelling in hard-bottom areas of Florida Bay indicated a stronger association of these lobsters with macroalgae than with seagrasses (Behringer & Butler 2006a), but juveniles of *P. argus* that dwell in mangrove edges or reef lagoons consume proportionally more small mollusks, while sub-adults/adults that dwell in coral reefs consume proportionally more crustaceans (Herrnkind *et al.*, 1975; Colinas-Sánchez & Briones-Fourzán, 1990; Cox *et al.*, 1997; Briones-Fourzán *et al.*, 2003).

7.3 Habitat specialists

The post-larvae of habitat specialists settle into the same location in which they will remain throughout their benthic life stages. Although individuals may undergo minor ontogenetic habitat shifts (e.g., juveniles may use microhabitats within adult habitats) or shift microhabitats in areas of different complexity to reduce predation, these shifts occur within the same site (Adams & Ebersole, 2009). Based on these criteria and on available life history information, *Panulirus* species that appear to fall into this category are *P. penicillatus*, *P. guttatus*, *P. echinatus*, *P. pascuensis*, *P. inflatus* and, with some doubt, *P. versicolor*, *P. marginatus*, and *P. homarus rubellus*. All these species dwell in crevice-rich habitats such as coral reefs or complex rocky bottoms, presumably throughout their benthic life, but vary in the extent of their geographical distribution and in their degree of mobility and gregariousness.

Panulirus penicillatus is the most longitudinally widespread species of spiny lobster, ranging from the Red Sea (30°E) to the Galapagos archipelago (90°W) (Holthuis, 1991). This species typically occupies the shallow, subtidal zone of coral reef slopes or rocky bottoms with clear water and high-energy waves (de Bruin, 1969; George, 1974; Briones & Lozano, 1982; Ebert & Ford, 1986). Juveniles and adults are known to occur in the same areas and to forage over the same habitat in which they dwell (de Bruin, 1969; Pitcher, 1993; Yoshimura *et al.*, 1994). In the Galapagos archipelago (Ecuador), 78% of 1414 individuals of *P. penicillatus* were found at depths of 0–5 m and the greatest densities occurred in small islands where the steeply sloping rocky coastline rapidly attains great depths (Hearn & Murillo, 2008). Holthuis & Loesch (1967) often found 50–100 individuals of *P. penicillatus* sharing large individual caves, implying that this species is highly gregarious. Movements of *P. penicillatus* appear to be restricted, as 467 individuals were recaptured on the same site of release or within 5 km of their original tagging site (Hearn & Murillo, 2008).

The pueruli of *P. guttatus*, a species that occurs throughout the wider Caribbean region, are known to settle directly into small holes in the coral reef

habitat, where the full size range of these lobsters occurs (Briones-Fourzán, 1995; Briones-Fourzán & McWilliam, 1997; Sharp *et al.*, 1997; Robertson & Butler, 2009). Man-made jetties built with large granite and limestone boulders also sustain populations of *P. guttatus* (Caillouet *et al.*, 1971). These lobsters occupy the entire coral reef habitat but tend to occur at higher densities in fore-reef zones exposed to wave action (Acosta & Robertson, 2003; Lozano-Álvarez *et al.*, 2007). They forage on the reef itself, usually close to protective recesses (Wynne & Côté, 2007), and consume small crustaceans, mollusks, and coralline algae, but also echinoderms, ascidians, and sponges (Colinas-Sánchez & Briones-Fourzán, 1990). Individuals of *P. guttatus* have a maximum home range of about 100 m and tend to remain on the same reef patch for several years, suggesting that this species may be distributed in relatively small, highly fragmented populations constrained to individual patches of coral reef (Lozano-Álvarez *et al.*, 2002; Negrete-Soto *et al.*, 2002; Robertson & Butler, 2009). *Panulirus guttatus* exhibits a rather low degree of gregariousness, with many individual lobsters occupying individual reef crevices (Sharp *et al.*, 1997; Briones-Fourzán & Lozano-Álvarez, 2008). Large males in particular defend their dens aggressively from conspecific intruders (Segura-García *et al.*, 2004). However, when reproductive activity in the population is more intense, *P. guttatus* lobsters are more attracted to conspecific chemical cues (Briones-Fourzán & Lozano-Álvarez, 2005) and show a more aggregated distribution in the reef patches in which they reside (Briones-Fourzán *et al.*, 2013).

Panulirus echinatus occurs in oceanic islands of volcanic origin across the Atlantic ocean and in rocky reefs of north-east Brazil. In Ascensión Island (South Atlantic), a small juvenile 9.5 mm CL was collected in the same habitat as adults (Manning & Chace, 1990). In reefs off north-east Brazil, juveniles and adults occupy the same habitats but, according to Vianna (1986), mature males occur to depths of 25 m whereas females are rarely found below 5 m in depth. Juveniles and adults were collected in trammel nets deployed on or near coral and rocky reefs in Pernambuco, where *P. echinatus* is quite abundant (Barreto *et al.*, 2009), and in traps

deployed on hard grounds around volcanic islands of the São Pedro and São Pablo archipelago (Pinheiro *et al.*, 2003). In this latter location, stomach content analyses revealed that adults of *P. echinatus* consume almost as much plant material (green algae, calcareous algae, and coralline algae) as animal food (mostly fish and crustaceans) (Goés & Lins-Oliveira, 2009).

The distribution of *P. pascuensis* appears to be restricted to a few south Pacific islands between latitudes 20°S and 30°S (Easter Island, Pitcairn Island, Salas y Gómez, and Rapa) (Holthuis, 1991; Poupin, 2003; Anonymous, 2011), where these lobsters dwell in rocky bottoms. No information on the juvenile stages of this species was found. In Easter Island, *P. pascuensis* has been decimated by over-fishing, but Boyko (2003) remarked that very large individuals may be partially protected from harvesting because they are difficult to sell to local restaurants. In Salas y Gómez, large individuals were observed dwelling alone or in groups of up to six individuals in caves along the rocky slope to depths of 36 m, but more often between 20 and 35 m (Anonymous, 2011).

Panulirus inflatus, a species endemic to the Mexican Pacific coast, dwells in shallow rocky habitats with relatively clear waters (Briones-Fourzán & Lozano-Álvarez, 1992; Pérez-González, 2011). In Zihuatanejo (Mexico), small juveniles of *P. inflatus* were observed dwelling among the profuse biota fouling the piles of concrete piers from just below the sea surface to a depth of 3 m (see Section 7.3), and large juveniles and adults were often found side by side in caves and crevices during the day. These lobsters appear to have a rather sedentary lifestyle, as suggested by multiple recaptures of the same individual lobsters in the same rocky outcrops (Lozano *et al.*, 1982) and the composition of their stomach contents, which included small invertebrates (bivalves, gastropods, crabs, sea urchins, polychaetes and sipunculids) typical of rocky bottoms (Lozano-Álvarez & Aramoni-Serrano, 1996).

Panulirus versicolor occurs in shallow waters of the Indo-Pacific, usually <15 m in depth, in areas ranging from exposed coral reef slopes with clear waters through to sheltered lagoonal or coastal areas with relatively turbid waters (Williams, 1986;

Pitcher, 1993), but small juveniles usually occupy small holes in the same areas in which adults dwell (Berry, 1971a; George, 1968; Kuthalingam *et al.*, 1980; MacDonald, 1982). In the Great Barrier Reef (Australia), individuals of *P. versicolor* were found to be gregarious and to have strong associations with small reef areas for considerable periods of time. The home range of adults of *P. versicolor* is in the order of 200–300 m although some individuals, in particular males, can move between several dens up to 400 m apart from each other in any 10-day period (Frisch, 2007, 2008).

According to Parrish & Polovina (1994), the pueruli of *P. marginatus*, a species endemic to the Hawaiian archipelago, settle directly into the adult grounds. Because benthic populations of these lobsters occupy individual banks that are isolated by the surrounding deep waters, their distribution greatly depends on the abundance of vertical relief and the height of bank summits (Polovina *et al.*, 1995). The mobility of these lobsters appears to be restricted, as 42% of 641 individuals were recaptured at their same sites of release and 97% within distances <1 km (MacDonald, 1984). *Panulirus homarus rubellus* dwells in rocky reefs, from the shallow intertidal surf zones to depths <10 m (Heydorn, 1969). Berry (1971b) collected individuals over the full size range (7–126 mm CL) from the same sampling sites in Natal (South Africa) and remarked that these lobsters were very gregarious.

7.4 Coexisting species: interspecific trade-offs

Given the great overlap in geographic distribution of many *Panulirus* species (Table 7.1), two or more species of this genus commonly coexist at regional or local spatial scales. To be able to coexist, similar species require some form of niche differentiation or resource partitioning that increases the strength of intra-specific competition relative to that of inter-specific competition (Amarasekare, 2003). In other words, coexistence of similar species may be promoted by trade-offs in species performance of different ecological functions (Kneitel & Chase, 2004). Trade-offs for regional coexistence include

a differential habitat use and the competition/colonization trade-off, which holds that species differ in their ability to disperse to and colonize new habitats versus their ability to compete once in a habitat, with strong competitors being weaker colonizers (dispersers) and weak competitors being strong colonizers. Trade-offs for local coexistence include, among others, differential use of resource types, susceptibility to predators, and fitness in a temporally variable environment (e.g., Tilman, 1994; Wang *et al.*, 2002; Kneitel & Chase, 2004).

For example, at the regional level, the five species distributed along the eastern coast of south Africa (*P. homarus rubellus*, *P. penicillatus*, *P. versicolor*, *P. longipes longipes*, *P. ornatus*) tend to be separated by abiotic environmental features such as water temperature and degree of turbidity, depth, habitat exposure, and tidal range (Berry, 1971a). In other areas of the Indo-west Pacific where *P. ornatus*, *P. versicolor*, *P. l. longipes*, *P. polyphagus*, and *P. penicillatus* are distributed, *P. polyphagus* occurs in muddy bottoms where the water is most turbid, *P. ornatus* exhibits a broad depth distribution, from reef lagoons to fore-reef zones down to 100 m in depth, including low-energy areas with greater coastal influence and water turbidity as well as areas with low coral cover, *P. versicolor* inhabits areas with prolific coral growth down to approximately 20 m in depth, *P. l. longipes* (or in some locations *P. l. bispinosus*) is more common in reef flats with stunted corals, and *P. penicillatus* occupies the high-energy reef crest area (George & Main, 1967; George, 1968, 1974; de Bruin, 1969; Pitcher, 1993; Coutures & Chauvet, 2003).

However, at a more local scale, if species A tends to co-occur with species B and C, this does not necessarily imply that species B and C also co-occur, because species A and B may co-occur in different sites than those where species A and C are present (Sfenthourakis *et al.*, 2005). For example, Plate 7.1 shows some locations where different species distributed along the eastern Pacific and the Atlantic oceans co-occur. In the Galapagos archipelago, where *P. gracilis* co-occurs with *P. penicillatus*, the former dwells under flat rocks or in cracks between rocks at depths >5 m whereas the latter occupies the more shallow (<5 m in depth), exposed

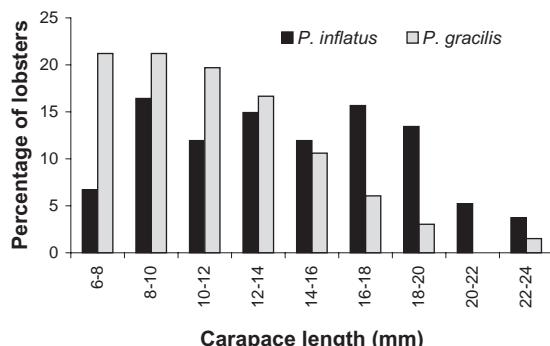


Fig. 7.3 Size distribution of small juveniles of *Panulirus inflatus* and *P. gracilis* co-occurring in Zihuatanejo, Mexico (E. Lozano-Álvarez, unpubl. data).

rocky areas (Holthuis & Loesch, 1967). Further north, along the Pacific coast of Mexico, where *P. gracilis* co-occurs with *P. inflatus* (Holthuis & Villalobos, 1961), the former occupies different types of habitat, from rocky bottoms with clear water to gravel-sand bottoms near river discharges where water can be considerably turbid, whereas *P. inflatus* occurs exclusively in rocky habitats and not in gravel-sand bottoms (Lozano *et al.*, 1982; Briones-Fourzán & Lozano-Álvarez, 1992; Pérez-González, 2011). Thus, the benthic distribution of both species greatly overlaps in rocky habitats. The two species can even share individual dens (caves), with *P. inflatus* typically occupying the deep recesses and *P. gracilis* the cave entrances. But as the carrying capacity of a particular rocky area becomes saturated, individuals of *P. inflatus*, which forage exclusively over the same rocky habitats, are able to displace individuals of *P. gracilis*, which can exploit food and shelter resources over different types of habitats (Lozano *et al.*, 1982; Lozano-Álvarez & Aramoni-Serrano, 1996). However, interestingly, both species appear to settle in similar habitats. In Zihuatanejo (Mexico), small juveniles of both species over the same size range (6–24 mm CL) were collected among the sessile biota (barnacles, small octocorals, sponges, and ascidians) fouling the concrete piles of a large pier at depths of 0–3 m, but twice as many individuals of *P. inflatus* ($N = 134$) than of *P. gracilis* ($N = 66$) were collected over the same sampling period. Also, the

size distribution of the small juveniles was more platykurtic for *P. inflatus* and more positively skewed for *P. gracilis* (Fig. 7.3) and hence the mean size was significantly larger ($t_{198} = 4.714$, $p < 0.001$; log-transformed data) for *P. inflatus* (14.3 ± 4.5 mm CL, mean \pm SD) than for *P. gracilis* (11.3 ± 3.7 mm CL) (E. Lozano-Álvarez, unpubl. data).

Panulirus argus, *P. laevicauda* and *P. echinatus* co-occur in north-east Brazil. *P. echinatus* occupies mostly offshore rocky bottoms but also abounds in inshore coral reefs (Barreto *et al.*, 2009) whereas, according to Fonteles-Filho (2000), *P. argus* occupies a much wider shelf area than *P. laevicauda*, which mainly occurs in the inner shelf area, and these two species avoid competition for food and shelter by occupying nursery and breeding grounds at different times of the year. Further north, across the wider Caribbean region, *P. argus* co-occurs with *P. guttatus* and the distribution of these species overlaps in the coral reef habitat. However, *P. guttatus* is more prevalent on the fore-reef habitat, over the middle and upper portions of the reef profile, and at the vault (i.e., the ceiling and walls) and deepest recesses of the dens, whereas *P. argus* is more prevalent on the back-reef and deeper reef habitats, over the lower portion of the reef profile, and at the floor and entrances of dens (Cailliet *et al.*, 1971; Sharp *et al.*, 1997; Lozano-Álvarez & Briones-Fourzán, 2001; Acosta & Robertson, 2003; Lozano-Álvarez *et al.*, 2007). Also, *P. guttatus* forages over the reef itself (Wynne & Côté, 2007), whereas *P. argus* forages over adjacent seagrass and hard-bottom areas (Cox *et al.*, 1997; Briones-Fourzán *et al.*, 2003). The degree of gregariousness (mediated by conspecific scents) is high in *P. argus*, a species that expresses antipredator group defense behavior (Herrnkind *et al.*, 2001; Dolan & Butler, 2006), but low in *P. guttatus*, a species that does not express this behavior (Briones-Fourzán *et al.*, 2006). Therefore, conspecific scents positively influence shelter selection by individuals of *P. argus* irrespective of season, size, or sex (Ratchford & Eggleston, 1998), but their influence on shelter selection by individuals of *P. guttatus* varies with size, sex, and intensity of reproductive activity (Briones-Fourzán & Lozano-Álvarez, 2005; Briones-Fourzán, 2009). The degree of den sharing by

congeners depends to some extent on the local abundance of each species and on the particular characteristics of individual dens, given that *P. guttatus* tends to prefer deeper dens than *P. argus* (Sharp *et al.*, 1997; Lozano-Álvarez & Briones-Fourzán, 2001; Guzmán & Tewfik, 2004). However, both species respond neutrally to the scents of each other (Briones-Fourzán *et al.*, 2008b), potentially explaining why, across the reef habitat, den sharing by conspecifics is more common than den sharing by congeners (Briones-Fourzán & Lozano-Álvarez, 2008).

Panulirus guttatus is also more vulnerable to predators than *P. argus* (Briones-Fourzán *et al.*, 2006; Lozano-Álvarez *et al.*, 2007; Briones-Fourzán, 2009), which could partially explain why the former occupies the deep recesses of caves while the latter occupies the entrance to the dens. A similar occupation of the inner space of shared dens is shown by individuals of *P. inflatus* and *P. gracilis* (as previously noted) and by individuals of *P. l. bispinosus* (the deep recesses) and *P. bruneiflagellum* (the entrances) in the Ogasawara Islands, Japan (Sekiguchi & George, 2005) suggesting that a differential vulnerability to predators is a trade-off promoting the local coexistence of other species of *Panulirus*.

7.5 Global and local threats to habitats used by *Panulirus* lobsters

In many marine ecosystems, habitat loss and habitat degradation (loss of quality) are the greatest threats to biodiversity and abundance of many species (Mangel, 2000). In particular, biogenic habitats that occur in close proximity to densely populated coastal regions exhibit the highest loss rates (Harrison *et al.*, 2006; Boström *et al.*, 2011). For example, at the global scale, the loss rates of seagrasses, mangroves, and coral reefs – essential habitats for many *Panulirus* species – range between 1% and 9% per year (Duarte *et al.*, 2008; Waycott *et al.*, 2009). Most of the causes of habitat loss and degradation are anthropogenic in origin, including adverse fishing practices, coastal development (which increases pollution, sediment runoff, and eutrophication), and climate change, but

their effects on coastal ecosystems are synergistic (Hughes & Connell, 1999; Strickland & Grosse, 2000). Thus, the general decline in production of *Panulirus* lobsters over the last few decades (Phillips & Melville-Smith, 2006) is possibly due not only to overexploitation, but to its combination with habitat loss and degradation, as has been suggested for *P. argus* in particular (Muñoz-Nuñez, 2009; Ehrhardt *et al.*, 2010; Puga *et al.*, 2010).

7.5.1 Fishing practices

Panulirus lobsters are fished with a variety of fishing methods that include trawl nets, traps, pots, tangle nets, and gill nets that are deployed from boats of many types and sizes, and in shallow habitats they are also caught by hand or with snares, hooks, or bully nets using hookah-, scuba- or free-diving (see Phillips & Melville-Smith, 2006). The pervasive damage that continued trawling inflicts on benthic habitats is well documented (e.g., Auster & Langton, 1999; Thrush & Dayton, 2002) but traps, pots, gill nets, and tangle nets also damage benthic habitats by crushing organisms upon contact with the bottom, by pulling up biotic structures upon being lifted from the bottom, and by dragging during storms (Chuenpagdee *et al.*, 2003; Lewis *et al.*, 2009). Boat propellers can cause extensive damage to shallow seagrass meadows and increase their fragmentation into ever smaller patches (Dawes *et al.*, 2004), while lost fishing gear and continued diving activities can have substantial impacts on coral reefs (Chiappone *et al.*, 2005; Sadovy, 2005). Moreover, irrespective of the fishing method, fishing effort is usually not distributed at random but is rather localized on particularly productive habitat patches or where aggregations of target species are known to occur (Seijo *et al.*, 2004; Bello *et al.*, 2005; Wynne & Côté, 2007). Improved capability to find these patches (e.g., by using GPS) is expected to both increase and concentrate fishing effort within specific areas, further increasing the potential for destroying or degrading critical habitat types (Caddy, 2008). In some locations, the removal of large predators can indirectly cause phase shifts in habitats. For example, according to Edgar *et al.* (2010), the impacts of the 1982/1983 El Niño on

the marine ecosystems of the Galapagos were probably magnified by the removal of large spiny lobsters and predatory fish by artisanal fishing through a cascade of indirect effects involving population expansion of grazing sea urchins. As a result, heavily grazed reefs with crustose coralline algae replaced former macroalgal and coral habitats.

7.5.2 Coastal development

The impacts of coastal development, which includes activities such as construction, agriculture, aquaculture, and hydrological alterations, can permeate an entire coastal marine ecosystem, especially in tropical areas with oligotrophic waters. For example, in Cuba, the extensive construction of dams and highways in the 1990s interrupted the natural run-off of nutrient rich fresh water to the coastal areas, significantly impacting the nursery habitats of *P. argus* (Ehrhardt *et al.*, 2010; Puga *et al.*, 2010). In Florida, extensive hydro-engineering of the Everglades caused a cascade of effects over time that resulted in the destruction or degradation of marine habitats used by different life stages of *P. argus* (Butler *et al.*, 1995; Herrnkind *et al.*, 1997; Dawes *et al.*, 2004; Butler, 2005). Seagrasses and coral reefs are particularly responsive to increases in nutrient and sediment run-off due to coastal development (Fourqurean *et al.*, 2003; Orth *et al.*, 2006). As water quality decreases, seagrasses are replaced by faster growing plant competitors like macroalgae and microalgae (Duarte, 1995). In the Bahamas archipelago, a 53-year comparison of near-shore environments using aerial imagery showed a more significant loss of patch reefs and seagrass areas near islands that had increasing rates of population and coastal development (Sullivan-Sealy, 2004).

7.5.3 Climate change and ocean acidification

The accumulation of carbon dioxide (CO_2) and other greenhouse gases in the atmosphere due to human activities is affecting marine ecosystems through climate change and ocean acidification (Raupach *et al.*, 2007). Climate change is already affecting reef-building corals across the world via

increases in coral bleaching events and disease outbreaks, which can cause widespread coral mortality (Hoegh-Guldberg *et al.*, 2005; McWilliams *et al.*, 2005; Harvell *et al.*, 2007), resulting in marked declines in live coral cover and in phase shifts from coral-dominated to fleshy algae-dominated ecosystems (Hughes, 1994; Gardner *et al.*, 2003; Bruno & Selig, 2007). The increase in ambient and seawater temperature is also expected to increase the strength and duration of hurricanes (Webster *et al.*, 2005), which can also cause losses of live coral cover (Gardner *et al.*, 2005). Because the magnitude of the immediate coral loss increases with hurricane intensity and with the time elapsed since the last impact, more intense and/or frequent hurricanes could potentially overwhelm the natural resilience of coral reefs (Nyström & Folke, 2001; Álvarez-Filip *et al.*, 2009a). Decreases in live coral cover do not immediately result in loss of available habitat because the reef framework can persist long after the death of corals (Álvarez-Filip *et al.*, 2009b) but ocean acidification, which enhances calcium carbonate dissolution, might eventually exacerbate the balance towards net reef erosion (Sheppard *et al.*, 2002; Harvell *et al.*, 2007; Hoegh-Guldberg *et al.*, 2007). As a result, coral reefs worldwide are becoming flatter and more structurally homogeneous (Álvarez-Filip *et al.*, 2009b). This loss of habitat complexity is already affecting many reef-associated species (e.g., Gratwicke & Speight, 2005; Pratchett *et al.*, 2008; Paddack *et al.*, 2009).

Another potential effect of more frequent and strong hurricanes would be an increase in partial destruction or fragmentation of seagrass–macroalgal habitats via changes in sediment levels, selective elimination of plant species, and migration of blowouts (Patriquin, 1975; van Tussenbroek, 1994; Fourqurean & Rutten, 2004; van Tussenbroek *et al.*, 2008). For example, in Bahía de la Ascensión, Mexico, the passage of two major hurricanes did not greatly impact areas with high seagrass coverage but resulted in further fragmentation of already fragmented seagrass meadows (Arellano-Méndez *et al.*, 2011). Increases in seawater temperature could also trigger ecosystem-wide changes in subtropical/temperate areas. For example, the high temperatures associated with the strong

1997–98 El Niño event ravaged the macroalgae populations throughout Bahía Tortugas (Baja California, Mexico), leaving virtually no settlement areas for *P. interruptus* at the same time that artificial collectors recorded a high pulse of pueruli influx into the bay (Guzmán del Prío *et al.*, 2003).

7.5.4 Potential effects of habitat loss

Little is known on the potential long-term effects of habitat loss and degradation for *Panulirus* lobsters (but see Herrnkind *et al.*, 1997). A major concern is whether population size and other ecological variables change linearly with habitat loss or whether they suddenly decline more rapidly below a “critical threshold” level of habitat (Swift & Hannon, 2010), but the potential for critical thresholds to occur depends on species-specific features (e.g., dispersal, area/edge sensitivity, predator-prey relationships, perception of patchiness) and seascape characteristics (e.g., fragmentation, matrix quality, rate of change) (Egginton *et al.*, 1998; Hovel & Lipcius, 2001; Boström *et al.*, 2006; Hovel & Regan, 2008; Swift & Hannon, 2010). That local populations of spiny lobsters are likely interconnected by the lengthy pelagic larval phase makes the possible scenarios more uncertain. However, in most *Panulirus* species, individual fitness tends to be positively related to population size or density, a situation known as the Allee effect (Allee, 1927). Because habitat loss reduces the carrying capacity of a seascape, there might be a critical threshold level of habitat below which Allee effects come into play. If these effects become strong, a population might no longer have the ability to reach or maintain itself at the carrying capacity of the remaining habitat (Stephens & Sutherland, 1999; Greene, 2003; Swift & Hannon, 2010). For ontogenetic shifters, an increase in fragmentation of nursery habitats may exacerbate demographic bottlenecks, while loss of structure may disrupt important linkages between juvenile and adult habitats by reducing foraging success and increasing predation mortality of juvenile lobsters (Caddy, 2008). Seagrass loss may also disrupt movement corridors between insular habitats. In Belize, for example, immigration and emigration rates of juveniles of *P. argus* were several times

higher on mangrove and coral islands surrounded by seagrass than on mangrove and coral islands surrounded by sand and rubble (Acosta, 1999), while in Bahía de la Ascensión (Mexico), large juveniles of *P. argus* exhibited greater mobility in lush seagrass areas bordered by coastal mangroves than in less vegetated areas away from mangroves (Lozano-Álvarez *et al.*, 2003b). The flattening and loss of structural complexity of coral reefs might deny access to suitable reproductive areas to adults of ontogenetic shifters and decrease the amount of microhabitats for all benthic stages of habitat specialists, potentially causing long-term population declines.

7.6 Habitat management

In response to the current threats to marine ecosystems in general and to exploited species in particular, it is now recognized that fishery management regimes should be expanded to include the very basis of healthy fisheries: the habitat itself (Rosenberg *et al.*, 2000). This recognition has led to the definition of “essential fish habitat” and to the emergence of the ecosystem approach to fisheries management (e.g., Conover *et al.*, 2000; Rosenberg *et al.*, 2000; Pikitch *et al.*, 2004; Ehrhardt *et al.*, 2010). Fisheries-related habitat management involves conservation, restoration, and mitigation of system functions that are crucial to the sustainability of economically significant species at all life stages (Stoner, 2003). Habitat management measures that may be particularly helpful to mitigate the loss or degradation of essential habitats for *Panulirus* lobsters are the establishment of marine protected areas and habitat enhancement (Langton *et al.*, 1996).

7.6.1 Marine protected areas

Marine protected areas (MPAs) are areas of the ocean designated to enhance conservation of marine resources and to help protect critical habitats for species that have been depleted through overfishing or habitat destruction (Conover *et al.*, 2000). However, the actual level of protection within MPAs varies widely: some allow certain

extractive activities such as recreational and/or commercial fishing, while others prohibit all kinds of fishing activities as well as the removal or disturbance of any living or non-living marine resource, except as necessary for monitoring or research to evaluate reserve effectiveness (Lubchenco *et al.*, 2003). Regardless, in this chapter we adopt the broad definition of MPAs and consider MPAs from the point of view of the protection of critical habitats for *Panulirus* lobsters with special reference to *P. argus*, because this species alone constitutes approximately 50% of the world catch of spiny lobsters (Phillips & Melville-Smith, 2006) but its landings have been declining in some Caribbean sub-regions for the last 10 years (Ehrhardt *et al.*, 2010).

It has been proposed that, in order to protect a target species, MPAs should be sized and spaced to enable a significant proportion of larvae to disperse to surrounding fished areas (e.g., Sale *et al.*, 2005). On the other hand, it has also been proposed that increasing the extent of critical habitats for a given species within a MPA can be a more effective strategy to enhance populations and prevent local extinctions than other management measures (Babcock & Pikitch, 2004). However, this approach requires substantial knowledge on the habitat requirements of the target species. For example, the obligate reef-dweller *P. guttatus* would require MPAs with large areas of coral reef habitat, whereas its sympatric species *P. argus* would require MPAs containing large areas of heterogeneous habitats including seagrass beds (nursery habitats) and coral reefs (adult habitats) (Acosta & Robertson, 2003). But from a metapopulation perspective, the location of MPAs (i.e., in source or sink habitats) is important because the persistence of benthic populations of lobsters depends not only on the amount and quality of nursery and adult habitats, but also on the influx levels of post-larvae, which depend on hydrographic features (Briones-Fourzán, 1994; Lipcius *et al.*, 1997, 2001; Butler *et al.*, 2001, 2005; Eggleston & Dahlgren, 2001; Stockhausen & Lipcius, 2001; Acosta, 2002). Moreover, for *P. argus*, simulation models have shown that relatively minor changes in the size and boundary conditions of a MPA (i.e., whether or not the MPA is adjacent to fished areas and the degree of fishing in

those areas) may result in major population-level responses, depending on dispersal dynamics and habitat availability (Acosta, 2002).

Nevertheless, at least in theory, a “good” MPA for *P. argus* should be located in a source location and contain sufficient habitat for all benthic life stages. Because larval production depends on adult biomass, the build-up of adult lobsters in a MPA is likely to increase larval output from the MPA (‘recruitment subsidy’) whereas the increase in density of lobsters within the MPA could eventually result in a net movement of individuals to adjacent fishing areas (“spillover”) (Lozano-Álvarez *et al.*, 1993; Childress, 1997; Bertelsen & Matthews, 2001; Lipcius *et al.*, 2001; Stockhausen & Lipcius, 2001; Acosta & Robertson, 2003; Cox & Hunt, 2005; Iacchei *et al.*, 2005; Butler *et al.*, 2006; Díaz *et al.*, 2011). Indeed, along the Florida Keys, the density and mean size of *P. argus* lobsters significantly increased over time in two relatively large MPAs (50,000 and 3000 ha) that contain the entire suite of habitats used by this species, but not in 12 other smaller MPAs (34–515 ha) that only contain adult habitats (Davis, 1977; Cox & Hunt, 2005). Interestingly, also in the Florida Keys, Eggleston & Parsons (2008) found that many *P. argus* lobsters moved into nearby MPAs in response to the disturbance caused by the recreational diving fishery outside the MPAs, a phenomenon they called “spill-in.” Lobster spill-in was particularly high into MPAs that contained relatively high densities of non-disturbed lobsters, presumably through mass-dependent conspecific chemical attraction from undisturbed sites. Spill-in may also underlie the occurrence of very large adults of *P. argus* (up to 204 mm CL) in a small MPA in Cozumel island, Mexico (Lozano-Álvarez *et al.*, 2003a). Eggleston & Parsons (2008) proposed that spill-in and spillover may potentially act in tandem, protecting fishery target species when disturbance is high, while also making them available to the fishery through both disturbance-mediated spill-in and natural MPA recovery.

However, large MPAs containing all the habitats used by a given target species may be difficult to establish. In this case, habitat management may have to be prioritized on a species-specific basis. For some species, places warranting special

protection would be historically important nurseries habitats, sites in which high densities of critical life stages occur in important habitat, or breeding sites (Langton *et al.*, 1996; Stoner, 2003; Levin & Stunz, 2005). In particular, Levin & Stunz (2005) posited that, for fish species where the exploited population is regulated by processes in the juvenile stage (as occurs in many *Panulirus* lobsters), juvenile habitats should be given a higher priority for conservation than adult habitats in order to increase post-settlement survival. A similar conclusion was reached by Ehrhardt *et al.* (2010), who proposed that the protection of shallow-water nursery habitats for *P. argus* should be of major importance to managers seeking to sustain viable fisheries.

7.6.2 Corollary: marine reserves and invasive species

Since its introduction in the early 1990s, the Indo-Pacific red lionfish (*Pterois volitans/miles* complex) has rapidly spread across the western Atlantic coast, including the Caribbean Sea and Gulf of Mexico (see Schofield, 2010). This invasive carnivore can cause deleterious changes in coral reef ecosystems via predation on native fishes and invertebrates, and competition with native predators (Albins & Hixon, 2008). However, lionfishes actually occur over mangrove, seagrass, patch reef, and deep reef habitats (e.g., Claydon *et al.*, 2009; Barbour *et al.*, 2010), that is, the same habitats used by *P. argus* and/or *P. guttatus*, and also tend to use similar microhabitats as these species. Because lionfish populations may particularly thrive in fully-protected MPAs, laboratory and field experiments are needed to assess the potential impact of lionfish on habitat use and shelter selection by *P. argus* and *P. guttatus*.

7.6.3 Habitat enhancement

Populations of ontogenetic shifters are more likely to be limited by the amount of the stage-specific habitat with the lowest carrying capacity than by gamete production, food supply, or adult habitat (Caddy, 2008). For many *Panulirus* lobsters, local demographic bottlenecks usually occur at the time of the first ontogenetic habitat shift due to con-

straints imposed by availability of crevice dens. These bottlenecks can lead to a temporary increase in predation-related mortality, disrupting functional connectivity between juvenile and adult habitats. Also, the foraging success of juvenile lobsters can be greatly reduced if appropriate dens are sparsely distributed over large areas, even if substantial food resources exist in areas beyond their foraging range (Walters & Juanes, 1993; Caddy, 2008). In such areas, adding structural elements ("artificial shelters") may provide juveniles with "stepping stones" (*sensu* Caddy, 2008) that may facilitate their access to more food resources (Lozano-Álvarez, 1995). For example, over the shelter-poor Puerto Morelos reef lagoon, Briones-Fourzán *et al.* (2003) found that resident sub-adults of *P. argus* (45–80 mm CL) exhibited a significantly lower nutritional condition than small (<15 mm CL) and large juveniles (15–45 mm CL), and speculated that the lack of suitable shelter for sub-adult lobsters in this location restricted their foraging activities to minimize their risk of predation. Indeed, in experimental sites over the reef lagoon where multiple artificial shelters (casitas) were subsequently deployed, the foraging range of sub-adults significantly increased relative to control (non-enhanced) sites (Briones-Fourzán *et al.*, 2007) and the nutritional condition of the three size classes of juvenile lobsters became similar (Briones-Fourzán *et al.*, 2009).

The artificial shelters most widely used to enhance juvenile habitats are hollow construction blocks and "casitas," probably because many spiny lobsters prefer low shelters close to the seabed (Spanier & Zimmer-Faust, 1988; Gristina *et al.*, 2009). According to Nonaka *et al.* (2000), in Japan, where there is a long tradition of habitat enhancement, artificial reefs made with construction blocks increase the catch of *P. japonicus* lobsters even in usually poor fishing grounds. However, construction blocks are particularly useful to alleviate lack or paucity of shelter for juvenile lobsters making the first ontogenetic habitat shift. Thus, in Biscayne Bay (USA), when extensive construction of a marina threatened to displace thousands of juveniles of *P. argus*, these lobsters readily occupied hundreds of concrete block structures that were temporarily deployed as alternative dens (Davis, 1985), as did juveniles following a mass mortality

of sponges, which constitute their preferred habitat over hard bottoms in Florida Bay (USA) (Butler & Herrnkind, 1997; Herrnkind *et al.*, 1997, 1999). Also in Florida, a significant increase in density of juveniles of *P. argus* after the addition of construction block dens had no effects on lobster mortality or nutritional condition but increased the short-term residency of lobsters (Behringer & Butler, 2006b). So-called “condominiums” (a double-stack of hollow concrete blocks forming a square) deployed over nursery habitats in Cuba and Mexico provide a useful tool to assess recruitment of juvenile *P. argus* into the fishery (de León *et al.*, 1991; Lozano-Álvarez *et al.*, 1994; Sosa-Cordero & Ramírez-González, 2004; Cruz *et al.*, 2007a).

7.6.4 Casitas and the controversy over their use

Casitas are a special type of large (1.5–2 m² in surface area) but low-lying (8–15 cm in entrance height) artificial shelters long used to commercially harvest *P. argus* lobsters in Cuba (where they are called “pesqueros,” Cruz & Phillips, 2000), in certain locations of Mexico (Lozano-Álvarez *et al.*, 1991b; Sosa-Cordero *et al.*, 1999; Briones-Fourzán *et al.*, 2000), and more recently in the Bahamas (Ehrhardt *et al.*, 2010). Smaller casitas (e.g., 1 m² in surface area and 4 cm in entrance height) have also been used to experimentally enhance shelter-poor juvenile/sub-adult habitats (Arce *et al.*, 1997; Sosa-Cordero *et al.*, 1998; Briones-Fourzán *et al.*, 2007; Ramírez-Estévez *et al.*, 2010). A long-standing controversy over the use of casitas is whether these structures simply attract lobsters already in the system (“attraction” hypothesis), thus increasing their vulnerability to predators, including humans, or actually increase production of lobster biomass (“production” or “enhancement” hypothesis), thus increasing their potential effects on other components of the benthic ecosystem (review in Briones-Fourzán *et al.*, 2007). However, multiple field experiments have shown that casitas increase production of lobster biomass primarily by enhancing lobster survival, because casitas (1) alleviate demographic bottlenecks by mitigating a limited supply of crevice habitat and reducing intraspecific competition for shelter, (2) allow lob-

sters to take advantage of abundant food resources over large open areas where predators would normally prevent them from doing so, and (3) increase the potential for gregariousness, thus extending the benefits of anti-predator group defense to lobsters of all sizes that occupy casitas (Eggerton *et al.*, 1990; Eggerton & Lipcius, 1992; Mintz *et al.*, 1994; Sosa-Cordero *et al.*, 1998; Briones-Fourzán & Lozano-Álvarez, 2001b; Briones-Fourzán *et al.*, 2007). The physical features of casitas are instrumental in achieving these effects because their large refuge area not only provides cover to many individual lobsters, but also to many other benthic animals as well, thus reducing interspecific competition for limited shelter resources (Lozano-Álvarez *et al.*, 2010), while their low height excludes many large predators and precludes those that are able to fit in casitas from attacking the lobsters beneath the casitas (Lozano-Álvarez & Spanier, 1997). Also, the increase in density of *P. argus* with casitas does not appear to significantly impact the abundance and diversity of the small invertebrates that constitute their prey, probably because these small animals are typically cryptic and sparsely distributed (Vidal & Basurto, 2003; Nizinski, 2007), and the “stepping stones” provided by casitas distribute the foraging activity of lobsters over wider areas (Lozano-Álvarez, 1995; Briones-Fourzán *et al.*, 2007).

It has been proposed that a controlled deployment of casitas within fully-protected MPAs may help to reduce local demographic bottlenecks by providing critical habitat to juveniles of *P. argus* and eventually increase lobster spillover from the MPAs to adjacent fishing areas (Briones-Fourzán *et al.*, 2007). But, interestingly, in MPAs where lobsters are not fished in deep habitats (e.g., because of strong currents), the use of commercial casitas to harvest lobsters in shallow habitats might work the other way around. For example, thousands of commercial casitas are distributed over a substantial portion of Bahía de la Ascensión and Bahía Espíritu Santo, two large, shallow bays located within the Sian ka'an Biosphere Reserve in Mexico (Sosa-Cordero *et al.*, 2008). During the 8-month fishing season, the local fishers continually harvest the legal-sized lobsters (and fishes of commercial value) from the casitas, thereby reducing their

potential impact on invertebrate prey (Vidal & Basurto, 2003). However, during the 4-month closed season all fishing operations completely cease, allowing many sub-adult/adult lobsters to migrate to deep offshore areas where the fishery does not operate, essentially turning the offshore habitats into a spatial refuge for the breeding population (Lozano-Álvarez *et al.*, 1993).

However, there are several reasons why casitas (and condominiums) should not be used to enhance the habitat of *Panulirus* lobsters just anywhere. First, these structures could probably work for tropical ontogenetic shifters but not for habitat-specialist lobsters (Briones-Fourzán, 1995; Okechi & Polovina, 1995). Second, they should probably not be used in tropical coastal areas where natural crevices abound (Lozano-Álvarez *et al.*, 1994; Lozano-Álvarez, 1995; Sosa-Cordero & Ramírez-González, 2004). Third, they should probably not be used in subtropical/temperate areas where changes in density of the local *Panulirus* species could potentially result in trophic cascades that could alter prey communities (e.g., *P. interruptus*: Tegner & Levin, 1983; Robles, 1997). Fourth, and perhaps most importantly, even for tropical species such as *P. argus*, the fishing and environmental impacts of extensive deployment of casitas should be properly monitored and controlled or else any production benefit might be quickly offset (Lozano-Álvarez, 1995). There is concern that this may eventually happen in the Bahamas where, according to Ehrhardt *et al.* (2010), there are currently in excess of 700,000 casitas that are never retrieved from the fishing grounds but are replaced at the rate of about 20% per year, fishing regulations are not respected, controlled, or monitored, and the environmental impact of these devices has not been assessed. In contrast, the production benefit achieved by the large-scale casita-based fishery in Cuba (with about 200,000 casitas in operation) and the much smaller-scale casita-based fishery in Mexico (with about 20,000 casitas in operation) is largely due to the proper management of fishing and environmental impacts (the “enhancement with fishing” scenario, see Powers *et al.*, 2003). In particular, both are limited-entry fisheries where ownership of casitas is warranted and the fishers comply with local regulations (Lozano-

Álvarez *et al.*, 1991b; Briones-Fourzán *et al.*, 2000; Cruz & Phillips, 2000; Sosa-Cordero *et al.*, 2008; but see Muñoz-Nuñez, 2009). Also importantly, the casitas used in these fisheries are widely spaced (e.g., 3.3 casitas ha⁻¹ over fishing grounds in Bahía de la Ascensión, Camarena-Luhrs *et al.*, 1996), a measure that may indirectly decrease their impact on seagrasses, wherein the bulk of the biomass lies below ground (e.g., van Tussenbroek, 1998).

7.6.5 Corollary: habitat enhancement and disease transmission

Another matter of debate is whether an increase in lobster density via habitat enhancement could increase the transmission of pathogenic diseases. For example, populations of *P. argus* across the Caribbean region are being attacked by a pathogenic virus (PaV1) that is potentially lethal to small juveniles, although the prevalence of overtly infected (“diseased”) lobsters varies widely in space and time (review in Behringer *et al.*, 2011). Based on results from laboratory experiments, it has been suggested that, in nature, PaV1 is most likely transmitted by contact and through water (Butler *et al.*, 2008). However, PaV1 appears to affect the normally gregarious behavior of *P. argus* lobsters. For example, in Florida Bay, most diseased lobsters were found solitary in crevice dens (mostly sponges), whereas many “healthy” lobsters (i.e., those not showing clinical signs of being infected) were found sharing dens (Behringer *et al.*, 2006). In laboratory experiments, healthy lobsters that were offered a choice between a den containing a diseased conspecific and a nearby, identical empty den, showed preference for the latter in the absence of predators (Behringer *et al.*, 2006) and in the presence of a caged octopus (Behringer & Butler, 2010). These results suggest that avoidance of dens containing diseased conspecifics might reduce contact transmission rates of PaV1 and keep the overall levels of disease prevalence low.

However, in experimental casitas deployed over the shelter-poor Puerto Morelos reef lagoon, Lozano-Álvarez *et al.* (2008) recorded high levels of cohabitation between healthy and diseased lobsters, suggesting that where crevice dens are sparsely distributed over large open areas, healthy

lobsters make a trade-off between avoiding disease and avoiding predation risk. In Bahía de la Ascensión, an analysis of the distribution patterns of thousands of lobsters among hundreds of commercial casitas revealed that the presence of diseased conspecifics did not significantly affect the distribution of lobsters among casitas, and that the prevalence of disease was significantly lower in all benthic stages of *P. argus* using casitas in shallow, non-vegetated areas than in deeper, moderately to lushly vegetated areas (Briones-Fourzán *et al.*, 2012). Furthermore, the overall average prevalence of diseased lobsters was found to be similar in Bahía de la Ascensión, México (4.7%, Candia-Zulbarán *et al.*, 2012) and the Gulf of Batabanó, Cuba (4.8%, Cruz-Quintana *et al.*, 2011), where casitas are extensively used, as in Florida Bay (5%, Behringer *et al.*, 2011), where the use of casitas is forbidden. In conjunction, these findings suggest that (i) investment in disease avoidance by healthy lobsters is modulated by shelter limitation and predation risk, (ii) contact transmission rates of PaV1 may be lower in nature than in the laboratory, and (iii) water-borne transmission rates of PaV1 may be modulated by exposure of habitats to solar ultraviolet radiation (which can damage viral particles) and the local amount of vegetation (via the degree of shading) (Briones-Fourzán *et al.*, 2012). Clearly, there remains much to be investigated about the potential effects of habitat enhancement on transmission rates of PaV1 (and other pathogenic diseases) among *P. argus* lobsters and, conversely, on the effect of pathogenic diseases on shelter selection and habitat use by *Panulirus* lobsters in general.

7.7 Conclusions

The scope of this chapter was limited to the habitats and microhabitats used by *Panulirus* lobsters. All the tropical/subtropical species in this genus represent valuable resources at local and regional scales, but the fact that they all inhabit relatively shallow-water habitats makes them particularly susceptible to overfishing and to the combined effects of multiple stressors that affect the habitats that they use. There is considerable knowledge on

the habitats used by adults of most *Panulirus* species and this knowledge has provided an important tool to study the evolution of *Panulirus* and the phylogenetic relationships among the species/subspecies than conform the genus (George & Main, 1967; George, 2006). However, from the ecological, fisheries management, and habitat conservation perspectives, it is important to determine which habitats are used by the different benthic life stages on a species-specific basis. Unfortunately, the amount of knowledge about this issue is very limited for many *Panulirus* species, so much so that their particular life history strategies (habitat specialist, habitat generalist, or ontogenetic shifter) remain to be determined. More knowledge about this issue exists for those species that support the most important fisheries, which (perhaps not coincidentally) tend to be ontogenetic shifters (e.g., *P. argus*, *P. cygnus*, *P. interruptus*, *P. ornatus*). However, both major phylogenetic lineages of *Panulirus* appear to contain ontogenetic shifters and habitat specialists (and possibly also habitat generalists), so care should be taken not to make generalizations about the life history strategies of these spiny lobsters.

In particular, more research is needed into the mechanisms by which the pueruli of different species settle and survive in different habitats. An extension of the “target area hypothesis” (*sensu* Lomolino, 1990) would predict that larger “islands” of habitat (e.g., extensive seagrass meadows) may serve as more effective target areas for settlers because they are more likely to be detected (by active settlers) or intercepted (by passive settlers). Field and laboratory experiments suggest that pueruli of the ontogenetic shifters *P. argus* and *P. cygnus* are able to assess the quality of a potential settling habitat using different types of cues (Phillips & MacMillan, 1987; Goldstein & Butler, 2009; Zito-Livingston & Childress, 2009), and that settling in a different habitat than that used by adults significantly decreases post-settlement mortality rates (Acosta & Butler, 1999). However, nothing is known on whether or how the pueruli of habitat-specialist *Panulirus* are able to assess the quality of their settlement habitats (e.g., coral reefs) or how they cope with the high predation rates typical of these habitats.

Little is known also on the interspecific trade-offs that promote the coexistence of *Panulirus* species at regional or local spatial scales. At the regional scale, an important trade-off appears to be a differential habitat use (e.g., the several *Panulirus* species that coexist across the Indo-West Pacific: George, 1968, 1974; de Bruin, 1969; Berry, 1971a; Pitcher, 1993; Coutures & Chauvet, 2003), but the competition/colonization trade-off could potentially explain the regional coexistence of some species (e.g., *P. inflatus* and *P. gracilis*: Lozano *et al.*, 1982; Lozano-Álvarez & Aramoni-Serrano, 1996). At local scales, important trade-offs appear to be differential use of resources types and vulnerability to predators (e.g., *P. argus* and *P. guttatus*: Cox *et al.*, 1997; Sharp *et al.*, 1997, Acosta & Robertson, 2003; Lozano-Álvarez *et al.*, 2007; Wynne & Côté, 2007; Briones-Fourzán & Lozano-Álvarez, 2008). Examination of the potential for species trade-offs at different scales would be an important ecological issue for the establishment of MPAs for coexisting species.

There is no doubt that essential habitats for the benthic stages of *Panulirus* lobsters are being increasingly lost or degraded throughout the world.

The move towards an ecosystem approach to management of *Panulirus* fisheries should include ecological safeguards to protect the habitats used by these species (e.g., MPAs), but this measure requires substantial knowledge on the life history strategies and the habitats used by different life stages of the target species. Because the extended larval phase of *Panulirus* lobsters provides some level of connectivity among many local populations (i.e., metapopulations), the siting of marine reserves also requires knowledge on circulation features and the most likely pathways that can assure the arrival of post-larvae to suitable areas for further development. Many *Panulirus* populations undergo local demographic bottlenecks that disrupt the connectivity between the juvenile and adult habitats, and habitat enhancement is now considered as a viable alternative to fill the gaps interrupting this connectivity (Briones-Fourzán *et al.*, 2007; Caddy, 2008). However, sufficiently long field experiments should be conducted first to examine the potential effects of habitat enhancement on other components of the ecosystem, and permanent monitoring and assessment programs should be established to detect potential longer-term effects.

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Chapter 8

Homarus

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Abstract

The chapter provides an overview of the life history and fisheries of the two clawed lobster species of the North Atlantic: the American lobster, *Homarus americanus*, and the European lobster, *H. gammarus*. The authors highlight new findings on the ecological factors affecting population dynamics, connectivity, and trophic interactions. The American lobster supports the most productive lobster fishery in the world. Although populations have been increasing in the northern part of the species' range, likely because of a favorable environment and predator depletion, stocks in the south have been declining with increasingly stressful summer temperatures and disease. The relatively small stock of European lobster has receded at the extremes of the historic range, but populations in the central part of the range have remained stable for several decades. The authors identify a need to better resolve spatial patterns of demographic and ecosystem processes that will serve stock assessments and management of these species.

Key Words: *Homarus americanus*; *Homarus gammarus*; Europe; Atlantic Canada; New England; clawed lobster; metapopulations; body size; larva; nurseries; fisheries; stock enhancement; trophic dynamics; population dynamics

8.1 Introduction

The American lobster, *Homarus americanus* Milne-Edwards, 1837, and the European lobster, *H. gammarus* Linnaeus, 1758, are the only extant representatives of their genus within the Family Nephropidae. These clawed lobsters are large-bodied, conspicuous, and ecologically and economically important. *Homarus americanus* supports the most productive lobster fishery in the world (FAO,

2012). Both species are intrinsically interesting as model systems in many biological fields. For these reasons *Homarus* may be among the most studied marine invertebrates. Two extensive monographs are foundation references for *H. americanus*: the now classic Herrick (1895, 1911) and the more recent authority published a century later (Factor, 1995). The literature on the European lobster may have a deeper history than its new world counterpart, as its taxonomic history suggests, but to our

knowledge no single text gives a comprehensive review of the species' biology. A recent review provides the most current phylogeographic status and ecological overview of the marine clawed lobsters as a group (Wahle *et al.*, in press). The volume of literature on the American lobster now far exceeds that for the European lobster, most likely because of its tremendous commercial value. Nonetheless, the two species are similar in many respects, and much remains to be learned about each if their fisheries are to be effectively managed.

This chapter updates the earlier edition by Cobb & Castro (2006). The pace of ecological and economic change experienced by lobster fisheries in less than a decade warrants an update. As with the previous version, our intent here is not a comprehensive review of all literature on *Homarus*, but rather, in keeping with the theme of this volume, a summary of issues of current importance primarily to fishery scientists, managers, and stakeholders in the industry. Over the past two decades, there has been growing concern over the ecological changes that have led to dramatic changes in ocean fisheries around the world (Jackson *et al.*, 2001; Estes *et al.*, 2011), and specifically in the North Atlantic (Worm & Myers 2003; Frank *et al.*, 2007). The clawed lobsters are no exception. Signs of depletion and ecosystem degradation manifest themselves in the densely developed coastal habitats of Europe and eastern North America where *Homarus* species reside. American lobster populations especially have seen large unexplained shifts in abundance in recent decades. Building on the earlier edition, we highlight new research in the peer-reviewed and technical literature published since the first edition. Our focus is on processes and mechanisms that influence population dynamics of the two species, and their implications for fisheries and management.

8.2 Species overview

Lobsters of the genus *Homarus* are found only in the North Atlantic Ocean, where they form the basis of important fisheries (Fig. 8.1). *Homarus americanus* is found on the western side of the Atlantic, ranging from Labrador, Canada, to shelf

waters off North Carolina, USA. *Homarus gammarus*, in the eastern coastal Atlantic, ranges from north of the Arctic Circle in Norway to Morocco, including the United Kingdom and the northern coast of the Mediterranean. The fossil record of the genus *Homarus* extends to the root of the clawed lobster Family Nephropidae, which emerged during the lower Cretaceous (Tshudy & Babcock, 1997). Williams (1995) speculated that the two recent species differentiated during the Pleistocene, but there is little new information to evaluate that hypothesis. The two species are very similar anatomically, distinguished only by color and a ventral tooth on the rostrum, present in *H. americanus* but absent in *H. gammarus*. They can be distinguished genetically but the differences between the species are slight (Williams, 1995; Ulrich *et al.*, 2001; Tam & Kornfield, 1998; Tshudy & Babcock, 1997). A little-known and rare species found in South Africa, formerly *Homarus capensis*, was reassigned to the new genus *Homarinus* on the basis of distinct morphology and molecular genetics (Kornfield *et al.*, 1995; Tam & Kornfield, 1998). Despite their convergent morphology, according to this analysis *Homarinus* and *Homarus* are less closely related to each other than *Homarus* is to *Nephrops*.

Homarus primarily occurs from the low intertidal to depths exceeding 50 m (Wahle *et al.*, in press). *Homarus americanus* extends to 100 m in the southern part of its range, but has been found to depths as great as 700 m at the continental slope where it inhabits burrows in the walls of submarine canyons. The American lobster lives in a wide variety of habitats, but is most restricted to shelter-providing habitats early in life. Rocky substrate is the most common habitat, but clawed lobsters may burrow in cohesive mud or dig bowl-like depressions in sand.

Both species of *Homarus* support valuable commercial trap fisheries. Despite its more compressed geographic range, landings of the American lobster are currently some 20-fold greater than that of the European lobster (Fig. 8.2). Since the 1980s overall landings of the American lobster have increased dramatically, but not uniformly. In the Gulf of Maine and Atlantic Canada, for example, lobster landings are currently at historic highs, while the fishery in southern New England is near

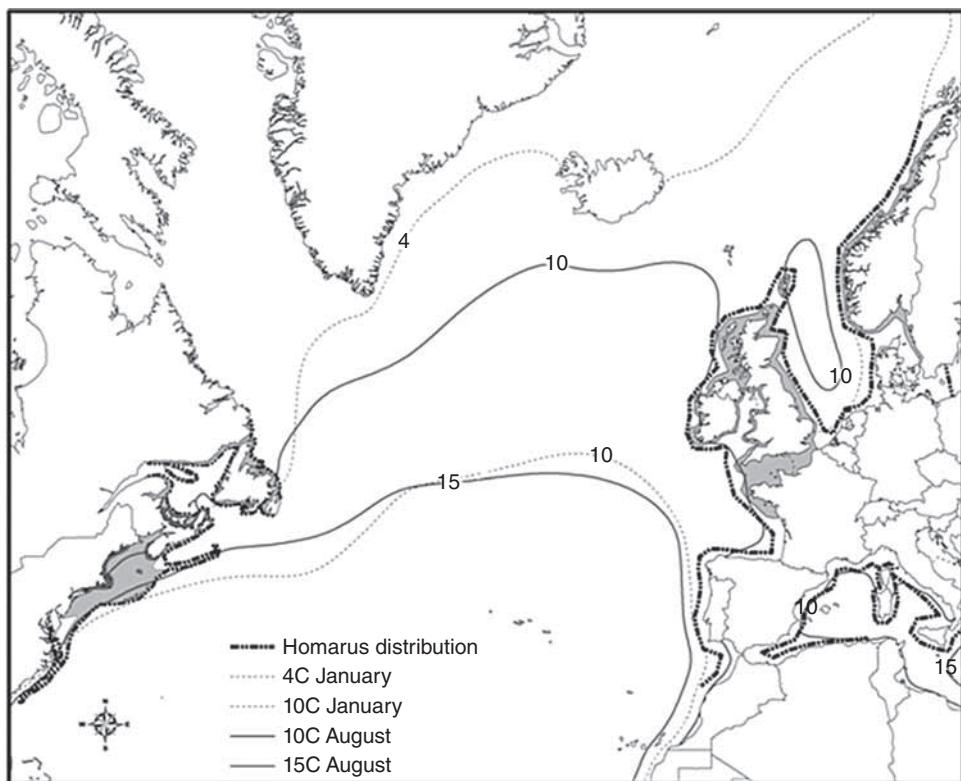


Fig. 8.1 Geographic distribution of *Homarus americanus* and *H. gammarus* in the North Atlantic relative to seasonal isotherms. Dotted boundary is species geographic range; areas in gray are prime commercial fishing grounds.

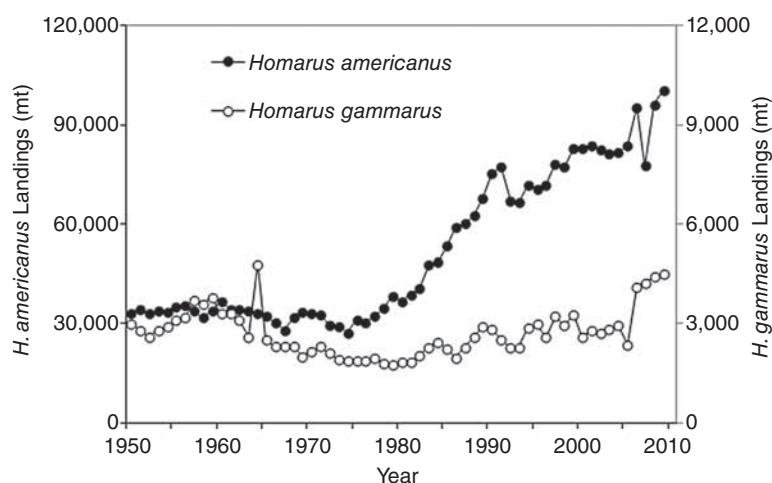


Fig. 8.2 Commercial catch of the two species of *Homarus* 1950–2010. Note 10-fold difference in scales of abundance for the two species. Data from FishStatJ, a tool for fishery statistics analysis. Release: 1.0.1. 2012.

collapse. Possible explanations for this contrast will be examined below. The European lobster supports a much smaller trap fishery which, today, is limited to the mid-latitudinal portion of the species' range.

8.3 Life-history overview

The stages of the life cycle of both species of *Homarus* are virtually identical. Three larval instars and one postlarval instar are pelagic. Following settlement to the sea bed, by the late-stage post-larva, early juveniles are cryptic and remain strongly associated with shelter. As they grow they range over increasing distances and in the case of *H. americanus* become entrained in seasonal inshore–offshore movements that track optimum water temperatures (Jury, 1999). The conspicuous ontogenetic changes in behavior and habitat have prompted the description of different ecological phases of the American lobster that can be useful in stage- or age-based modeling (Wahle & Steneck, 1991; Lawton & Lavalli, 1995; Lavalli & Lawton, 1996; Waddy & Aiken, 2000; Incze *et al.*, 2003).

The onset of sexual maturity comes sooner and at a smaller size for males than females, but mating success tends to be greater for males that are larger than their mates (Atema & Voigt, 1995). Size at maturity varies regionally and may be related to temperature. In the western Atlantic, where the latitudinal thermal gradient is steeper, females in southern New England for example mature at approximately 70–80 mm carapace length (CL), (~4–5 years), whereas those in the colder Bay of Fundy only some 300 km away mature at about 100 mm (~8 or 9 years) (Factor, 1995; Wahle & Fogarty, 2006). Differences between males and females in allometric growth of the abdomen and claws represent sex-specific investment in secondary sex characteristics, that result in males claws and female abdomen growing proportionately larger.

Adults are long-lived and iteroparous, capable of reproducing many times. The lobster mating system is polygynous whereby larger, competitively dominant males are more successful in obtaining mating shelters and in courting females. Courtship

and mating have been reviewed in detail by Atema & Voigt (1995). Females approaching molt assess the males, probably by way of chemical cues, and choose to cohabit with a male for one to several days prior to molting. Mating usually takes place shortly after the female molts; a spermatophore is deposited internally by the male in the seminal receptacle of the female. Sperm may be stored for several years (Talbot & Helluy, 1995). There is a period of mate guarding after copulation. Females may mate between molts, while hard-shelled (Dunham & Skinner-Jacobs, 1978; Waddy & Aiken, 1990), particularly if they are not inseminated. Females occasionally may mate with more than one male and multiple paternity in a brood has been detected genetically (Nelson & Hedgecock, 1977; Jones *et al.*, 2003).

Fertilization is external; as eggs are extruded from the oviduct they pass over the seminal receptacle and stored sperm is released through paired grooves (Talbot & Helluy, 1995; Aiken *et al.*, 2004). Females carry fertilized eggs cemented to the pleopods of the abdominal segments for 9–11 months. Relative to other marine decapods of similar size (e.g., spiny lobsters and crabs), *Homarus* egg sizes are large, clutch sizes small, and brood period long (MacDiarmid & Sainte-Marie, 2006).

The eggs are generally extruded in the summer or fall, and hatch the following spring–summer, producing a prelarva which rapidly molts into the first larval stage (Talbot & Helluy, 1995). Three pelagic zoeal stages last, in total, 2 weeks to 2 months, depending upon temperature (MacKenzie, 1988; Ennis, 1995). Metamorphosis to a lobster-like body plan occurs at the molt from Stage III to postlarva. The metamorphosis is accompanied by changes in behavior and habitat preference. The postlarva remains pelagic but swims forward using its pleopods; this is the only life stage in which the primary propulsion comes from these appendages. Two to 4 days after metamorphosis bottom-seeking behaviour appears, and the postlarva, upon discovering appropriate nursery habitat, makes the transition from pelagic to benthic environment and becomes a permanent resident of the sea bed (Cobb *et al.*, 1989). The newly settled young-of-year *H. americanus* are quite habitat-specific and are relatively easily captured by divers using airlift suction samplers (Wahle & Steneck, 1991, 1992; Wahle &

Incze, 1997) or vessel-deployed passive collectors (Incze *et al.*, 1997; Wahle *et al.*, 2009, *in press*). In contrast, despite extensive efforts, *H. gammarus* young-of-year have proven elusive (Mercer *et al.*, 2001; van der Meeren, 2003). It is not clear whether they simply are uncommon, and rarely settle in densities high enough to detect by these methods, or if they are yet to be found in unexpected habitats (van der Meeren, 2003). Nonetheless, early juvenile *H. gammarus* (<25 mm CL) are frequently captured in small mesh (9–11 mm) traps used by the shrimp (*Palaemon*) fishery in shallow (<20 m) mixed sediment and kelp habitats in Ireland (Oliver Tully, unpub. observations).

The juvenile phase of the life cycle is characterized by an early shelter-restricted period in which the lobster emerges infrequently from its burrow, followed by an increase in range of movement and habitat choice. The transition from planktonic to benthic habitat is thus associated with a corresponding change in diet (Sainte-Marie & Chabot, 2002). Analysis of RNA–DNA ratios (a measure of recent growth) revealed a temporary slowing in growth rate between the planktonic postlarval stage and recently settled young-of-year lobsters captured on the sea bed (James-Pirri & Cobb, 1997). This may reflect the trade-off of food for safety from predation associated with early benthic life (Wahle, 1992).

Benthic lobsters are omnivorous, feeding on a great range of benthic organisms. The range of prey species and amount consumed changes as a function of lobster size, temperature, prey availability, and molt cycle. Stomach content analysis of four size categories of Canadian *H. americanus* showed an ontogenetic shift in prey preferences (Sainte Marie & Chabot, 2002). There was a decrease in proportion of diet comprising soft animal tissue and an increase in the consumption of rock crabs (*Cancer irroratus*) as lobsters grew. Gendron *et al.* (2001) found that a diet lacking in rock crab resulted in reduced growth and ovary development in *H. americanus*. Fish used as bait is often found in the diet and could be an important contributor to lobster biomass production (Saila *et al.*, 2002; Grabowski *et al.*, 2010; Bethoney *et al.*, 2011). A diet consisting exclusively of fish, however, can have negative consequences for lobster health (Thusty *et al.*, 2007).

8.4 Growth and age

8.4.1 Components of growth

The patterns of growth and the intrinsic and extrinsic mechanisms controlling the molt increment and intermolt period have been studied intensively and has been reviewed in several times in recent years (Fogarty, 1995; Waddy *et al.*, 1995; Chang *et al.*, 2001; Hartnoll, 2001; Wahle & Fogarty, 2006).

Growth rate is usually expressed as an increase in size over time. Time (age), therefore, is a key variable. Age determination remains an elusive challenge in crustaceans, however, because of the absence of morphological age markers. Although, the “age pigment” lipofuscin has been used with some promising results, the method remains expensive, cumbersome, and fraught with its own uncertainties (see Sheehy, 2001; Wahle *et al.*, 2006, Giannini, 2008). As this volume goes to press, a new chapter in the crustacean age determination challenge is emerging with the discovery that cuticle layers accumulating in the eye stalk and gastric mill may be useful in age determination (Kilada *et al.*, 2012).

Annual growth increments have also been inferred from modes in the size distribution corresponding to early age classes in field collections from nursery grounds (Hudon, 1987; Wahle *et al.*, 2004; Gendron & Sainte Marie, 2006). Modal analysis becomes less useful, however, as lobsters grow because of highly variable growth rates.

Direct measurements of change in size over time have been gathered from tag return data that, in turn, have been used to parameterize growth models (reviewed in Wahle & Fogarty, 2006). Many studies describe growth using the von Bertalanffy function; however, empirical models that incorporate the probability of molting and the size increase at molting are perhaps more consistent with observed growth trajectories (e.g., Chen & Kennelly, 1999; ASMFC, 2009; Wahle & Fogarty, 2006). This section provides a brief overview with emphasis on recent advances.

Growth rate in crustaceans is influenced by molt increment and the time interval between molts. These two parameters have been estimated from observations of lobsters reared in laboratory and tag-recapture studies or caging experiments in the

field, but can be difficult to obtain for the largest individuals that molt infrequently and may not grow normally in captivity. The Hiatt growth equation is the linear regression analysis of the relationship between premolt and postmolt size (Fogarty, 1995; Wahle & Fogarty, 2006). The resultant slope gives a measure of proportional growth (=growth factor). For lobsters of both species in the commercial size range (~80–90 mm CL) the growth increment is around 5–10% (*H. americanus*: Wilder, 1963; Comeau & Savoie, 2001; Wahle & Fogarty, 2006; *H. gammarus*: Bennett & Lovewell, 1983; Agnalt *et al.*, 2007; O. Tully, unpublished).

The onset of maturity not only affects allometric growth of claws and abdomen, it also has a strong negative effect on the growth increment, and that effect is especially strong in females. Molt increment as a proportion of initial size typically is relatively constant prior to maturity, but declines with increasing size during the adult years. This observation has been used to justify a “broken stick” approach to modeling growth factor as a function of size: American lobster at the southern (warmer) extreme of their range have a steeper decline in post-maturity molt increment, suggesting the onset of maturity brings a greater cost in warmer regimes (Plate 8.1A,B; Bergeron, 2011). This may explain why adult sizes tend not to be as great as they are in northern, cooler regimes. Regional differences in allometric growth are already well documented for the American lobster, and likely reflect environmental effects, although heritable differences cannot be ruled out (Cadrin, 1995, 2000; MacCormack & DeMont, 2003).

Injury or trauma and limb loss (autotomy) (Juanes & Smith, 1995) can also reduce molt increment. Autotomy is an energetic cost to the individual and reduces growth rate. In *H. americanus*, Cheng & Chang (1993) found that autotomy decreased molt increment by 30–40%, and that the onset of the molt was hastened or delayed, according to when in the molt cycle the limb loss occurred. Even the injury associated with tagging can impact molt increment: *H. americanus* marked with streamer tags during premolt had smaller increments than those tagged in post- or intermolt. (Comeau & Savoie, 2001).

Disease is another trauma that can negatively affect growth. Epizootic shell disease in particular leads to measurable reductions in growth increment (Castro *et al.*, 2006; Stevens, 2009; Tlusty and Metzler, 2012). Disease-induced changes in molting behavior have been documented (Castro *et al.*, 2006) that may result from altered levels of the molting hormone ecdysone (Jacobs *et al.*, 2012). Although molting may help rid the lobster of shells that have been compromised by the disease, it may also have a detrimental effect on reproduction and growth (Castro *et al.*, 2006; Stevens, 2009). Recent research suggests shell disease leads to significant changes in gene expression that induce a hormonal state similar to that in premolt healthy lobsters (Tarrant *et al.*, 2010, 2012). Lobsters with shell disease also show decreased expression in thoracic muscle of arginine kinase involved in energy metabolism, which could indicate an energetic drain in diseased lobsters (Tarrant *et al.*, 2010, 2012). The overall effect on growth is still not clear.

Intermolt period is often estimated from knowledge of the proportion of tagged individuals molting in a year, using the “anniversary method” (Hancock & Edwards, 1967). Growth increment data for tagged commercial size female *H. gammarus* in Ireland reveal modes indicating that 63% of lobsters had molted 1 year following release, 10% had molted twice, and the remainder had not molted at all. Thus, even with relatively invariant molt increments for the commercial size range, size at age will be highly variable. This fact is further supported by age estimates based on lipofuscin (Sheehy *et al.*, 1999).

Intermolt period increases with size and mature female lobsters molt less frequently than males of the same size, no doubt in part because egg brooding inhibits the molt and thereby extends the intermolt period. As with molt increment, intermolt period is also influenced by environmental factors, primarily water temperature (Conan, 1985; Waddy *et al.*, 1995; Aiken & Waddy, 1995).

Combining an increasing intermolt period and a declining molt increment, as a proportion of premolt size, produces the characteristic stepped growth function. Growth trajectories resulting from a probabilistic, stepwise growth model used in stock assessment for *H. americanus* (Chen & Kennelly,

1999) illustrate the strong differences in growth between two oceanographically and thermally contrasting regions of New England, USA (Plate 8.1C,D).

Many environmental factors influence the progression of the molt cycle, and, among them, temperature is of paramount importance. Between 8°C and 25°C there is a proportional relationship between temperature and growth rate: metabolic rates are faster and molt intervals may be shorter at warmer temperatures (Waddy *et al.*, 1995). *Homarus americanus* in the relatively warm waters of the southern Gulf of St. Lawrence have higher growth rates than do those from the nearby, but colder Bay of Fundy (Campbell, 1983; Comeau & Savoie, 2001). Wahle *et al.* (2001) grew young-of-year *H. americanus* in field cages at two sites in the Gulf of Maine separated by 10 km. Mean temperature differed by 2°C, and the CLs at the warmer site were, on average, 6 mm larger after 3 months. In southern New England, young-of-year lobsters that settle earlier in the season are larger at each instar and have a higher growth rate than those that settle at the end of the season (James-Pirri *et al.*, 1998). By the end of the first growing season early settlers were 30–50% larger in CL than late settlers. Within the normal thermal range, metabolic rate and electron transport system activity in *H. gammarus* are correlated with temperature, and there appears to be no metabolic compensation for temperature change that would modulate this effect (Tully *et al.*, 2000).

8.4.2 Age determination

Age determination in crustaceans has been a long-standing challenge since all hard parts are shed at each molt, making impossible the use of techniques used in vertebrates, notwithstanding the most recent emerging results in Kilada *et al.*, (2012). In *Homarus*, age may be estimated by modal analysis of size-frequency distributions for the few year classes after settlement (e.g., Wahle & Fogarty 2006; Gendron & Sainte Marie, 2006), but, after that, variation in growth rate obscures cohort modes. Size-at-age relationships can be generated from animals in culture, or from tag and recapture growth data, but for various reasons these are quite

variable and less than fully satisfactory. An accurate alternative to size-based methods of deriving age would be a boon to growth modeling.

The “age pigment,” lipofuscin, is a by product of cellular metabolism. It accumulates in all cells at a rate determined by metabolic rate of the individual and is quite stable after formation and therefore has met with some success in crustacean age estimation.

Sheehy (1989, 1990) noted the occurrence of lipofuscin in a wide variety of crustaceans. To date, success with this aging technique has been found with shorter-lived and warm-water species such as the western rock lobster *Panulirus cygnus* (Sheehy *et al.*, 1998) and the blue crab *Callinectes sapidus* (Ju *et al.*, 2003). Studies of *H. americanus* and *H. gammarus* confirm the potential of the technique but suggest caution in its use. Lipofuscin quantities, but not CL of hatchery-reared *H. gammarus* tagged and released into the wild at 3 months of age, bore a significant relationship to the known age at recapture 5–9 years later (Sheehy *et al.*, 1996). Similarly, in *H. americanus* reared for 4–27 months at a constant warm temperature in the laboratory, CL-corrected lipofuscin accumulation was strongly correlated with chronological age (Wahle *et al.*, 1996). Further analysis of larger untagged *H. gammarus* of unknown age suggested that lobsters recruiting to the fishery may comprise as many as 7 year classes, and that very large males and females may attain ages of 42 and 74 years, respectively (Sheehy *et al.*, 1999). More recently, lobsters released from a hatchery in Norway showed a close linear relationship between lipofuscin accumulation and age ($r^2 = 0.88$) but age and size also were closely correlated ($r^2 = 0.78$), suggesting in this case lipofuscin data would add little to increase the precision of age estimates (Uglem *et al.*, 2005). In a study of known-age laboratory-reared *H. americanus* up to 5 years old, Giannini (2008) found a strong relationship between body size, lipofuscin accumulation, and age; however, lipofuscin concentrations also became increasingly variable with age, and of little more help than body size in predicting age.

Lipofuscin accumulation is not solely time-dependent, however, and its rate is subject to environmental effects. For example, lobsters raised for

22 months at three seasonally varying temperature regimes showed seasonal oscillations in accumulation of lipofuscin and lipofuscin accumulation was related to the number of degree-days to which the lobsters were exposed (Tully *et al.*, 2000). The strong relationship between temperature and metabolic rate suggests that thermal history must be accounted for to resolve age-classes accurately. Sheehy & Bannister (2002) therefore developed a temperature correction for better year-class identification. A fundamental assumption then, is, that to know an individual's age, one must know its thermal history. Environmental variables other than temperature may also play a role. Antioxidants in the diet of the Norway lobster (*Nephrops norvegicus*) significantly reduced the accumulation of lipofuscin, which would lead to underestimation of age (Castro *et al.*, 2002). This and other techniques for age determination in crustaceans must therefore be further refined and standardized before it becomes a routine technique of the fisheries biologist's tool kit.

8.5 Maturation

8.5.1 Size at onset of maturity

Studies of reproductive maturation in lobsters make the distinction between physiological and functional maturity that is important to estimating the size at maturity. For example, the testes may be physiologically capable of producing sperm well before the male lobster reaches a size functionally competent to mate. And although the simplest indicator of functional maturity in females is the clutch of eggs among the pleopods under the abdomen, the ovaries may be physiologically capable of producing viable eggs well before the first clutch appears. Moreover, females that do not extrude eggs every year can be erroneously classed as immature, even if they have spawned previously, if their pleopods have not been inspected for signs of maturity. Therefore, a multiple indicator approach that involves examining external morphology and dissection of the gonad provides stronger evidence of physiological maturity.

Allometric enlargement of the abdomen in females and claws in males also has been used to

determine size at "morphometric" maturity. However, the gradual nature of the allometric change makes it difficult to be precise in assigning age and size at maturity with this method alone (Conan *et al.*, 2001). Size at maturity estimates are, therefore, sensitive to methodology, and the precision of the estimates depends on sample sizes and variance around the maturity ogives fitted to the data. These are important considerations when evaluating regional differences in size at maturity.

Size and age at maturity are dependent on summer water temperature and vary across the geographic range of the lobster (Table 8.1). For example, female *H. americanus* vary widely in the median size of maturity, from 70 mm CL or less in the relatively warm southern New England and southern Gulf of St. Lawrence to approximately 100 mm in the colder Bay of Fundy (Waddy *et al.*, 1995). Estrella & McKiernan (1989) observed that female size at maturity differed by 21 mm CL within 0.5 degree of latitude. Delayed maturation in cooler waters has been also documented in offshore American lobster (Little & Watson, 2003, 2005). Selective harvesting of large individuals has been suggested as a mechanism that could favor maturity at a smaller size, but to date there is little evidence to support this (Landers *et al.*, 2001).

Size at functional and physiological maturity of female *H. gammarus* also varies geographically (Table 8.1; Tully *et al.*, 2001). For example, the median size at which females bear eggs ranged from 80 to 140 mm CL, with the smaller sizes consistently found within the North Sea (Table 8.1; Free *et al.*, 1992; Tully *et al.*, 2001; Lizarraga-Cubedo, 2003; Laurans *et al.*, 2009). However, some of the variability may be less related to true regional differences than a consequence of limited sampling and differences in methodology (O. Tully, pers. comm.).

Male *H. americanus* have sperm present in the vas deferens when they are as small as 45–50 mm CL apparently irrespective of geographic location (Krouse, 1973; Briggs & Mushacke, 1980; Conan *et al.*, 2001). Similar studies are not available for *H. gammarus*. Small males, however, are not likely to be capable of mating with larger females because larger males tend to be more successful in courting and acquiring mates (Templeman, 1934; Atema & Voigt, 1995). Male functional maturity may also

Table 8.1 Geographic variability in size at female maturity of *Homarus*. Researchers have used different methods and definitions of maturity.

Region	Size at 50% maturity	Maturity definition	Reference
<i>H. americanus</i>			
Georges Bank and offshore Gulf of Maine	79	Physiological	Little & Watson 2005
Southern New England Shelf	82	Physiological	
Rhode Is to New Jersey offshore	92	Physiological	
New Hampshire (Great Bay)	83	Physiological	
New Hampshire (Isle of Shoals)	86	Physiological	Little & Watson 2003
Fundy	108	Physiological	Campbell & Robinson 1983
Eastern Nova Scotia	92		
Northumberland St	78		
Gulf of St Lawrence	68–73	Physiological	Comeau & Savoie 2002a
<i>H. gammarus</i>			
Scotland (east)	80	Morphometric	Lizarraga-Cubedo <i>et al.</i> , 2003
Scotland (west)	98	Morphometric	
Ireland (Nwest)	96	Physiological	Tully <i>et al.</i> , 2001
Ireland (West)	92	Physiological	
Ireland (southwest)	94	Physiological	
Ireland (southeast)	95	Physiological	
France (northwest)	103–106	Functional	Laurans <i>et al.</i> , 2009
England (north east)	90	Physiological	Free <i>et al.</i> , 1992
England (south)	82	Physiological	
Wales	100	Physiological	

be related to competition for females, and therefore the abundance and size distribution of males in the local population. The distinction between physio-logical and functional maturity in males is therefore quite important. Gosselin *et al.* (2003) showed that the amount of sperm deposited in a female *H. americanus* varies according to the size of the female, suggesting that males gauge the amount of sperm transferred, and that larger males transfer more sperm than do smaller ones. Where the fishery removes a large proportion of the larger males while protecting females (through maximum size restrictions and v-notching), there may be reason for concern about the potential for sperm limitation, especially in the larger females.

The reproductive schedule is better known in *H. americanus*. While a lobster population may spawn annually, only a fraction of the mature females may spawn in any given year, and some may skip a year or more. Once female American lobsters are mature, they generally produce a clutch

of eggs every second year. In general, molting and spawning occur in alternate years for females less than 120 mm CL (Waddy *et al.*, 1995). Temperature and age may alter the cycle. Small females inhabiting the warmest waters may molt and spawn the same summer while larger, older females (>120 mm CL) exhibit a three-year cycle, spawning in two consecutive years then molting in the third (Waddy *et al.*, 1995; Comeau & Savoie, 2002a).

In Norway, Agnalt *et al.* (2007) reported that molting and reproduction of *H. gammarus* alternated in a two year cycle for >90% of female lobsters and the proportion of lobsters berried annually varied from 19–58%, indicating a lower spawning frequency than in Ireland or France. Laurans *et al.* (2009) showed, in France, that 70% of females over 115 mm are ovigerous annually. Mark recapture data for female *H. gammarus* from Ireland indicate that approximately 20% of female lobsters between 87–110 mm CL spawn annually, although some may molt and spawn in the same year. Consistent

with *H. americanus*, therefore, the scope for growth and reproduction in *H. gammarus* is partly dependent on environmental temperature with populations living in higher temperatures having a higher frequency of molting and spawning than those in colder waters.

8.5.2 Clutch size and fecundity

Clutch size, the number of eggs carried by a female at any one time varies with size of the individual. Lifetime egg production (fecundity) is the sum of eggs produced over all clutches. To estimate clutch size it is important to account for the fact that egg diameter increases with development (Tully *et al.*, 2001). Thus the loss of eggs may not be detectable by simply measuring clutch volume over time. This would argue for standardizing the stage of egg development at which fecundity is estimated by the volumetric method. Clutch size estimates are significantly different at different egg development stages at a given body size in *H. gammarus* (Tully *et al.*, 2001). Although clutch volume and egg number are expected to scale as the cube of CL, many studies have found a linear relationship between CS and CL. This may be due to egg loss during incubation among the larger females ((Latrouite *et al.*, 1984, Bennett ,1987).

In a comparative study, Tully *et al.* (2001) found that the size specific fecundity of *H. gammarus* was similar in different regions in Ireland and within the range of other studies in France and UK. *Homarus americanus* clutches are generally larger than *H. gammarus* clutches at all sizes. According to Tully *et al.* (2001) clutch size (CS) in *H. gammarus* varied with CL as the power function $CS = 0.0044 \times CL^{3.16}$ while for *H. americanus* it was $CS = 0.0048 \times CL^{3.255}$. For a female of 100 CL this would translate to a clutch size of 9200 eggs in *H. gammarus*, versus 15,800 eggs in *H. americanus*. These estimates are sensitive to the stage of egg development as egg loss occurs during incubation.

The clutch size-to-body size scaling relationship may not vary greatly in *H. gammarus* (Tully *et al.*, 2001; Lizarraga-Cubedo *et al.*, 2003). However, regional differences are recognized in *H. americanus* and may relate to differences in the onset of maturity and abdomen allometry (Estrella &

Cadrin, 1995; Fogarty, 1995). Maturity at a smaller size may initiate egg production younger age, but it will also constrain brooding capacity and clutch size, and may limit the maximum attainable body size. Fecundity estimates for management purposes should therefore be calculated on a regional basis (MacCormack & DeMont, 2003).

Some management measures in a lobster fishery aim to conserve a target female life time fecundity. If a female carries 15 clutches in a lifetime then a female *H. americanus* that lives out her full reproductive life expectancy might produce 750,000 eggs (Cobb *et al.*, 1997). However, female lobsters in heavily fished populations may be functionally semelparous, producing only a small fraction of their potential life time fecundity (Fogarty & Gendron, 2004). This is why some *Homarus* fisheries on both sides of the Atlantic have adopted special, regulatory, conservation measures for females, such as v-notching and maximum size limits. V-notching involves marking the tail of an egg-bearing or mature female to increase her contribution to egg production before she can be harvested.

Egg loss during incubation can impose significant loss of reproductive potential. Reports vary regarding egg losses during the brooding period. Nemertean egg predators and fungal infections are the cause of loss in some species (Shields *et al.*, 2006). Losses of 15–50% of the egg mass during incubation have been reported in the American lobster (Perkins, 1971; Campbell & Brattey, 1986; Savoie & Maynard 1991). Handling during the harvesting process may also cause egg loss (Talbot & Helluy, 1995). Ovigerous females with epizootic shell disease have been observed to molt before hatching their eggs, losing the entire clutch (Castro *et al.*, 2006). The high mortality of mature females, coupled with loss of an entire clutch, could dramatically reduce the reproductive potential of a lobster population.

8.6 Larval and pre-settlement dynamics

Larval production and transport are critical components of the dynamics of lobster populations. Over

the past decade or so, major inroads have been made to our understanding of the linkages between larval production, advection, behavior, and the early benthic recruitment. A considerable amount of work addresses abundance, distribution and transport of *H. americanus* larvae. However, similar work on larvae of *H. gammarus* is scarce, most likely due to the low abundance of planktonic and early benthic stages (Nichols & Lawton, 1978; Nichols & O'Ceidigh, 1984; Tully & O'Ceidigh, 1987). In both species, the postlarvae are generally found at the sea surface (neustonic) and the earlier stages are more widely distributed throughout the water column. All stages undertake limited diel vertical migrations (Nichols & Lovewell, 1987; Tully & O'Ceidigh, 1987; Harding *et al.*, 1987; Annis, 2005). Abundance of *H. gammarus* at the sea surface tends to be higher at dawn and dusk (Tully & O'Ceidigh, 1987). In both species, diel vertical migration complicates the estimation of larval abundance. Behavioral studies of larval and postlarval *H. americanus* responses to thermoclines in the laboratory (Boudreau *et al.*, 1991; 1992; Annis 2005) suggest that larvae prefer to remain above approximately the 12°C isotherm.

On the basis of drift bottle results, Rogers *et al.*, (1968) speculated that passive advection, would be insufficient to carry of larval *H. americanus* from southern New England's offshore canyons where they would hatch to inshore lobster grounds. A simple physical model coupled with postlarval swimming, however, suggested that swimming could considerably enhance a postlarva's chances of making it to nearshore nurseries (Katz *et al.*, 1994). Subsequent more sophisticated coupled bio-physical larval transport models, developed for both species of *Homarus*, are challenging long-held views about long distance larval connectivity. To date, models have been developed for the Gulf of Maine and New England shelf waters (Incze & Naimie, 2000; Xue *et al.*, 2008; Incze *et al.*, 2010), the southern Gulf of St. Lawrence (Chassé & Miller, 2010), and Irish coastal waters (Anon, 2008). The physical models are typically forced with tides, winds, heat fluxes, and marine (boundary conditions) and freshwater fluxes. In all cases, the model interface allows the testing of different spawning stock distributions, temperature-dependent larval

development times, larval vertical distributions, and mortality rates, because of uncertainty in these processes. Despite the touted potential for long-distance advection, often in excess of 200–300 km (e.g., Harding *et al.*, 1987), connectivity matrices generated by these models suggest that most larvae are generally transported less than 100 km (Plate 8.2). Furthermore, in the Gulf of Maine model the closer to shore larvae hatched the more likely they were to be retained in the source area. Model predicted spatial patterns of settlement along the Gulf of Maine coast over a 3-year period were consistent with observed young-of-year densities. However, patterns of postlarval concentration predicted for the Gulf of St. Lawrence bore little resemblance to spatial patterns in the harvest, suggesting other factors, such as the availability of benthic habitat, may ultimately limit adult abundance. Such modeling exercises are extremely useful in stock definition and in revising spatial management strategies. Uncertainties stem from temporal variability in the physical and biotic mechanisms that control benthic recruitment. Assumptions about the rate of larval mortality can dramatically affect these source-sink dynamics. For the purposes of the Gulf of Maine model, a 7% mortality rate was assumed, based on a previous mass-balance analysis of larval input versus fishery production for a segment of the Maine coast (Incze *et al.*, 2003). While our understanding of the mechanisms of larval retention and export have improved dramatically, the sources and magnitude of mortality during the planktonic stages remain largely a black box that would be a valuable topic of future research.

8.7 Postlarval settlement and benthic recruitment

8.7.1 Settlement indices

Settlement in lobsters is the process by which post-larvae recruit to the sea bed. Laboratory and behavioral studies have revealed a suite of cues that may stimulate or inhibit settlement, including temperature, geological substrata, algae, and the presence of predators and conspecifics (Boudreau *et al.*, 1990). Previous field experiments demonstrated

that the cumulative number new settlers counted and removed in experimental habitat units at weekly intervals over the settlement season closely matched the count in comparable units sampled only once at the end of the settlement season (Wahle & Incze 1997). Further surveys demonstrated a significant correlation between postlarval supply and young-of-year recruitment. In practice, therefore, the so called “settlement index” in large scale monitoring is a single count of the number of newly recruited young-of-year lobsters at the end of the postlarval settlement season in the early autumn (e.g., Incze *et al.*, 1997, Wahle *et al.*, 2004).

Success in quantifying settlement and young-of-year recruitment of the American lobsters, first by painstaking visual surveys (Hudon, 1987; Gendron & Sainte-Marie, 2006), followed by diver-based suction sampling (Fig. 8.3A; Wahle & Steneck, 1991; Incze & Wahle, 1991), and later by vessel-deployed passive collectors (Fig 8.3B; Incze *et al.*, 1997; Palma *et al.*, 1999; Wahle *et al.*, 2009b) has opened a window on the correlation between larval supply and benthic recruitment and the mechanisms that drive them (Hudon & Fradette, 1993; Wahle & Incze, 1997; Incze *et al.*, 1997). To date similar surveys in search of recently settled young-of-year European lobsters have come up empty handed (Mercer *et al.*, 2001). Given the very low abundance of European lobster relative to its American counterpart, it is likely that recruitment densities of young-of-year are so low that the probability of detection is extremely small.

The settlement index provides insights into both pre- and post-settlement processes. Spatially and temporally variable settlement patterns are extremely useful in revealing processes influencing larval supply – such as temperature, wind and surface flow. A small island in coastal Maine, a few kilometers long, became the outdoor laboratory to demonstrate these effects. Larval tows and benthic suction sampling revealed high numbers of planktonic postlarvae and correspondingly high settlement rates on the island’s windward side (Wahle & Incze, 1997). As long-term monitoring stations were established in New England and Atlantic Canada, and time series accumulated, more geographically comprehensive analyses became possible. This demonstrated a relationship between the

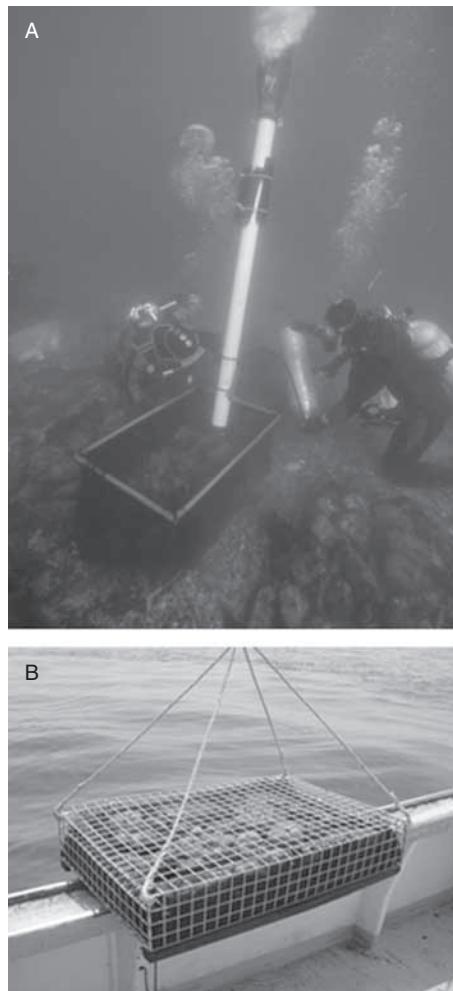


Fig. 8.3 Divers suction sampling (A) and a cobble filled passive collector (B) used in settlement surveys of *Homarus americanus*. (Photos by R. Wahle).

production of postlarvae and the abundance of newly settled young-of-the year (Incze *et al.*, 1997, 2000). With expanded sampling coverage, patterns of local and regional variability in benthic recruitment and the mechanisms behind them emerged (Incze *et al.*, 1997; Palma *et al.*, 1999; Steneck & Wilson, 2001).

Most recently, in an analysis of the correlation between settlement times series and satellite image derived sea surface temperature time series, Jaini (2011) identified areas of the sea surface with annual temperature anomalies, such as that over

Georges Bank, that might be useful predictors of annual variability in the lobster settlement at coastal areas in Rhode Island some 150 km away. Spatial correlations in the annual settlement signal among multiple monitoring stations suggest that annual variability in American lobster settlement are coherent at scales of hundreds of km (Pershing *et al.*, 2012). The Pershing analysis points to temperature and large scale prevailing wind indices as being the strongest correlates of annual variability in settlement. Together with the previously mentioned modeling results, suggesting limited larval transport along the coast, it would seem that large scale weather patterns explain the large-scale coherence in interannual variability among separate larval peaks (Pershing *et al.*, 2012).

8.7.2 Settler – fishery recruit relationship

One goal of settlement monitoring and research on juvenile life stages is to determine if a functional relationship can be described between settlement and recruitment to the fishery. In the framework of a mass-balanced life-history model and knowledge of egg production, young-of-the-year densities and the amount of suitable nursery habitat, Incze *et al.* (2003) estimated that it would take a larval mortality rate of 7% per day to achieve observed young-of-the-year densities and fishery landings on a segment of the Maine coast.

Well before settlement surveys were feasible, a 20-year data set on pelagic abundance of *H. americanus* larvae and postlarvae gathered by Scarratt (1964) in the southern Gulf of St. Lawrence, was pivotal in provoking research into the mechanisms linking larval settlement and recruitment to the fishable stock. At the time, Scarratt (1973a) concluded that there was no relationship between post-larval abundance and stock size. A reanalysis of that data set (Fogarty & Idoine, 1986), and several other spatial and temporal correlation analyses suggested varying degrees of correlation between egg or larval production, and fishery recruitment (Newfoundland: Ennis & Fogarty, 1997; Nova Scotia: Miller, 1997). With the European lobster, Sheehy & Bannister (2002) cleverly side-stepped the lack of larval or settlement time series to infer the consequences of variable settlement on fishery

recruitment. Using thermally corrected lipofuscin concentration to determine age and assign lobsters of a wide size range to age cohorts, they showed that large differences in year-class strength could be inferred for *H. gammarus* in Bridlington Bay (UK). They also demonstrated that geographically separated populations have different thermal histories, and so must be treated separately. By examining wind field data for each year, they concluded that years with greater onshore winds were positively correlated with year-class strength.

The advent of widespread and routine settlement monitoring by suction sampling has resulted in a spate of new analyses of the settler-to-recruit relationship. Spatial correspondence between settlement “hotspots” and regions with high commercial landings suggested a predictive relationship between settlement and fishery recruitment might be borne out (Steneck & Wilson, 2001). Encouraged by a consistent ability to follow cohorts through several years, Wahle *et al.* (2004) developed a predictive model for Maine and Rhode Island (Plate 8.3). Projections from the settlement index to fisheries landings were made using a logistic growth model with a range of ages at recruitment to account for growth variability. The settlement index-based model accurately predicted time trends in Rhode Island fishery recruitment, as measured by the state’s fishery independent trawl survey, until 1996. The onset of epizootic shell disease that year, considerably augmented juvenile natural mortality and required a revision of the predictive model. The revised model now includes the joint effects of settlement and shell disease prevalence as predictors of pre-recruit abundance (Wahle *et al.*, 2009b).

8.8 Meta-population structure

Lobster populations are subdivided by geographic and oceanographic features into interconnected sub-populations, which in aggregate, form the meta-population spanning the species’ geographic range. Ideally stock assessments are conducted on discrete stocks representing relatively closed populations with uniform demographic rates. In practice, stock definition has proven to be a challenge

for *Homarus* because of uncertainties about the extent of connectivity among sub-populations.

Historically, morphometric analysis has been one approach to assess stock structure (Cadrin, 2000; Conan *et al.*, 2001). The reliability of that singular approach is questionable, however, given the phenotypic plasticity of lobster body shape (e.g., Wahle & Fogarty, 2006). Recent developments in molecular genetic techniques have made possible significant advances in our understanding of the population structure of both European and American lobster. Building on earlier allozyme work by Tracey *et al.* (1975) and DNA sequencing work by Harding *et al.* (1997), the recent study by Kenchington *et al.* (2009) is perhaps the most comprehensive analysis of genetic structure of the American lobster to date. Kenchington and co-workers suggest the geography of genetic structure of *H. americanus* reflects the history of shrinking and expanding geographic ranges during Pleistocene glacial advance and retreat (Plate 8.4). The pattern of population structure reported in their study is “best explained by a balance between genetic drift and migration.” While considerable spatial differentiation appears to have occurred over the past 12,000 years in the southern part of the species’ range, the likely refuge during glaciation, lobsters further north in the Gulf of St. Lawrence and Scotian Shelf are relatively undifferentiated, hypothetically, because they were the result of only a few founder events that re-established the modern population. Finer scale sampling may reveal further differentiation, however. For example, on a smaller scale, using nine microsatellite loci Crivello *et al.* (2005) discovered that lobsters from the western end of Long Island Sound, a long, narrow and poorly flushed embayment, were genetically distinct from those in the eastern sound and offshore. The difference was much greater than would be predicted by geographic distance, and may relate to the a recent mass mortality event in the western Long Island Sound in 1999 (Crivello *et al.*, 2005).

The genetics of population structure of the European lobster has also been coming to light recently. Along the Norwegian coast, microsatellite and mitochondrial DNA studies confirmed the genetic differentiation of lobsters from north of the Arctic

Circle (Tysfjord region) and other parts of Norway (Jorstad *et al.*, 2004). This study also distinguished lobsters from Tysfjord and a location 142 km away along the Norway’s convoluted coast. They suggested that locally discrete populations may be maintained by hydrographic conditions allowing little larval dispersal between the two regions. Triantafyllidis *et al.* (2005) used mtDNA to look for genetic differentiation across the entire range of *H. gammarus*. The analysis indicates the existence of four genetically differentiated subpopulations: northern Norway, Mediterranean, Netherlands, and Atlantic. The existing knowledge of larval biology and dispersal and information on movement of adult lobsters both suggest that *H. gammarus* occur as discrete local populations at scales smaller than those suggested by Triantafyllidis *et al.* (2005). On the other hand, Ulrich *et al.* (2001) determined that the small population of *H. gammarus* on the island of Helgoland has diverged from others in the North Sea most likely by geographic isolation.

Larval transport and movement of adult lobsters are the modes by which sub-populations interact, and this exchange may play an important role in the resilience of stocks to harvesting pressure. In a meta-population model of the southern New England American lobster stock, Fogarty (1998) concluded that as little as a 10% larval subsidy from offshore to inshore would suffice to maintain the inshore population at what would be, otherwise, unsustainable levels of fishing mortality. In general, if a sub-population receives a net subsidy from an external source it is likely to be able to sustain higher levels of fishing pressure than without the subsidy, an argument that may be useful in planning spatial refuges (Fogarty & Botsford , 2007).

The larval transport modeling described in Section 8.7.2 makes important inferences about the degree of connectivity among stock assessment units, and could be an important tool in spatial fisheries management. The key uncertainty in these models is how larval and postlarval mortality rates determine effective exchange rates between populations.

Benthic migrations may also contribute significantly to source-sink dynamics. Although a considerable number of tagging studies have documented long-distance migration in the American lobster

(Cooper & Uzmann, 1973; Caddy, 1986; Fogarty, 1998; Comeau & Savoie, 2002b), given high rates of exploitation, it is unlikely that a large proportion of lobsters above harvestable size get the opportunity to move very far before they are caught. On the other hand, it is well known that a large number of mature v-notched females from the Gulf of Maine turn up in the southern New England harvest where notching tails is not practiced (R. Glenn, Massachusetts Division of Marine Fisheries, pers. comm.). V-notching and protection of lobsters above the maximum landing size are means of conserving broodstock. If these components of the reproducing population undertake benthic movements they could contribute significantly to spatial dynamics of egg and larval production that should be incorporated into stock assessments.

Interpretations of the extent of, and processes leading to, metapopulation structure in both species of *Homarus* remain controversial. Population genetic analysis at a higher spatial resolution can only help reconcile diverging views of the scale of connectivity.

8.9 Post-settlement mortality sources

8.9.1 Predators and habitat-mediated survival bottlenecks

Demersal and benthic fishes have long been recognized to be major predators of *H. americanus* (Herrick, 1911; van der Meeren 2000, 2001, 2003). The widespread depletion of groundfish, including cod, in the northwest Atlantic is strongly correlated with the upsurge in American lobster, crab (*Chionoecetes opilio*), and northern shrimp (*Pandalus borealis*) abundance in recent decades (Acheson & Steneck, 1997; Worm & Myers, 2003), suggesting these predators play a central role in population regulation. Further time series analysis of US National Marine Fisheries Service trawl survey time series in the Gulf of Maine points to a strong inverse correlation between the abundance of the American lobster (kg tow^{-1}) and the aggregated abundance of four species of groundfish (Atlantic cod, cusk, longhorn sculpin, monkfish, and wolffish), as well as the singular abundance of cod (Boudreau

& Worm, 2010). *Homarus americanus* is also reported from stomach of a more nearshore assemblage including striped bass (*Morone saxatilis*), shorthorn sculpin, (*Myoxocephalus scorpius*), cunner (*Tautogolabrus adspersus*), and white hake (*Urophycis tenuis*) (Steimle *et al.*, 2000; Nelson *et al.*, 2003). On the other hand, groundfish stomach analyses from the southern Gulf of St. Lawrence and Georges Bank found little evidence of predation on lobster by Atlantic cod, Greenland cod (*Gadus ogac*), winter flounder (*Pleuronectes americanus*), yellowtail flounder (*P. ferruginea*), thorny skate (*Raja radiata*), or spiny dogfish (*Squalus acanthias*) (Garrison & Link, 2000; Steimle *et al.*, 2000; Watts & MacPherson, 2002; Hanson & Chouinard, 2002; Link & Garrison, 2002). These seemingly contradictory findings have led to some debate on the role of groundfish, and particularly cod, as chief predators of lobster. To reconcile these differences one must ask whether the fish analysed co-occurred in space or time with lobster, and, if so, whether they were large enough to consume the lobsters present.

A field experiment by Norden (2003) with American lobster postlarvae illustrates the gauntlet of predators settling lobsters face as they approach the sea bed. Postlarvae were tethered along a vertical, monofilament line at several depths between the surface and a known rocky nursery habitat. Most of the mortality occurred within 2 m above the sea bed. Palma *et al.* (1998, 1999) further observed that once settled, mortality of early juvenile *H. americanus* appears to be very low compared with that of the rock crab, *Cancer irroratus*, which is much more fecund, matures quickly, and settles at much higher densities than *Homarus*.

Although far fewer studies address predation on *H. gammarus*, the greater diversity of benthic fishes, wrasses in particular, suggests the potential that young lobsters contend with high predation rates in coastal Europe and Scandinavia (Ball *et al.*, 2001) observed predation on juvenile *H. gammarus* by gobies, (*Pamatoschistus minutus*), rockling (*Ciliata mustela*), and green crabs (*Carcinus maenas*). The Norwegian hatchery-release program avoided summer releases because of the high predation risk to lobsterlings at that time (van der Meeren pers. comm.). The European lobster

becomes more cryptic in the presence of predators, and this behavioral response is used to advantage in culture settings to suppress aggression among juveniles (van der Meer, 2003).

Demographic bottleneck models in various forms have been proposed for lobster and other shelter-dwelling crustaceans to account for the interactive effects on survivorship of size-specific shelter availability and size-specific predation risk (Caddy, 1986; Wahle & Steneck, 1991, 1992; Beck, 1995, 1997; Wahle, 2003). A survival bottleneck will occur if lobsters run out of sheltering habitat before they outgrow their predators; thus changes in the size composition of available shelters or predators can alter the strength of the bottleneck and have important demographic implications. Observations that American lobster abundance, in the wake of declines in predators, expanded into habitats with less shelter (Boudreau & Worm, 2010) are consistent with the hypothesis that the demographic bottleneck has relaxed in some sectors of the species' range.

8.9.2 Evidence of density-dependence

The role of density-dependence in lobster population regulation has been the topic of long-standing debate. Habitat and shelter has long been cited as a potential limiting factor in lobster populations (Wahle *et al.*, in press). Given the relatively low densities in *H. gammarus* populations, it is unlikely that intraspecific crowding is a factor in their population dynamics. *Homarus americanus* is much more likely to be subject to density-dependent controls. On the basis of correlation analyses between spawner-recruit and postlarval times series and fishery recruitment, Fogarty & Idoine (1986) and Ennis & Fogarty (1997) first suggested density-dependent processes might be operating in *H. americanus*. These analyses have been questioned because they depend on the tenuous assumption that the populations in question are closed (Wahle, 2003). Nonetheless, there is support for the existence of crowding effects even during the early benthic phase. For example, field experiments conducted in a region of Maine that consistently sees high settlement rates suggest that lobster postlarvae do not settle at saturating densities and that juve-

niles start to be subject to shelter limitation as they grow (Wahle & Incze, 1997). Non-linear relationships observed between young-of-year and resultant 1- and 2-year-old lobsters in suction sampling data times series from Rhode Island and Maine cobble nurseries further substantiate the existence of density-dependent controls during the early benthic phase (Wahle *et al.*, 2004). Additional support for density-dependence comes from direct observations of shelter competition in field experiments in naturally occurring dense populations. In a field experiment in Maine, Steneck (2006) varied the space among artificial shelters configured in an array on otherwise shelterless seabed. Lobsters moving in from the surroundings populated the shelters. In the widely spaced configuration where shelters were several meters apart, most shelters were occupied, but in the closely spaced array with shelters about 0.5 m apart, shelter occupancy was considerably lower, and lobsters were frequently observed in agonistic bouts with neighbors, with the larger contender typically evicting its neighbor from shelter. Further research is needed to quantify the role of crowding and resource limitation in *Homarus* population dynamics

8.9.3 Disease

Prior to the mid-1990s, reports of disease affecting wild stocks of *Homarus* were rare and largely restricted to pathologies associated with captivity (Wickins & Lee, 2007; Cawthron 2011). In 1996, epizootic shell disease (ESD) appeared in coastal Rhode Island and southern Massachusetts, and in the summer of 1999 a mass mortality event occurred in Long Island Sound off New York and Connecticut. The two episodes were associated with warmer than average summers, and heightened concern over the interaction of climate change and disease. Pearce & Balcom (2005) reviewed the scientific analysis of the cause of the Long Island Sound die off. They also described three new diseases or syndromes (co-occurring symptoms) associated with the event: (i) paramoebiosis caused by the parasitic amoeba, *Neoparamoeba pemaquidensis* (Robohm *et al.*, 2005); (ii) calcinosis, believed to be caused by a physiological reaction to high water temperatures (Dove *et al.*, 2004); and (iii) idiopathic blind-

ness (Maniscalco & Shields, 2006). Further north in the Gulf of Maine, another emergent pathogen, *Vibrio fluvialis* (and possibly *Hyphomicrobium indicum*), was implicated in mortalities in American lobsters (Tall *et al.*, 2003). Below we focus in some depth on recent developments in our understanding of ESD; a recent compendium of research on the topic is available in the *Journal of Shellfish Research*, 3(12) 2012.

Epizootic shell disease presented as deep shell lesions along the anterior dorsal carapace, rapidly spreading to all parts of the dorsal surface (Smolowitz *et al.*, 2005). The pathology of the lesions differed from classical shell disease in that the pillars of chiton remained while the degradation occurred in the other polymers in the carapace (Smolowitz *et al.*, 2005). Although there is scientific consensus that the characteristic shell lesions in shell disease are caused by bacteria that invade the carapace of the lobster from the surface of the shell, there evidence is lacking to link a single bacterium with the disease. (Fisher *et al.*, 1976; Malloy, 1978; Chistoserdov *et al.*, 2005; Getchell, 1989; Quinn *et al.*, 2009; Smolowitz *et al.*, 1992, 2005). This is due to the inherent difficulties in studying a cutaneous disease with open lesions prone to secondary infection. Glenn & Pugh (2006) observed that ESD disproportionately affects older lobsters that do not shed their exoskeleton as often as juveniles, and that egg-bearing females have a disproportionately high incidence of the disease, ostensibly because they must delay their molt.

Koch's postulates state that in order to establish a cause–effect relationship between a bacterium and a disease, the microorganism must (i) be found in all organisms suffering from the disease, but not in healthy ones; (ii) it must be isolated from a diseased organism and grown in pure culture; (iii) the cultured microorganism should cause disease when introduced into a healthy organism; and (iv) it must be reisolated from the inoculated, diseased host, and shown to be identical to the original specific causative agent. Unfortunately, these criteria cannot be fulfilled in the case of ESD. It is difficult to satisfy Koch's postulates for pathogens such as those associated with ESD or other infectious diseases that are not culturable and may have an unknown host or environmental component (Fre-

dricks & Relman, 1996). Analysis to date suggests that EDS is caused by opportunistic pathogens that take advantage of a compromised shell. Possible suspects include the recently isolated bacteria *Aquimarina 'homaria'*, and *'Thalassobius' spp.*, which are commonly found in the lesions (Chistoserdov *et al.*, 2012; Quinn *et al.*, 2012). In laboratory-reared lobsters, a compromised shell is necessary to transmit the disease (Quinn *et al.*, 2012). Injury by v-notching, however, did not affect the appearance of the disease or the rate of infection (DeAngelis *et al.*, 2010). Environmental contaminants may play a role. The strength of the shell can be compromised by alkylphenols that interfere with the incorporation of tyrosine into the cuticle, delaying the hardening process and possibly disrupting the antibacterial properties of the epicuticle (Laufer *et al.*, 2005; Jacobs *et al.*, 2012; Kunkel *et al.*, 2012). Walker *et al.* (2005) found that methoprene, a pesticide, also adversely affected the synthesis and incorporation of chitoproteins into post-molt shells.

Homerding *et al.* (in press) found that lobsters from eastern Long Island Sound had a weaker immune system than those from either the western Sound or Maine. Lobsters with ESD showed significant reduction in plasma antimicrobial activity and hemocyte phagocytosis, as well as higher bacterial loads in the hemolymph. Given this evidence of endocrine disruption, it is perhaps not surprising that aggression and mating behavior is also affected by ESD. In behavior experiments, diseased males lost more frequently in paired fights with non-diseased males of equal size, although female lobsters did not actively avoid males with the disease (Rycroft *et al.*, 2012).

Given these severe physiological effects, it is not surprising that ESD has had adverse population-level consequences. The abundance of lobsters in southern New England began to decline coincident with a rise in shell disease prevalence. The relatively straightforward predictive relationship between young-of-year and subsequent pre-recruit abundance changed dramatically after 1996, indicating an increased rate of mortality. The revised predictive model now incorporates shell disease prevalence (Wahle *et al.*, 2009a). Other potential variables such as temperature and predator abundance

did not add significantly to the explanatory power of the model. In laboratory studies, Stevens (2009) found direct evidence for increased mortality during molting associated with shell-diseased lobsters. A shift in sex ratio also occurred in 1997 pointing to a disproportionate loss of females in the southern New England area. The declining young-of-year index and fishery recruitment since the onset of ESD have prompted fishery managers of the Atlantic States Marine Fisheries Commission (ASMFC) to declare a recruitment failure in the southern New England lobster stock. In 2010 fishery managers recommended a moratorium on lobstering in southern New England, but it was rejected after much deliberation in favor of less severe conservation measures. The future of the southern New England lobster fishery remains of great concern.

A multitude of environmental factors may interact to increase the probability of onset or severity of this disease. To date, a prevailing interpretation is that warming temperatures may play a key role, although there is not scientific consensus on this question. From 1970 to 2002, sea surface temperatures at Woods Hole, Massachusetts, were warming at the rate of approximately 0.04°C per year, and have recently been consistently well above 20°C during the summer (Nixon *et al.*, 2004). Temperature time trends vary locally, but there was no dramatic upturn in temperature in coastal southern New England in the years immediately preceding or during the onset of EDS to make a compelling case for warming as the sole factor initiating the disease. Nonetheless, lobster immune systems function begins to weaken at temperatures above 22°C (Steenbergen *et al.*, 1978). Moreover, the spatial pattern of high ESD prevalence along the New England coast correlates with warmer regions south of Cape Cod, and its northward expansion since the late 1990s appears to have stalled against the gradient of declining temperatures (Glenn & Pugh, 2006). In the laboratory, however, Tlusty & Metzler (2012) found that lobsters held at 10–20°C developed ESD, but that the bacteria were most virulent at 15°C, well below summer thermal maxima in southern New England, and well within the physiological optimum for lobsters. In another laboratory study, both injured (v-notched) and

uninjured lobster held in ambient flow-through systems equally developed shell disease with cold winter temperatures (DeAngelis *et al.*, 2010). Warming temperatures, therefore, may be only one of several environmental factors suspected in the onset and spread of ESD.

Evidence for the role of other environmental factors in the spread of EDS is still equivocal. Environmental pollutants can negatively impact the health of crustaceans, leading to disease directly through toxicity or indirectly through immunosuppression. Evidence of a possible link between contaminant metals and shell disease has been provided in several studies as reviewed in LeBlanc and Prince (in press). They did not find statistical differences in trace metals concentration in the hepatopancreas between shell diseased and non-diseased lobsters in Rhode Island, although several metals were found in the sediments that were similar or exceeded sediment quality guidelines. DeGuise *et al.* (2004, 2005) verified that methoprene and resmethyltin suppress the immune system of adult lobster, and Walker, *et al.* (2005) further found that methoprene caused high mortality rates in postlarvae, and that in adults it accumulates in the hepatopancreas, gonad, epithelial tissue, and, most significantly, the eyestalks.

Perhaps the most startling result of the recent research on lobster disease was the discovery of additional pathologies apparently found in lobsters from southern New England. In the so-called 100-Lobster-Study of intensively studied lobster collected from Narragansett Bay, Rhode Island, Shields *et al.* (in press) identified several previously unknown syndromes (Shields *et al.*, in press). For example, over half the lobsters from this sample were afflicted with idiopathic (=unknown cause) blindness and at higher severity levels than a control site (Maine). Maniscalco & Shields (2006) found a similar result for Long Island Sound. Fifteen percent of the lobsters had necrotizing hepatopancreatitis, a newly described disease with unknown consequences. These two syndromes suggest exposure to an environmental contaminant (Shields *et al.*, in press). Although the 100-Lobster-Study is admittedly a limited sample, it is clear that ESD should be examined as part of a larger suite of health issues for the American lobster. The

multi-faceted nature of the ESD and associated syndromes make it a complex problem. It is clear that multiple stressors exist in the environment and that southern New England lobsters have experienced physiological and endocrine changes that affect their ability to molt, reproduce, and survive. The emergence of these new diseases may reflect both opportunistic invasions and anthropogenic disruptions. Developing the appropriate management response remains a challenge, yet management decisions must be guided by sound theory and empirical data.

Epidemiological models need to be developed for ESD to generate testable predictions about the outcome of different disease management strategies at large scale and over the long term. Such models developed for other species may help guide the way. Feehan *et al.* (2012) recently field tested a predictive model on disease outbreak following a hurricane in Nova Scotia and was able to predict massive mortalities in caged sea urchins by an opportunistic paramoeba, a situation that emulates the “perfect storm” that occurred prior to the 1999 Long Island Sound disaster with the American lobster.

8.10 Homarus in a changing ecosystem

Coastal environments inhabited by both species of *Homarus* have been undergoing considerable change over the past century from global and regional anthropogenic effects. The literature on the topic falls into two categories: (i) global climate change effects, and (ii) altered foodweb effects.

8.10.1 Global climate change effects

Climate change effects include ocean warming and acidification. The literature on observed and projected effects on *H. americanus* is reviewed in Chapter 4 of this volume. In 2007, the Union of Concerned Scientists undertook an assessment of projected climate change effects on different resource sectors of the US northeast, marine fisheries among them. Projections were made under high and low carbon emissions scenarios used in a selec-

tion of current climate change models (Frumhoff *et al.*, 2007). This area of the northwest Atlantic, spanning the geographic range of the American lobster, has the steepest latitudinal gradient in sea surface temperature on the planet (Longhurst, 1998; Frank *et al.*, 2007), so the consequences of climate warming vary along the coast. For example, in the Mid-Atlantic Bight and southern New England summer sea temperatures by mid-century are predicted to frequently exceed thermal stress thresholds for this species, resulting in the likely loss of suitable nearshore habitat. Mortality events, such as the one in Long Island Sound, brought on by high temperatures and hypoxia (Pearce & Balcom, 2005), are likely to become more frequent. Deep waters and offshore banks along this segment of the continental shelf, where the sea bed is removed from the extremes of summer warming may become a refuge for lobsters. In the cooler waters of the Gulf of Maine and Bay of Fund, by contrast, warming may enhance growth, reproduction, and settlement.

Concern over the effects of ocean acidification on marine calcifying organisms from anthropogenic increases in atmospheric CO₂, has heightened since the phenomenon was documented globally in the past decade (Orr *et al.*, 2005). Assessments of acidification effects on *Homarus* are only just beginning and the implications are unclear. For example, in a recent study of *H. gammarus* larvae, Arnold *et al.* (2009) found that sea water acidified to pH levels predicted over the next century had no effect on larval development, but significantly increased calcification of the exoskeleton. In benthic juvenile *H. americanus* reared in acidified waters, Reis (2011) attempted to explain the varied responses of marine calcifiers, including crustaceans and mollusks, to an increasingly acidic environment. These relatively preliminary findings suggest that under the highest pCO₂ scenarios, and at excessive 25°C temperatures for lobsters, juvenile lobsters will be able to acclimate, at least in the short term (less than 6 months), by increasing the net calcification of their exoskeleton. Future research needs to evaluate the effect of chronic exposure to acidified conditions over a range of seawater temperatures to more fully understand the effects of ocean acidification.

8.10.2 Altered food webs

Marine foodwebs throughout the North Atlantic have been altered dramatically by the depletion of large predatory groundfish (Frank *et al.*, 2006, 2007). Frank and co-workers observed that increases in the abundance of mid-level consumers such as forage fish and crustaceans to relaxed predation has been most evident in simpler, less diverse ecosystems where fewer unexploited predator species can play the functional role of those removed. Perhaps it should be no surprise then that the American lobster may have responded more dramatically to groundfish depletion than its European counterpart. In Chapter 1 of this volume, Phillips *et al.* review these effects for *H. americanus* in some depth in a case study comparison with the sub-tropical spiny lobster, *Panlirus cygnus*. To our knowledge studies of *H. gammarus* in a foodweb context are lacking.

In contrast to the collapsing American lobster population in the southern part of the species range, abundance of the lobster in the Gulf of Maine and parts of Atlantic Canada have surged to unprecedented levels in the past few decades in the wake of severe groundfish depletion. While we cannot rule out other contributing factors, the strong correlation between the decline of fish and the increase in lobster has been taken to indicate a cause–effect relationship (Acheson & Steneck, 1997; Worm & Myers, 2003; Boudreau & Worm, 2010; Wahle *et al.*, in press). Evidence in support of this hypothesis has been accumulating in a variety of forms. For example, Zhang and Chen (2007) used Ecopath modeling to quantify changes in the Gulf of Maine ecosystem during the groundfish depletion of the 1980s and 1990s. The mass-balanced model suggests that while the estimated biomasses of Atlantic cod (*Gadus morhua*) and cusk (*Brosme brosme*) decreased by nearly a half from 1980s to 1990s, the separate biomasses of shelled mollusks, crabs, lobster, and herring doubled or even more than tripled. Interviews of fishermen in southern Nova Scotia revealed the strong view that groundfish depletion was the cause of lobster increases on their fishing ground, a perception supported by groundfish and lobster time trends in fishery independent trawl surveys (Boudreau & Worm, 2010). In video-

monitored predation experiments, Wahle *et al.* (in press) observed significantly lower numbers of fish attacks and lobster mortality in the Gulf of Maine than in southern New England, where predator diversity is higher. From trawl survey time series spanning three decades they also report a more dramatic downward shift in predator body mass in the Gulf of Maine than in the south.

While the evidence for top-down forcing as the explanation for the boom in lobster abundance in this region has been gathering force, bottom-up effects may also play a role, primarily as bait subsidies to the lobster energy budget. Because traps in the Canadian and US fishery have escape vents, small lobsters may enter a trap, consume bait and leave. Herring bait can be detected in stomach analysis. As it is assimilated over time it gives an altered nitrogen stable isotope ratio in lobster tissue from that observed in lobsters feeding on a bait-free natural diet. Grabowski *et al.* (2010) measured a stronger herring signature in lobster tissue and higher growth rates in fishing areas where herring bait was used during the summer fishery. Regardless of the cause, with lobster landings now at historic highs, and groundfish and other fisheries seriously depleted, harvesters in Maine and parts of Atlantic Canada are perilously dependent on this single fishery. It is hard to imagine how the region's working waterfront would recover from a collapse of lobsters.

8.11 Harvest and management of wild populations

8.11.1 Gear type and methods

There are both inshore and offshore fisheries for *H. americanus*. The inshore fishery is carried out by smaller vessels (ranging from skiffs to vessels about 15 m in length) usually carrying one or two crew. The offshore vessels typically average 39 m in length, and accommodate three or four crew members. In Europe *H. gammarus* is fished primarily inshore (<5 km from the coast) by vessels ranging in length from 6–15 m. In some areas such as the North Sea fishing has recently developed in deeper waters.

The offshore fishery for *H. americanus* on the continental shelf and canyons started as a trawl fishery in the late 1950s. This peaked in the 1970s and was gradually replaced by a trap fishery by the 1980s. The offshore trawl fishery was important for the development of markets for larger lobsters and the refrigerated holding systems that held them at sea. Today regulations limit the catch of trawlers to 100 per day or 500 per trip. In some states trawl landings are prohibited, and in others there are small trawl fisheries primarily targeting lobsters during or after the molt when they are found in deep muddy pockets. There is no trawl fishery for *H. gammarus* although they are occasionally seen as by-catch in the groundfish fisheries. Higher by-catch occurs in the fixed net fisheries targeting spider crab (*Maja brachydactyla*) or the spiny lobster (*Palinurus elephas*). Trap numbers in the European fishery are high and can number over 2000 in larger (10–15 m) vessels. Usually 500–700 traps may be hauled per day with a soak time of 2–3 days.

Traps used to capture lobsters vary in designs, shapes and sizes, although there is a maximum size allowed overall in some fisheries (Miller, 1995). Traps can be fished as singles (one trap, one buoy) or as a trawl (American) or string (European) (i.e., 10–50 traps placed on one ground line with two or three surface marker buoys). In the American fishery, rectangular lobster traps are constructed of either wood lath, or more often vinyl-coated wire-mesh. The basic two-chamber trap contains a “kitchen” where the bait is hung, and a “parlour” area with at least two escape vents. Lobsters enter the kitchen through the entrance funnels and then move through another no-return funnel to the parlour. Escape vents and lath spacings are sized to allow sublegal lobsters to leave the trap. European style round traps have a single opening on the top and vary from “hard eye” traps to D-shaped “soft eye” traps with single or, rarely, double parlours. Hard eye traps have an entrance constructed from solid piping or a funnel whereas “soft eyes” have a mesh entrance where the roof of the entrance is of loose mesh hanging towards the floor of the entrance.

Traps are usually retrieved using a hydraulic hauler that allows for rapid re-deployment after

they are emptied and re-baited. Bait may vary from region or port, usually reflecting local availability and price. Herring and skate are sought after for the attractive smell and endurance properties, but other species are also used. In the *H. americanus* fishery in Long Island Sound, fish racks of any species from local fish retail stores are frequently used. Artificial bait is currently being evaluated. The first products used cow hide for durability but after bovine spongiform encephalopathy (BSE or “mad cow disease”) became prevalent in bovine herds, this was discouraged.

8.11.2 Commercial exploitation

The lobster resource in Canada and the USA is the most productive lobster fishery in the world and one of the most valuable of fisheries of eastern North America. Reported lobster landings are currently at or near historically high levels in both countries (Fig. 8.2, FishStatJ, 2012; DFO, 2012; NMFS, 2012). Catches have increased dramatically since the 1980s likely because of changes in environmental and ecological conditions affecting lobster production (see Section 10). There have been recent severe declines in the stocks in southern New England that may reflect continued ecological or environmental change and effects of near coastal habitat disruption.

The principal landings of *H. gammarus* now occur in the United Kingdom, Ireland, the Channel Islands and northern France. Landings have historically averaged 2500 t per year and are important to the fishing communities throughout their range (Mercer *et al.*, 2001). Declines in the *H. gammarus* harvest have occurred throughout Europe over the past 50 years (FishstatJ, 2012). There was a major collapse population in Norway beginning in the 1960s. Sweden, Denmark once logging a few hundred tonnes annually, now generate on the order of 10 t per year. Landings from the Mediterranean countries –Turkey, Italy, Yugoslavia and Algeria – in some cases quite significant, have fallen to zero.

The total landings in a given year and area is a function of lobster abundance, fishing effort, and catchability. Many factors affect catchability including the bait, trap design, soak time, molt status, the

number of traps, temperature, and the presence of other lobsters in the trap or other species in the trap (Cobb, 1995). Laboratory studies of the behavior of *H. americanus* indicate that only a small portion of lobsters that encounter the traps actually enter them and are subsequently captured (Karnofsky & Price, 1989). The relationship between catch rate and abundance or density and between effort and fishing mortality is therefore complex (Addison & Bell, 1997; Addison & Bannister, 1998). Encounter probability depends upon the lobster having the external or internal motivation to leave its shelter (i.e., state of hunger, gender, reproductive status, time of day, water temperature, light level, odor cues). Catchability is lowest during ecdysis (Miller, 1990) but increases in early post-molt when feeding levels increase to recover from molting (Ennis & Fogarty, 1997). Many fishermen plan their maximum effort to correspond to the period after the molt. In general, *Homarus* is nocturnally active and leaves its shelter when light intensity falls below $2 \times 10^{-2} \mu\text{W}/\text{cm}^2$ (Weiss, 1970; Jury *et al.*, 2005). In deeper or murkier water with lower light levels, it is possible that lobsters are more active or active for longer periods. However, *in situ* video evidence indicates that entry rates to traps in *H. americanus* do not increase at night (Jury *et al.*, 2001).

Temperature also strongly affects catchability. McLeese & Wilder (1958) observed activity to increase linearly with temperatures between 2°C and 10°C, to remain constant between 10–20°C, and increase again above 20°C.

Miller (1990) estimated effective area fished by comparing trap catches and diver surveys and found that trap catches do not reflect the sex ratio, size composition, or reproductive status of the lobsters in the area adjacent to the traps. Tremblay & Smith (2001) used comparisons between direct estimates of density and trap catches of American lobster to demonstrate seasonal differences in effective areas fished.

Trap-saturation effects (decreasing catch rates with increasing catch) occur as a result of the interaction between lobsters already captured by the gear and lobsters approaching or trying to enter the trap (Fogarty & Addison, 1992). Addison & Bell (1997) modeled the capture process involved in *H. gammarus*. *In situ* video analysis confirmed the

importance of intraspecific interactions to catch rates (Jury *et al.*, 2001).

Intense gear-competition, where lobsters approaching gear may choose between more than one trap can also reduce catch per trap. This has been reported for a variety of crustaceans including American lobster (Waltz, 1989), European lobster (Addison & Bannister, 1998), blue crab (*Callinectes sapidus*), crayfish (*Orconectes virilis*) (Momot, 1998), and brown crab (*Cancer pagurus*) (Tully *et al.*, 2006a). Crecco (2000) found widespread and persistent evidence of gear-saturation in the US lobster fishery. High trap densities can result in a non-linear relationship between fishing effort and fishing mortality, making management through effort controls complex (Gendron & Brethes, 2002)

8.11.3 Fishery management

Canada and the USA use different schemes to divide up the ocean into management zones. Canadian fisheries are managed federally throughout by the Department of Fisheries and Oceans. There are 41 Canadian Lobster Fishing Areas (LFAs), each with its own season, varying in length from 8 weeks to 8 months. Other management strategies in the LFAs include restrictions on licences and number and type of traps.

In the USA individual states retain some sovereignty over their waters out to 3 miles (5.5 km) from shore, beyond which fishing grounds fall to federal management. This creates a rather complicated management structure. Federal (National Marine Fisheries Service) and state agencies coordinate fishery management of fisheries, such as the lobster that are harvested in both federal and state waters. Fishing activity in federal waters is managed by the New England Fishery Management Council, while fisheries in state waters are managed by the Atlantic States Marine Fisheries Commission (ASMFC) under an interstate fishery management plan. The ASMFC currently uses six areas; Maine has further divided their coast into seven lobster zones co-managed with the fishermen. Area management has the advantage of allowing adaptive harvesting rules reflecting local tradition and stock abundance. The major disadvantage is that enforcement is complicated.

In Europe lobstering is an entirely inshore fishery managed by the Common Fisheries Policy (CFP) which sets a minimum landing size (87 mm CL; Browne 1999). Otherwise each country must manage its own fishery, but must demonstrate to an EU Commission that its management plan is non-discriminatory to fishermen from other countries. National level management is generally centralized or regionalized in some countries and regional differences in minimum size regulations (usually between 87–90 mm) and input controls (vessels and traps) occur. Fishermen voluntarily v-notch lobsters in Ireland and the United Kingdom. V-notched lobsters are legally protected. In some areas there may be what can be described as “pseudo-limited entry” regimes where specific licences or permits are required to fish for lobster, but the number of such permits is rarely strictly limited. ICES currently does not assess European lobster stocks and generally there are few formal and regular scientific assessments being produced at national level. Length cohort analysis and egg per recruit assessments have been produced in Ireland (Tully *et al.*, 2006b) and United Kingdom, but as yet the output of such assessments have not been used to develop new management measures. The positive effects on reproductive potential in *H. gammarus* of a v-notching program in Ireland was demonstrated by Tully (2001). The spawning contribution from v-notched lobsters in Irish stocks may be significant given that catch rates of v-notched lobsters are, in some regions, 20–25% of all female catch rates and v-notched lobsters are larger than other female lobsters.

The American lobster has traditionally been managed through input controls such as licencing and trap limits. Technical regulations include v-notching, minimum and maximum CL and prohibition on possession of ovigerous females. The rationale for these measures has been based on the yield and egg per recruit considerations, preserving the breeding populations and marketing factors. These analyses have been used as qualitative guides to regulation rather than hard targets. Historically, an egg per recruit (EPR) reference point has been used in both the USA and Canada. In Canada, the management target has been the doubling of EPR relative to 1995 levels (Fogarty & Gendron, 2004). In the USA, the target has been to maintain $F_{10\%}$, a

fishing mortality rate below a threshold that would preserve a brood stock giving at least 10% of the egg production of an estimated virgin stock. However, a recent review of the assessment process in the USA has concluded that none of the assessment methods were able to adequately estimate EPR or $F_{10\%}$ (ASMFC 2009). The most recent stock assessment (through 2007) adopted a new approach (ASMFC 2009).

The University of Maine (UMaine) statistical catch-at-age model is now used to estimate abundance and mortality of male and females lobsters by size for each stock unit. This model uses size transition matrices to represent growth similar to that used for *Jasus* lobster stocks in New Zealand (Chen & Kennelly, 1999; Breen *et al.*, 2002) and for sea scallops in the northeast USA. The model calculates spawning stock biomass per recruit and is fit by maximum likelihood to landings and surveys data.

Trends in indicators of natural mortality, abundance, and fishery performance were also examined in a traffic light approach. Revised reference points include median reference abundance and median exploitation rate thresholds for combined sexes over 20 years in the Gulf of Maine, Georges Bank, and southern New England. The assessment further recommends that stock status be determined by comparing the average reference abundance and average exploitation rate for combined sexes during the most recent three years to stock specific thresholds values.

Output controls such as total allowable catches (TACs) have not been used in the North American fishery except for one fishing area off southern Nova Scotia. There are two examples of closed areas in Canada, one in Bonavista Bay and one in LFA 40 for fixed lobster gear on Brown's Bank, Nova Scotia. The latter example was established in 1979 to protect a large concentration of reproductive females on Brown's Bank. Impacts from this marine protected area on lobster stocks are unclear (Petruny-Parker *et al.*, 2005). Extensive studies were conducted in Bonavista Bay by Rowe (2001) showing differences in some lobster population parameters inside and outside the reserve, but the data suggested no change in densities or proportion of ovigerous females.

8.12 Mariculture and population enhancement

Scientists, fishermen, and fishery managers have long prophesized the commercial demise of *Homarus* fisheries. Over a century ago, Herrick (1895) citing a 25% decline in New England landings of *H. americanus* between 1889 and 1892 was motivated to write, "These figures illustrate very forcibly the decline which, unless speedily checked, threatens to destroy this valuable fishery." Similarly, J.N. Cobb (1899) noted alarming declines in the lobster catch (and catch per trap) in Maine. Clearly, by the end of the 20th century the fishery did not collapse, but expanded. However, some fishing areas in the USA and Canada appear to be truly overfished and the catch has declined significantly, leading to calls for "rebuilding" the population to a level at which managers and fishermen can agree that the landings are stable. Proposed solutions run the gamut, from restocking hatchery-reared young, to installation of artificial reefs, to meeting biological reference points in the fishery, to high-tech mariculture. Despite technological advances in aquaculture, here we note the lack of progress toward truly intensive lobster mariculture, and give a brief overview of research on stock and habitat enhancement efforts.

8.12.1 Mariculture

Intensive mariculture, the culturing of marine organisms in high-density, technically sophisticated facilities, for lobsters has been examined and touted since the mid 1880s (Aiken & Waddy, 1995; Nicosia & Lavalli, 1999, Wickins & Lee, 2007). Research in the 1970s and 1980s, primarily on *H. americanus*, demonstrated the feasibility of lobster mariculture. This has been reviewed by Aiken & Waddy (1995) in considerable detail. Little progress has been made since that review. The chief constraint to developing the culture of *Homarus* to commercial scale is the unfavourable cost benefit of such projects. Despite consumer appetite for lobster, the remarkable increase in landings by the natural fishery has been able to meet demand at reasonable prices. The demand is for lobsters that weigh about 500 g, the weight of lobster near the

minimum legal size in many areas. Consumer preference and legal constraints on holding or selling lobster smaller than minimum size discourages the development of a market for smaller lobster that would be more economical to produce. Because of this, Aiken & Waddy (1995) advocate the development of a market for small lobsters although, as they point out, commercial constraints, particularly of providing warm water and effective feed, are formidable. Research attention has re-focused on population enhancement or restocking programs in which lobsters are cultured to a young age but a size at which predation is less likely (Wahle, 1992). Extensive aquaculture ("sea ranching") also has been suggested, but economic analysis for *H. gammarus* ranching in Norway where the fishery is nearly completely collapsed, is still negative (Moksness *et al.*, 1998).

8.12.2 Stock enhancement

Common sense suggests to many that contributing young to a population should increase the number of adults available to the fishery. This reasoning led, for many years, to the proliferation of lobster hatcheries whose primary goal was to rear and release larvae. Despite the continuing lack of evidence that the release of hatchery-produced young can economically make an impact on the population, there were 20 or more lobster hatcheries in the USA, Canada, and Europe between 1880 and 1900 (Nicosia & Lavalli, 1999). Early efforts at stock enhancement for clawed lobsters in Norway and the USA involved lobster "parks" in which ovigerous females, captured in the fishery, were held until their eggs hatched. When this was seen as ineffective, rearing eggs separated from the female in jars was tried with great success – up to 93% of the eggs hatched into first stage larvae and were released into the environment. The release of millions of stage I larvae probably made little difference to the population. Later efforts reared lobsters to the fourth (postlarval) stage before release (Nicosia & Lavalli, 1999) but still without demonstrable enhancement of the population. However, rearing lobsters to 5–12 months of age in a hatchery before release holds more promise. The hatchery-release program in Norway's Kvitsoy Island is perhaps the

best example of a local fishery that benefitted tangibly from stock enhancement; however, this small fishery numbers its catch only in hundreds of lobsters per year. As yet, such a program does not seem economically viable at a large scale (Bannister & Addison, 1998; Agnalt *et al.*, 1999).

8.12.3 Habitat enhancement

The enhancement of population size by providing additional appropriate habitat is often suggested under the assumption that habitat is limiting the growth of the target species. Artificial reefs primarily are targeted at finfish production, and while lobsters certainly are found at artificial reefs intended for finfish (Briggs & Zawacki, 1974), reef building is not frequently targeted at crustaceans. An exception are shell reefs constructed to mitigate habitat-loss for juvenile Dungeness crab *Cancer magister* (Dumbauld *et al.*, 2000).

Artificial reefs designed specifically for *Homarus* have been built on both sides of the Atlantic. In 1965, a 3000 m² reef of large sandstone boulders was placed 2.5 km from the nearest known good lobster habitat in Northumberland Strait, Canada (Scarratt, 1968). Colonization was slow, after 2 years biomass was low, although the size of individual lobsters was larger than that in nearby natural lobster ground. After 7 years, the reef communities were similar to natural areas and lobster populations had similar characteristics as well (Scarratt, 1968, 1973b).

There is a positive relationship between lobster size and shelter size (Cobb, 1971). Larger lobsters will choose, or construct, larger shelters. They also may maintain a minimum distance between occupied shelters through aggression (Lawton & Lavalli, 1995). These observations were used to fabricate shelters for a reef in Rhode Island, USA (Sheehy, 1976). The shelter units had either three small crevices or a single large crevice and were sited in arrays on a featureless sand substrate about 0.6 km from a rocky habitat. Vagrant lobsters arrived within a week. A year later, lobsters ranging from postlarvae to egg-bearing females resided on the reef and the biomass of lobsters was higher than in the nearby rocky area. Occupancy by small and medium lobsters was higher in the more closely

spaced arrays. Planning for appropriate inter-neighbour distance may be a critical design feature for clawed lobster reefs (Sheehy, 1976).

The utility of combining the disposal of solid waste and artificial reefs was explored in the UK. Pulverized fuel ash, waste from burning coal, was compacted into bricks stacked underwater into 4 × 1 m conical units in array on sandy substrate at 10 m depth in Poole Bay on the south coast of England (Jensen *et al.*, 1994, 2000a,b). Although the nearest known natural lobster habitat was over 2 km distant, the reef was occupied within weeks by vagrant lobsters. Settlement later by postlarvae was inferred from the presence of very small lobsters. The size distribution of lobsters on the reef and in the fishery were similar initially, but later the reef saw more larger lobsters than are found in the fishery (Jensen *et al.*, 2000a,b). This may have been a result of lower fishing effort on the reef or perhaps because the crevices in the reef units were larger than in the natural habitat.

The impact of new habitat in the form of a specially designed reef for lobsters in Rhode Island was examined by Castro *et al.* (2001) and Castro (2003). Rock rubble was placed on featureless shell-mud substrate forming 6 replicate reefs, each 10 × 20 m. Lobsters populated the reef by postlarval settlement and immigration from the surroundings. The development and dynamics of the lobster population of the reef was monitored by trapping, tagging and diver surveys for 5 years (Castro, 2003). Before the reef was built few lobsters were found on the soft sediment of the site; within 3 months vagrant lobsters had moved in. After the first year, lobster density on the reef was equal to or greater than nearby natural areas. Lobsters on the reef were larger in each year after the first than in nearby (2 km) rocky areas. A few tagged lobsters were recaptured numerous times on the reef suggesting a long residence time by some individuals. Postlarval settlement on the reef compared favorably to settlement density in natural beds monitored nearby.

The relationship between crevice size and lobster body size (Cobb, 1971) was incorporated into models of the creation of interstitial spaces by different sizes of stone (Barry & Wickins, 1992; Wahle, 1992b). In planning for an artificial reef for

lobsters of all sizes it would be useful to estimate the numbers and sizes of habitable crevices in reefs made of different size rock. If a reef were planned with enough shelters for all sizes, it might reduce the chances of a local demographic bottleneck. Immigrants and newly settled recruits to the reef would have to be accommodated and, if juveniles were seeded, would compete for shelter with the seeded population. Such models of crevice size are important to an initial understanding of the constraints on habitat use as well as the practical question of what rock sizes to use in constructing a reef for *Homarus*, or for any lobster (Spanier, 1994).

8.13 Conclusions and future research

Despite the large amount of scientific knowledge accumulated on the two species, and the fact that one of them comprises the largest lobster fishery in the world, the key to wise management remains elusive. The large commercial value of the North American fishery, and its recent dramatic upswings in abundance and catastrophic mass mortalities, have prompted a large amount of recent research activity on *H. americanus*.

The American lobster has increased substantially in the cooler, northern part of its range, and this expansion has resulted in an overall increase in landings. In contrast, populations in the southern part of the range are collapsing, leading fishery managers to consider, but eventually reject, a ban on lobstering in this region. The steep latitudinal thermal and biogeographic gradient across the species' range are likely at the foundation of the contrasting regional dynamics of lobster populations. Fishing down predators, thermally mediated range expansion and bait subsidies may explain the increases in the north, while physiologically stressful temperatures compounded by disease likely explain the losses in the south. Further understanding of these dynamics requires more knowledge of the interaction of the American lobster with its ecosystem. This will require a better information on the spatial dimension of bottom-up and top-down trophic effects, disease epidemiology, and physiological and genomic responses to climate change.

Stocks of the European lobster may have receded at the extremes of the species' historic range, but for several decades its abundance and fishery in the central part of its range has remained stable, if low. Forthright attempts at stock enhancement in Europe have been made without significant impact, except at a very local scale, and have not yet proven cost effective. Nonetheless, the scientific focus on enhancement of this species has provided valuable quantitative information on the efficacy of lobster stock enhancement.

Important advances have been made in our understanding of larval source-sink dynamics in both species, by a combination of coupled bio-physical models, population genetics, and satellite imagery. Both modeling and genetic evidence suggest populations self-recruit at a smaller spatial scales than larval dispersal potential might suggest. Future modeling efforts would benefit by expanding the geographic domain to include a larger portion of the species range, as well as refinements of behavioral parameters, such as the vertical distribution of larvae which can dramatically affect the range of advection. Despite important advances and rapidly developing tools, population genetic studies have yet to catch up with larval source-sink modeling to resolve questions of connectivity at fine geographic scales.

The development of stage-structured models has been a great advance in population modelling and stock assessment. If further advances are made in age-determination, we may be able to employ age structured models with more confidence. Understanding regional differences in demographic rates, such as growth and reproduction, will also further refine these models. The reproductive and population-level consequences of strongly size selective harvesting, especially of males, remains poorly understood for *Homarus*, although examples may be found in other exploited species.

Integrating an understanding of the demographic and ecosystem processes discussed above into stock assessment and management will result in better stock definition and an improved ability to differentiate losses due to fishing from losses due to emigration and natural mortality. Improved spatial resolution of these processes should be a goal of future research on *Homarus* as it is in other fisheries.

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Chapter 9

***Jasus* and *Sagmariasus* Species**

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Abstract

The six spiny lobster species of the genera *Jasus* and *Sagmariasus* are the basis of some of the most important spiny lobster fisheries found in the Southern Hemisphere. These species inhabit rocky reef and foul ground habitats in shallow coastal waters. Many aspects of the biology of this group of spiny lobster species appears to be similar despite their circumglobal geographic range and their taxonomic diversity. Of the six lobster species, only *J. lalandii*, *J. edwardsii* and *Sagmariasus verreauxi* exist as more extensive populations on larger land masses that are all important resources as regional fisheries. The remaining three species, *J. caveorum*, *J. frontalis* and *J. tristani* (the last species is expected to be synonymized with *J. paulensis*), exist on small isolated oceanic islands and seamounts. In recent years there is new evidence that changes in ocean climate are beginning to show significant impacts on populations of several of the species of these genera. Given the biology of these species, especially their larval biology, it is likely that further change in ocean climate has the potential to greatly affect the production of these lobster species.

Key Words: *Jasus edwardsii*; *Jasus lalandii*; *Jasus frontalis*; *Jasus paulensis*; *Jasus caveorum*; *Jasus tristani*; *Sagmariasus verreauxi*; spiny lobster; Palinuridae

9.1 Species and distribution

George and Maine (1967) divided the Family Palinuridae into two main evolutionary lineages, Stridentes and Silentes, based on the presence or absence of the stridulating organ at the base of the antennae. The stridulating organ is used for communication and defence (Bouwma & Herrnkind, 2009; Staaterman *et al.*, 2010), allowing members

of the Stridentes to make a rasping sound by rubbing the plectrum, a basal extension of the antenna, over the antennular plate (Palero *et al.*, 2009). The genera *Panulirus*, *Justitia*, *Palinurus*, *Palinustus*, *Linuparatus*, *Puerulus* and *Palibythus* belong to the Stridentes group, whereas the genera *Jasus*, *Sagmariasus*, *Projasus* and *Palinurellus* belong to the Silentes group (George, 2006). Recent molecular data generally supports the division

between the Stridentes and Silentes, with the Stridentes forming a monophyletic group. However, the Silentes were paraphyletic as *Palinurellus* is more closely related to the Stridentes than to the other members of the Silentes, and it is likely that *Palinurellus* is a transitional lineage between the two groups (Tsang *et al.*, 2009). Initially it was thought that the ancestral Palinuridae stock originated from less specialized species that inhabited deep waters, such as *Puerulus* and *Linuparus*, which subsequently diversified and invaded shallow waters (George & Maine, 1967; George, 2005). Contrary to this hypothesis, Tsang *et al.*'s (2009) research indicates that the Silentes group are the basal stock for the Palinuridae, probably originating from the Southern Hemisphere, in the shallow-water of onshore habitats and subsequently diverging into offshore, deep-water locations.

The genus *Jasus* (Parker, 1883) is the most diverse of the Palinuridae genera in the Southern Hemisphere, comprising five species that are distributed throughout the temperate waters of the South Pacific, South Atlantic and South Indian Oceans (Plate 9.1). All five species are biologically and morphologically very similar (see Table 10.1 in Booth, 2006), and there is relatively little genetic divergence between the five species (Ovenden *et al.*, 1997). *Jasus edwardsii* (Hutton, 1875), commonly known as the red rock lobster or southern rock lobster, is distributed throughout New Zealand from the Three Kings Islands to the Auckland Islands, on seamounts in the Tasman Sea (Booth, 2000) and in southern parts of Australia south of about 30°S (Phillips *et al.*, 2000). *Jasus edwardsii* was previously known as *Jasus novaehollandiae* in Australia until the two species were synonymised in 1990 (Booth *et al.*, 1990). A second continental species, *Jasus lalandii* (H. Milne Edwards, 1837) or Cape rock lobster, is found throughout western South Africa between Walvis Bay, Namibia (23°S) and East London, Cape Province (28°E) (Pollock, 1986). The other three *Jasus* species have highly restricted distributions associated with isolated oceanic islands and seamounts. *Jasus paulensis* (Heller, 1862) is found on the isolated islands of Île St Paul and Île Amsterdam, as well as nearby seamounts in the southern Indian Ocean (Webber

& Booth, 1988; Holthuis, 1991; Booth, 2006). The range of this species appears likely to be extended by new DNA evidence (J. Groeneveld, pers. comm.) which indicates there are insufficient differences to differentiate the species from *Jasus tristani* (Holthuis, 1963), which is found in the Southern Atlantic Ocean at the Tristan da Cunha Archipelago, Gough Island and on the Vema Seamount (Heydorn, 1969). *Jasus frontalis* (H. Milne Edwards, 1837) is restricted to the Juan Fernandez Archipelago and the waters around Islas Desventuradas, west of Chile (Holthuis, 1991; Yáñez *et al.*, 2000), and *Jasus caveorum* (Webber & Booth 1995) has only been recorded from the non-emergent Foundation Seamount chain (35°S, 120°W) in the east South Pacific Ocean from depths below 140 m (Webber & Booth, 1995).

The genus *Sagmariasus* is represented by a single species, *Sagmariasus verreauxi* (H. Milne Edwards, 1851), commonly known as the pack-horse, green or eastern rock lobster, or pawharu in Māori. The species was previously placed in the genus *Jasus*, but was given a separate subgenus, *Sagmariasus*, because it differed from the other *Jasus* species in both morphological and behavioural aspects (Booth, 2006). In 2002 *Sagmariasus* was elevated to genus level as the differences were considered sufficient to warrant full genus status (Booth *et al.*, 2002). The separation between *Jasus* and *Sagmariasus* has since been validated by molecular genetic data (Palero *et al.*, 2009; Tsang *et al.*, 2009). *Sagmariasus verreauxi* has been found throughout New Zealand from Bluff to Cape Reinga, although it is only common in north-eastern New Zealand (Kensler, 1967; Booth, 2011). It is also found in the Chatham Islands, Kermadec Islands and in eastern Australia from Tweed Heads in New South Wales (28°S) down to Tasmania (42°S), and west through the Bass Strait to Port MacDonnell (140°E) (Holthuis, 1991; Montgomery & Craig, 2005). The species appears to be extending its range southward in south-eastern Australia with increasing numbers of these lobsters captured off eastern Tasmania, which has been linked to the strengthening of the Eastern Australian Current as a result of climate change processes (Johnson *et al.*, 2011).

Table 9.1 Reproductive parameters for *Jasus* and *Sagmariasus* species.

	J. edwardsii	J. lalandii	J. paulensis.	J. tristani	J. frontalis	S. verreauxi
Female size at sexual maturity (mm CL): min (L_{50})	58 (63–104) ^{1,2,6,7}	45 (53–65) ^{8,9,10}	(65–75) ¹³	(56–60) ^{10,14}	(75–77) ^{17,18}	150–170 ^{20,21}
Female age at maturity (yrs)	3–7 ¹	5 ¹¹			7 ¹⁸	7–8 ^{22,26}
Egg-bearing (hatch) season	Win/spr (spr) ¹	Win/spr (spr) ¹¹	Win (spr) ¹³	Win (spr/sum) ^{15,16}	Win/spr (spr/sum) ^{17,19}	Spr/sum (sum) ²¹
Brood period (mo)	3.5 ¹	2.5–4 ^{11,12}	4–6 ¹³	4–6 ^{15,16}	2.5–6 ^{17,18,19}	2–3 ²¹
Clutch size min–max $\times 10^3$	44–660 ³	33–490 ⁹		7–137 ¹⁴	61–524 ⁹	387–2040 ⁹
Duration of phyllosoma stage (mo): wild (cultured)	12–24 ⁴ (7–12) ⁵	14–18 ¹¹ (10) ¹²				8–12 ²³ (6–12) ²⁴
Duration of the puerulus stage: (cultured)	9–25 ²⁵	>31 ¹²				25 ²⁴

¹Annala *et al.* (1980); ²Linnane *et al.* (2009); ³Green *et al.* (2009); ⁴Booth & Phillips (1994); ⁵Kittaka *et al.* (2005); ⁶Linnane *et al.* (2008); ⁷Smith & Ritar (2007); ⁸Cockcroft & Goosen (1995); ⁹Annala (1991); ¹⁰Pollock (1991a); ¹¹Pollock (1986); ¹²Kittaka (1988); ¹³Grua (1960) (incorrectly referred to as *J. lalandii*); ¹⁴Pollock & Goosen (1991); ¹⁵Roscoe (1979); ¹⁶Heydorn (1969); ¹⁷Arana *et al.* (1985); ¹⁸Dupre (2003); ¹⁹Dupre (2000); ²⁰Montgomery (1992); ²¹Booth (1984); ²²Booth (2006); ²³Booth (1986); ²⁴Kittaka *et al.* (1997); ²⁵Booth & Kittaka (1994); ²⁶Montgomery *et al.* (2009).

Note that *J. caveorum* is not included in the table as virtually nothing is known about the reproductive parameters of this species except that the females carry eggs in winter (Webber & Booth, 1995). Also, *J. tristani* and *J. paulensis* are likely to be synonymised on the basis of recent DNA evidence (J. Groeneveld, pers. comm.).

9.2 Reproduction, life history and growth

Species of *Jasus* appear to have similar reproductive strategies based on the information available (Table 9.1). Compared to other Panulirid species, *Jasus* species take a relatively long time to reach sexual maturity with females reaching maturity between 3 and 7 years of age, at an average carapace length (CL) of between 53 and 104 mm, depending on species and locality. *Sagmariasus verreauxi* females reach sexual maturity at a much larger size of 150–170 mm CL. Little information is available on the size and age at which males reach sexual maturity for most species of the genera. *Jasus edwardsii* males become sexually mature between 55 and 85 mm CL (MacDiarmid, 1989; Turner *et al.*, 2002) but they may not get the

opportunity to breed until they are much larger because aggression between males may prevent small males from mating with females (MacDiarmid, 1989).

Breeding of *Jasus* species occurs in winter shortly after the female moults, providing her with fresh ovigerous setae on which to carry her eggs, and to ensure that moulting does not occur while she is carrying eggs (MacDiarmid & Kittaka, 2000). During mating, male *Jasus* and *Sagmariasus* lobsters deposit a short-lived spermatophore on the sternum of the female, which is usually immediately followed by egg extrusion. The close timing between mating and egg extrusion requires a high level of synchrony between mating and egg maturation. Egg maturation in *J. edwardsii* can be predicted based on the moult date and carapace length (MacDiarmid & Kittaka, 2000), and experiments

have shown that delaying mating for 5 days after the peak maturation date reduces the fertilization success by around 55%, and delaying mating for 10 days after peak maturation reduces the fertilization success by around 98% (MacDiarmid & Kittaka, 2000).

Reproductive success is correlated with size for both male and female *J. edwardsii*. Fecundity of the largest females can be more than an order of magnitude greater than the fecundity of the smallest females, and larger females produce larger eggs (MacDiarmid & Kittaka, 2000; Green *et al.*, 2009). Large males control the mating access to females and will mate with the majority of the females in a den (MacDiarmid, 1989). Furthermore, larger males produce more sperm than smaller males resulting in larger clutch sizes, and, thus, the reproductive output of lobster populations that have a low abundance of large males may be constrained by sperm limitation (MacDiarmid & Butler, 1999). However, females may mate with multiple small males to increase their fertilization rate. Large males will also conserve their sperm by varying the size of their spermatophore they deliver according to the size of the female, with larger females receiving larger spermatophores (MacDiarmid & Butler, 1999).

Eggs hatch in spring to summer after brooding for between 3 and 6 months for most *Jasus* species, and somewhat shorter for *S. verreauxi*. Hatching in *J. edwardsii* occurs at sunrise with the first larval stage a very short-lived naupliosoma that develops into a 2-mm-long phyllosoma within 30–60 minutes (MacDiarmid, 1985; Kittaka, 1997). The phyllosoma grows continuously by up to 17 moults (instars) for *Jasus* and *Sagmariasus* species, before metamorphosing into a non-feeding puerulus (Kittaka, 1988; Illingworth *et al.*, 1997; Kittaka *et al.*, 1997). Phyllosoma also undergo a series of distinct morphological stages with some stages including several moults, with 11 stages identified for both *J. edwardsii* and *J. lalandii* larvae (Kittaka, 1988, 2000).

The larval period for *Jasus* and *Sagmariasus* species is very long, with phyllosoma estimated to spend between 9 and 24 months in the plankton (Booth, 1986; Pollock, 1986; Booth & Phillips, 1994). The leaf-shaped, transparent phyllosoma

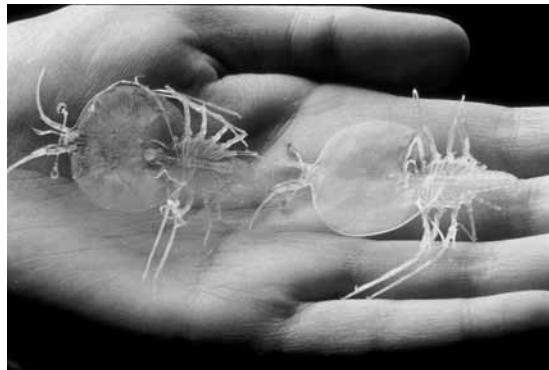


Fig. 9.1 Final-stage phyllosoma larvae of *Jasus edwardsii*.

have a very poor horizontal swimming ability until the late development stages (Kittaka, 1994). After hatching the early phyllosoma are transported hundreds of kilometres offshore where the majority of their development occurs, often within large ocean gyres (Bruce *et al.*, 2007). Late-stage phyllosoma are dispersed widely offshore (Fig. 9.1) (Chiswell & Booth 1999, 2005), with metamorphosis from phyllosoma to puerulus most often occurring beyond the continental shelf, on average around 200 km offshore (Jeffs *et al.*, 1999, 2001). The mechanisms by which pueruli make their way over this distance in order to reach shallow coastal waters where they settle is poorly understood (Fig. 9.2). Jeffs *et al.* (2005) reviewed the range of cues that may be used by pueruli to orientate toward the coast, including underwater sound, water chemistry, magnetic fields, celestial cues and hydrodynamic waves, but they found little evidence for any long distance orientation cues directing the shoreward movement of pueruli.

Given the long duration of the larval period, the poor horizontal swimming ability of phyllosoma and the speed of ocean currents it is theoretically possible that phyllosoma could be dispersed over extensive areas of the Southern Hemisphere. Booth & Ovenden (2000) sampled the south Atlantic Ocean, southern Indian Ocean and the Tasman Sea for mid- to late-stage *Jasus* phyllosoma. In general they found the greatest densities of phyllosoma within a few hundred kilometres of known adult populations, and densities declined with increasing

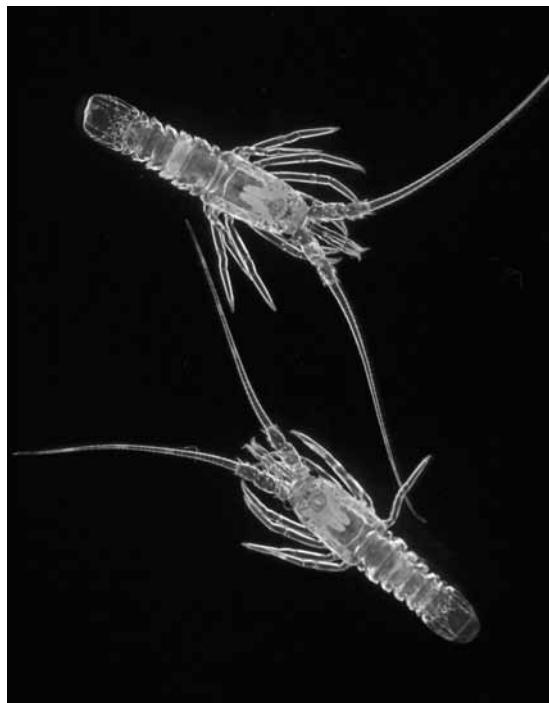


Fig. 9.2 Pueruli of *Jasus edwardsii*, the white digestive gland indicating that settlement has taken place.

distance from adult populations. *Jasus edwardsii* phyllosoma were caught southwards of South Australia and east across the Tasman Sea to the western coast of New Zealand. *Jasus paulensis* phyllosoma were only caught near their breeding area (Île Amsterdam) in the middle of the southern Indian Ocean, and *J. lalandii* phyllosoma were mainly found off the east and west coasts of South Africa. Unexpectedly, relatively high numbers of *J. lalandii* phyllosoma were also found around Île Amsterdam, although no adult *J. lalandii* have even been caught in this area. Phyllosoma were never caught upstream of the prevailing current from their respective adult habitat. The close association between adult and larval distributions suggests that on a broad geographic scale, *Jasus* larvae are retained close to their natal location, possibly through physical ocean processes and/or behavioural strategies.

Studies on the distribution of *J. edwardsii* phyllosoma and pueruli around New Zealand have

found that nearly all mid- to late-stage (Stages V–XI) phyllosoma were caught offshore beyond the continental slope, from just seaward of the slope to 1300 km from the mainland (Booth, 1994; Booth *et al.*, 1998; Jeffs *et al.*, 2001). It was previously assumed that because of their shape and poor swimming ability, phyllosoma had no control over their horizontal dispersal. However, there is some evidence that late-stage phyllosoma begin to actively make their way back towards shore because late-stage phyllosoma have been found to be on average 49 km closer inshore than mid-stage phyllosoma (Chiswell & Booth, 1999, 2005). Final-stage phyllosoma have well developed pleopods that may enhance their horizontal swimming ability (Chiswell & Booth, 2005), although the concept of directed shoreward swimming in final-stage phyllosoma is subject to some debate (Phillips & McWilliam 2010). In contrast to the wide dispersal of phyllosoma, *J. edwardsii* pueruli are rarely caught more than 100 km from the coast (Booth, 1994), although pueruli have been caught up to 330 km from the coast (Booth & Chiswell, 2005). McWilliam and Phillips (1997) hypothesized that phyllosoma will delay metamorphosis until they have accumulated a specific level of energy reserves, presumably sufficient to sustain their journey to the coast. Furthermore, they proposed that the highest concentrations of pueruli are typically found in areas of high productivity, which are often associated with continental shelf breaks and inshore margins of oceanic eddies and currents (Phillips & McWilliam, 2009). However, energy storage levels do not appear to be a simple metamorphosis trigger for *J. edwardsii* because Jeffs *et al.* (2001) found that newly metamorphosed pueruli had a wide range of lipid reserves (21–40% of dry body mass), which did not correspond to any measured environmental variables, such as distance offshore.

Modelling data supports the theory that lobster populations can be self-recruiting despite their long larval period. Chiswell & Booth (2008) modelled the dispersal of *J. edwardsii* phyllosoma and pueruli around New Zealand based on satellite-derived ocean currents, and predicted settlement levels were generally in agreement with levels observed on the coast. The model found larvae were

dispersed between four major geographic areas: the east coast of the North Island, the east and south coasts of the South Island, the far north of the North Island and the Chatham Islands. The *J. edwardsii* population on the east coast of the North Island is mainly self-recruiting. Larvae originating from this region become entrained and then retained in the area by the Wairarapa Eddy, a 100 km diameter semi-permanent eddy that circulates off the south-east coast of the North Island (Chiswell & Roemich, 1998; Chiswell & Booth, 1999). A small percentage of larvae from the far north of the North Island, and from the South Island are also transported to this region. The Fiordland population of *J. edwardsii* is also thought to be mainly self-recruiting, with the majority of pueruli that settle on the south and east coasts of the South Island originating from the Fiordland region. In contrast, the far north region of the North Island is mainly supplied by larvae that are transported up the west coast of both islands, while larvae settling on the Chatham Islands originate from a wide variety of sources. Although the majority of settlers are likely to originate from local sources, there is ocean modelling evidence that a small percentage of *J. edwardsii* larvae settling in New Zealand may originate from Australia (Chiswell *et al.*, 2003).

Oceanographic modelling of larval dispersal of *J. edwardsii* in Australia reached similar conclusions to those in New Zealand, with apparent potential for recruitment back to the broad area of larval release (Bruce *et al.*, 2007). In the Australian system, larval flow is generally from west to east with recruitment in easterly management jurisdictions of Tasmania and the Victorian eastern zone supplemented by larvae thought to be arriving from the west. Larvae are found within offshore eddy systems and these also provide an element of westward flow.

Limited information is available on the natural diet of phyllosoma. Studies on the mouthpart morphology and feeding behaviour of *J. edwardsii* and *S. verreauxi* phyllosoma indicate that phyllosoma are opportunistic predators and will grab at anything that comes into reach of their pereiopods (Cox & Bruce, 2003). The mouthparts of early-stage (Stage I–III) phyllosoma of both species are better suited to consuming soft prey such as poly-

chaete worms, medusae and ctenophores, while later stages have a greater ability to manipulate and tear their prey, making them potentially more adept at consuming larger and fleshy prey, such as fish larvae and mussel flesh (Johnston & Ritar, 2001; Cox & Johnston, 2003, 2004). Comparison of zooplankton abundances with *J. edwardsii* phyllosoma abundances shows a strong correlation between the abundance of mid- to late-stage (Stages V–XI) phyllosoma and the abundance of gelatinous zooplankton, while late-stage phyllosoma (Stages IX–XI) were strongly correlated with shrimp and amphipod biomass (Jeffs, 2007). These results, along with those of Cox & Johnston (2003, 2004), suggest that phyllosoma prey on gelatinous zooplankton, as well as some crustaceans in the later stages of development. This mixed opportunistic diet also has support from food chain tracing methods using signature lipids (Jeffs *et al.*, 2004). More recently researchers have turned to molecular genetic techniques to try to identify the prey of phyllosoma. Suzuki *et al.* (2006, 2008) isolated Cnidaria, Urochordata, Teleostei, Oomycetes, Myctozoa, and fungal DNA from the hepatopancreas of several species of *Panulirus* phyllosoma, supporting Cox and Bruce's (2003) laboratory observations that phyllosoma are opportunistic predators. Cultured early-stage *J. edwardsii* phyllosomas reared exclusively on a diet of jellyfish (*Aurelia aurita*, *Dactylogestra pacifica*, *Stauropora mertensi* and *Aequorea coerulescens*) for 2 months grew faster than phyllosoma reared on the current 'best diet' of *Artemia* nauplii and mussel gonads, indicating that the gut physiology of phyllosoma is well-suited to a diet of jellyfish (Kittaka, 2005).

Spiny lobster pueruli resemble juveniles in morphology, but are almost totally transparent. The strong-swimming pueruli have poorly developed mouth parts (Nishida *et al.*, 1990) and rely almost exclusively on stored energy for the duration of their journey back to the coast (Jeffs *et al.*, 1999). *Jasus* pueruli have only been observed to be active at the surface during the night (Jeffs & Holland, 2000), and, likewise, the greatest surface abundances of pueruli of other genera have been caught at night, particularly during a new moon phase (Acosta *et al.*, 1997; Phillips & Pearce, 1997;

Acosta & Butler, 1999; Yoshimura *et al.*, 1999). Upon arrival at the coast *J. edwardsii* pueruli settle into small rocky crevices in shallow waters typically less than 20 m deep (Booth & Tarring, 1986). Settlement mainly occurs at night and can occur at any time throughout the year, although it is often highest during winter and summer (Booth, 1994). Inter-annual settlement levels can vary by 10-fold or more, and there is some evidence that settlement levels are sometimes correlated with subsequent juvenile lobster abundance (Booth & McKenzie, 2009). In some parts of New Zealand, pueruli settlement is strongly influenced by climatic conditions. In the south-east coast of New Zealand, levels of pueruli settlement are correlated with strong southerly winds that occur more frequently during El Niño conditions. Strong southerly winds are thought likely to assist the shoreward transport of phyllosoma and pueruli dispersed off the south-east coast of New Zealand and this may be important in terms of conserving the biochemical reserves of the puerulus needed for subsequent settlement processes (Booth *et al.*, 2000; Wilkin & Jeffs, 2011).

The pueruli of *J. edwardsii* moult into juvenile lobsters 1–3 weeks after settlement, depending on water temperature (Booth & Stewart, 1993). Growth is rapid in the first 3 years, with wild lobsters reaching 38 mm CL after 1 year, 58 mm CL after 2 years and 75 mm CL after 3 years (McKoy & Esterman, 1981; Annala & Bycroft, 1985). Growth of male and female lobsters is similar until they reach sexual maturity; thereafter, the growth of females slows markedly as they invest more energy into egg production (Booth, 2006). *Jasus edwardsii* reaches a maximum weight of 8 kg and a maximum length of 580 mm total body length (TBL) for males, and 430 mm TBL for females (Holthuis, 1991; National Rock Lobster Management Group, 2010).

Sagmariasus verreauxi is the largest of the Palinurid lobsters, achieving a maximum size of 700 mm TBL and a maximum weight of 20 kg (Holthuis, 1991; MacDiarmid & Booth, 2003; National Rock Lobster Management Group, 2010). Little information is available on the growth of small juveniles of *S. verreauxi*, but lobsters are predicted to reach 101–110 mm CL after 5 years,

and 167–178 mm CL after 10 years (Montgomery *et al.*, 2009).

9.3 Ecology and behaviour

Jasus and *Sagmariasus* species are shallow water Palinurids, mainly inhabiting rocky reefs and light foul ground from the intertidal zone down to about 200 m depth, although some species have occasionally been taken from depths of 400 m (Biais, 1987; Holthuis, 1991; MacDiarmid & Booth, 2003). *Jasus lalandii* is typically found in depths of less than 60 m (Holthuis, 1991), whereas *J. caveorum* has only been found on seamounts between 140 and 180 m deep (Webber & Booth, 1995).

Early *J. edwardsii* juveniles (<20 mm CL) are solitary, and normally occupy small holes and crevices in shallow coastal waters. These juvenile lobsters become increasing communal as they develop, and older juveniles and sub-adults (>20 mm CL) are commonly found in large aggregations inside rocky dens (Butler *et al.*, 1999). Aggregations were found to provide a greater level protection from predators in lobsters larger than 20 mm CL, but not for early juveniles (Butler *et al.*, 1999). During the mating season males become aggressive and both sexes tend to be more solitary (MacDiarmid & Booth, 2003).

Jasus lobsters are nocturnal, emerging from their dens to feed at night. Lobsters are opportunistic feeders, ingesting a wide variety of sessile invertebrates; primarily molluscs, crustaceans, polychaetes and echinoderms, as well as some algae (Beurois, 1971; McKoy & Wilson, 1980; MacDiarmid & Booth, 2003; Redd *et al.*, 2008). *Jasus tristani* consumes a greater percentage of kelp and sessile invertebrates, such as sponges, hydroids and bryozoans, than other *Jasus* species, which is likely to be a result of the general paucity of benthic fauna in the Tristan da Cunha Archipelago (Pollock, 1991b). This response of diet to habitat has also been seen in *Jasus edwardsii* where consumption rates of ascidians, urchins and gastropods varied with lobster density and thus competition for preferred prey (Guest *et al.*, 2009). Cannibalism, particularly in early juveniles, can cause high mortality in cultured lobsters (James *et al.*, 2001; Thomas

et al., 2003), and field experiments using tethered *J. edwardsii* (30–52 mm CL) found that 16% of all predation events were caused by free-roaming, larger conspecifics (Oliver *et al.*, 2005). Natural cannibalism rates in the wild are unknown, although Beurois (1974) reported that high levels of cannibalism occurred in the deep-sea populations of *J. paulensis* living around Île Amsterdam and Île St Paul.

Predation interactions between urchins, grazing molluscs and *Jasus* species are of interest in several areas, especially in the context of the effects of fishing. *Jasus edwardsii* are known to predate on abalone, which appears to both increase the size at emergence from cover of abalone juveniles and reduce the yield from the abalone fisheries (Pederson *et al.*, 2008). The interaction between these abalone and lobster fisheries appears more complex in South Africa in some areas where urchins provide limited shelter for juvenile abalone so that predation of urchins by *J. lalandii* potentially increases abalone mortality (Mayfield & Branch, 2000; van Zyl *et al.*, 2003). The predation of urchins by lobster is also of interest because of changes in grazing patterns of urchins when released from predation by lobster (Arana, 1987; Andrew & MacDiarmid, 1991; Shears & Babcock, 2002). The loss of the macroalgal canopy from grazing appears to have surprisingly little effect on biodiversity off eastern Tasmania (Edgar *et al.*, 2004), although more extensive grazing of the reef results in barren areas with substantially reduced productivity and biodiversity (Pederson & Johnson, 2006; Ling, 2008). Rock lobster predation of urchins also appears to mitigate climate change-driven range expansion of the barren forming urchin *Centrostephanus rogersii* off eastern Australia (Ling *et al.*, 2009). The ability to handle and eat urchins appears to generally increase with lobster size (Ling *et al.*, 2009), with *J. lalandii* below 68 mm CL being unable to eat the urchin *Parechinus angulosus* (Mayfield *et al.*, 2001).

Most *J. edwardsii* lobsters show high site fidelity and are resident for the majority of the year, moving less than 3 km from their tagging location (Kelly, 2001; Gardner *et al.*, 2003; Linnane *et al.*, 2005; Barrett *et al.*, 2009; Freeman *et al.*, 2009). During the breeding season lobsters undergo seasonal

inshore–offshore movement associated with moulting and breeding. In New Zealand females have been found to move inshore to moult prior to breeding during autumn, remaining there until spring when they move out to deeper waters to release their eggs beyond the reef edge. Males only move inshore for a brief period in spring for mating and moulting and then move to deeper waters to feed over the sand (MacDiarmid, 1991; Kelly, 2001; MacDiarmid & Booth, 2003).

Occasionally, long distance migrations of juvenile *J. edwardsii* have been reported, although these appear to be restricted to specific locations. In New Zealand, movements usually occur during spring and summer and often cover distances of more than 100 km, with a maximum distance of 406 km recorded (Street, 1971; 1995). The purpose of these migrations is unclear and there is no evidence of returning migrations. Booth (1997) hypothesized that the migrations may be important in maintaining populations of lobsters around the country by countering the effect of larval drift, as lobsters are always observed moving against the prevailing coastal current (Street, 1995; Booth, 1997). The largest *J. edwardsii* migrations observed in New Zealand were from the Otago coast to Fiordland and south Westland (Street, 1995). Unusually large movements of these lobsters have also been observed off the York Peninsular region in South Australia with animals travelling over 100 km to the adjacent Eyre Peninsular and Kangaroo Island (Linnane *et al.*, 2005). These movements were mainly by immature females so the behaviour is consistent with Booth's (1997) hypothesis that these movements are an effort to counteract larval drift. Longer distance (>10 km) movements of juvenile female lobsters have also been observed in north-eastern Tasmania (Gardner *et al.*, 2003).

Sagamariasus verreauxi also exhibit long distance migrations of up to 1070 km, which appear to be associated with the onset of sexual maturity. Maturing lobsters move in a north-west direction around the north-eastern coast of the North Island of New Zealand towards Cape Reinga where there is a particularly large population of adult *S. verreauxi*. Unlike the occasional migrations of *J. edwardsii*, almost all *S. verreauxi* migrate (Booth, 1979, 1997).

9.4 Predators and disease

Spiny lobster phyllosoma are preyed upon by a range of coastal and pelagic fishes, sometimes comprising a significant proportion of the stomach contents of fish (Phillips & Satstry, 1980). Pueruli are also preyed upon by fishes, both benthic and pelagic, as well as octopus. Early juveniles are preyed upon by a wide variety of predators including fish, crabs, octopus and small sharks (MacDiarmid & Booth, 2003; Oliver *et al.*, 2005; Mills *et al.*, 2008), while large lobsters are only susceptible to being preyed upon by very large fish and sharks (Booth, 2006). Behavioural studies with *J. edwardsii* show that juvenile lobsters significantly reduce their activity in the presence of large predatory fish, presumably to reduce their predation risk, and that this behaviour was found to be innate to both cultured and wild lobsters (Mislan & Babcock, 2008; Oliver *et al.*, 2008).

Octopus predation of lobsters in pots increases mortality in many jurisdictions. Research on temporal and spatial patterns of predation has produced mixed conclusions with apparently clear seasonal trends in South Australia (Brock & Ward, 2004), while there were no apparent seasonal trends in Tasmania (Harrington *et al.*, 2006). However, Pecl *et al.* (2009) showed that mortality of lobsters due to octopus increased in years with higher average water temperature, suggesting vulnerability from climate change. Hunter *et al.* (2005) showed that octopus predation in lobster pots represented a case of depensation where predation risk increased as stocks declined and catch rates fell.

There is a paucity of information on the occurrence of diseases in wild populations of *Jasus* and *Sagmariasus* lobsters. Most of the information on diseases of spiny lobsters comes from cultured lobsters and a number of them are associated with poor husbandry (Diggle, 1999). The main diseases known to naturally affect species of *Jasus* and *Sagmariasus* are bacterial diseases (shell disease, vibriosis, *Leucothrix* sp.), fungal infections (*Haliphthoros* sp.), peritrich ciliate infestations and parasitic infections (*Carcinonemertes* sp., *Paramphiascopis* sp.) (Diggle *et al.*, 2000; Bruce *et al.*, 2003; Shields, 2011). Disease outbreaks can cause severe mortalities in cultured lobsters (e.g., Diggle *et al.*,

2000), but the natural rates of disease infection and mortality in wild lobsters are mostly unknown.

The most common disease known to affect wild *Jasus* and *Sagmariasus* lobsters is shell disease, which is the blackening and erosion of the exoskeleton of crustaceans. It is caused by a number of species of chiton-degrading bacteria and fungi such as *Vibrio* sp., *Aeromonas* sp., *Pseudomonas*-like sp. and *Fusarium solani*. In spiny lobsters, tail infections, or tail fan necrosis, appears to be the most common form of shell disease. Musgrove *et al.* (2005) isolated three species of *Vibrio* bacteria from tail fan necrosis tissue of *J. edwardsii* and inoculated them onto healthy lobsters. These lobsters subsequently developed tail fan necrosis demonstrating the causal relationship between *Vibrio* bacteria and the disease. Mild cases of shell disease are not fatal, though damaged lobsters are of lower market value. Mortalities usually occur through secondary infection via the damaged exoskeleton (Evans *et al.*, 2000). Tail fan necrosis is common in captive lobsters (Bryars & Geddes, 2005), but incidence in wild lobsters was previously thought to be low (Musgrove *et al.*, 2005). However, there is evidence that high fishing pressure and repeated handling of undersized lobsters increases the incidence of tail fan necrosis in wild *J. edwardsii* (Breen *et al.*, 2005). In support of this, incidence of tail fan necrosis in *J. edwardsii* was found to be significantly lower in lobsters caught inside a no-take Marine Protected Area (MPA) than in lobsters caught outside the MPA (2% versus 17%) (Freeman & MacDiarmid, 2009).

9.5 Population dynamics

The very long larval period of *Jasus* and *Sagmariasus* lobsters means that larvae are dispersed over a wide area, and, therefore, it is very unlikely that there would be a stock–recruitment relationship for any particular area. Therefore, the extent of populations are likely to be largely recruitment driven rather than dependent on the size of the breeding population (Booth, 2006). Recruitment levels of *J. edwardsii* pueruli can vary by 10-fold or more, and in some areas the abundance of *J. edwardsii* pueruli are strongly correlated with the subsequent

abundance of early juveniles (Breen & Booth, 1989; Booth *et al.*, 2000).

The factors that influence the recruitment of *Jasus* and *Sagmariasus* lobsters are poorly understood. Climatic conditions are thought to have an impact on recruitment in some areas, such as the south-east coast of New Zealand, where levels of pueruli settlement are correlated to strong southerly winds. However, no similar correlation between southerly winds and pueruli settlement was found for the east coast of Tasmania (Booth *et al.*, 2000), but for the same species in South Australia significant correlations between wind stress and data from puerulus settlement monitoring sites indicated that wind influenced settlement patterns (Linnane *et al.*, 2010a). Coastal wind patterns also appear to mediate the settlement of pueruli of *Jasus lalandii* in parts of South Africa (Groeneveld *et al.*, 2010).

Fishing pressure and minimum legal size limits largely determine the population structure of current lobster populations. In overexploited populations, such as the population of *J. frontalis* in the Juan Fernandez Archipelago, a very small percentage of the population is above the minimum legal size (Arana & Olate, 2000; Yáñez *et al.*, 2000). The natural rate of mortality (M) of *Jasus* and *Sagmariasus* populations is largely unknown, although M is estimated to be 0.18 for *J. frontalis* (Arana & Olate, 2000), and typically between 0.1 and 0.2 for *J. edwardsii* (Booth, 2006).

9.6 Harvest of wild populations and their regulation

All species of *Jasus* and *Sagmariasus* are regularly exploited commercially, with the exception of *J. caveorum*, and all fisheries are considered fully exploited. Historical commercial exploitation of *Jasus* and *Sagmariasus* species has tended to follow a typical pattern, initially an intense exploitation of populations with huge catch rates, followed by a rapid decline in population size, and then relatively consistent landings after the implementation of management controls (Booth, 2006). *Jasus edwardsii* from Australia and New Zealand supports the largest commercial fisheries of *Jasus* species, with

Table 9.2 Commercial fisheries production totals for *Jasus* and *Sagmariasus* species for 2009. Statistics from FAO (2011).

Species	Country	2009 landings (tonnes)
<i>J. edwardsii</i>	Australia	3,499
<i>J. edwardsii</i>	New Zealand	3,058
<i>J. lalandii</i>	South Africa	2,100
<i>J. lalandii</i>	Namibia	50
<i>J. paulensis</i>	France (Île Amsterdам & Île St Paul)	390
<i>J. tristani</i>	St Helena	380
<i>J. frontalis</i>	Chile (Juan Fernandez)	58
<i>S. verreauxi</i>	Australia	122
<i>S. verreauxi</i>	New Zealand	36

a combined annual catch of more than 6550 t in 2009, followed by *J. lalandii* from South Africa. *Jasus paulensis* and *J. tristani* support modest-sized fisheries (Table 9.2), although both fisheries provide an important income source for their respective countries (Pollock *et al.*, 2000).

Management controls are now in place for all commercial *Jasus* and *Sagmariasus* fisheries, with most fisheries having a total allowable commercial catch (TACC), a minimum legal size, and protection of ovigerous females. In addition, all relevant countries, with the exception of some parts of New Zealand, have a closed fishing season and most countries have regulations on the type of fishing gear allowed to be used (Booth, 2006).

Jasus and *Sagmariasus* populations are also subjected to heavy recreational harvesting pressure, particularly in Australia, New Zealand and South Africa. Information on recreational harvest levels is limited, but it is estimated that recreational harvest comprises 10–12% of the TACC for *J. edwardsii* in New Zealand (Kim *et al.*, 2004; Haist *et al.*, 2005), 10% of the TACC for *J. edwardsii* in Tasmania (Lyle *et al.*, 2005) and 7–25% of the total allowable catch (TAC) for *J. lalandii* in South Africa (Cockcroft & Mackenzie, 1997).

9.6.1 South Africa and Namibia

West Coast rock lobster *J. lalandii* are distributed generally close to shore from about 23°S in Namibia to about 28°S in South Africa (Pollock, 1986). The trap and hoopnet fishery for this species lies between 25°S in Namibia and 34°S in South Africa, a distance of some 1055 km (Pollock, 1986; Pollock *et al.*, 2000). Recent mitochondrial (mt)DNA data gathered from 235 adult individuals collected at eight sampling sites throughout the distribution range does not justify the recognition of separate fishing stocks over this range (Matthee *et al.*, 2007). Despite this, the Namibian and South African fisheries for *J. lalandii* are managed completely independently.

The development of the South African *J. lalandii* fishery and the trends in commercial landings are well documented (Pollock, 1986; Cockcroft & Payne, 1999; Pollock *et al.*, 2000; Melville-Smith & van Sittert, 2005). Commercial exploitation commenced in the late 1800s and expanded during the early 1900s, eventually stabilizing at catches of about 10,000 t, a level maintained from about 1950 to 1965. Catches declined during the 1960s, most likely as a result of overfishing. The lobster fishing grounds were divided into fishing zones and areas in the early 1980s and a tail mass production quota was replaced by a whole landed mass total allowable catch (TAC) for each zone/area at about the same time (Pollock, 1986). By the mid-1980s catches had stabilized between 3500 and 4000 t, a level at which catch rates seemed to be increasing (Cockcroft & Payne, 1999). This period of relative stability in the fishery was followed by a period characterized by a coast-wide decline in the somatic growth rates of juvenile and adult lobsters (Pollock *et al.*, 1997; Hazell *et al.*, 2002), reductions in the minimum legal size to reduce mortalities resulting from the discarding of undersized lobsters, and a decline in TAC to its lowest ever level of 1500 t in the 1995/96 season (Cockcroft & Payne, 1999). The period between the late 1980s and early 1990s was also marked by a major shift in resource availability from the traditional fishing grounds on the West Coast to the more southern fishing grounds, with far-reaching social, economic and manage-

ment implications (Cockcroft *et al.*, 2008). The early 1990s was also the start of a major influx of lobsters into an area traditionally associated with a lucrative abalone fishery (Tarr *et al.*, 1996; Mayfield & Branch 2000; Blamey *et al.*, 2010). The ecological, fisheries and resource management implications of this influx have been severe (Cockcroft 2001 Blamey *et al.*, 2010; Haley *et al.*, 2011) and are likely to cause challenges in the future management of both rock lobster and abalone resources. The temporal coincidence of the shifts in lobster distribution with events such as onset of reduced somatic growth and increased lobster walkouts (Cockcroft 2001) suggests environmental forcing factors which are still poorly understood.

An Operational Management Procedure (OMP), which uses commercial catch rate data, survey data that is collected independently of commercial fishing activity and somatic growth rate to set the TAC for the lobster resource, was introduced to the fishery in 1997 (Johnston & Butterworth, 2005) and has been used with some modifications since then. The initial target for the 1997 OMP was to achieve an increase of 20% of the 1996 biomass of the lobster resource by the year 2006. By 2003 the resource had improved to 16% above the 1996 level, but by 2006 the resource biomass had decreased again dramatically to 18% below the 1996 level. This decline was due to recruitment failure and continued slow growth (Johnston & Butterworth, 2010). In response, the commercial TAC was decreased by 10% for three consecutive seasons in an attempt to rebuild the resource to a new target (20% recovery above 2006 levels by 2016). In 2009 lobster abundance was estimated to have increased from 18,500 t in 2005/06 to 22,700 t (3.4% of pristine levels) in 2008/09. The TAC for the 2009/10 season was increased to 2,393 t, 53 t higher than the previous season.

The equitable redistribution of fishing rights via the medium-term (2001/2002) and long-term rights allocation processes in 2006 introduced significant changes to the lobster fishery. The long-term rights allocation process for West Coast rock lobster resulted in the commercial fishery being divided into distinct Nearshore and Offshore components with the split in TAC between these components

based on resource availability (80% to Offshore and 20% to Nearshore components). The Offshore component (245 rights-holders) consists of individuals/companies who use traps deployed from large vessels in deep water. The Nearshore component (812 rights-holders) consists of individual rights-holders who are restricted to their zone, or area, of residence (based on Territorial User Rights Fishery (TURF) system) and to the use of ringnets from small vessels in shallow water (Cockcroft *et al.*, 2008). This rights allocation dispensation is currently under review.

The history of the Namibian fishery for *J. lalandii* has been thoroughly reviewed (Tomalin, 1993; Grobler & Noli-Peard, 1997; Pollock *et al.*, 2000). After a period of instability in the 1980s, the 1990s were characterized by an effort to rebuild the resource (Grobler & Noli-Peard, 1997) via conservative TACs which increased gradually from 100 t in 1991/92 to 300 t in 1998/99. With one exception, the TAC was caught in full during this period (Pollock *et al.*, 2000). The TAC was raised to 400 t in 2000/01 and remained at around that level until 2006/07 after which it was reduced to around 350 t in 2008/09. The TAC has not been caught in full since 2000/01 and commercial landings have ranged from just over 300 t to just under 200 t during this period (Maletzky, pers comm.). The Namibian fishery for *J. lalandii* is strongly influenced by environmental conditions such as wind stress, swell height and dissolved oxygen content of the bottom water (Grobler & Noli-Peard, 1997).

9.6.2 Australia

The Australian fishery for *J. edwardsii* occurs across five different jurisdictions, with significant catches in the States of South Australia, Victoria and Tasmania. In the past Aborigines fished lobsters across the range of this species and a small indigenous harvest continues today (Gardner *et al.*, 2011). The resource has been harvested commercially since European settlement with the need for regulation recognized in the late 1880s, resulting in rules such as prohibition of the possession of ovigerous females and a minimum legal size. Legislation continued to evolve with much debate on gear restrictions in the early 1900s and conflict

between states over fishers moving across state borders. Controls on the number of pots per vessel were implemented at this time.

Markets have adapted to changes in technology throughout the development of the fishery. The adoption of diesel engines and the development of refrigeration after the Second World War meant that more harvested lobsters could be shipped to major population centres in eastern Australia, which led to expanded markets. Soon after this there was a rapid expansion into the American market for frozen lobster tails. Today, most of the commercial lobster catch is transported live into Asia, although the domestic market remains important for *S. verreauxi*, which is the premium seafood in the Sydney market (Liggins *et al.*, 2009).

Concerns about declining catch rates led to a shift to output controls in the commercial fisheries with most stocks now under individual transferable quota (ITQ) management (1993 – southern South Australia *J. edwardsii*, 1994 – New South Wales *S. verreauxi*, 1998 – Tasmania *J. edwardsii*, 2000 – Victoria *J. edwardsii*, 2003 – northern South Australia *J. edwardsii*). The small catch of *J. edwardsii* taken in Western Australia (30–50 t) is the only Australian fishery for *Jasus* that remains managed only under input controls (Anon., 2010b; Phillips *et al.*, 2010).

The outcome of ITQ management has been mixed with stock rebuilding occurring in some jurisdictions (e.g. New South Wales) but not in others. Large-scale and prolonged decline in the recruitment of *J. edwardsii* stock into the harvestable biomass occurred in the period 2005–10 which resulted in a sustained decline in stock and catch rates (Linnane *et al.*, 2010b) (Fig. 9.3). Significantly, this decline across the broader region was not apparently caused by the same widespread process because exceptionally low settlement of puerulus was recorded in Tasmania, while record high settlement was occurring in South Australia and western Victoria. In the later locations, the declines in the fishery appeared to be linked to periods of exceptional cold water upwellings that affected post-settlement productivity (Linnane *et al.*, 2010c,d).

In contrast to the recent history of most Australian *J. edwardsii* fisheries, the *S. verreauxi* fishery

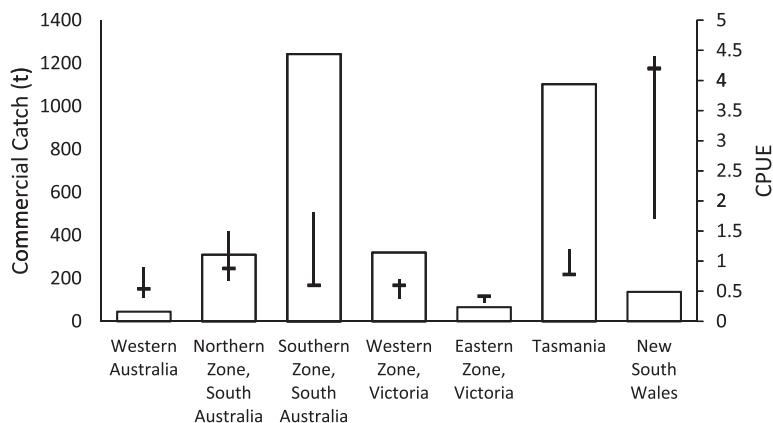


Fig. 9.3 Catch (bars) and catch rate of *Jasus* and *Sagmariasus* species by jurisdiction. Catch data is for the most recent year, generally 2010. Catch rate is shown as highest and lowest yearly value for the last decade with the most recent value indicated by the horizontal bar. Catch rate data for the New South Wales *Sagmariasus* fishery (Anon. 2010a) are kg per trap-month, while catch rate in the Western Australian (Anon. 2010b), South Australian (Linnane *et al.*, 2010c,d), Victorian (Hobday *et al.*, 2007) and Tasmanian (Gardner *et al.* (2011) *Jasus* fisheries are expressed as kg per potlift. Catch rate data for the Western Australian fishery is from the Esperance Rock Lobster Managed Fishery component.

has undergone steady recovery and the market price for catch shares has almost tripled over the past 4 years (Liggins *et al.*, 2009).

The recent history of ITQ implementation in Australian rock lobster fisheries has resulted in evolution of the industry. There has been increasing separation of ownership of quota units from the catching sector with an increasing proportion of fishers reliant on leasing of quota (van Putten *et al.*, 2011). This trading of units occurs in well-linked market networks which can be used by processors to regulate prices unless there are barriers to control the size of quota unit holdings (van Putten *et al.*, 2011). Trading and leasing of quota units has created a process that can lead to the fleet being rationalized with fewer vessels taking more of the catch, with this efficiency gain then being capitalized into the value of quota units (van Putten & Gardner, 2010). In theory this capitalization of future cash flows into the asset value of quota units should promote stewardship of the resource with conservative TACs favoured by industry (Wilen, 2006). However, commercial fishers have tended to oppose lower TACCs in declining *J. edwardsii* stocks which is explained in part by imperfect

rights and competition with recreational catch and MPAs (Bradshaw, 2004).

9.6.3 New Zealand

The New Zealand spiny lobster fishery is primarily based on *J. edwardsii*, with commercial catches of *S. verreauxi* only comprising around 1% of all commercial landings of spiny lobsters in the country (FAO Fisheries Department, 2011). Commercial fishing for lobsters in New Zealand began in the early 1900s, expanding greatly after the Second World War with the development of overseas markets (Booth, 2000). A maximum annual catch of 10,900 t was reported for *J. edwardsii* in 1968 but landings declined rapidly over the next 6 years to <4000 t per annum (FAO Fisheries Department, 2011). Commercial landings for *J. edwardsii* have been relatively stable since the late 1980s with an annual catch of 3000–4000 t (FAO Fisheries Department, 2011); however, fishing effort required to maintain catch levels has steadily increased (Booth, 2000).

The commercial lobster fishery in New Zealand is managed as three stocks, the North and South

Island *J. edwardsii* stock (NSI), the Chatham Island *J. edwardsii* stock (CHI) and a single New Zealand *S. verreauxi* stock (PHC). Currently, the main commercial fishery for *J. edwardsii* is along the south and south-western coasts of the South Island, and down the east coast of the two main islands. The Chatham Island fishery for *J. edwardsii* commenced in 1965 producing a record catch of >6000 t in 1968, but landings have declined greatly in the last 30 years and the Chatham Island fishery has only yielded 300–600 t per annum since the early 1980s (Booth, 2000). *Sagmariasus verreauxi* is commercially fished mainly from the northern regions of the North Island. Annual catches are typically less than 40 t, with a maximum catch of 64 t recorded in 1996 (FAO Fisheries Department, 2011).

New Zealand's spiny lobster fishery has been managed by the Quota Management System since 1990, whereby commercial fishers must own quota, i.e. their fishing share of the TACC. Fisheries in New Zealand are required to be managed so that stocks are maintained near or above B_{MSY} , the biomass required to sustain the maximum sustainable yield (MSY). Each year the TAC and TACC for the upcoming year is set for each of the nine lobster quota management areas (CRA 1–9) based on MSY calculations (Booth, 2000). In recent years the lobster TACC has been nearly, or fully, caught for all areas, except CRA 4 (Wellington region), which has had a voluntary commercial catch limit in place (National Rock Lobster Management Group, 2010). The total TACC for the 2009/2010 year was 2761 t (National Rock Lobster Management Group, 2010). Additional fisheries management controls include a minimum legal size (54 mm tail width for males and 60 mm for females for most areas), closed seasons for some management areas (e.g. management areas CRA 3, 6 and 7), and the prohibition of taking ovigerous females or soft-shelled lobsters (Booth, 2000; National Rock Lobster Management Group, 2010). There is no restriction on the number of fishing vessels or the type of trap used, but traps must have gaps to allow the escape of small lobsters (Booth, 2000). Increasingly commercial rock lobster fishing interests have become more engaged in the management of their local stocks, often developing and implement-

Table 9.3 Export statistics for New Zealand spiny lobsters between 2005 and 2009 (SeaFIC Export Database).

Year	Total quantity exported (tonnes)	Value (NZ\$, millions, FOB)
2005	2,419	113.93
2006	2,412	127.05
2007	2,250	121.42
2008	2,639	179.52
2009	2,447	184.23

ing their own sets of management measures (Miller & Breen, 2010; Yandle *et al.*, 2011).

For several years starting in 1999 commercial quota holders were able to use their quota to harvest pueruli, with every tonne of quota for legal-sized lobsters retired from the commercial fishery a fisher was allowed to take 40,000 (30kg) of pueruli or early juveniles for aquaculture (Booth, 2000). A number of groups took advantage of the scheme to harvest more than 50,000 lobsters but the huge variability in the natural supply of pueruli, combined with the relatively slow growth rates of the lobsters in aquaculture systems, curtailed continued harvesting.

Total exports of lobster from New Zealand have remained similar over the last 5 years, with between 2250 and 2640 t exported per annum (Table 9.3). However, lobster prices have markedly increased over that period from NZ\$38–51 kg⁻¹ in 2005 to NZ\$<82 kg⁻¹ in 2009 (for chilled, live lobsters), resulting in a NZ\$70 million (Free on Board) increase in export earnings (SeaFIC Export Database). The vast majority of lobsters commercially harvested in New Zealand are exported live, mostly to Hong Kong, but also to Japan and China (Fig. 9.4). There is also a small market in the USA for frozen tails. More recently, export prices have continued to increase to <NZ\$102 kg⁻¹ for live New Zealand lobster in Hong Kong (Ministry of Fisheries, 2011).

9.6.4 Other *Jasus* fisheries

Commercial fishing of *J. paulensis* began in 1928 with the construction of a canning factory on Île St

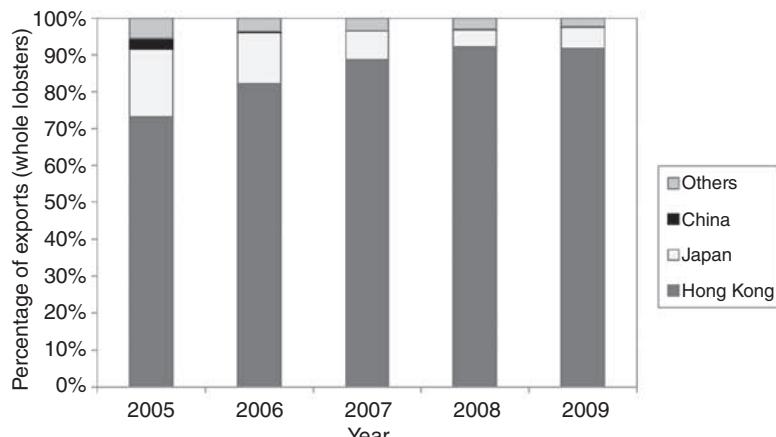


Fig. 9.4 Changing destination countries of New Zealand's whole lobster exports, both fresh and frozen (Source: SeaFIC Export Database). Note that the percentage of lobsters exported to Hong Kong is artificially inflated as some of the lobsters are subsequently forwarded on to China. Export statistics for the first three quarters of 2010 show that the percentage of all lobsters that are exported from New Zealand that are sent to Hong Kong has dropped to 85%, and the quantity exported to China has risen to 9% as a result of a new free-trade agreement between New Zealand and China (Ministry of Fisheries, 2011).

Paul, but was discontinued shortly after because of a disease outbreak amongst the workers living on the island. Commercial harvest recommenced in 1950 when a ship equipped with canning facilities visited the islands. Over the next 6 years between 214 and 255 t of *J. paulensis* lobster tails were canned annually, equating to an annual landing of approximately 5000 t (Holthuis, 1991). Fears of overfishing saw the instigation of a number of control measures including the setting of a TACC, a minimum legal size, protection of ovigerous females, and a closed season (Booth, 2006). Commercial landings have been less than 1000 t since the 1960s and in recent years annual landings have been around 400 t (Biais, 1987; Holthuis, 1991). The *J. paulensis* fishery at St Paul and Amsterdam Islands is conducted from a Réunion Island-based vessel with associated motorized dories. Annual catches have increased gradually from 340 t in 2001 to 400 t in 2010 with catch per unit effort (kg per pot) increasing over this period (Duhamel, pers comm.). *Jasus paulensis* were captured from various seamounts on the south-western Madagascar Ridge during exploratory surveys undertaken in 2010 and 2011, confirming that its distribution

extends approximately 2500 km west from St Paul and Amsterdam Islands. The complete absence of *Jasus lalandii* during these recent surveys suggests that it does not occur on the south-western Madagascar Ridge, and that the catches of *J. lalandii* attributed to these seamounts during the late 20th century (see Romanov 2003) were more likely to be *J. paulensis* (Groeneveld, pers. comm.).

Populations of *J. tristani* at the Tristan da Cunha archipelago and Gough Island have been commercially exploited since the 1950s. Approximately 300 t of lobster tails were harvested during the 1960s (Roscoe, 1979), but landings have stabilized at around 300–500 t (whole weight) since 1980 (FAO Fisheries Department, 2011). Intensive commercial harvest of the small population of *J. tristani* on Vema Seamount in the 1960s reduced the population so dramatically that after 2 years of commercial fishing the population was considered 'fished out' (Heydorn, 1969). Over the last 50 years the *J. tristani* population on Vema Seamount has shown no sign of recovery indicating that larval recruitment to the seamount is very small or has been interrupted by the removal of the adult population (von der Heyden *et al.*, 2007). Commercial

exploitation of *J. tristani* occurs around the islands of much of the Tristan da Cunha Archipelago (Tristan da Cunha, Inaccessible and Nightingale Islands) and Gough Island (Pollock *et al.*, 2000). Fishing around Tristan da Cunha is conducted by islanders using trap and hoopnets from motorized dinghies while the fishing around the other islands is conducted from a large long-line factory freezer vessel operating out of Cape Town, South Africa, under licence to the government of Tristan da Cunha, a British Overseas Territory. The resource is managed via individual TACs for each island along with size limits and gear restrictions. Annual catches have increased gradually from 331 t in 2001 to 442 t in 2010 (Glass, pers. comm.). The lobster fishery obtained Marine Stewardship Council (MSC) certification as a sustainable commercial fishery in June 2011. The benefits of MSC certification are not only viewed from a marketing perspective, but also as a means of facilitating the enhancement of future resource management capacity on Tristan da Cunha (Venn, pers. comm.).

The earliest accounts of *J. frontalis* on the Juan Fernandez Archipelago from the mid-1700s stated that the lobsters were present in such abundance in the intertidal areas of the islands that they were frequently hit by boat hooks when going to and from shore (Walter, 1776). Commercial fishing for *J. frontalis* began in the late 1800s when lobsters were commercially harvested from shallow waters (<15 m) (Albert, 1898), but as fishing pressure increased lobsters were harvested from deeper and deeper waters (Holthuis, 1991). Despite the implementation of control measures, including a minimum legal size of 98 mm CL, a closed season from May to September, and prohibition of taking

ovigerous females (Holthuis, 1991; Arana & Olate, 2000), landings have decreased markedly from 100 t in 1959 down to 1 t in 2003 (FAO Fisheries Department, 2011). Assessment of the state of the fishery in 1997 showed that the population was overexploited with less than 9% of the population over the minimum legal size (Arana & Olate, 2000; Yáñez *et al.*, 2000). In 2004 landings of *J. frontalis* increased dramatically to 47 t, and have remained at a similar level over the following 5 years (Arana *et al.*, 2011; FAO Fisheries Department, 2011). However, this sudden increase in landings most likely reflects the discovery of new fishing grounds, rather than a rapid recovery of the population. Recent modelling using the scant catch data available suggests that current fishery is unsustainable in the long term (Eddy *et al.*, 2010).

The population of *J. caveorum* on the Foundation Seamount Chain does not support a regular commercial fishery but at least 20 t of *J. caveorum* have been taken since its discovery in 1995 (Booth, 2006).

9.7 Aquaculture

Lobsters of the genera *Jasus* and *Sagmariasus* have been the focus of aquaculture research for over 30 years. The long and complex larval culture of spiny lobsters has hampered the development of effective hatchery methods, and to date, only a relatively small number of lobsters have been reared from egg to juvenile in laboratories (Table 9.4). *Sagmariasus verreauxi* is the only species to be cultured from egg to adult (J. Kittaka, pers. comm. in Booth, 2006). Further substantial research and develop-

Table 9.4 Culture duration of the phyllosoma and puerulus stage of *Jasus* and *Sagmariasus* species.

Species	No. of instars	Larval duration (days)	No. of pueruli per batch	Puerulus duration (days)
<i>J. edwardsii</i>	17 ¹	250–437 ^{1,2,3}	1–9 ^{1,2,3}	9–25 ⁴
<i>J. lalandii</i>	15 ⁵	306 ⁵	1 ⁵	>31 ⁵
<i>S. verreauxi</i>	16–17 ^{6,7}	189–359 ^{6,7}	168 ⁶	25 ⁶

¹Illingworth *et al.* (1997); ²Kittaka *et al.* (2005); ³A. Ritar, TAFI, pers. comm.; ⁴Booth & Kittaka (1994); ⁵Kittaka (1988); ⁶Kittaka *et al.* (1997); ⁷Moss *et al.* (2000).

ment on the larval culture of these spiny lobsters will be required before commercial-scale production of spiny lobster larvae will be possible.

The nutrition of cultured spiny lobster larvae is a major issue impeding the development of commercial production of cultured juvenile lobsters. Currently, the most common diet for phyllosoma is *Artemia salina* nauplii for early-stage phyllosoma and mussel gonad (*Mytilus* species or *Perna canaliculus*) for later stages (Kittaka, 1994). While mussel gonads appear to be nutritionally satisfactory for phyllosoma they are expensive and impractical for commercial-scale culture. More recently attempts have been made to develop a formulated diet for phyllosoma but these have met with limited success (Kittaka & Booth, 2000; Tong & Moss, 2000; Williams, 2001). Similarly, a diet of mussels has proven to produce the best growth rates in juvenile *Jasus* and *Sagamariasus* lobsters to date (Crear *et al.*, 2000; Jeffs & Hooker, 2000; Ward *et al.*, 2003; Ward & Carter, 2009). In general, formulated diets are often attractive and readily ingested by lobsters, but produce poorer growth and food conversion ratios than mussels (Crear *et al.*, 2000; Tolomei *et al.*, 2003), indicating that the higher growth of lobsters on a diet of mussels is because of their better nutritional value. Considerable research has been conducted on determining the optimum protein, lipid, and carbohydrate dietary levels for *Jasus* lobsters (e.g. Crear *et al.*, 2001; Johnston *et al.*, 2003; Ward *et al.*, 2003; Simon, 2009; Simon & Jeffs, 2011), and, yet, formulated diets are still inferior to a diet of fresh mussels.

Globally, the current aquaculture of spiny lobsters is based on the on-growing of wild-caught pueruli and early juveniles in sea cages, primarily *Panulirus ornatus* in Southeast Asia, especially Vietnam. The ecological impact of large scale collection of pueruli from the wild is difficult to assess, although research indicates that localized collecting only removes a small proportion of the available pueruli from the wild, and that the natural predation and mortality of pueruli or early juveniles is much higher (Bannerot *et al.*, 1992; Butler & Herrnkind, 1992; Forcucci *et al.*, 1994). In New Zealand, many thousands of pueruli of *J. edwardsii* have been collected for commercial aquaculture,

but the economics of on-growing lobsters is doubtful at present as the cost of pueruli collection and maintaining on-growing systems is relatively high (Booth, 2006).

In parts of New Zealand and Australia commercially fished adult *J. edwardsii* are sometimes held in 'holding pots' or 'caufs' for short periods to take advantage of fluctuations in market prices. In South Australia a 30-week study was conducted to investigate the effects of holding lobsters for longer periods both without feeding and with being fed mussels or a formulated pelleted feed (Bryars & Geddes, 2005). Fed lobsters increased in size by up to 18%, and survival was between 83% and 98% in the fed treatments and 65% in the unfed treatment. However, there was also a high incidence of tail fan damage in all treatments with between 36% and 51% of lobsters developing tail damage during the experiment. These results show that while good survival and moderate growth can be obtained through long-term holding of adult lobsters in sea cages, the extremely high feeding rate and high incidence of tail fan damage, that would reduce the market price of animals, would make long-term holding of lobsters uneconomic.

9.8 Marine protected areas

A number of studies have demonstrated that Marine Protected Areas (MPAs) result in increased density of harvested species, such as lobsters of the genus *Jasus* within the MPAs (Kelly *et al.*, 2000; Shears *et al.*, 2006; Barrett *et al.*, 2009; Freeman & MacDiarmid, 2009). Shears *et al.* (2006) compared the densities of *J. edwardsii* in a fully protected MPA, a partially protected MPA that allowed recreational but not commercial fishing, and an unprotected area. Lobster densities prior to establishment of the MPAs were similar at both MPAs. Twenty eight years later lobster densities at the fully protected MPA had increased 11 times and lobster biomass had increased 25 times. In contrast, there was no significant change in lobster numbers at the partially protected MPA and the densities of lobsters within the partially protected MPA were not significantly different from a nearby fully-fished area. These results clearly demonstrate that no-take

MPAs allow lobster populations to recover, but partially protected MPAs do not provide protection for long-lived, highly exploited species such as *J. edwardsii*.

Consideration of the location of MPAs is important if the objective is to increase lobster abundance within the protected area. Assessment of four MPAs in South Africa found that only one of the MPAs showed a significant increase in lobster numbers. The other MPAs appeared to be poorly sited, containing large areas of unsuitable substrate for lobsters (Mayfield *et al.*, 2005). Freeman *et al.* (2009) found that *J. edwardsii* rarely crossed areas of muddy substrate between patch reefs, and thus the design of MPA boundaries should encompass the reef edges to prevent edge effects. More rarely, movement of lobsters is so limited that MPAs with boundaries bisecting a reef may still result in rebuilding of lobster stocks within the MPA (Barrett *et al.*, 2009).

Marine protected areas have been widely used as research sites due to the cost effectiveness of sampling where there is access to high density of lobsters (Barrett *et al.*, 2009). Benefits to research also comes through access to lobsters of large size that are rarely encountered in fished areas, which is especially valuable for ecological studies involving *Jasus* (e.g., Ling *et al.*, 2009; Pederson *et al.*, 2008). Although MPAs have an established literature of their use and benefit as research sites, the larger scale use of MPAs as fisheries management tools has been more problematic in *Jasus* fisheries. Their impact on lobster populations was evaluated by Buxton *et al.* (2004) using population modelling and they concluded that MPAs were limited in terms of their usefulness as a fisheries management tool, especially for the Tasmanian rock lobster and abalone fisheries, but also for quota-managed fisheries in general. This was because they considered the catch was displaced rather than reduced by MPAs placed within ITQ fisheries and also because of spatial differences in the productivity of areas that are closed or open to fishing activity (Haddon *et al.*, 2003). Hobday *et al.* (2005) modelled the effect of MPAs on the Victorian *J. edwardsii* fishery and concluded that MPAs would slow or reverse stock rebuilding under ITQ management. This expectation appeared to hold with stocks of *J. edwardsii* falling rapidly across most of the Victo-

rian coastline following introduction of a large MPA network, with CPUE approximately half that of adjacent jurisdictions of South Australia and Tasmania (Phillips *et al.*, 2010).

9.9 Managing ecosystem effects of fishing

Ecosystem-based fisheries management is increasingly important in management of *Jasus* and *Sagamia* fisheries, with consideration of issues such as bycatch, protected species interactions, habitat impacts of fishing gear and ecosystem interactions through reduction of lobster biomass.

Bycatch is monitored continuously in some jurisdictions, either by industry in logbooks or through observer programmes (Frusher & Gibson, 1998; Brock *et al.*, 2007). The programmes have shown that across southern Australia, the most common bycatch animals that are not returned alive are the leatherjackets (Monacanthidae) and wrasse species (Labridae). Rates of bycatch can be substantially reduced through the use of escape gaps which are mandatory in some jurisdictions (Frusher & Gibson, 1998; Linnane *et al.*, 2011). Protected species are occasionally captured and killed as bycatch in lobster pots, including cormorants and pinnipeds (Frusher *et al.*, 2003). Of special concern in the South Australian *J. edwardsii* fishery is the potential for drowning of pups of the endangered Australian sealion (*Neophoca cinerea*), although this is minor risk relative to that from gillnets, and it can be prevented by incorporating sealion exclusion spikes within the pots (Goldsworthy & Page, 2007).

Interactions with threatened and endangered species can also occur through entanglements with buoy lines, particularly with cetaceans and turtles. Cetacean entanglements in the Victorian *J. edwardsii* fishery average one or two per year with mitigation through an industry code of practice and a trained response team (Anon, 2009). The New Zealand *J. edwardsii* fishery interacts with critically endangered populations of Hector's dolphin (*Cephalorhynchus hectori*) through entanglement in gillnets used for harvesting baitfish used in the lobster fishery (Dawson & Slooten, 2005). In this

case, mitigation has been attempted with the use of MPAs, although this appears inadequate because dolphins are highly mobile and remain vulnerable when outside the MPAs (Slooten, 2007). Turtle entanglements in buoy lines occur occasionally with documented entanglements for hawksbill, loggerhead, green, olive ridley and leatherback turtles (Limpus, 2009). Entanglements of leatherback turtles (*Dermochelys coriacea*) have received most attention because these are a regular, although now rare, visitor to Bass Strait, which separates the Victorian and Tasmanian *J. edwardsii* fisheries (Bone, 1998; Anon, 2003). The survival prospects for this species in the Australian region are bleak so even the low entanglement rates, estimated at around one per decade, are of concern (Frusher *et al.*, 2003; Limpus, 2009).

Ecosystem effects of fishing can occur through changing the abundance of prey items of rock lobsters as a consequence of harvesting of rock lobsters. *Jasus edwardsii* fisheries along eastern Australia are being managed with performance measures related to biomass of large lobsters in attempt to maintain predation of urchins as described previously (Gardner *et al.*, 2011).

9.10 Conclusions

The six species in the genus *Jasus* and the sole *Sagmariasus* species share a great many similarities in aspects of their biology and of their ecology. All species live mostly in shallow coastal waters where they are associated with rocky reef or foul ground habitats. Despite this narrow coastal range of the reptant stage of the lifecycle of these lobsters, all seven species appear to have extended oceanic larval development, with the larval dispersal potential for extending their natural range. However, three species, *J. frontalis*, *J. caveorum*,

and *J. tristani*, which is set to be synonymized with *J. paulensis*, are all confined to small oceanic islands and seamounts, which in a number of instances are swept by persistent ocean currents, which would tend to remove larvae from the vicinity. *Sagmariasus verreauxi*, also has a restricted distribution when compared with *J. lalandii* and *J. edwardsii*, and especially when compared with many other members of the Palinuridae, such as the *Panulirus ornatus*, which is found from the east coast of Africa, across most of Asia and into the centre of the Pacific Ocean. How these highly constricted populations maintain sufficient localized recruitment, despite a history of intensive fishing pressure in some instances, remains somewhat of a mystery. These populations may be particularly vulnerable, as there are indications from a number of spiny lobster populations, including species of *Jasus* and *Sagmariasus*, that the larval supply and juvenile recruitment processes, and even adult growth rates, are being greatly influenced by climatic perturbations. In general the life history of spiny lobsters makes their populations very resilient to poor fisheries management, with the recovery of populations depleted by harvesting often occurring quickly with a year or two of naturally high recruitment. However, if as predicted, global climate change increases the rate and extent of perturbations in our oceans, and these are compounded by gradual latitudinal shifts in seawater temperatures, then the resilience of lobster populations will be tested. Therefore, it is vital that the management of these important fisheries takes into account these short- and long-term changes to the marine environment. An obvious priority would be to improve our understanding of the basis of the large fluctuations in the recruitment of these lobster species, especially in terms of the larval processes, which are poorly understood at present for all spiny lobster species.

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Chapter 10

Panulirus Species

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Abstract

Spiny lobsters are among the most valuable species in the world's oceans. Because of this they have been a focus of research and several have become among the most studied exploited marine animals. Commercial fisheries exist wherever they occur and because they are generally shallow water species they have been subject to intensive fishing worldwide. The maintenance of the sustainability of the fisheries for spiny lobsters has seen wide-ranging research programs conducted over many years including studies of the biology and ecology of the lobsters and the environments and habitats in which they occur. This chapter concentrates on changes and developments in *Panulirus* lobster fisheries since 2006, as part of the ongoing quest for sustainable management of existing fisheries as well as increased production through enhancement and aquaculture. Important species including *Panulirus cygnus*, *Panulirus argus*, *Panulirus interruptus* and *Panulirus ornatus* are given special attention.

Key Words: *Panulirus cygnus*; *Panulirus argus*; *Panulirus interruptus*; spiny lobsters; catches; aquaculture; sustainability

10.1 Species and distribution

Lipcius and Eggleston (2000) succinctly summarized the systematics, evolution and morphology of the more than 20 species of *Panulirus* found in the tropical and subtropical waters of the world's oceans. Variously known as 'rock' or 'spiny' lobsters (and even rocklobsters in Australia), depending on local traditions and trade requirements, they provide a valuable source of seafood and exports

for a large number of countries. Lavalli & Spanier (2010) published a comprehensive review of the Infraorder Palinura in *Treatise on Zoology: Anatomy, Taxonomy, Biology*. This monumental reference will set a new standard in this area.

The worldwide distribution of *Panulirus* lobsters is shown in Plate 10.1A–F. In some areas there is a wide range of species. For example some 10 species are recorded from India but the fisheries are confined to *Panulirus polyphagus*, *P. versicolor*,

P. ornatus and *P. homarus*. Outside of India, fisheries are based on almost all *Panulirus* species but not all have been successfully managed. For example fisheries for commercial *Panulirus marginatus* in the Hawaiian Islands, *P. pascuensis* at the Easter Islands, and *P. japonicus* in Taiwan have essentially disappeared in these areas, although the same species may be fished in other areas.

Data on *Panulirus* spp. up to 2005/06 were reviewed by Phillips & Melville-Smith (2006). This review concentrates on changes and developments in those fisheries since 2006, as part of the ongoing quest for sustainable management.

10.2 Life history, growth and reproduction

The life cycle of all *Panulirus* species is complex and includes a long oceanic larval phase, which varies in length among species (see diagrammatic life history for *Panulirus cygnus*, Fig. 10.1). In the western rock lobster *P. cygnus*, it is estimated to be 7–14 months (Phillips *et al.*, 1979; Rothlisberg, 1988). In the California spiny lobster *Panulirus*

interruptus the phyllosoma stages go through 11 moults during an estimated larval period of 7.75–12 months (Johnson, 1960; Peñaloza-Mayorazgo, 2008). Tropical species, in contrast, may have shorter oceanic cycles. In *Panulirus ornatus* for example, the larval phase is estimated to be only 4–7 months (Dennis *et al.*, 2001).

Spiny lobsters hatch as planktonic phyllosoma larvae (about 1–2 mm long) and develop through a series of moults, increasing in size. After developing in offshore waters, phyllosoma return towards the continental shelf where the final stage larvae metamorphose into the puerulus, a non-feeding stage (about 30 mm in total), which then swims towards the coast.

When the puerulus stage settles, it moults after a few days to weeks into a benthic juvenile stage. Small juveniles (often called post-pueruli) are usually found in shallow coastal reefs and larger juveniles and adults in deeper water offshore. It is in these depths that they reach maturity, that mating takes place and that the life cycle is completed.

For many spiny lobster species there are data on female fecundity, growth rates of juveniles, age at

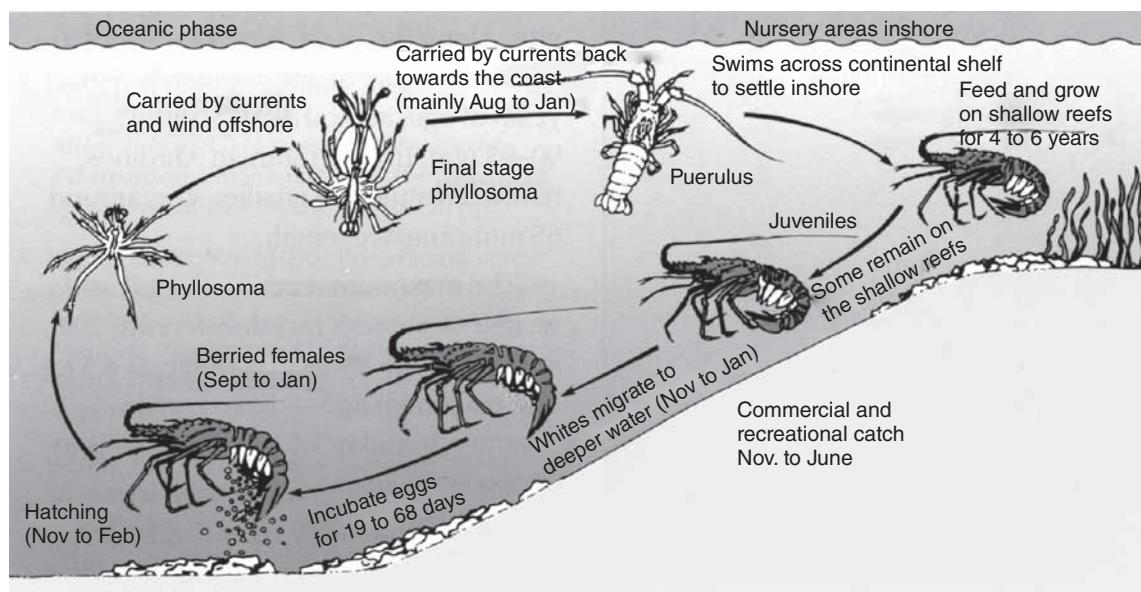


Fig. 10.1 Schematic life history of the western rock lobster, *Panulirus cygnus*. Kailola, P. J., *et al.* (1993). Reproduced with permission of Australian Fisheries Resources. Bureau of Resource Sciences, Canberra, Australia.

maturity in the wild, natural diets of the juveniles and adults and natural densities in the wild, as well as some information on cannibalism and health. By contrast, there are few data on the ecology of the larvae and puerulus stages of *Panulirus*, except for *P. cygnus* in Western Australia (Booth & Phillips, 1994); *P. argus* off the Cuban and Florida coasts (Butler & Herrnkind, 2000; Yeung & Lee, 2002); *P. japonicus* off Japan (Yoshimura *et al.*, 1999; Sekiguchi & Inoue, 2002); and for *P. interruptus* in the California current ecosystem (Guzmán del Prío, *et al.*, 1996; Arteaga Rios *et al.*, 2007).

Growth rates are a key component of stock assessment models for any species. In the case of *Panulirus* lobsters, the need to have reliable information on this important parameter has encouraged considerable research on the subject in most of the commercially important species (e.g. Smale, 1978; Phillips *et al.*, 1992; Skewes *et al.*, 1997). Studies on *P. interruptus* have used a number of methods from which the age of males and females at minimum legal size (82.5 mm carapace length (CL)) was estimated in a range of 4 to 7 years and 6.5 to 9 years, respectively (Vega-Velázquez, 2006). As with all decapods, lobsters of this genus grow rapidly to maturity, but slow down thereafter. Growth rates are highly variable across the genus, with tropical species tending to grow very much faster than their temperate relatives. For example maturity is reached approximately 6–7 years after settlement in *P. cygnus* (Chittleborough, 1976), a temperate and subtropical species, whereas by comparison it is reached after only 2 years in the tropical species *P. homarus* (Smale, 1978).

As with growth, the necessity to have a good understanding of reproduction in a managed fishery has encouraged much research on this subject in the commercially fished species within the genus. Obviously size at maturity of females and males varies for different species in the genus, but research has shown that this parameter can vary substantially both spatially (e.g. in *P. cygnus*, Melville-Smith & de Lestang 2006; *P. homarus*, Mohan, 1997; *P. argus*, Arango & Marquez, 1995; and *P. guttatus* Robertson & Butler, 2003) and temporally (e.g. *P. marginatus*, Plaganyi *et al.*, 1989; DeMartini *et al.*, 2003; and *P. cygnus*, Melville-Smith & de Lestang, 2006) for the various species.

The temperate species in this genus tend to have a well-defined breeding season during which they carry one brood (*P. interruptus*, Vega-Velázquez, 2003b) or more broods of eggs (*P. cygnus*, Chittleborough, 1976). By comparison, the tropical species tend to spawn throughout the year (e.g. *P. inflatus* and *P. gracilis* Briones-Fourzán & Lozano-Álvarez, 1992; Villalejo Fuerte & Velázquez Abunader, 2007; Pérez-González *et al.*, 2009). Overall therefore, the tropical species produce more eggs per year on average than the temperate species, but are likely to have a shorter life expectancy than their temperate relatives due to higher mortality rates that are generally considered to be a feature of the warm tropical water environments.

Chubb (1994) documented that the onset of breeding season may also vary both spatially and temporally in some species of *Panulirus* and *Jasus* genera. For example, in the case of *P. interruptus* (Vega-Velázquez *et al.*, 1991) showed that a latitudinal (north–south) gradient along Baja California in commencement and seasonal peak of breeding, which begins in November–December at the northernmost areas of its range 3–4 months later in the southernmost areas (Vega-Velázquez *et al.*, 1992a, 1996a, 1997). In addition, Vega-Velázquez (2003b) demonstrated that the timing of breeding of *P. interruptus* is strongly temperature dependent. El Niño and La Niña condition impacts were particularly evident at the onset and duration of breeding. Warmer temperatures during El Niño periods significantly accelerated breeding, while the contrary happened under cold temperatures during La Niña years. Taking into account the synchronism between environment and breeding the lobster fishery in Baja California is managed by flexible and dynamic strategies to guarantee, when necessary, the adjustments in the opening and closing dates of the fishing season (Vega-Velázquez *et al.*, 2010b).

10.3 Predators and diseases

The phyllosoma larval, puerulus, juvenile and adult stages are all subject to predation (Phillips & Melville-Smith, 2006). Phyllosoma and pueruli are often part of the stomach contents of pelagic fish (Phillips & Sastry, 1980) and near-shore fish prey

on pueruli and small juveniles (Howard, 1988). Larger juveniles and adults fall prey to octopus, sharks and fish, as evidenced in Cuba (Cruz & Phillips, 2000).

Rock lobsters are more susceptible to developing health problems including infectious diseases when they have been stressed, injured, have just moulted or are about to moult, have had unsuitable feed or been held at a high stocking density (see reviews in Shields *et al.*, 2006; Shields, 2011). Stress often occurs when lobsters are held in water of suboptimal quality and during capture and transport, especially if they have been held in air during this process. The majority of diseases identified in rock lobsters to date have been the result of opportunistic infections rather than primary pathogens. Opportunistic pathogens commonly include bacteria, fungi and protozoa that are present in the lobster's environment but do not cause disease unless lobsters are stressed or damaged by some of the factors outlined above.

Some of the more common disease problems seen in rock lobster include 'white tail', caused by an intracellular protozoan parasite, tail fan necrosis or shell disease, weak lobsters (often the result of a generalized bacterial infection) and fouling of the gills and carapace. 'Turgid lobster syndrome' in which the soft areas of the lobster bulge from the harder shell, and pink-fleshed lobsters are conditions that are sometimes seen and may have a number of causes. Further investigation is needed to identify the range of environmental, physiological and disease conditions that can result in the last two syndromes. 'Milky haemolymph' syndrome in spiny lobsters has been investigated by Nunan *et al.* (2010).

10.4 Ecology and behaviour

A very thorough review of juvenile and adult ecology was undertaken by Butler *et al.* (2006) and of behaviour by Childress & Jury. (2006). *Panulirus* lobsters are widespread and numerous, particularly on rocky and coral substrates, though some members of the genus, such as *P. polypagrus*, are found on soft muddy bottom. Without exception, they remain hidden by day and emerge to forage

nocturnally so as to avoid their many predators. All members of the genus are non-specialist feeders, foraging on a wide range of food items.

In the relatively few *Panulirus* species for which this information is recorded, there is a general trend for the juveniles to be found in shallow inshore areas (e.g. *P. argus*, Butler & Herrnkind, 2000; *P. japonicus*, Yoshimura & Yamakawa, 1988; *P. cygnus*, Phillips *et al.*, 2001), shallower than those depths at which the bulk of the adult population is to be found. For *P. interruptus* there is some information on the feeding ecology and habitat preferences of early juveniles in central Baja California (Castañeda-Fernández *et al.*, 2005a; Castaneda-Fernandez *et al.*, 2005b). Recently settled pueruli and small juveniles of *P. interruptus* commonly inhabit rocky habitats which have dense plant cover, particularly the surf grass *Phyllospadix* spp., at depths of 0–4 m. A study has shown that juvenile California spiny lobsters have a strong preference for *Phyllospadix* sp. (Castañeda-Fernández *et al.*, 2005a). Juveniles and sub-adults are highly gregarious. Juvenile lobsters usually spend their first 2 years in the near-shore surf grass beds.

Early juvenile spiny lobsters tend to be solitary in the small holes or dens that they choose, but as they grow they become gregarious. For example Fitzpatrick *et al.* (1990) showed that in *P. cygnus*, over 95% of newly settled pueruli and post-pueruli (6–10 mm CL) were solitary, but less than 20% of animals that had been settled for about a year (i.e. 20–25 mm CL) were solitary. Their gregarious behaviour is considered an effective antipredator strategy (Butler *et al.*, 1999). Natural mortality rates of lobsters, but particularly juvenile animals, are extremely high. Herrnkind & Butler (1994) estimated mortality of *P. argus* to be 96–99% in the first year after settlement and Phillips *et al.* (2003) had similarly high estimates of 80–96% for *P. cygnus* juveniles at the end of their first year after settlement. In the case of *P. cygnus*, as few as 3% of settling pueruli are estimated to survive to recruit into the fishery 3.5 years after they first settled as pueruli (Phillips *et al.*, 2003).

Several species of *Panulirus* undertake substantial migrations as they approach or reach sexual maturity (e.g. *P. argus*, Kanciruk & Herrnkind, 1978; *P. ornatus*, Bell *et al.*, 1987; *P. cygnus*, Phil-

lips, 1983). Once settled in their dens spiny lobsters can stay for long periods of time, often occupying the same holes, or same home range, for months or even years (Chittleborough, 1974).

10.5 Population dynamics and regulation

Exploitation rates on commercially fished populations of spiny lobsters, where they have been measured, are frequently high (e.g. 0.71–0.83 for *P. argus* in Chinchorro, Mexico (Sosa-Cordero *et al.*, 1996), 1.43 for male and 0.8 for female *P. polyphagus* trawled off Bombay, India (Kagwade, 1994), and 0.92–2.30 for *P. cygnus* caught by pots in different regions of the fishery in Western Australia (Wright *et al.*, 2006). For *P. interruptus* in Baja California, Mexico (Vega-Velázquez, 2003a), average fishing mortality (F) estimated from cohort analysis models was 0.21 for females and 0.22 for males, whereas F maximum was 0.91 and 0.92, respectively. Long time series of pueruli, early post-pueruli and pre-recruit abundances and their relationship to subsequent commercial and recreational landings have provided managers with the ability to predict catches in the *P. cygnus* fishery (Caputi & Brown, 1986; Caputi *et al.*, 1995; Melville-Smith *et al.*, 2004) and the Cuban catch component of the *P. argus* fishery (Cruz *et al.*, 1995).

10.6 Harvest of wild populations and their regulations

All commercial *Panulirus* fisheries are now considered fully exploited. This is an important point, because the nature of fishing is an aggressive activity, with participants seeking to achieve higher or more valuable catches. With the lack of ability for fishers to increase their catch size we have seen a strong trend towards value-adding to the catch, usually by marketing live lobsters to the highest paying customers who are often on the other side of the world to where the catch is made.

Most of the large fisheries for this genus have management measures such as input or output controls, legal minimum sizes and others (Table 10.1). Controls are variable in their scope and enforce-

ment, but as a generalization it could be said that management controls in the African and Asian sub-regions are few and weak – though there are exceptions – Japan and South Africa being cases in point.

As with the lack of management controls on the African and Asian continents, there is also a lack of information in the FAO statistics on the landings of spiny lobsters throughout these regions. We have endeavoured to present information on the landings of those species that contribute amongst the largest spiny lobster tonnages on world markets. We acknowledge that in several cases (in particular *P. longipes*, *P. polyphagus* and *P. ornatus*), the landings in Table 10.2 are gross underestimates of actual catches.

Regulations in some commercial lobster fisheries have been extreme. For example the U.S. National Marine Fisheries Service (NMFS, now NOAA Fisheries) and a Federal District Court ruling halted lobster (*P. marginatus*) fishing in the Hawaiian Islands in mid-2000. This closure was precipitated by pressure from several environmental lobby groups who considered that the lobster fishery was contributing to the starvation of the monk seals by harvesting one of the seals' food sources (Tighe, 2000; Environment News Service, 2000).

In the following section, we have selected a few *Panulirus* fisheries for more detailed discussion. These fisheries have been chosen because they are widespread in terms of global coverage and in most cases are very productive.

10.6.1 Australia and Papua New Guinea

Panulirus cygnus

The western rock lobster, *P. cygnus* is found only in temperate and subtropical waters off the west coast of Australia. The juveniles populate the shallow inshore limestone reefs and the breeding stock is found offshore (35–90 m) and at the Abrolhos Islands, which are situated on the continental shelf edge (Phillips *et al.*, 2000a). The Western Rock Lobster Fishery currently has around 280 boats and a long history of operating under input controls, but the fishery is in the throws (since the 2010/11 season) of moving to output management.

Table 10.1 Management measures in effect in selected *Panulirus* fisheries in 2011.

	P. argus	P. argus	P. argus [§]	P. argus	P. argus	P. argus/ P. laevicauda ⁶	P. cygnus	P. interruptus	P. interruptus
Bahamas ⁵	British Virgin Is.	Mexico	Cuba	USA	Brazil	Australia	Mexico	USA	
Catch 2009 ¹	7138	40	469	4124	1827	7268	7634	1816	323
Year ITQs introduced	no	No	no	no	no	no	2010/2011	no	no
TAAC (tonnes)	no	No	no	no	no	no	5500	no	no
Number of licences	no	2140	1250	432	Pot	no	278	1250	N/A
Minimum legal size	yes	Yes	yes	yes	309	Dive	yes	Yes	yes
Berried females protected	yes	Yes	yes	yes	yes	no	no	Yes	no
Number of boats	no	No	898	189	914	1486+	278	565	200
Type of gear specified	Casitas, Diving	Pots; and Scuba	Casitas, Pots and Diving	Casitas and Jaulones	Pots and Diving	Pots and Diving, and shelters	Pots	Pots	Pots
Number of pots	N/A	No	N/A	N/A	492,253 ⁹	no	31700	2896	no
Characteristics of Pots	N/A	No	N/A	N/A	yes	no	Yes	no	no
Escape gaps	N/A	No	N/A	N/A	no	no	Yes	yes	yes
Sanctuaries	yes	Yes	yes	?	yes	yes	Yes	no	yes
Closed season	yes	Yes	yes	yes	yes	yes	Yes	yes	yes
TACC	no	No	no	no	N/A	no	Yes	no	no
Recreational fishing allowed	no	Yes	no	no	yes	no	Yes	no	yes

	P. ornatus	P. ornatus	P. ornatus	P. ornatus/P. polyphagus/P. homarus/P. versicolor	P. ornatus/P. homarus/P. longipes	P. ornatus/P. homarus/P. longipes	P. japonicus
Australia Queensland ⁴	Papua New Guinea ³	Torres Strait ^{2,3}	India	Kenya	Somalia	Japan ⁸	Indonesia
CATCH 2009 ¹	192	114	236	2400 ⁷	82	500	1300
Year ITQs Introduced	2009	No	no	no	No	No	no
TAAC (tonnes)	195	No	No	?	No	No	No
Number of licences	11	No	13	no	N/A	N/A	N/A
Minimum legal size	yes	Yes	Yes	For export	no	yes	no
Berried females protected	Yes	No	No	no	Yes, Not enforced	yes	no
Number of boats	11	No	47	no	no	No	N/A
Type of gear	Diving	Diving inc. hookah	Diving inc. hookah	Gill, tangle and trawl nets	Pots and Tangle nets	Tangle nets, Trawling, traps and diving	Various
Number of pots	N/A	N/A	N/A	N/A	N/A	No	N/A
Characteristics of pots	N/A	N/A	N/A	N/A	N/A	No	N/A
Escape gaps	N/A	N/A	N/A	N/A	N/A	No	N/A
Sanctuaries	Green zones	No	No	yes	yes	yes	?
Closed season	yes	No	Yes, for hookah	no	no	No	?
TACC	195	No	Nominal	no	no	no	No
Recreational fishing allowed	yes	Yes	yes	no	no	no	?

¹FAO 2011²Licence cap in place for fully transferable licences (24 primary boats), however Traditional Inhabitant licences are not capped.³Berried females rarely encountered in area of fishery⁴Queensland waters south of 14° south latitude are closed to commercial fishing for lobster⁵Patricia Briones -Fourzan pers. comm. Mexico⁶René Schäfer Brazil⁷No FAO Data, Khan (2006)⁸Co-managed at the Prefectural level⁹The number of traps available to the fishery has been based on the number of active trap certificates issued by the state of Florida through the LTC (Florida Fish and Wildlife Conservation Commission unpubl. data).

Table 10.2 Landings (t) of *Panulirus spp.* For 1997–2009 (*from FAO, 2011 and **from some other sources). The FAO data are best considered indicative of the scale of landings of each species from each area, rather than being accurate representations.

		2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
Western Australian spiny lobster*	<i>Panulirus cygnus</i>	14433	11273	8983	11387	13591	12.305	10441	8678	8990	7634
Caribbean spiny lobster*	<i>Panulirus argus</i>	39639	33153	40360	36739	41839	37075	34053	32272	34366	31638
Long legged spiny lobster*	<i>Panulirus longipes</i>	1716	1924	1782	2082	1889	2059	2041	2041	1962	2424
California Spiny Lobster (USA** and Mexico***)	<i>Panulirus interruptus</i>	2413	2051	2228	2350	2135	2097	2229	1908	2394	2139
Tropical spiny lobsters nei*	<i>Panulirus spp.</i>	13581	14685	13914	17040	16867	18641	16738	13566	15036	21257
Ornate lobster** (Torres Strait Australia and Papua New Guinea)	<i>Panulirus ornatus</i>	625	283	481	665	896	1111	462	678	391	342

*From FAO, 2011. **Data on *P. ornatus* from Plaganyi *et al.* (1989).

**From California Fish and Game Department, USA. Compiled by Matthew Kay.

***From Lobster Program of Instituto Nacional de Pesca (INAPESCA)/CRIP-La Paz (México). Compiled by Armando Vega V.

The intention is to introduce a new quota based management plan for the fishery in 2013. Until then, the fishery will operate in a transition phase that retains many of the former input controls.

Until very recently, the fishery was landing average catches of around 11,000 t and was valued at around US\$300 million, making it Australia's most valuable single species fishery. However, in recent times the fishery has experienced a serious downturn in landings (Fig. 10.2) see details below. In addition to the commercial catch, recreational fishers take about 225 t a year (de Lestang *et al.*, 2010). The ability of this fishery to continue is assisted by analysis of a comprehensive fisheries database, some of which dates back to the 1960s (e.g. catch, effort, length frequencies, fishery-independent breeding-stock surveys, puerulus settlement monitoring, recreational catch monitoring); an extensive set of management controls (including a limited fishing season and legal minimum and maximum sizes); and an effective compliance programme. Apart from good governance structures

which support this valuable fishery, its sustainability has been maintained by a very intensive research programme that has been conducted for many years (Phillips *et al.*, 2010).

The size of the breeding stock has been measured using data from both a commercial at-sea monitoring programme and an annual fishery-independent breeding-stock survey (Chubb, 2000). When the breeding stock fell to low levels in the early 1990s, management initiatives succeeded in returning it to what were considered to be safe levels (Phillips & Melville-Smith, 2005). However, intense maintenance of the breeding stock was always going to be necessary under input controls because of declines brought on by effective effort increases resulting from improvements in fishing efficiency as a result of technology changes (e.g. improved GPS positioning, bottom discrimination and seabed mapping tools, etc.).

The second important research contributor to maintaining sustainability in this fishery has been the ability to predict future catches up to 4 years

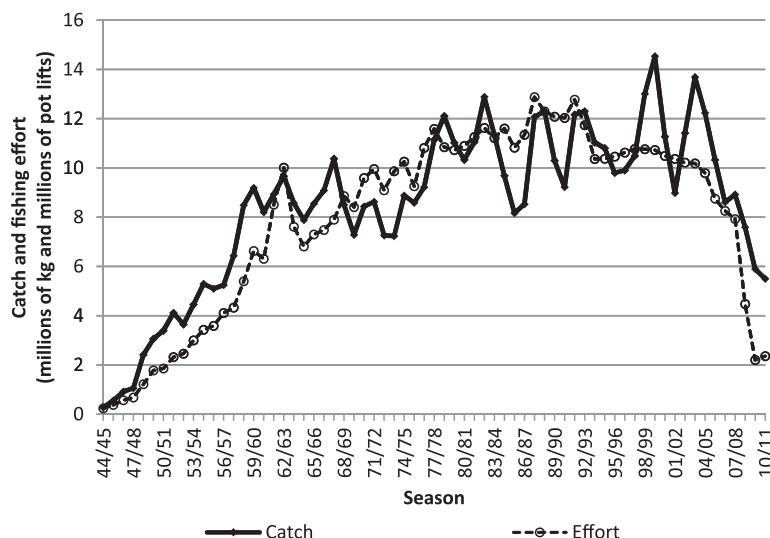


Fig. 10.2 Seasonal western rock lobster, *Panulirus cygnus*, catch and nominal fishing effort from 1944/45–2010/11. Data from FAO, 2011 and Department of Fisheries, Western Australia.

ahead of time. Environmental effects have been shown to drive the level of puerulus settlement each season (Caputi *et al.*, 2003). These settlement levels are in turn highly correlated with catches 3–4 years later (Phillips, 1986; Caputi *et al.*, 1995, 2003), which provides a means of predicting future catches and managing the fishery accordingly. The resulting seasonal fluctuations in puerulus settlement have led to high variability in catches (Fig. 10.3) but fishers have acquired sufficient scientific knowledge to understand that catches fluctuate for environmental reasons and to take this into account in their fishing operations.

Since the 2006/07 season there has been a severe decline in puerulus settlement across the fishery, and the level recorded in 2008/09 was the lowest in the long-term data series that has been monitored since 1968 (Department of Fisheries 2011), and well below the levels expected given prevailing environmental conditions at the time. A risk assessment workshop undertaken in April 2009 (Brown, 2009) aimed at assessing the cause of the low puerulus settlement was unable to identify a specific cause for the decrease in settlement. The workshop concluded that the responsible factors were likely to be changes in environmental conditions and productivity in the eastern Indian Ocean, and/or a

decline in the abundance of breeding stock. There have been signs of improvement in puerulus settlement and the 2010/11 settlement is above that of the previous three seasons (Department of Fisheries, 2011).

It was recognized early on that the downturn in settlement would impact landings in the foreseeable future and if no action was taken, this would also affect the state of the broodstock. As a result, effort reductions were introduced in the fishery in 2007/08, 2008/09 and 2009/10. Furthermore, in the 2008/09 season a catch limit of 7800 t was imposed on the fishery and in 2009/10 a competitive total allowable catch (TAC) of 5500 t was introduced. Individual catch limits of 5500 t were introduced in 2010/11 in the transition to management by output control. Another important development has been adoption of reference points focusing on maximum economic yield (MEY) rather than maximum sustainable yield (MSY) for the fishery.

Factors affecting the resilience of the several temperate fisheries, one of which was the western rock lobster fishery, have been examined in Melville-Smith (2011). The review covered a range of potential factors that can impact population resilience under the broad headings of climate change, fishing, coastal development, introduced marine

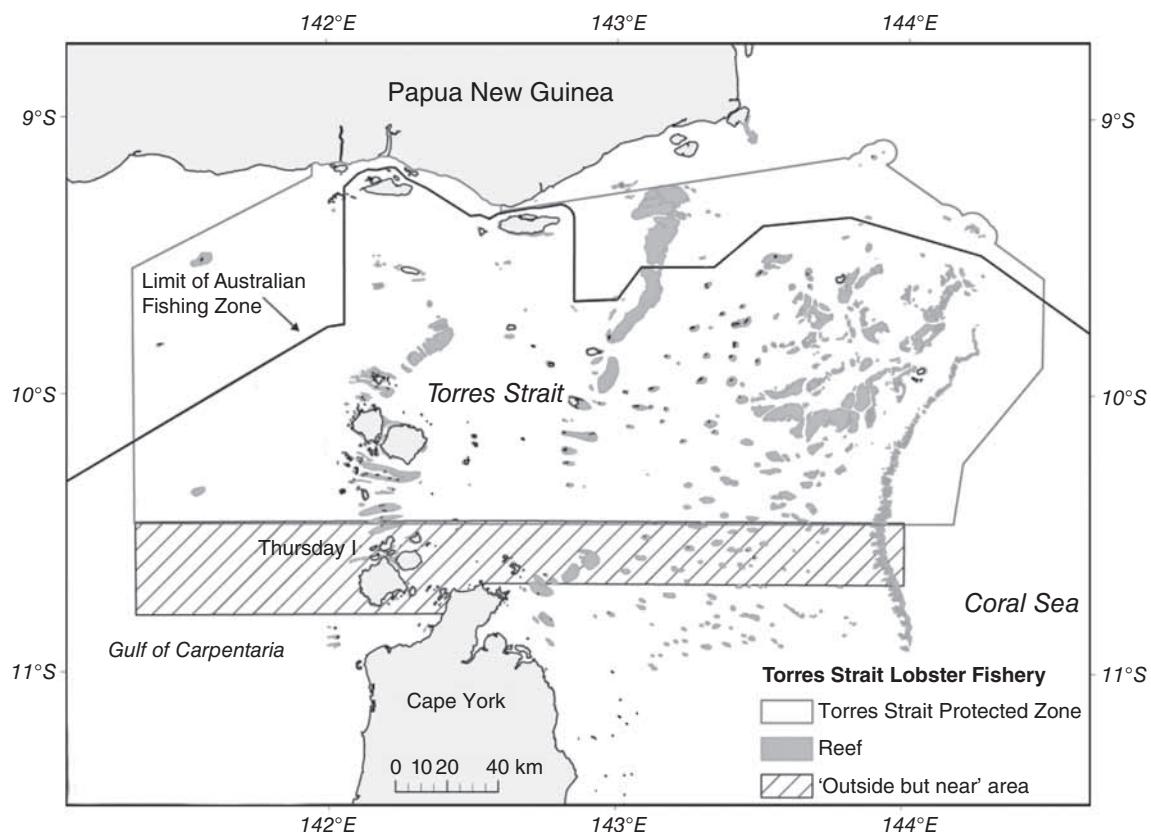


Fig. 10.3 The area in which the *Panulirus ornatus* fishery, jointly managed by Australia and Papua New Guinea, is located. Cape York and Thursday Island on the bottom of the figure is Australian territory; Papua New Guinea is in the northern part of the figure. Adapted from Bureau of Rural Sciences (2005) and courtesy of the Australian Fisheries Management Authority and Geoscience Australia.

pests, infectious diseases and the socio-economic influences associated with fishery management. The conclusion was identification of a single responsible factor is tempting when fished populations fail. However, it is likely that in most cases the failure of populations to recover can be attributed to a combination of causal factors and the way that managers of the fishery respond. While causal factors remain unclear in the case of the western rock lobster fishery, the decisive response by management in drastically reducing exploitation rates and rebuilding brood stock has been appropriate and positive.

The fishery was awarded Marine Stewardship Council (MSC) certification as a well-managed fishery in March 2000, the first in the world to

receive this imprimatur. It continues to maintain Certification.

Panulirus ornatus

There has been an artisanal fishery on *P. ornatus* in the Torres Strait and the east coast of Papua New Guinea for hundreds of years. Commercial fishing in Australian waters began in the area in the late 1960s and is restricted to the indigenous Torres Strait Islander people, who derive from it a significant portion of their income (Phillips *et al.*, 2000a). There is also a commercial dive fishery for *P. ornatus* along the north coast of Queensland, Australia. This is not discussed here, but the management arrangements are reported in Table 10.1.

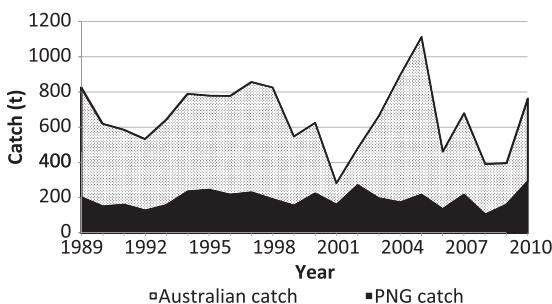


Fig. 10.4 Annual *Panulirus ornatus* catches 1989–2010 caught by PNG and Australian dive fisheries. Flood, M. J., Marton, N. & George, D. (2011). Reproduced with permission of Australian Bureau of Agricultural and Resource Economics and Sciences, Canberra.

The fishery (see Fig. 10.4) is managed as a joint authority fishery between the Australian and Queensland governments and under an agreed treaty between Australia and Papua New Guinea (PNG). Under the treaty, the catch is shared between PNG and Australia. This is achieved by Australia endorsing PNG boats to fish in Australian waters (Williams, 2004).

Diving is the method of fishing, with fishers freediving to about 4 m, or using hookah to around 20 m, from small outboard powered dinghies and returning their catches to land-based processors or processing vessels. There are currently upwards of 500 dinghies and about 25 small freezer boats being used in the Australian and PNG fishery (Williams, 2004). It is possible to catch these lobsters by trawling and during the 1970s and 1980s prawn trawlers targeted migrating animals, but this fishing method was banned in 1984 because of the danger to the breeding stock (Williams, 2004). Young lobsters grow quickly and first start recruiting to the commercial fishery about a year after settlement (Dennis *et al.*, 1997). In spring each year, most of the 3-year-old animals migrate from the Torres Strait to the north east and even the eastern reaches of the Gulf of Papua – a distance of up to 500 km (Moore & MacFarlane, 1984; Williams, 2004) (Fig. 10.3).

Recruitment to the fishery varies considerably and catches have fluctuated over the years. Since 1989 the abundance of *P. ornatus* over the approxi-

mate 25,000 square km of the Torres Strait fishery has been estimated using a dive/transect technique (Pitcher *et al.*, 1992). *Panulirus ornatus* is found throughout this area except in the centre of the fishery where the habitat is unsuitable silt and mud (Pitcher *et al.*, 1992). In 1989, there were an estimated 14 million lobsters in the Torres Strait, with about 8 million being legal size (Pitcher *et al.*, 1992). Ye *et al.* (2004) estimated the population size in 2002 at approximately 9 million lobsters of which the number of legal size lobsters was between 1 and 1.5 million, or 17% of the numbers of legal sized lobsters estimated in the 1989 survey (Ye *et al.*, 2004).

New regulations were introduced in 2002: an increase in the minimum legal size from 100 to 115 mm tail length; prohibition of commercial fishing in October and November; and banning the use of hookah gear from December to January (Ye *et al.*, 2004). Modelling results showed that these regulations would reduce the catch of age 1+ lobsters and increase the catch of age 2+ lobsters under higher fishing mortalities. In addition, there will be a positive impact on the spawning stock and thus on recruitment under high fishing pressure (Ye *et al.*, 2004).

Other developments: In 2003 the number of tenders that could be used to fish was reduced by 30% for Australian vessels. This requirement remains in place. Moon-tide hookah closure was introduced for 1 week during peak spring tide each month as an interim arrangement; this measure has been reintroduced annually. In 2005 the Tropical Rock Lobster Resource Assessment Group (TRLRAG) was established. A fishery-independent pre-season survey was introduced to support the development of a proposed quota-based management system. In 2006 a nominal TAC was agreed on and calculated for the first time. In 2007 13 Torres Strait vessel licences and 29 associated non-islander licence tenders were voluntarily surrendered in an open tender process to meet Australia's obligations under the Torres Strait Treaty. In 2008 the TRLRAG agreed to a new conversion factor of 2.677 for converting lobster tail weight to live weight. In 2009 a new stock assessment model was introduced. PNG cross-endorsed vessels took up their option under the Torres Strait Treaty to fish in

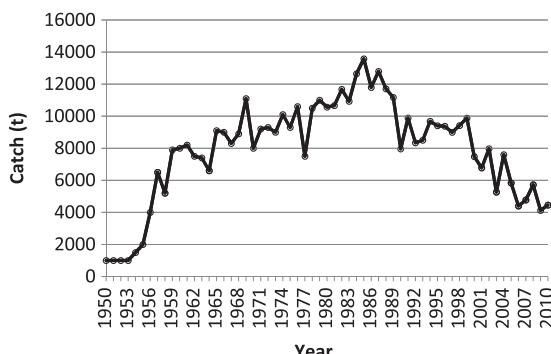


Fig. 10.5 Annual catches of *Panulirus argus* caught in Cuba- 1950 to 2010. From FAO (2011). The 2010 data obtained from Oficina Nacional de Estadísticas (ONE) de Cuba: Pesca en Cifras. Cuba 2010 (Enero-Diciembre de 2010)-Edición Junio 2011. 10 p. (<http://www.one.cu/Pescaencifras2010.htm>).

Australian waters for the first time since 2002 (Flood *et al.*, 2011)

The catches in Torres Strait by Australia and PNG are shown in Fig. 10.5. They have varied considerably over time and seldom reached the nominal TAC. In recent years, economic drivers, such as high fuel prices and a downturn in the export market are understood to have contributed to reduced effort in the fishery. In 2010, exporters of lobster tail received lower prices in the USA, largely as a result of the appreciation of the Australian dollar. Despite this, prices for live lobsters exported to China increased between 2009 and 2010. The gross value of production (GVP) has been decreasing every year since 2004–05, at an average rate of 18% per year, resulting in a 64% decrease since 2004–05. The decline in GVP has largely been due to decreasing catch. The GVP in 2009–10 was \$A6.7 million. Between 2008–09 and 2009–10, beach prices fell by 15% to \$A24.70kg (Flood *et al.*, 2011).

10.6.2 Cuba

Panulirus argus

The spiny lobster *P. argus* is the most valuable single-species fishery in the Cuban archipelago. Lobster fishing is carried out over an area of 34,618 km², associated with shallow embayment's

and reef lagoons. The most recent history of the Cuban lobster fishery was by Puga *et al.* (2010), who described the major changes in management measures from 1970–2010. Major changes included drastic reduction in the number of vessels from 310 in 1980–89 to 176 in 2010, a decrease from 45,161 to 17,712 days of fishing by 2010, and the closed season was increased from 90 days to 150–65 during the same period (Puga *et al.*, 2010). The fishery involves about 1280 fishermen operating 300,000 fishing gears (Cruz & Phillips, 2000; Puga *et al.*, 2009; Muñoz-Nuñez, 2009) during the 8-month coastal season (1 June to 31 January) in four management regions, which are divided into 10 smaller fishing zones, each controlled by a fishing enterprise. The boats vary in length from 10 to 18m and are concentrated on the south coast (75%), in the Gulf of Batabanó and south-eastern region, and 25 % in the northern region (Cruz *et al.*, 1990).

The state (Cuban government) organizes agencies and institutions to be in charge of administering the means of production. The Ministry of Fishery (MIP) was the Government agency that since 1975 has been totally responsible for all fisheries policy, planning, management, regulation, production and commerce of lobster (Joyce, 1997), until 2008 when after a restructuration it was integrated into the Ministry of Food industries (Ministerio de la Industria Alimentaria (MINAL)) (Puga *et al.*, 2010). Thus, the Cuban state-owned fisheries are managed under a somewhat highly centralized system, different from what occurs in most other countries. The assignment of fishing zones, boats, fishermen and industrial plants is an important feature of the Cuba lobster fishery. A strategic biological catch and effort quota is used to control fishing capacity (Puga *et al.*, 2010). The Fisheries Research Centre (Centro de Investigaciones Pesqueras (CIP)) is the scientific branch of the (MINAL) that coordinates the ‘Catch Bureau’ – small groups of specialists – that collects the biological information from the provincial Fishing Associations (the productive branch). Based on their studies, the CIP proposes the fisheries regulations to the Advisory Commission on Fishing (ACF). Once the ACF has analysed and approved these regulations, it submits them to the Minister

of the MINAL. Finally, the regulations approved by the MINAL are published by law decree and implemented by the Division of Fishing Regulations. The control and enforcement is then carried out by the Fishing Inspection Office (ONIP) (Muñoz-Nuñez, 2009; Puga *et al.*, 2010).

The Cuban fishery has been regulated for more than 75 years. The principal regulations governing the fishery are a legal minimum size which until 2004 was 69 mm CL but is now 76 mm with a maximum legal size of 140 mm for females. In addition, there is now an increased closed season (Puga *et al.*, 2010) that helps to safeguard the reproductive females during spawning, protect the new recruits and allow the growth of the lobsters. Recruitment to the fishing grounds shows a pronounced seasonal cycle: from March to May it coincides with the decrease in the average size of lobsters and the arrival of the smallest lobsters (pre-recruits) into the fishery (Cruz *et al.*, 2001). Strict control is also exercised via prohibition of taking berried females and females with spermatophores, number of fishing gears and boats, and boat replacement (Baisre & Cruz, 1994; Muñoz-Nuñez, 2009).

The majority (70%) of the fishing gears are artificial shelters, called ‘pesqueros’ (Cuban casitas) and are made from trunks of a coastal palm tree (*Coccothrina miraguana*) or from fibrocement sheets and palm trunks. The remaining 30 % are ‘jaulones’ (rectangular traps joined by 40 m pieces of nets, which are trap-like set nets), which have replaced Antillean traps (Cruz *et al.*, 1993; Cruz and Phillips, 2000). In Cuba, the catch rate is highest in June just after the beginning of the fishing season; 95% of ‘pesqueros’ catches are made then because lobsters enter the ‘pesqueros’ in the fishing area during the closed season, from February to May. Fishermen call the beginning of season, when 88% of the catch comes from the ‘pesqueros’, ‘levante season’ (June–September); during the mass migration season, called ‘recalo season’ (October–February), 70% of the catch comes from ‘jaulones’ (Puga *et al.*, 1996; Cruz & Phillips, 2000). The seasonal migrations of *P. argus* are characteristic of adult populations, and the concentration and subsequent movements, which are influenced by meteorological processes (intensity of winter fronts, depressions, hurricanes and conti-

ntental cold-air mass), have a great influence on catch volumes (García *et al.*, 1991).

In 1990 the lobster fishery collapsed (Fig. 10.5) due to a very poor recruitment (Baisre & Cruz, 1994). Puga *et al.* (1992) explained that hurricane Gilbert in 1988 most likely affected the lobster nursery grounds of the Gulf of Batabanó causing an increase in the mortality of juveniles. Besides the negative impact of this natural meteorological event on the recruits, Cruz (1999) argues that the intensive exploitation during the 1980s caused recruitment overfishing. A further analysis of the minimum legal size (MLS) that was in place during that time supports the latter argument. Analysing the curves of retention of ovigerous female spiny lobsters presented by Cruz & Bertelsen (2008) for the south of Cuba, it can be estimated that with a CL of 69 mm around 10–20% of the females carry eggs. This indicates that during all the years the Cuban lobster fishery followed this measure as the MLS limit, the spawning stock was most likely fished to a point that it did not have the reproductive capacity to replenish itself and to compensate for the loss caused by the fisheries (i.e. recruitment overfishing).

The Cuban shelf is close to its maximum exploitation (Claro *et al.*, 2001). Puga *et al.* (2005) developed an age-structured bioeconomic model for the fishery, which can be used to estimate reference points, such as the fishing effort for maximum sustainable yield per recruit, or the maximum economic yield per recruit. It was determined that recruitment has decreased since 1988 and it was suggested that effort should be adjusted (decreased) in order to achieve MEY. Since the decline of Cuban lobster fisheries production around the mid-1980s, the Cuban Ministry of Fisheries has tried to improve the economic efficiency and management of fisheries through stricter measures and new regulations (Baisre, 2004). However, as in many other coastal regions of Latin America and the Caribbean, a lack of resources has hindered the implementation and enforcement of these regulations (Charles *et al.*, 2007). Though the fishery experienced a slight increase in production after these regulatory efforts, the spiny lobster stock has not yet recovered from overfishing (Muñoz-Nuñez, 2009). Illegal lobster fishing is rampant in the

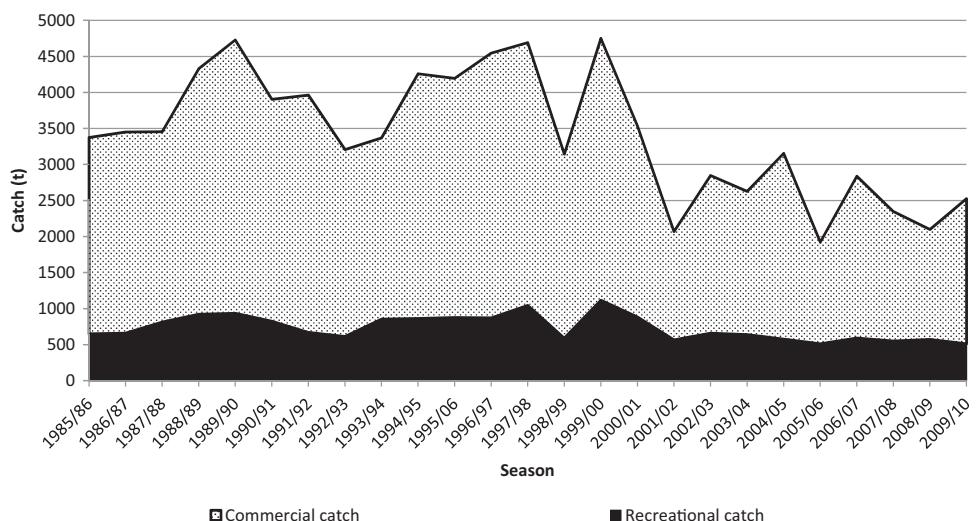


Fig. 10.6 Commercial and recreational spiny lobster landings of *Panulirus argus* in Florida, USA, from 1993/94 through the 2009/10 fishing seasons (FAO, 2011).

Cuban waters and contributes to the overfishing problem (Fuentes-Rodrigues, 2008; Muñoz-Nuñez, 2009). Hopefully the recent management changes will be effective, but with the continual decline in the catches to 4124 t in 2009 (Fig. 10.6), the future of the fishery is uncertain.

Exports of lobsters from Cuba averaged US\$70 million per year (Holmyard & Franz 2006) with over 60% of the catch exported as frozen precooked lobster (Puga & de León, 2003). These products are exported mainly to the markets of the European Union, Japan and Canada (Holmyard & Franz, 2006).

10.6.3 USA (Florida)

Panulirus argus

The Caribbean spiny lobster, *P. argus*, supports one of Florida's most valuable commercial fisheries as well as an intensive recreational fishery, with large annual sales of recreational lobster fishing permits (Gulf of Mexico Fisheries Management Council, 2011). The fishery is located principally on Florida's extreme south-eastern coast, especially along the Florida Keys archipelago, where approximately 90% of the state's landings occur. The rapid growth of this heavily capitalized fishery in the 1970s and

1980s evoked considerable management concern, which culminated in the implementation of management efforts in both the commercial and recreational sectors. Beginning in 1991, Florida required all amateur lobster fishers to possess a recreational spiny lobster permit, purchased as an additional endorsement to the state's saltwater fishing license. Then, in 1993, the state implemented the Lobster Trap Certificate Program (LTCP) in the commercial sector with the goal of reducing fishing effort by reducing the number of lobster traps. These management efforts have shaped the course of the spiny lobster fishery in Florida in the past two decades.

During the 1993/94 fishing season, the first year that the LTCP-mandated reduction in the number of lobster traps in the Florida spiny lobster fishery was implemented, commercial lobster trappers accounted for 69% of total state-wide landings and landings by commercial divers accounted for approximately 2% of the total (i.e. commercial and recreational combined) state-wide landings (see Fig. 10.6). After the inception of the trap reduction programme, though, there was a progressive shift in total landings away from commercial trappers toward commercial divers, and by the 2001/02 season the latter group accounted for more than 10% of total landings. This shift in allocation was the result of a significant increase in dive-caught

lobster during the first month of the fishing season in the Florida Keys and as commercial divers began to extensively use permanent underwater habitats to increase their catch efficiency. These underwater habitats have been made illegal. In an effort to limit this allocation shift, a bag limit regulation of 250 lobsters per day was placed on commercial divers beginning with the 2003/4 season.

In recent decades a slight shift in the relative landings from the commercial fishery toward the recreational dive fishery has been observed. Until the 1999/2000 season, the relative proportion of total landings accounted for by the recreational sector averaged 22%, and only exceeded 24% during one season (1993/4). However, since the 2000/01 season the relative proportion of landings by the recreational fishery has averaged in excess of 25%. It is important to note that the years when relative recreational proportions were much higher than average coinciding with those of record-low total landings. This is likely because nearly all of the recreational fishery effort occurs early in the season when abundance is highest, while the commercial sector effort is spread throughout the season. Though the shift in relative landings from the commercial to the recreational sector appears to have hit a plateau in the past few years, the relative proportion accounted for by the recreational sector is still above historic numbers.

Ehrhardt & Fitchett (2010) reported that despite management practices to achieve sustainability, commercial landings for Florida spiny lobster have experienced a drastic decline (57%) since 2000 (see Fig. 10.7). This is cause for concern not only for economic reasons, but for issues of sustainabil-

ity. In addition to the downturn in landings, the commercial fishery has been affected by low prices for the product in the last couple of years (Vondruska 2010). According to Vondruska (2010), the combination of reduced landings and market price would have had a more severe economic impact were it not that there have been very substantial reductions in fishing effort which have led to increases in vessel and trip productivity. Vondruska (2010) has provided 5-year averages for the periods 1987–88 to 1991–92 compared with 2005/06 to 2009/10 that show that the number of vessels in the fishery, trips per year and hours fished per year has declined over those periods by 64%, 60% and 52%, respectively.

An annual index of *P. argus* post-larval (puerulus) abundance, estimated with a generalized linear model with significant mean sea-level effects, shows a 36% decrease in annual puerulus supply since 1988 (Ehrhardt & Fitchett, 2010). In addition, local Florida spawning stock biomass estimated from an age-structured sequential population analysis decreased 57% from 1988 to 2010. Puerulus abundance follows a highly correlated ($R = 0.76$) trend with a 12-month delayed spawning stock abundance, which supports the contention that the Florida spawning population is a significant contributing factor to post-larval recruitment in Florida. Residuals about the puerulus on spawning stock abundance function follow closely an interannual North Atlantic Oscillation Index signal. This residual effect is thought of as a secondary regional population effect on Florida puerulus recruitment. The Florida spiny lobster stock is exploited with no fishing mortality controls due to the Pan Caribbean recruitment concept adopted in Florida spiny lobster management. Therefore, Ehrhardt & Fitchett (2010) concluded that the potential of recruitment overfishing exists if fishing mortality controls to protect local spawning stock abundance, such as catch quotas, are not introduced.

A workshop report (SEDAR 8 Update Assessment Workshop Report 2010) examined the state of the fishery and resulting management advice. They pointed to new evidence (Hunt *et al.*, 2009, cited by SEDAR 8 Update Assessment Workshop Report 2010) indicating that the south-eastern USA stock depends on external recruitment from

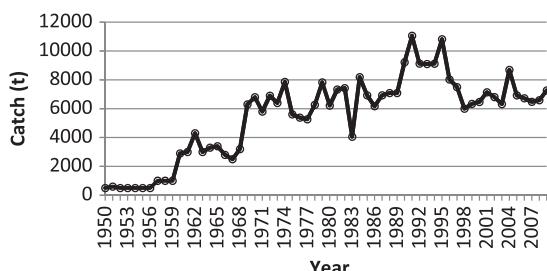


Fig. 10.7 Annual catches of spiny lobsters *Panulirus argus* 1950–2009 for Brazil. Reproduced with permission of FAO.

upstream Caribbean populations, as precluding the stock from being assessed in isolation of other regions within the geographical distribution of the species. Since recruitment to the US stock in Florida appears to be largely derived from stocks outside of US waters, stock recruitment relationships based solely on south-east US data could be meaningless. The declines in catch the fishery were not addressed in the Research Recommendations of the Committee.

The Gulf of Mexico Fisheries Management Council met in 2011 to consider an amendment to the Fishery Management Plan for Spiny Lobster in the Gulf of Mexico and South Atlantic. The proposed amendment is to ‘Establish annual catch limits and accountability measures for Caribbean spiny lobster; remove several other species of lobster from the FMP; redefine biological reference points; update the framework process; and establish or modify other management measures.’ In December 2011 the National Marine Fisheries Service announced the approval of Amendment 10 establishing the new arrangements (Southeast Fishery Bulletin FB11-98, 2011). This includes catch limits for spiny lobsters, an annual catch limit of 7.63 million lbs (3468 t) and an annual catch target of 6.59 million lbs (2995 t). These new arrangements should do much towards achieving sustainability of the spiny lobster fishery.

10.6.4 Brazil

Panulirus argus and *Panulirus laevicauda*

The Brazilian fishery was the world’s second largest producer of spiny lobsters in the 1980s. Several species contribute to the landings, with *P. argus* and *P. laevicauda* making up around 80% and 15% of the catch, respectively, and the balance of the catch being made up of a variety of other species (Ehrhardt & Aragão, 2006). The fishery began in the mid-1950s with the catches made by artisanal (small scale) sail-fleet fishers who sold to industrial processors for export. With the help of government subsidies from 1967 to 1988 (Government Decree 221/67), the fishery quickly became the main export fishery in the country.

Catches, based on figures provided by Fonteles-Filho (2000), peaked at almost 11,000 t in 1991,

and from 1991 to 1997 were between 6000 and 9000 t. The data presented in Fig. 10.7 are from FAO statistics and are only for reported landings of *P. argus*. The landings suggest that the fishery is maintaining its long-term catch level, although the fishing area increased considerably since 1985.

According to Ehrhardt & Aragão (2006) at the time of their publication there were 3336 sailboats, 2572 motorized wooden boats and five industrial vessels in the fishery, representing an enormous amount of capacity in this fishery. The same authors noted that traps and gillnets were the main fishing gear used at the time, but an increasing number of boats were using diving equipment assisted by compressors – a practice which is prohibited by law. According to R. Schärer (Terramar Institute, Brazil, pers. comm.), the fishing power has now been increased with the use of several types of recycled steel drums as lobster aggregating devices (LAD) (Plate 10.2A,B). The LADs positions are marked using GPS for easy harvesting.

Since Ehrhardt & Aragão’s (2006) publication, there has been a prohibition of gill nets, but according to R. Schärer (pers. comm.), even after a buy-back programme which cost the government US\$10 million, gill nets continue to be widely used illegally in several areas of the fishery.

According to R. Schärer (pers. comm.) in 2007 the legal fishing effort (boats fishing with traps) was reduced to achieve a theoretical maximum fishing effort of 40 million traps/year, but lack of enforcement has instead led to increased use of gillnets and hookah compressor. In the period since the reduction of effort there has been an increase of lobster exports which the Fisheries Ministry has interpreted as a positive response to the new management measures, but which R. Schärer has interpreted as being almost exclusively due to the increases in the illegal fleet operations. On the positive side, there was an increase to the closed fishing season introduced in 2009, from four to six months, to help protect egg bearing lobsters which are legally permitted to be harvested (R. Schärer, pers. comm.).

Whilst this fishery does have management regulations (see Table 10.1) there appears to be a lack of respect for, or enforcement of these regulations.

According to Chaffee (2001) (Scientific Certification Services, USA, pers. Comm.) some fishing, is taking place during the closed fishing season, illegal fishing methods (diving) are being used and undersized lobsters are being caught and marketed locally as well as overseas. Ehrhardt & Aragão (2006) estimated the amount of undersized lobster landed in the fishery as being between 10% and 30% by weight of the total catch.

In the long term, landings in this fishery appear unlikely to be sustainable. The spawning potential of the stock is considered to be at <15% of pristine levels (Ehrhardt & Aragão, 2006) and this combined with high exploitation rates and lack of adequate enforcement do not bode well for the future of this fishery.

10.6.5 Baja California Mexico and California USA

Panulirus interruptus

The spiny lobster *P. interruptus* is distributed within the temperate-subtropical environment of the California Current Ecosystem (CCE), between approximately 35° and 23.5° north (Fig. 10.8) from San Luis Obispo California to near the southern tip of the Baja California peninsula (Vega-Velázquez, 2003a, 2006). Known as red lobster or California spiny lobster, *P. interruptus* is fished commercially in Mexico in an area from the border with the USA to Todos Santos, near Cabo San Lucas. However, the main portion of the population is between Cedros Island and Punta Abreojos along the coast of Mexico, which account for near 67% of the total catch of this species (Vega-Velázquez, 2006). The southern range of distribution this species overlap with the range of two tropical species, *P. inflatus* and *P. gracilis*, due to a mix of temperate and warm water in a transitional zone at southwest Baja California (Vega-Velázquez & Lluch Cota, 1992; Vega-Velázquez, 2006). *Panulirus interruptus* is also fished both commercially and recreationally in California in the USA.

Studies based on a mitochondrial DNA analysis of *P. interruptus* along the Pacific coast of Baja California (García-Rodríguez & Pérez-Enríquez, 2006) and including the gulf of California (Pérez-

Enríquez, R. & García-Rodríguez, 2009), indicated that there is a single population.

Baja California, Mexico

The *Panulirus interruptus* fishery in Baja California, for which Ayala *et al.* (1988), Vega-Velázquez & Lluch Cota (1992) and Vega-Velázquez *et al.* (1996) have provided a thorough history, dates from the turn of the 20th century. In Baja California the fishery has been traditionally conducted by limited access rights granted to licensed cooperatives, although a modification to fishing law in 1992 allows the entrance of producers belonging to the private sector (Vega-Velázquez *et al.*, 1997). The private sector, which is represented by 25 cooperatives, controls most of lobster grounds and almost 98% of total production (Vega-Velázquez *et al.*, 2010b). The limited access includes a clear delineation of a fishing zone through concessions lasting 20 years, or permits by 4 years, and a maximum number of boats and traps by cooperative or private producers (Vega-Velázquez *et al.*, 1997). Approximately 2605 members belong to the cooperatives (private sector), and are distributed in 48 fishing towns along western Baja California. Commercial harvest is conducted with baited wire traps deployed from small boats ('pangas') ranging from 3 to 6 m in length. During the 2009–10 and 2010–11 fishing seasons 564 boats operated by 1250 fishermen used 28,296 traps, (Vega-Velázquez *et al.*, 2010a). This fishery is among the most economically important resources in Baja California, the average price (US dollar) for live lobster, mainly exported to Asian markets, increased from \$18/kg in 2000–01 to \$44–52/kg in (2010–11), and generated a landed value of around US\$77 million in the 2010–11 season (Vega-Velázquez *et al.*, 2011a).

Catches by commercial fishers in Mexico available since 1928 (Fig. 10.9), and also commercial fishers in the USA, show long-term trends and interannual fluctuations of the landings series from California and Baja California. Phillips *et al.* (2000c) showed that changes in the catches of *P. interruptus* in Baja California over a long period tended to be higher 4 years after ENSO episodes that cause high sea levels and a strong poleward

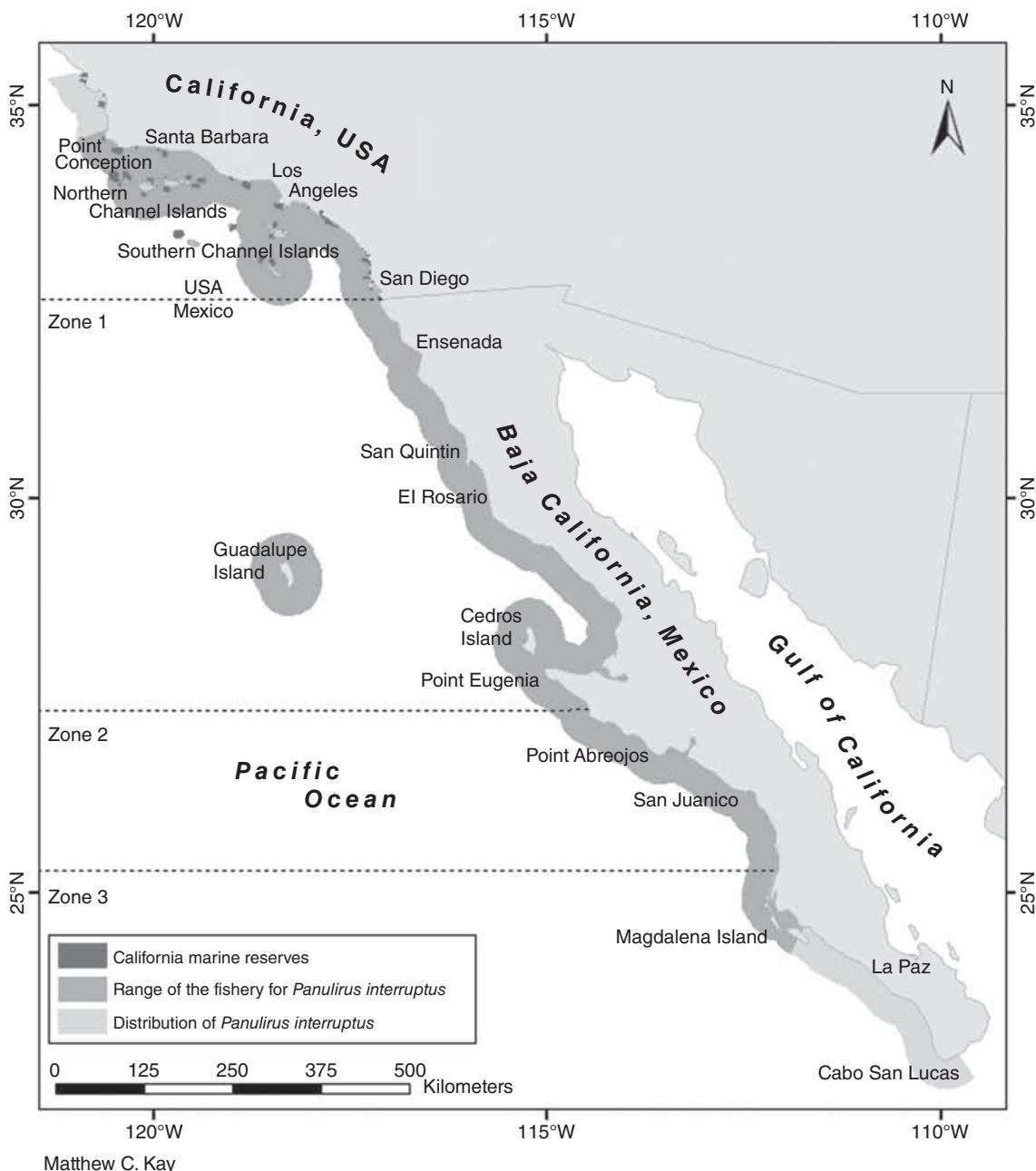


Fig. 10.8 Map of southern California, USA, and Baja California, Mexico showing the distribution of *Panulirus interruptus* and the areas fished for *Panulirus interruptus* in both countries. Compiled by Matthew Kay.

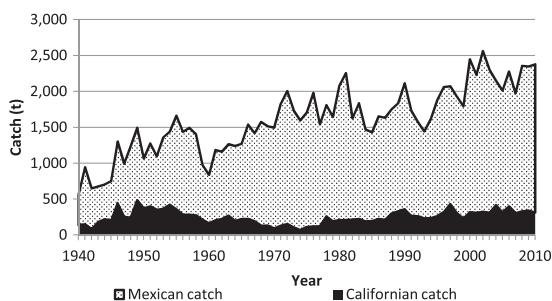


Fig. 10.9 Catches of *Panulirus interruptus* in Baja Mexico and California USA between 1998 and 2010. Data supplied by Armando Vega and Kristine Barsky (CDFG).

flow. Vega-Velázquez & Lluch (1992) found evidence of a relationship between sea surface temperature and lobster catch. Arteaga-Rios *et al.* (2007) found that settlement of *P. interruptus* pueruli was significantly correlated with lobster catches 5 years later in Bahia Tortugas, central Baja California, which appears to be related to the recruitment to the fishery, suggesting that such relationship would be useful for predicting catches of this species.

The management system is under Federal Government control and research for stock assessment and management is carried out by the National Institute of Fisheries (Instituto Nacional de Pesca (INAPESCA)) through the Regional Centre of Fisheries Research (CRIP) located in Ensenada (Baja California) and La Paz (Baja California Sur). Harvest control rules are established by official communications of the Mexican government through the 'Official Gazette' Diario Oficial de la Federacion (DOF). The main control rule of this fishery since 1997 is to maintain the fishery at a level to harvest the maximum surplus production while maintaining the population biomass at values above the Bo/2 biomass estimate (where Bo is the estimated theoretical virgin population biomass). Regulations applied to this fishery are based on minimum size by species, closed season by zones, limiting fishing effort and trap design (Vega-Velázquez, 2006). The fishery harvest strategy is based on all governmental specifications for the fishery as stated in Regulations (NOM-006-PESC-1993, updated 15 June 2007). These strategies have

been considered and included in a Management Plan which was developed by INAPESCA, and includes a scientific research plan (Vega-Velázquez *et al.*, 2010b).

Institutional mechanisms are in place for coordination and co-management to facilitate collaboration between fishermen and technical personnel of INAPESCA (Vega-Velázquez *et al.*, 1997). These arrangements start from the collection of data to discussion of research results, where recommendations for management are openly and transparently discussed before their submission to fisheries authorities (Vega-Velázquez *et al.*, 2000; Vega-Velázquez, 2006). The first of these mechanisms was the 'Comité Técnico Consultivo de la Pesquería de Langosta del Pacífico' (Technical consulting committee for the Pacific lobster fishery), created during 1988, from which was originated the 'Taller I de Langosta' (Annual lobster workshop). There is also a 'Subcomité Estatal de Langosta' (state lobster subcommittee) operating since 2003, within the framework of the 'Consejo Estatal de Pesca y Acuacultura' (State council for fisheries and aquaculture) for each State (Baja California Sur and Baja California).

Both the state councils and fishery subcommittees achieved a legal mandatory status by the new fishing law (Ley General de Pesca y Acuacultura Sustentable) enacted since 2007 (DOF 24 April 2007). Also, the most recent modification of the lobster fishery regulations set by the Official Mexican Norm (Norma Oficial Mexicana NOM-006-PESC-1993) (DOF 15 June 2007) established that each state must have a lobster subcommittee and if a lobster stock is shared by two states then a regional committee must be created. Since 1997–98, the Mexican official research institution (INAPESCA) has set reference points at MSY (incorporating biomass, fishing mortality, effort and rate of exploitation) using a Biomass Dynamic Model, particularly for biomass maximum sustainable yield (BMSY) (Vega-Velázquez *et al.*, 2000). Management decisions are taken depending on the ratio of current biomass (B) to BMSY – where $B/BMSY < 1$, the stock is considered to be under its optimum biomass level and where > 1 , over its optimum biomass level. In Vega-Velázquez (2003a) and Vega-Velázquez (2006) the Biomass Dynamic

Model, as well as several analytical models, were used to provide more advice to management. Vega-Velázquez (2006) also applied a bio-economic model to take into consideration the value of the fishery. In the latest analysis, using the Biomass Dynamic Model (Hilborn & Walters, 1992) and utilizing the catch and effort time series from 1960–61 to the 2009–10 seasons, Vega-Velázquez *et al.* (2010a) found that the biomass ($B = 14,120$ t) in the last five seasons compared with BMSY (9402 t) is 1.5 larger, meaning that the stock is above its target biomass. Vega-Velázquez *et al.* (2010a) also found that Fishing Mortality (F) was 0.10, half the FMSY (0.20). Effort (f) was 2,218,377 trap-hauls (average 2007–10). On the basis of these references points Vega-Velázquez *et al.* (2010a,b) concluded that the lobster fishery is sustainable. Though the biomass, catch and effort values have been within the MSY parameters, Vega-Velázquez *et al.* (2010) recommended that effort should *not* be increased due to economic reasons based on the bioeconomic analysis (Vega-Velázquez, 2006).

Chavez & Gorostieto (2010) made a bioeconomic assessment of the *Panulirus interruptus* fishery in Baja California using a FISMO model. Recommendations for a gradual decrease in fishing mortality and an increase in the minimum size were made aimed at improving the volume of the catch and future profits. A target of MEY was also recommended for the fishery.

A recent series of studies conducted by agreement between Stanford University (Dr Fiorenza Michelli, Principle Investigator) and The Northwest Centre of Biological Research (CIBNOR), funded by the United States National Science Foundation (Linking Human and Biophysical Processes in Coastal Marine Ecosystems of Baja California OCE 0410439) was finalized (Michelli, 2010). The study yielded 47 articles and many PhD theses. Many are already published but others are in press or still in manuscript form and the reader is referred to the report for details. Among these are the studies regarding the lobster fishery impacts on the ecosystem (Shester, 2008a,b) that provided estimates on the amount and composition of retained and discarded bycatch as well as the bait used in the fishery. Shester (2008a) estimated that the total incidental (non-target) catch was approximately

13% of landed lobster catch by weight: He also showed that traps have a minimal impact on the benthic ecosystem and that ghost fishing was not significant as additional cause of mortality to spiny lobsters or other species (Shester, 2008a). Ghost fishing mortality through lost lobster traps was estimated to be between 1% and 2% of total landed lobster catch annually and has likely been reduced because biodegradable traps were implemented in the fishery in 2007 (Shester, 2008b).

Of special interest was the development of an Ecopath food web model including 23 species or functional groups (Morales-Zarate *et al.*, 2011). This model was used to examine the relative importance of fishing and ecological interactions on the food webs and identify species that may play a key role in the webs dynamics, using a methodology developed by Libralato *et al.* (2006; ‘keystoneness’ index). The total system throughput was 496.25 t/km²/year, of which 56% is for internal consumption, 29% is for respiration, 14% becomes detritus and only 1% is removed through commercial fishing. The model suggests that even for exploited populations, predation and competition have greater influences than current fishing effort. Spiny lobster showed the highest ‘keystoneness’ index value. Thus, overexploitation of this species could have impacts on the entire ecosystem.

Another publication of interest is that of Ramirez-Rodriguez & Ojeda-Ruiz (2012) on spatial management of small-scale fisheries on the west coast of Baja California Sur. Ley-Cooper *et al.* (in press) have recently completed a study within the Biosphere Reserve of Sian Ka'an, Mexico (SK), which is a MPA where restricted access fishing is allowed. Commercial catch rates were examined, and lobsters over a wide size range were tagged throughout the 2010/11 fishing season, to assess fishing mortality rates and movement patterns in Bahía Espíritu Santo-SK. Lobster tag recovery data were analysed using a modified Brownie model parameterized to account for lobster tag-reporting, and the lobster tag-retention rates. This allowed the estimation of instantaneous rates of lobster natural and fishing mortality, considering catchability and fishing effort. The model indicated that exploitation rates in the study area were high, >0.94. Changes in catch per unit of effort and catchability throughout

the season explain how the ‘casita/campo’ system allows for a seasonal replenishment of juveniles and adults, which has kept the landings relatively stable for the past decade.

On the basis of the fishery sustainability and bio-ecological indicators, an independent evaluation carried out by the Marine Stewardship Council (MSC) recommended that the central Baja California Lobster Fishery for *P. interruptus* satisfied the conditions to be awarded again in 2011 the MSC certification as a well-managed fishery (MSC 2011).

California, USA

Commercial harvest of *P. interruptus* in California, USA, represents less than ~20% of the combined total from US and Mexican waters, but it is among the most economically important commercial fisheries in California and generated nearly US\$7 million landed value in 2007 (Harty *et al.*, 2010). Commercial harvesting is conducted with baited wire traps deployed on the seafloor, while the use of nets (fixed or towed) or diving equipment is prohibited. Traps are deployed individually (i.e. are not physically connected) and retrieval is conducted using hydraulic pot haulers on modern vessels ranging from ~6–13 m in length.

Commercial harvest dates to the mid-1800s when lobster were fished primarily along the mainland coast. By the early 1900s, when catches increased due to the advent of gasoline engines and offshore fishery expansion (Bell, 1973), encampments of fishermen were well established in the Northern Channel Islands and distant markets in cities such as San Francisco had existed for decades (Stimpson, 1856; Jordan, 1887). The capacity of these early markets and fishermen was significant, and by 1909 the fishery was closed for 2 years due to concerns of overharvesting (Wilson, 1948). A long-term (120 year) historical study of the effects of fishing on *P. interruptus* indicates size structure truncation and decreased mean size throughout California (McArdle, 2008). Other recent and ecologically relevant research elucidates antipredator acoustic signalling (Petak *et al.*, 2009; Staaterman *et al.*, 2009) and suggests predation upon other invertebrates including the sea cucumber *Pach-*

ythone rubra (Eckert 2007) the sea hare *Aplysia californica* (Kicklighter *et al.*, 2005) and the purple sea urchin *Strongylocentrotus purpuratus* (Matassa, 2010).

The US fishery for *P. interruptus* has a long history of regulatory change (Bell, 1973). In California both commercial and recreational fishing are permitted. Current regulations set by the California Fish and Game Department (CFGD) include a limited fishing season, a minimum legal size and release of all undersize lobsters. Since the 1976–77 season it is required that commercial traps must be fitted with rectangular escape ports to reduce retention of undersize lobster (Barsky & Swartzell, 1992). Additionally, in 1996 the commercial fishery was restructured into a limited entry regime (<http://www.dfg.ca.gov/>) and since July 2005 commercial lobster operator permits are allowed to be transferable.

MPAs are fast becoming an important factor in the management of all California near-shore fisheries. Earliest reserves, which were small and isolated, led to increased lobster abundance or size (Parnell *et al.*, 2005; Iacchei *et al.*, 2005) and have been supplemented by reserve networks at the Northern Channel Islands (established in 2003) and along the mainland from Point Conception to the US–Mexico border, including the Southern Channel Islands . Research at the Northern Channel Islands network indicates increased abundance and mean size (Kay *et al.*, 2012a) and reduced mortality inside reserves (Kay & Wilson, 2012). These findings are corroborated by a tagging study in which adult *P. interruptus* moved average distances that were shorter (even across long time scales) than the dimensions of reserves (Kay *et al.*, 2008). Although fisheries benefits (e.g. increased yield) via spill-over have not been observed in fishery landings or trap performance (Guenther, 2010; Kay *et al.*, 2012a), abundance gradients inside reserves suggest net emigration of lobsters from these reserves (Kay *et al.*, 2012). These gradients of abundance were modified by habitat features known to influence spiny lobster distribution and mortality rates (e.g. Mai & Hovel, 2007; Loflen & Hovel, 2010).

Management of *P. interruptus* in US waters includes a thriving open access recreational fishery for which participants must possess an annual

California fishing license, ocean enhancement stamp, and (since 2008) lobster report card. Until recently, the majority of harvest in the recreational sector was conducted by skin and scuba divers (Barsky *et al.*, 2004; Ben-Horin *et al.*, 2006) who are allowed to capture lobsters by hand but forbidden from using foreign objects (e.g. spears, hooks, lassos) to ensnare lobsters. In 2007, a CDFG creel survey found that circular hoop nets are now the dominant gear type (<http://www.dfg.ca.gov/marine/newsletter/0109.asp#spinylobster>). Recent increases in hoop net popularity, as well as modifications that enhance capture rates of traditional designs (Neilson *et al.*, 2009), have raised concern about increased capacity of this sector. Historical estimates (Frey, 1971; cited in Shaw 1986) and recent analysis of recreational report card data suggest that recreational harvest may equal approximately half of the commercial catch.

A number of management and fisheries research issues are pending or on the horizon for this fishery. Perhaps most important of these is a stock assessment recently completed by the California Department of Fish and Game (CDFG). The assessment team and a report by a Technical Review Panel (TRP) (Cope *et al.*, 2011) indicate that available biological data are not sufficient to support classic surplus production models, Leslie depletion models, or a statistically based size-structured stock assessment. Consequently, the assessment is based upon catch and effort data used in a fishery simulation model (FISMO) developed by Chávez (2005). Initial results indicate that the fishery is sustainable, and that sustainable yields likely range from 335 to 375 t (Cope *et al.*, 2011). However, the TRP cautions that long-term sustainability may be uncertain due to capacity changes in both the recreational and commercial sectors, low rates of report card return for recreational fishermen, uncertainty around life history parameter used in stock assessments estimates and the absence of biological data that describe population trends and demographic rates of *P. interruptus* throughout the entire Southern California Bight. In addition to the stock assessment, CDFG has identified this fishery as a priority for a fisheries management plan (FMP), as described and mandated by California's Marine Life Management Act (MLMA, 1998). CDFG is currently

moving forward with the FMP process (<http://www.dfg.ca.gov/marine/lobsterfmp/>).

Interest in a trap limit remains high among many commercial fishermen who are concerned about latent capacity, especially as rising ex-vessel prices (from ~ \$20/kg in 2005–06 to ~ \$40/kg in 2010–11) displacement due to marine reserves, transfer of latent permits to active fishermen, and a burgeoning recreational sector all lead to increased effort. Capacity adjustments to the commercial sector may stimulate similar actions for the recreational sector, and allocation within and between sectors promises to be a contentious and difficult consideration for managers. Range expansion of the southern sea otter (*Enhydra lutris*), once common south of Point Conception, may drastically impact populations and fishery landings of *P. interruptus* (USFW, 2005). Management relevant research contributions for the near future will include monitoring of new reserves, expanded fisherman–scientist–manager collaboration, optimization of harvest/effort, spatially explicit descriptions of population structure and life history parameters for assessments, and recruitment studies that scale stock-recruitment dynamics and explore connectivity between the US–Mexico stocks (e.g. Pringle, 1986).

10.6.6 India

Panulirus polyphagus

Commercial exploitation of lobsters began in the 1950s and targeted *P. homarus*, *P. ornatus*, *P. polyphagus*, *P. versicolor* and also *Thenus orientalis* and the deepwater *Puerulus sewelli*. The peak landings occurred in 1985 (4075 t) but since then there has been a sharp fall in catches and growing instability in the stocks (Radhakrishnan *et al.*, 2005).

We have chosen data on *P. polyphagus* to present here, but the trends in the catches are similar for other *Panulirus* species in India. India is not the only country that catches *P. polyphagus*, a species which is widespread across South East Asia (see Fig 11 in Phillips & Melville-Smith, 2006). *Panulirus polyphagus* occupies a 1–10 m depth range along the south-west coast and 75% of all landings is caught by shrimp trawlers. The remainder of the lobster catch is taken in shallow water by traps, gill

nets and trammel nets. Other species including *P. ornatus*, *P. homarus*, *P. versicolor*, *P. penicillatus* and *P. longipes* are also caught in small quantities, depending on the area.

Stock assessment studies on *P. polyphagus* carried out at Mumbai indicate a high exploitation ratio (0.81 for males and 0.68 for females), and between 1996 and 2000 an exploitation rate of 78% was estimated for this slow growing species with 7–8 years of fishable life span (Radhakrishnan & Manisseri, 2003). Between 2007 and 2010 catches from the fishery averaged only 600 t/year, of which 5–24% were scyllarids (J. Kizhakudan, CMFRI, India, pers. comm.).

Currently no management regulations are in force to control fishing of *P. polyphagus* in India, except that a 300 g minimal size for export of *P. polyphagus* was adopted in 2003 (Radhakrishnan et al., 2005). Minimum sizes for export were also introduced for *P. homarus* and *P. ornatus*, but other recommendations, such as a minimum legal size, closure of the fisheries during the peak spawning season in the southern region of India, and a ban on trammel nets, have not been introduced.

10.6.7 Kenya and Somalia

Panulirus homarus megasculptus (mostly)

Panulirus fisheries on the African coast generally have few regulatory controls. We have included lobster-fishing regulations used in two countries, Kenya and Somalia, as examples (Table 10.2). According to Kulmiye (pers. comm., University of Nairobi, Kenya) most, but not all, of the Somalian catch is *P. homarus* and landings are currently around 2100 t whole weight. The Kenyan catch is made up of at least five species (*P. homarus*, *P. longipes*, *P. ornatus*, *P. penicillatus* and *P. versicolor*) and the annual production is approximately 70 t. The FAO records show a catch of 500 t, but this is unreliable as an identical catch is reported annually.

10.6.8 Indonesia

The spiny lobster catch in Indonesia is of several species (*P. homarus*, *P. longipes*, *P. peni-*

cillatus, *P. polyphagus* and *P. versicolor*) Tewfik et al., 2009). There are very few regulations for the fishery (see Table 10.1).

Catches have increased rapidly in recent times (Fig. 10.10)

10.6.9 Japan

Management of spiny lobster fisheries in Japan is a co-management process with the fishermen and the Prefectural Government. For further details see Nonaka et al. (2000). A recent book on Fisheries management in Japan (Makino, 2011) does not deal specifically with lobsters but clearly describes the whole process of management of coastal fisheries in Japan.

Yamakawa, (2007) provides further information specific to lobsters. Catches of *Panulirus japonicus* in Japan (Fig. 10.11) do fluctuate, but attempts are

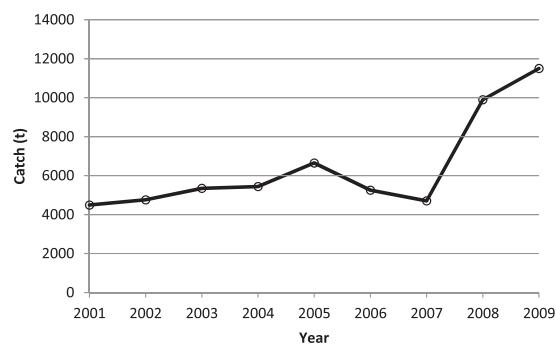


Fig. 10.10 Catches of spiny lobsters in Indonesia 2001–2009 (FAO, 2011).

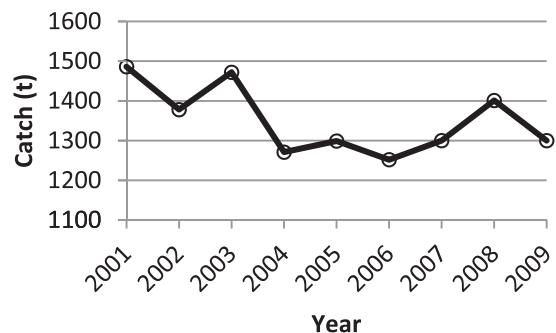


Fig. 10.11 Catches of *Panulirus japonicus* in Japan 2001–2009 (FAO, 2011).

made by the fishers, in coordination with the Prefectural Governments, to stabilize the annual catches. The coastal fisheries management system in Japan is characterized by community-based management in which fishermen are organized into fisheries cooperative associations (FCAs) that are exclusively granted coastal fishing rights under the authority of prefectural government. The management system in FCA is mainly based on spontaneous, self-motivating rules by fishermen, as well as compliance with the prefectural ordinance. Thus, co-management that is coordinated by fishermen and the government functions effectively as a fundamental framework. Management measures for lobster fisheries largely depend on ‘input control’ and ‘technical measures’. They include establishment of closed season or closed areas, introduction of various constraints for gear (type of nets, mesh size, thickness or quality of the net yarn, number of nets per boat), fishing recess around new-moon nights, rotation system of closed areas, limitation for allowable body size for landing, and release of berried females or small individuals. In recent years, efficacy of conventional management measures has been reinvestigated based on scientific management models, and gaps between optimal versus actual measures may exist in some cases. A management model based on the optimal in-season allocation of fishing effort considering the shifts in market price, catchability and operation costs was presented using the theory of maximum principle. Also, an optimal fishery model, which aims to integrate the effective utilization of recruited stocks and the reproductive management, was proposed by introducing a concept of economic value of the spawning stock.

10.7 Aquaculture and enhancement

10.7.1 Aquaculture

Countries recently involved in research in this area include Australia, New Zealand, Cuba, Brazil, Mexico, Singapore, India, Peoples Republic of China, Brazil, Japan, Vietnam and Thailand. In addition, we understand that Ireland, People’s Republic of China, United Kingdom, Spain, Sey-

chelles, Sri Lanka, Iran, Saudi Arabia, Thailand, Burma, Croatia, Tahiti, Mexico and Norway all have some involvement or interest in spiny lobster aquaculture. Phillips & Matsuda (2011) published a ‘Global Review of Spiny Lobster Aquaculture’ hence in this chapter we will summarize data in the review or update from the data in the review.

Larval culture

The complete larval development under laboratory conditions has now been achieved for six species of *Panulirus* (Table 10.3). The time required for larval development of the spiny lobsters under laboratory conditions varied considerably. For example, *P. japonicus* took between 307 and 391 days and *P. longipes* 281–294 days. Studies in Mexico include those of Diaz-Inglesias & Baez-Hidalgo (2010) and Diaz-Inglesias *et al.* (2011) on *P. interruptus*. Recently has *P. argus* been reared in captivity from egg to the benthic juvenile stage with an observed pelagic larval duration of 140–198 days (mean 174 days (Matsuda *et al.*, 2008).

In Australia the main species being examined for complete aquaculture are *P. ornatus* and *Jasus edwardsii*. Considerable research effort underway to achieve this objective (Phillips & Matsuda (2011) but little of the research has been published as it is considered ‘commercial in confidence’. A dramatic development was announced by Barnard *et al.* (2011), who reported not only that they had achieved the complete larval rearing of *P. ornatus* but that they had produced an F2 generation of aquacultured *P. ornatus*. Rogers *et al.* (2010) predicted commercial hatchery production by this company and grow-out of tropical rock lobster *P. ornatus* in Australia within ~3 years. On 13 December 2011 the Queensland Government announced the official opening of a Tropical Rock lobster Pilot Commercial Hatchery in Cairns, Australia (Department of Employment, Economic Development and Innovation, 2011).

Research for lobster aquaculture in Mexico began around 2002. Experimental rearing phyllosoma larvae produced in a laboratory during 2003–06, at CICESE in Ensenada, only reached the Stage VI (Álvarez *et al.*, 2004). Because of difficulties

Table 10.3 Species of *Panulirus* sp. lobster where complete larval development has been achieved in the laboratory.

Species	Number of instars	Duration of phyllosoma stages in the laboratory (months)	Duration of puerulus stage in the laboratory (days)	Author(s)
<i>Panulirus japonicus</i>	20–31	7.5–12.6	9–26	Kittaka & Kimura (1989); Yamakawa <i>et al.</i> (1989); Sekine <i>et al.</i> (2000); Matsuda & Takenouchi (2005)
<i>Panulirus longipes bispinosus</i>	17	9.1–9.5	–	Matsuda & Yamakawa (2000)
<i>Panulirus penicillatus</i>	20	8.3–9.4	–	Matsuda <i>et al.</i> (2006)
<i>Panulirus homarus</i>	–	5.5–8	–	Murakami, K. (2006)*
<i>Panulirus argus</i>	18–21	4.5–6.5	11–26	Goldstein <i>et al.</i> (2006); Matsuda <i>et al.</i> (2008)
<i>Panulirus ornatus</i>	23–24	4–6.5	9–25	M G Kailis Group (Barnard, R) (2006); Northern Fisheries Centre 2007 (Jones, C. pers. comm.)
<i>Panulirus versicolor</i>	–	6–7	–	Australian Institute of Marine Science 2007 (Smith <i>et al.</i> , 2009) Barnard R (2010)*

*Pers. comm., not published

rearing larvae successfully, research moved to fattening of pueruli captured in the wild with artificial collectors (Díaz-Iglesias and Baez-Hidalgo, 2010). These authors reported that from initial average length of 6.91 mm CL and 0.21 g weight of 11 pueruli, after 221 days (2008–09) and 8 moults these increased to 34.2 mm CL and 35.4 g, under an environmental temperature of 19.4°C. However, despite promising results, the main problem was the low abundance of pueruli in northern Baja California areas, as only 11–12 pueruli were caught per collector per year; which was the same problem reported by Serfling & Ford (1975).

The National Institute of fisheries (INAPESCA) of Mexico, in coordination with several cooperatives, has initiated in 2010–11 an experimental research project to assess the aquaculture potential of the commercial lobster species in northwest Mexico. Experiments with pueruli of *P. interruptus* reared in floating cages in ponds have been carried out in the facilities of the Cooperative ‘Leyes de Reforma’ located in Bahía Asunción, BCS. An experiment con-

ducted from June 2010 to June 2011 with 15 pueruli, averaging 7.8 mm CL, showed an average increase of 25.3 mm LC (Vega-Velázquez *et al.*, 2011b). These preliminary results, together with the greater abundance of pueruli in central-southern areas of Baja California, indicate a promising prospect for culture of such species. Thus, we recommend support for long-term research leading to comprehensive evaluation of the aquaculture potential of *P. interruptus*, and other tropical species (*P. gracilis* and *P. inflatus*) including the possible impacts of removing puerulii in the wild population, as well as to develop biotechnology for production and rearing of larvae and pueruli in laboratories.

Grow-out of pueruli and juveniles

Partial aquaculture involving raising wild pueruli or juveniles collected from the ocean is also an area of current interest. Countries that are currently, or were formerly, involved directly in research include Australia, New Zealand, India, Vietnam, Cuba,

Table 10.4 Total aquaculture production of spiny lobsters over the last 12 years*.

Country	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
Philippines	10	19	27	17	10	18	19	19	23	64	72	64
Singapore	12	11	6	10	6	11	14	5	8	2	4	4
Vietnam**	1000	500	600	1000	1127	1200	1120	1200	1900	1400	720	1003
Cuba	2	1	22	13	11	3	1					
Taiwan	12	18	6	1								
Indonesia			5	10	10	10	20	50	100	100	292	338
India										3	3	5

*Data from FAO

**Not an exact match with FAO data

Singapore, South Africa, Bahamas, Malaysia, Mexico, Turks and Caicos, Namibia, Philippines, USA, Indonesia, British Virgin Islands and New Caledonia.

Vietnam is currently producing more than 1000 t of cage raised *P. ornatus* (the ornate spiny lobster), *Panulirus homarus homarus* (the scalloped spiny lobster), *Panulirus stimsoni* and *P. longipes longipes* annually (Phillips & Matsuda, 2011) and Table 10.4, which are exported to China, Japan, Hong Kong and Thailand (Tuan *et al.*, 2000; K. Williams, CSIRO Marine Research, Queensland, Australia, pers. comm.). Some of these pueruli are caught in other countries and transported to Vietnam for grow-out.

10.7.2 Enhancement

Conan (1986) comprehensively reviewed enhancement of lobsters. It involves many types of protection of the early life history stages to increase yields from the fisheries. As pointed out by Conan (1986), ‘References on recruitment enhancement are extremely scarce’.

Japan has pursued a plan for stock enhancement of the Japanese wild stocks of *P. japonicus* and in addition to encouraging culture of the larvae, and has a programme of research into the best methods for safe release of pueruli and young juveniles into the wild. Field experiments with *P. argus* have clearly demonstrated that with appropriately designed artificial structures, recruitment to local populations can be increased (Butler & Herrnkind, 1997). Briones-Fourzan & Lozano-Alveraz (2001)

and Briones *et al.* (2007) clearly demonstrated that artificial habitats (casitas) used by fishers can increase the density, survival and persistence of juvenile *P. argus* in habitat-limited environments in Mexico (see also new developments described in Chapter 7).

10.8 Management and conservation

The funding for research, and, therefore, by implication, the sincerity with which authorities manage their *Panulirus* fisheries, is variable over the range of the species. There appear to be several regional localities where declining annual landings based on FAO by country statistics (FAO, 2011) would indicate that the fisheries might be severely depleted. Catches in Taiwan declined to about 1 t per year by 2002 (FAO, 2011). The overall reported catches, for some of the more commonly caught species of this genus (Table 10.2), show no sign of decline. However, it is unclear whether this is as a result of more effort being applied to make the catches.

A lack of effort or TAC controls beyond relatively basic restrictions preventing the retention of berried animals or those below a minimum size is quite widespread, even in some of the larger *Panulirus* fisheries (Table 10.1). Despite resilience of lobsters to intense fishing pressure, such weak management controls threaten to inevitably result in stock collapses. Fortunately, the wide distributional range of most species in this genus, combined with their long and complex offshore larval phase, does provide an element of robustness to the

likelihood of any species being fished beyond the possibility of recovery.

In recent times there has been intense interest in the use of MPAs in managing fish populations (Pauly *et al.*, 2002; Roberts *et al.*, 2001; Hilborn *et al.*, 2004). Research into the response by rock lobster populations to MPAs has been a focus of attention, particularly in the *J. edwardsii* fishery in New Zealand (Kelly, 2000; Davidson *et al.*, 2002), but also in the *P. argus* fishery in Florida (Bertelsen & Cox, 2001; Lipcius *et al.*, 2001; Acosta, 2002). It may be that this form of easily applied management restriction will be the solution to maintaining and restoring lobster populations in countries where effective input and output controls are too complex and/or expensive to manage and enforce.

10.9 Conclusions

Managing fisheries sustainability is a dynamic process. While some future questions in each lobster fishery have been identified here, it is inevitable that unforeseen issues will arise. The challenge for fisheries researchers, managers, and industry, is to have the foresight to identify these potential problems and to have the continued means and ability to address them.

Change is inevitable, but not necessarily recognized as occurring. The global markets for lobsters have changed significantly, even in the last 10

years. In Plate 10.3 we have illustrated to changes in sales of live and cooked/frozen rock lobsters over the last 10 years. Each country has its own special needs and requirements for lobster colour, size, form of delivery, price acceptability, etc., so these changes are much more than mere localities for delivery. These changes are brought about by many things such as, changes in affluence, availability of product, changes in community acceptance of product styles, economic downturns or upturns, natural disasters (e.g. the 2011 tsunami) and other phenomena such as the SARS virus. These types of changes also affect the needs for research by way of maintenance of supply, size of animals, and form of product sold.

Over the last 15–20 years we have seen an increasing call for sustainable management of fisheries. Initially this was essentially management of the stock(s) of the fishery, and gradually the ecology of these resources. This has included economic and social aspects of the fisheries but in most cases without real objectives, collection of valid data or performance measures. This is changing and lobster fisheries are increasingly finding that all of these aspects are now required for successful management in a modern world. This is now expanding to ecosystem management (see Chapter 1). There are new calls for multiple-species models, and a complete raft of additional information, not just on the target species, is required as input to these models to make them operational.

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Chapter 11

Palinurus Species

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Abstract

Spiny lobsters belonging to the genus *Palinurus* have been fished for centuries in the Mediterranean Sea and the northeast Atlantic Ocean between Norway and the Cape Verde Islands, and for at least the past 50 years in the southwest Indian Ocean, off South Africa, Mozambique, and on the submerged seamounts along the South West Indian Ridge. Six extant species are known to science, two from relatively shallow shelf-waters (<200 m; *Palinurus elephas* and *P. gilchristi*), two from deeper continental shelf and slope habitats (200–600 m; *P. delagoae* and *P. mauritanicus*), and two from geographically isolated islands and submerged seamounts and ridges (*P. barbareae* and *P. charlestoni*). The previous edition of this Chapter reviewed historical research and fisheries information up to 2005 – subsequent research on this genus accelerated to produce upwards of 40 peer-reviewed articles between 2005 and 2011. These recent studies focused on three broad topics: molecular analyses to evaluate gene flow and population genetic structure; marine protected areas (MPAs) to enhance heavily fished lobster populations and create spillover onto nearby fishing grounds; and the influence of oceanic processes on larval dispersal, their settlement on the seafloor and juvenile ecology. Alternative gene flow patterns in different *Palinurus* spp. suggest wide dispersal of pelagic larvae by ocean currents, but also that hydrographical barriers in the open ocean can give rise to genetically structured populations. The identification of separate stock management units, together with the positive responses of *P. elephas* to protection in MPAs and of *P. gilchristi* to reduced fishing effort, provide important milestones towards developing sustainable management strategies for these high-value, and often over-exploited spiny lobster stocks.

Key Words: *Palinurus*; gene flow; larval dispersal; marine protected areas; spillover; larval settlement; fisheries management; harvest of wild populations; protection; enhancement; ocean processes; seamounts

11.1 Introduction

More than 50 years of published information on the distribution, life history and fisheries of *Palinurus* lobsters was reviewed in a previous edition of this book (Groeneveld *et al.*, 2006a) and by Goñi & Latrouite (2005). These two timely reviews preceded a boom period in scientific research on *Palinurus* lobsters, with upwards of 40 scientific articles being published between 2005 and 2011. These recent studies have focused on three broad topics: molecular analyses to evaluate gene flow and population genetic structure; marine protected areas (MPAs) to enhance heavily fished lobster populations and create spillover onto nearby fishing grounds; and the influence of oceanic processes on larval dispersal, their settlement on the seafloor and juvenile ecology. This chapter expands the information base provided in the previous two reviews by including the many new findings accumulating after 2005.

11.2 Species and distribution

11.2.1 Present-day distributions

Six extant *Palinurus* species are now recognized, consisting of three species in the northeastern Atlantic and Mediterranean Sea (*P. elephas*, *P. mauritanicus* and *P. charlestoni*) and three in the southwestern Indian Ocean (*P. gilchristi*, *P. delagoae* and *P. barbatae*). The existence of these six taxa is supported by morphology and by an analysis of the mitochondrial DNA 16S and COI regions, which show sequence divergences of 3–8% between the recognized species (Groeneveld *et al.*, 2007).

The new addition to the genus is *Palinurus barbatae* (Groeneveld *et al.*, 2006b), which was described from specimens captured by a fishing vessel on a seamount at Walters Shoals, Madagascar Ridge (33°9'–16'S 44°49'–56'E; Fig. 11.1). Morphology and mitochondrial (mt)DNA analyses placed *P. barbatae* closest to *P. delagoae*, which is found in deep-shelf waters off eastern South Africa and Mozambique. No female gene flow could be detected between these two taxa, and they were separated by at least 27 mutational steps, translat-

ing to a mtDNA divergence of 5% (Gopal *et al.*, 2006).

Palinurus barbatae was first thought to be restricted to Walters Shoals, but trapping surveys in 2010 and 2011 found specimens on seamounts of the Southwest Indian Ridge, as far east as 55°E (Johan C. Groeneveld, *et al.*, 2012). Spiny lobsters reported from the deep-water ridges of the southwest Indian Ocean by Soviet and Ukrainian vessels during the late 20th century (Romanov, 2003) were therefore most likely *P. barbatae*, which now appears to be widespread on southwest Indian Ocean seamounts. These seamount populations are separated from each other by deep intervening waters, and are connected by drifting larvae only.

The distributions of the other five *Palinurus* species were summarized by Groeneveld *et al.* (2006a). *Palinurus gilchristi* is endemic to the south coast of South Africa, where it occurs in moderately deep water (50–200 m), extending up to 250 km offshore on the Agulhas Bank (Fig. 11.1). *Palinurus delagoae* is a deeper-water species (150–600 m) occurring between 17°S in central Mozambique and 32°S in eastern South Africa. *Palinurus elephas* inhabits shallow waters extending to 200 m deep in the western Mediterranean (as far eastwards as Croatia and Crete) and is widespread in the northeast Atlantic Ocean, including the occidental coast of North Africa, Madeira, the Canary Islands and the Azores, and as far north as the Hebrides and southern Norway (Fig. 11.2). The distribution of *P. mauritanicus* often overlaps with that of *P. elephas*, but generally they occur deeper (40–600 m), and are distributed in the Eastern Atlantic from western Ireland (53°N) to southern Senegal (14°N) and in all the western Mediterranean from Gibraltar to Sicily, west of 16°E (Fig. 11.3). *Palinurus charlestoni* is endemic to the Cape Verde Islands (14–17°N), roughly 600 km from the West African coast, where it occurs at depths of 50–400 m (Fig. 11.3).

11.2.2 Effects of climate change on past distribution patterns

Recent population expansions have been shown for several *Palinurus* species, and these expansions appear to be relatively consistent with climatic and

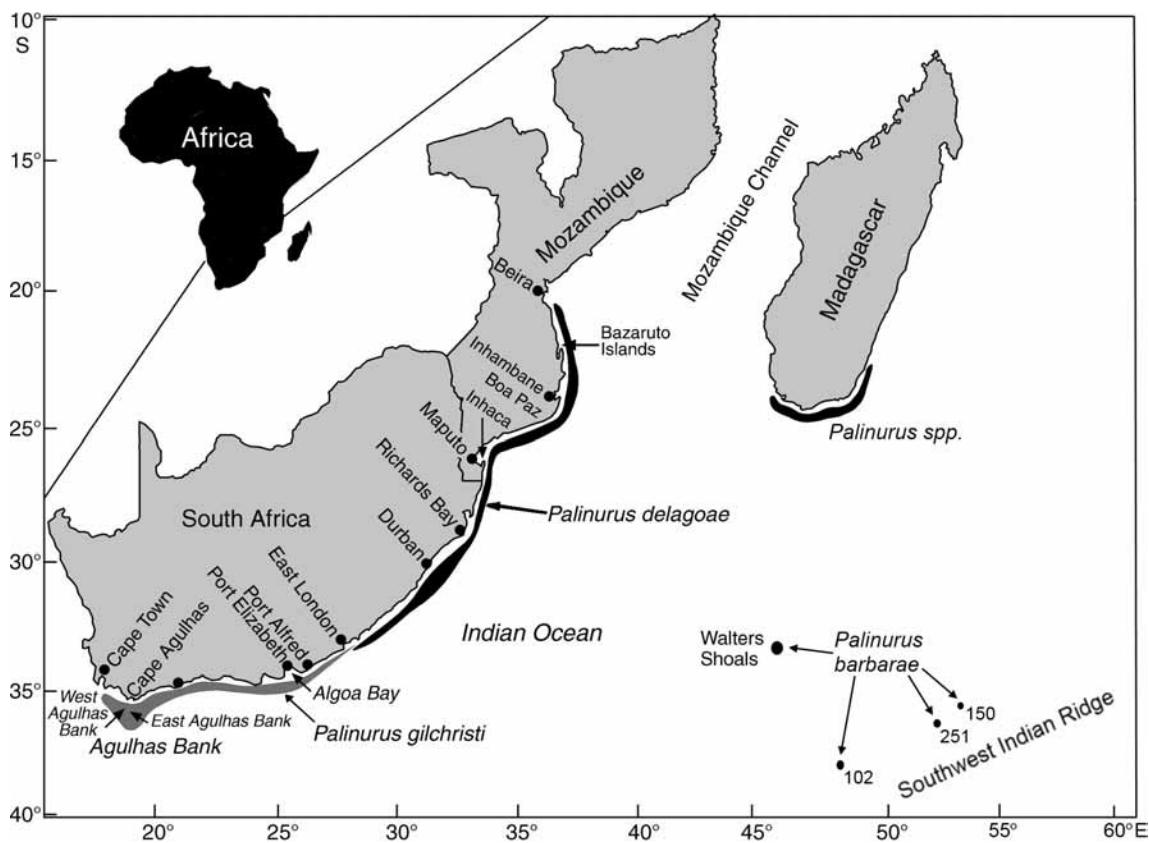


Fig. 11.1 Distribution of the southwest Indian Ocean spiny lobster species, *Palinurus gilchristi* and *Palinurus delagoae* along the offshore continental shelves of South Africa and Mozambique and of *Palinurus*. *barbareae* at Walters Shoals (Madagascar Ridge) and the seamounts of the Southwest Indian Ridge. Numbered seamounts are as in Romanov (2003). The *Palinurus* species from the south coast of Madagascar has not yet been identified.

sea-level changes wrought by late Pleistocene events, particularly the impacts of glacial and interglacial intervals. Estimates for *P. gilchristi* population expansions are as recent as 5300–10,600 years ago (Tolley *et al.*, 2005), and may be explained by the inundation of the Agulhas Bank (average depth <200 m) when sea levels increased by >150 m after the retreat of the last glacial maximum (LGM). Present-day *P. gilchristi* occupies rocky habitats on large parts of the Agulhas Bank. *Palinurus delagoae* population expansions were estimated at 9000–40,000 years ago, depending on mutation rate assumed, and Gopal *et al.* (2006) similarly suggested a habitat expansion following on the LGM.

Palinurus elephas population expansions were estimated at 26,100–42,900 years ago in the Atlan-

tic, and 32,200–52,900 in the Mediterranean (Babbucci *et al.*, 2010). Babbucci *et al.* (2010) suggested that ‘glacial–interglacial intervals repeatedly modified the extent of habitat availability in association with ice cover and coastline regression causing local extinctions, particularly in the Mediterranean Sea’. The recent glacial events appear to have had a smaller impact on *P. mauritanicus*, which occurs in deeper, cooler waters (Palero *et al.*, 2008). Using polymorphic microsatellite markers and depth distributions, Palero *et al.* (2010) found that the shallow water species *P. elephas* and *P. gilchristi* have larger historical effective population sizes than the deep water species, *P. mauritanicus*, *P. delagoae* and *P. barbareae*. The deep-water species are therefore more sensitive to overfishing, and

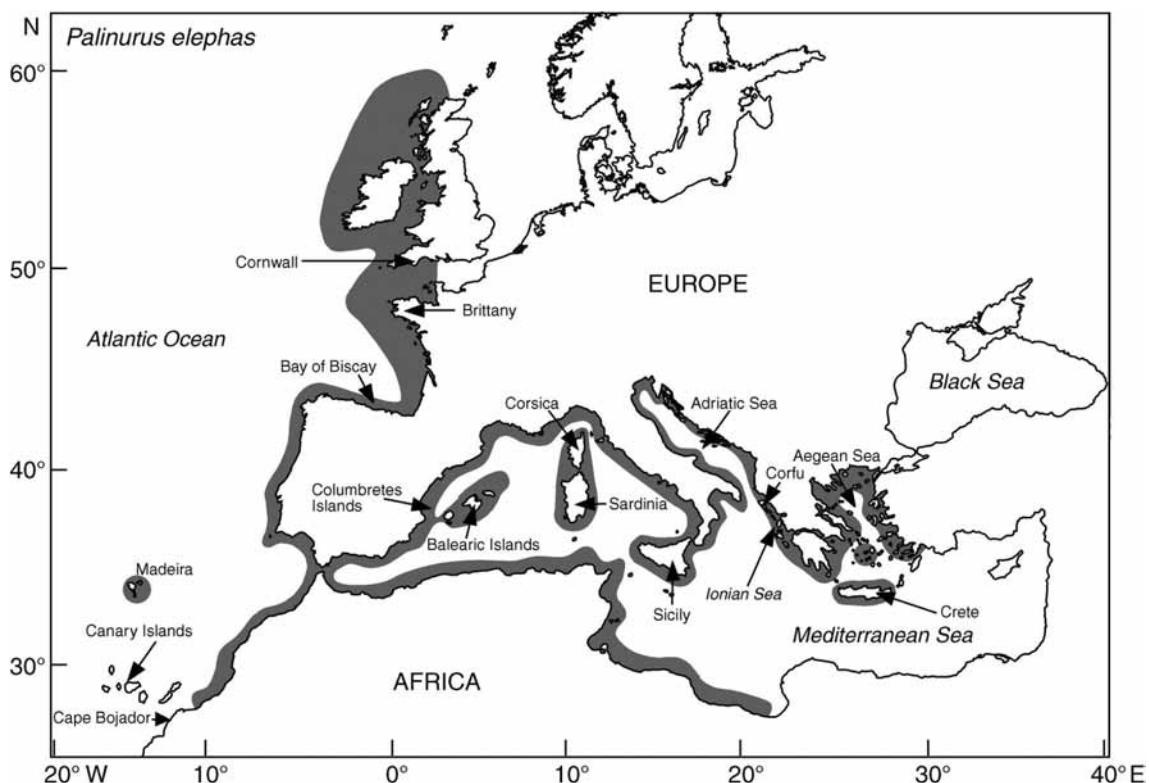


Fig. 11.2 Distribution of *Palinurus elephas* in the Western Mediterranean Sea and north-east Atlantic Ocean, including the occidental coast of North Africa, Canary Islands and the Azores (not on map).

overexploitation would have a larger effect on their long-term genetic diversity.

11.3 Biology and ecology

11.3.1 Reproductive biology

Various criteria have been used to estimate the carapace length (CL) at which female spiny lobsters reach maturity, including estimation of physiological maturity (development of ovigerous setae) and functional maturity (egg-bearing). Discrepancies between estimates in the literature are therefore often the result of the criteria used by different authors, as well as the sampling period, number and size range of the specimens (Chubb, 2000). Size at maturity is often age-specific instead of size-specific, so that differences may further be explained on the basis of geographical variation in growth

rates, which depend on food availability, population density, or water temperature (Goñi *et al.*, 2003a).

Female *P. gilchristi* achieves sexual maturity at a smaller size at Port Alfred (59–62 mm CL) than at Algoa Bay to Cape Agulhas (64–71 mm) (Groeneweld & Melville-Smith, 1994), and *P. delagoae* reach maturity at 67.3–71.2 mm CL off eastern South Africa (Groeneweld, 2000) and at 70 mm CL off Mozambique (Brinca & Palha de Sousa, 1983). Functional maturity of *P. elephas* is reached at 95 mm CL in Brittany (Latrouite & Noël, 1997; smallest berried female = 92 mm CL) and in Ireland females reach physiological maturity at 82 mm CL and males at 84.5 mm. Females of a protected population in the Western Mediterranean attained physiological and functional maturity simultaneously at a mean CL of 76–77 mm, while males were physiologically mature at 82.5 mm, but at the same age (Goñi *et al.*, 2003a). However, off

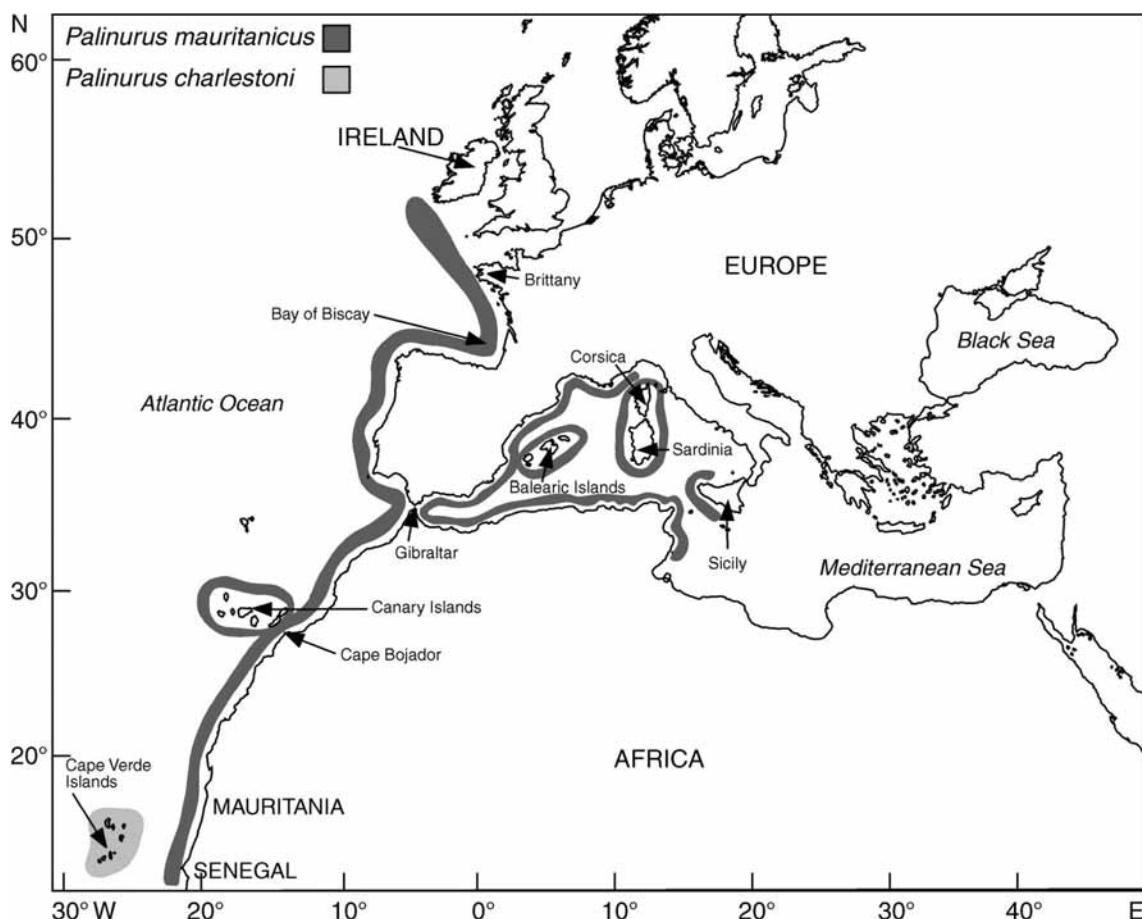


Fig. 11.3 Distribution of *Palinurus mauritanicus* in the Western Mediterranean Sea, north-east Atlantic Ocean, and occidental coast of North Africa. *P. charlestoni* (also shown) is endemic to the Cape Verde Islands.

Corsica, Marin (1987) observed a 1-year lag between female physiological maturity (achieved at 76–80 mm CL) and functional maturity (86 mm). Males reached maturity (testis weight/body size) at a mean CL of 76 mm. *Palinurus charlestoni* females begin to bear eggs at 90–100 mm CL, and the mean size of functional maturity is 110 mm (Carvalho & Latrouite, 1992). Despite these discrepancies, it is clear that the northern hemisphere *Palinurus* species achieve maturity at a larger size than their southern counterparts.

Mating and fertilization have been described for *P. elephas* (Mercer, 1973), *P. delagoae* (Berry, 1969) and *P. mauritanicus* (Maigret, 1978). After a courtship between two hard-shelled individuals, the male deposits two soft spermatophores of a

milky-white gelatinous texture on the surface of the last sternal plate of the female. Females with spermatophores are infrequently observed, and Hunter *et al.* (1996) showed that spermatophores are labile and disappear after a maximum of 10 days in *P. elephas*. Oviposition occurs soon after mating, and external fertilization is achieved when the female scratches open the spermatophore during egg extrusion, using the fifth pair of walking legs (Berry & Heydorn, 1970; Mercer, 1973).

At least 20% of *P. gilchristi* females caught in traps carry eggs throughout the year. However, the ovaries of the majority of females ripen in June with spawning taking place in July and August (Groeneveld & Rossouw, 1995). Egg-bearing percentages are highest between July and October

(60–85% of females), declining towards November. Egg incubation therefore takes 4–6 months to complete. More than 50% of *P. gilchristi* females >80 mm CL also bear eggs in March, suggesting that larger females may spawn twice per year, during autumn and spring.

The breeding period of *P. delagoae* is better defined with only one brood of eggs annually. Freshly spawned eggs first appear in September, eggs about to hatch first occur in April and hatched eggs are evident from May to July (Berry, 1973; Brinca & Palha de Sousa, 1983). Incubation of eggs takes about 5–6 months. The seasonal egg-bearing cycle can also be inferred from the ovarian cycle; most ovaries ripen in November to December, whereas 90% of females have inactive ovaries in April (Berry, 1973). No reproductive data are available for *P. barbareae* from Walters Shoals.

In the Western Mediterranean, egg-bearing in *P. elephas* may start as early as June and peaks in September (Gamulin, 1955; Campillo & Amadei, 1978; Marin, 1985; Goñi *et al.*, 2003a). In Greece, females with eggs have been observed from August to November (Moraitopoulou-Kassimati, 1973). Egg incubation lasts 4–5 months and hatching

occurs in December to February. In the Atlantic, mating occurs from June to October depending on the region and egg-bearing peaks in September to October (Vasconcellos (de), 1960; Gibson & O'Riordan, 1965; Mercer, 1973; Hunter *et al.*, 1996; Latrouite & Noël, 1997; Hunter, 1999). Egg-incubation lasts 6–10 months and hatching occurs in March to June.

Egg-bearing females of *P. mauritanicus* are found year round, although the main spawning season extends from August to January, roughly coinciding with breeding in *P. elephas*. Hatching of *P. mauritanicus* eggs in captivity may last 14 hours (Maignret, 1978). The breeding period of *P. charlestoni* starts in June, reaching a maximum in August to November. Hatching starts in November, peaks in December to January and ebbs in February. No egg-bearing females occur in March to May and incubation lasts for 4–5 months (Carvalho & Latrouite, 1992).

Fecundity (external eggs carried on the female abdomen) in two southern hemisphere *Palinurus* species and in *P. elephas* increases linearly with size (Fig. 11.4). *Palinurus gilchristi* appears to be the most fecund, followed by *P. delagoae* (Groeneveld

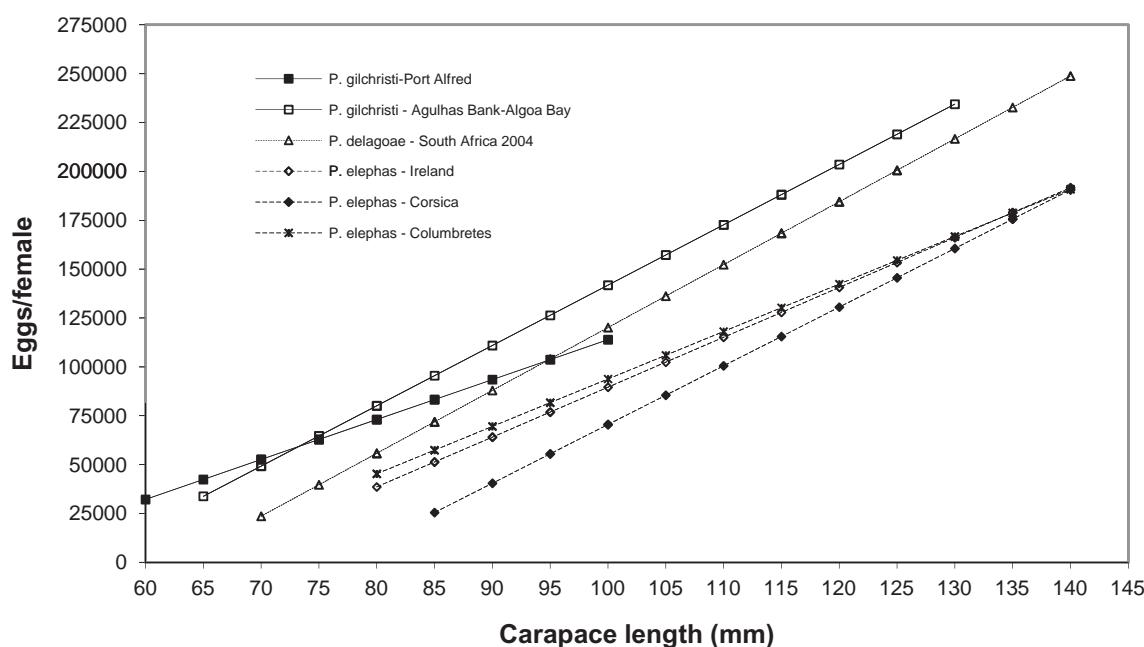


Fig. 11.4 Relationships between female fecundity and lobster size of *Palinurus gilchristi*, *P. delagoae* and *P. elephas*.

et al., 2005). These species are much more fecund than *P. elephas* (Goñi *et al.*, 2003a) where maximum relative fecundity (MRF: 119 eggs/g) in western Mediterranean populations is reached at intermediate sizes of 100–110 mm CL (Goñi *et al.*, 2003a). Fecundity of *P. elephas* near Ireland (Mercer, 1973) compares well with the western Mediterranean, where it is somewhat higher in a protected population at the Columbretes Islands (Goñi *et al.*, 2003a) than in an exploited population off Corsica (Campillo, 1982). The fecundity of *P. gilchristi* is lower at the eastern-most limit of its distribution (Port Alfred; size at MRF = 72 mm CL) than between Algoa Bay and Cape Agulhas (size at MRF = 77 mm CL) (Groeneveld, 2005). Few data are available for *P. mauritanicus* and *P. charlestoni*, and fecundity-size relationships are still unclear. Maigret (1978) estimated that *P. mauritanicus* females with a CL of 140–157 mm carry only about 60,000 eggs. Large *P. charlestoni* females of 140–180 mm CL may spawn between 120,000 and 350,000 eggs (Carvalho & Latrouite, 1992), which compares well with *P. elephas*.

Egg loss during incubation is estimated at 14–17% in *P. gilchristi* (Groeneveld, 2005), 10–16% in *P. delagoae* (Groeneveld *et al.*, 2005), 10% in Atlantic *P. elephas* (Mercer, 1973) and 26–28% in western Mediterranean populations of *P. elephas* (Marin, 1985; Goñi *et al.*, 2003a). The range of egg losses within the *Palinurus* genus therefore appears to be from 10% to 28%, over an incubation period of 4–10 months. Discrepancies between egg loss estimates may be explained on the basis of geographical variation (temperature) and specimens capture and handling methods.

Eggs hatch into leaf-like, transparent planktonic phyllosoma (Cunningham, 1892), which are adapted to a long offshore drifting life during which they are dispersed by ocean currents. *Palinurus elephas* larvae measure 2.9–3.9 mm total length (TL) at hatching (Williamson, 1983) and are larger than those of other species within the Palinuridae (Kittaka & Ikegami, 1988). Bouvier (1914) described 10 phyllosoma stages from natural plankton samples, and Kittaka *et al.* (2001) provides a full description of six phyllosoma stages (from hatching to puerulus) identified under culture conditions. Although the duration of the pelagic larval

life of *P. elephas* in the wild is estimated from 5–6 and up to 10–12 months depending on the region, the larval cycle is much shorter under culture conditions, ranging from 65 days (6 instars) to 149 days (nine instars), depending on temperature and food type (Kittaka & Ikegami, 1988; Kittaka *et al.*, 2001).

A single *P. mauritanicus* Stage I phyllosoma of 2.9 mm TL was found by Maigret (1978) in December off Mauritania. The absence of larvae in the plankton in January to April, soon after hatching, suggests that phyllosoma are then offshore from the continental shelf. More recently, Palero & Abelló (2007) described the first Stage I phyllosoma larvae of *P. mauritanicus* using a scanning electron microscope. The larvae came from gravid females captured off Morocco, and hatched in captivity in April. The total phyllosoma length (TL) was 2.9 mm (CL = 1.7 mm). Berry (1974) described several phyllosoma stages of *P. delagoae* hatched out in captivity. The size of the larvae increased as follows: Stage I, TL = 3.3 mm and CL = 2 mm; Stage III, 3.8 mm and 2.5 mm; Stage IV, 6.4 mm and 4.4 mm; and Stage VI, 9.2 mm and 6.1 mm, respectively. Larvae of *P. gilchristi* and *P. delagoae* are pelagic for at least 4 months (Pollock, 1995).

The final phyllosoma stage metamorphoses into a free-swimming puerulus, which settles on the substratum. After settlement, the puerulus moults into the first benthic juvenile stage (post-puerulus), which resembles adult lobsters. Guerao *et al.* (2006) provided the first detailed morphological description of a *P. mauritanicus* puerulus. It was transparent and had morphological characters that confirmed its role as a transitional phase: i.e. well-developed pleopods for swimming with internal appendices bearing coupling hooks to allow for settling in benthic habitats.

11.3.2 Larval dispersal patterns and recruitment of pueruli

Most of the known populations of *Palinurus* lobsters occur in regions dominated by strong ocean currents or in the paths of large ocean gyres (Table 11.1). These currents may play a major role in the dispersal of their phyllosoma, and therefore also on

Table 11.1 Habitats and life history traits of the *Palinurus* species inhabiting the NE Atlantic, Mediterranean Sea and the SW Indian Ocean. Numbers in parenthesis refer to references shown below.

Species	Ocean currents and water quality	Depth/substrate/temperature	Larval ecology and settlement	Juvenile and adult ecology
<i>P. elephas</i> (Fabricius, 1787)	Gulf Stream in Atlantic & oligotrophic Mediterranean water (1) Clear shelf waters	Shore to 200 m depth on rocky, coralline substrate with micro-caves, 12–16°C (2, 3)	Fecundity low, eggs hatch inshore (15) Early larvae large (2–3 mm TL), located inshore and in surface waters to 36 m (15) Late larvae offshore in eddies, currents (15) Larval life short in culture (min. 65 days), longer in nature (8) Pueruli settle in sheltered habitats between 10 and 90 m when SST rises (9)	Continued juvenile movement to find optimal shelter (14) Ontogenetic shallow to deep juvenile migrations (2) Pre-reproductive spring inshore & post-reproductive autumn offshore movements, dist. <5 km (2) Moults in spring-summer (2) Attains larger sizes in Atlantic than Mediterranean Longevity = +25 y (14)
<i>P. mauritanicus</i> Gruvel, 1911	Portugal Current and deeper Mediterranean waters (1) Turbid subsurface waters	180–600 m depth at shelf-edge canyons, and muddy, coraline substrata near rocky outcrops (1, 2)	Fecundity low, early larvae large (2.9 mm TL) (10) Phyllosomas move offshore, and may develop near bottom (10)	Sex and size composition vary with depth, season (10) Females undergo reproductive migrations (10) N to S size increase in CL suggests N-wards larval drift, settlement in a nursery, return migrations (10) Moults in Sep-Dec; CL [∞] = 203 mm and lives for 21 y (10) Seasonal movements between depth strata (4) Max CL = 270 mm
<i>P. charlestoni</i> Forest & Postel 1964	Canary Current and clear, back eddy flow around islands (1)	100–400 m depth; Steep, rocky grounds, 13–14°C (4)	No data	

continued

Table 11.1 continued

Species	Ocean currents and water quality	Depth/substrate/temperature	Larval ecology and settlement	Juvenile and adult ecology
<i>P. delagoae</i> Barnard, 1926	Eddies in Mozambique Channel and Agulhas Current upper reaches	<i>var. delagoae</i> and <i>natalensis</i> at 150–600 m depth, rock, muddy substrata, high organic content, coral fragm. 12–14°C (5, 6)	Eggs large, fecundity > than in <i>P. elephas</i> (3); Larvae pelagic for 4 mo and pueruli settle >600 m depth (6)	Size increase from 450 to 150 m depth suggests inshore ontogenetic migrations (12) Females with eggs aggregate in shallow water in summer (3) Juvenile counter-current migrations to redress downstream larval displacement (13)
<i>P. gilchristi</i> Stebbing, 1900	Aguilhas Current (1); Clear cold subsurface waters	50–200m depth, rocky substrata, 9–11°C (3)	Eggs large, fecundity > than in <i>P. elephas</i> (3) Phyllosoma drift downstream in eddies inshore of Agulhas Current (11)	Moults in Aug–Jan (6) Max CL = 180mm; lives for >30y Size gradient along migration route from nursery to adult habitat (3, 11) Long-distance juvenile counter-current migrations to redress down-stream transport of larvae (11)
<i>P. barbareae</i> Groeneveld <i>et al.</i> , 2006b	Eddy formed by retroflection of E. Madagascar Current; eddies around seamounts	>100 m on seamounts of the Madagascar Ridge and SW Indian Ridge (7)	No data	Moults in Oct-Dec (3) Max CL = 140mm & lives for >30y Max CL = 186 mm (7)

References: (1) Holthuis 1991 (2) Goní & Latrouite 2005 (3) Groeneveld *et al.*, 2006a (4) Carvalho & Latrouite 1992 (5) Berry & Plante 1973 (6) Berry 1973 (7) Groeneveld *et al.*, 2006b (8) Kittaka *et al.*, 2001 (9) Díaz *et al.*, 2001 (10) Maigret 1978 (11) Groeneveld & Branch 2002 (12) Cockcroft *et al.*, 1995 (13) Cockcroft & Branch 2002 (14) Diaz 2010 (15) Mercer 1973.

the distribution and abundance of the extant populations. However, phyllosoma are very infrequently caught, and larval dispersal patterns are therefore mostly inferred from spatial and temporal patterns of puerulus settlement, and from population genetic structure.

Díaz (2010) showed that post-larval densities of *P. elephas* were higher to the north of Majorca Island than to the south, and that this pattern was consistent with the prevailing currents and likely larval supply routes around the Balearic Islands (Fig. 11.5). The Algerian current (poor in larvae)

that brings Atlantic waters through the Straits of Gibraltar influences the south of the island, while the northern shores are bathed by the Northern Balearic Current – the latter accumulates larvae and presumably connects northern Majorca lobster populations with productive lobster grounds to the north and east of the Mediterranean basin. It is important to note that optimal habitats for *P. elephas* settlement stages (holes bored into the limestone by date mussel *Lithophaga lithophaga*; Díaz *et al.*, 2001) and adult lobsters (coralligenous substrates at 50–100 m depth; Goñi & Latrouite, 2005) abound

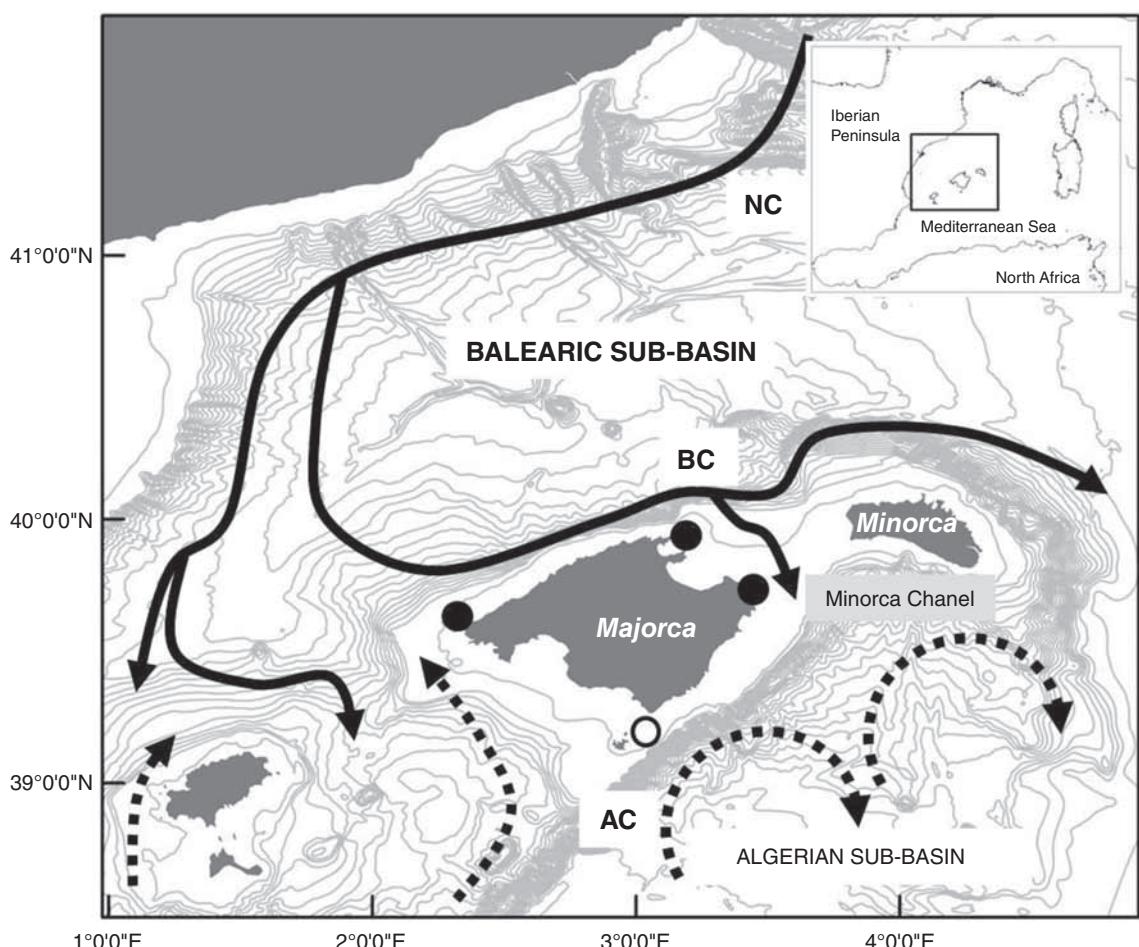


Fig. 11.5 Balearic archipelago showing bathymetry, Northern Current (NC) and Balearic Current (BC) in solid lines and the Algerian Current (AC) in dashed lines. Long-term underwater visual sampling sites for *Palinurus elephas* post-larvae and early juveniles are shown as solid dots (higher recruitment) and open dots (lower recruitment). Produced with permission from Diaz *et al.*, 2010.

throughout the Balearic Islands – thus habitat limitations cannot explain the relative absence of spiny lobsters in the south of the island.

Recent observations of the distribution of *P. elephas* post-pueruli suggest that settlement may occur over a wider bathymetric range and broader range of substrates than previously thought (Abelló *et al.*, 2008). Post-pueruli have been observed at 73 m depth (Díaz, pers. obs.) and appear regularly in commercial lobster fishing nets at similar deep waters (S. Mallol, pers. obs.) and also on artificial collectors placed on sandy bottoms (Díaz *et al.*, 2004). Furthermore, Díaz 2010 observed few movements of early benthic stages, thus casting some doubt on earlier theories of ontogenetic movements from shallow- (settlement habitat) to deep waters (adult habitat) (Table 11.1). Pueruli and post-pueruli of *P. mauritanicus* have been found in trawls between 78 and 329 m (Guerao *et al.*, 2006) and at 400 m depth (Maigret, 1978) and Groeneveld (2002) speculated that *P. delagoae* pueruli settle at depths of 100–600 m.

Several recent studies have used population genetic analyses to infer metapopulation structure and likely larval dispersal pathways for *P. elephas* (Palero *et al.*, 2008; Babbucci *et al.*, 2010), *P. delagoae* (Gopal *et al.*, 2006) and *P. gilchristi* (Tolley *et al.*, 2005), respectively. Markers for mtDNA (*COI* and control region genes) and polymorphic microsatellite loci (see Palero & Pascual, 2008) revealed two genetically separated groups of *P. elephas*, from the Atlantic and Mediterranean basins respectively, and the observed pattern can be explained by limited gene flow (or larval dispersal) between the two water bodies without complete lineage sorting (Babbucci *et al.*, 2010). Genetic structure within each of the two basins was also shown, with differentiation between Brittany and Scotland/Ireland populations in the Atlantic (Palero *et al.*, 2008), and between eastern (Cyclades) and western Mediterranean populations (Babbucci *et al.*, 2010). Palero *et al.* (2008) attributed the differentiation between the Brittany and Scotland/Ireland populations to the large effect of the Gulf Stream on larval dispersal and gene flow patterns. The limited exchange between the eastern and western Mediterranean populations is similar to several other marine species, such as European

clawed lobster *Homarus gammarus* (Triantafyllidis *et al.*, 2005), and compatible with an ‘isolation by distance’ model (Babbucci *et al.*, 2010).

mtDNA variation in *P. delagoae* in the southwestern Indian Ocean showed a shallow genetic partitioning between populations off southern Mozambique and those off eastern South Africa (Gopal *et al.*, 2006). This partitioning supports earlier morphological studies that suggested the occurrence of two populations along the southeast African coast, i.e. var. *natalensis* from South Africa and var. *delagoae* from Mozambique (Berry & Plante, 1973). The boundary between the two populations is consistent with the interface between the Mozambique Channel eddies and the upper Agulhas Current. Although some larvae doubtlessly disperse across this interface, others will be retained in the slow-moving anti-cyclonic eddies moving southwards along the Mozambique shelf-edge (see Fig. 11.1). Larval retention in these eddies through a combination of life-history attributes and behaviour will eventually give rise to shallow genetic partitioning between the two populations (Gopal *et al.*, 2006).

Palinurus gilchristi populations along the south coast of South Africa were found to be panmictic, based on an analysis of hypervariable mtDNA control region (Tolley *et al.*, 2005). The species is distributed below the strong southwesterly flowing Agulhas Current, leading to the expectation of unobstructed gene flow during the larval stage, when phyllosomas are presumably carried downstream by the Current. Puerulus settlement hotspots close to the downstream (westernmost) extreme of its range have been inferred from the preponderance of small juveniles near Cape Agulhas (Fig. 11.1; Groeneveld & Branch, 2002) – such juveniles (CL <55 mm) are scarce on traditional fishing grounds further upstream where adults occur (Pollock & Augustyn, 1982).

11.3.3 Moulting and growth

Moult ing and growth of *P. elephas* in the Western Mediterranean have now been determined over its entire size range, from data collected during an underwater visual census (all sizes from settlers to adults; Díaz, 2010) and from long-term tag-

recapture data (Goñi *et al.*, 2010). Juveniles moulted 8–12 times during the first year after settlement, each time growing by approximately 2 mm CL. Size increased from 7.5 to 8.0 mm CL at settling to 35 mm in the first year, and to 50 mm in the second year. The slower growth in the following years is as a result of fewer moults taking place, rather than a decrease in moult increments.

Earlier studies also showed that moult frequency is related to size, with juvenile *P. elephas* moulting two to five times per year (Corral, 1968; Marin, 1987; Cuccu *et al.*, 1999), and that after maturity moult frequency decreased faster in females than in males (Cuccu *et al.*, 1999; Follesa *et al.*, 2003). In the Mediterranean mature females moult one or two times per year, mainly in April to May (Marin, 1987), and possibly also in winter after hatching (Cuccu *et al.*, 1999; Goñi, unpublished data). In the Atlantic mature females appear to moult once per year, in June to August prior to mating (Mercer, 1973; Latrouite & Noël, 1997). Mature males off Ireland follow the same pattern, but with a more extended moulting season. Off the Columbretes Islands (Western Mediterranean) males were seen moulting *en masse* in February, and data from captive males show another moulting peak in the fall (Goñi, unpublished data).

Tagged male *P. elephas* in Corsica grew faster than females, with respective von Bertalanffy (VB) growth parameters of $CL_{\infty} = 166$ mm, $K = 0.151$ year $^{-1}$, $t_0 = -0.348$ y for males and $CL_{\infty} = 136$ mm, $K = 0.189$ year $^{-1}$, $t_0 = -0.342$ y for females (Marin, 1987). In a more recent tag–recapture study, Follesa *et al.* (2007a) proposed VB growth parameters of $CL_{\infty} = 167.9 \pm 54.5$ mm (SE), $K = 0.13 \pm 0.08$ year $^{-1}$, $t_0 = -0.399$ y for males and $CL_{\infty} = 120.2 \pm 11.51$ mm, $K = 0.21 \pm 0.05$ year $^{-1}$, $t_0 = -0.349$ y for females.

Palinurus elephas was previously believed to attain a larger maximum size in the Atlantic (200 and 170 mm CL for males and females off Brittany; Latrouite & Noël, 1997) than in the northwestern Mediterranean (175 and 160 mm CL respectively off Corsica; Campillo & Amadei, 1978; Table 11.1). In the Western Mediterranean larger lobsters (186 and 171.5 mm CL for males and females, respectively) are nowadays encountered in the Columbretes Marine Reserve after 20 years of pro-

tection (Goñi *et al.*, 2010). However, lobsters caught in the fishery off Tunisia in 2001 were as large or larger (180 mm and 200 mm CL for females and males, respectively; Quetglas *et al.*, 2004) than those reported in the Atlantic by Latrouite & Noël (1997). Estimates of maximum size should therefore be compared with caution, as they may depend on the level and pattern of exploitation, and may also be influenced by sample size, sampling method, habitat, season and depth.

Adult *P. mauritanicus* from Mauritania moult once per year between September and December (Maignret, 1978). Moult increments from a few tagged males of initial size 250–270 mm TL, were 30–40 mm TL. Using Maignret's data, Boitard (1981) proposed Von Bertalanffy growth parameters of $CL_{\infty} = 202.8$ mm, $K = 0.169$, $t_0 = -0.227$ for females. No data are available on the moult season or increment of *P. charlestoni* in nature, but moulting in commercial tanks has been observed in February and March.

Palinurus gilchristi exhibits a clear size-dependent moulting season during summer when the water temperature at 100 m depth is cooler than during winter because of an intense seasonal thermocline (Groeneveld & Branch, 2001). Setagenic development of the pleopods divide the moulting cycle into seven discrete moulting stages and sub-stages showing that the proportions of premoult lobsters in catches peak in September (25%), October (35%) and November (22%) (Groeneveld & Branch, 2001). Tagging data confirm the summer moult season, with an increase in proportions of small post-moult lobsters in catches in October (43%), November (60%) and December (98%), and in larger (>70 mm CL) post-moult lobsters in December (61%). *P. delagoae* adults off South Africa and Mozambique moult once per year, respectively in August to October (Berry, 1973) and August to January (Brinca & Palha de Sousa, 1983). A minor peak in April is probably a continuation of moulting of sub-adults, which moult more often.

Tagging data show that adult *P. gilchristi* and *P. delagoae* grow slowly, that annual growth increments decrease with increasing CL and that females grow progressively slower than males after reaching sexual maturity (Groeneveld, 1997; 2000).

Moult increments of *P. gilchristi* are smaller at Port Alfred than Algoa Bay to Cape Agulhas, and maximum observed CLs are also less at Port Alfred (110 mm versus 130 mm). The theoretical maximum lengths (CL_∞) of the Von Bertalanffy growth function grossly underestimate these values, but growth coefficients (*K*) are smaller at Port Alfred than elsewhere. In *P. delagoae*, the observed maximum CL is 180 mm, compared with length-based Powell-Wetherall estimates of 160–163 mm CL. The low value of *K* reflects slow growth towards CL_∞, which is consistent with a slow-growing and long-lived life strategy. The maximum observed CL of *P. barbareae* is 186 mm CL for males and 159 mm for females (Groeneveld *et al.*, 2006b).

Using a wide size range of specimens from a long-term protected population (8–170 mm CL), Díaz (2010) estimated that the largest *P. elephas* were approximately 25 years old, 10 years more than previously estimated in an exploited population of Corsica (Marin, 1987). *Palinurus mauritanicus* can attain 21 years (Maigret, 1978), and based on tagged individuals recaptured more than 13 years later, Groeneveld (unpublished) estimates that both *P. gilchristi* and *P. delagoae* may live for >30 years (Table 11.1).

11.3.4 Population structure, size composition and sex ratios

The CL of *P. gilchristi* caught in commercial traps range from 50 to 130 mm, but lobsters >125 mm are scarce. Long-term size composition differs markedly between sites, the mean CL increasing gradually from west to east (Groeneveld & Branch, 2002). Sex ratios vary with season, but generally there is parity or males outnumber females at most sites (Pollock & Augustyn, 1982; Groeneveld & Branch, 2002).

The CL of *P. delagoae* caught in trap and trawl fisheries range from 50 to 185 mm, with a marked absence of juveniles <50 mm. Off South Africa and Mozambique depth and latitude strongly influence size composition, with average CL increasing as depth decreases from 400 to 150 m (Cockcroft *et al.*, 1995; Palha de Sousa, 1998). The latitudinal trend shows a smaller average CL at the edge of the distribution range, south of Durban (see Fig.

11.1), and large variations in size composition in other areas (Cockcroft *et al.*, 1995). Trap fishing between 1994 and 1997 reduced the average CL in three areas off South Africa (Groeneveld & Cockcroft, 1997). Males dominate in length classes above 125 mm CL, and sex ratios of catches during the non-reproductive season (May to September) are fairly evenly spread across depth.

Information on the population structure of *P. elephas* originates from a variety of gear types, including traps/pots, diving, and trammel nets (Hepper, 1977), which together with the scattered nature of the data hamper temporal and spatial comparisons (Hunter *et al.*, 1996; Goñi & Latrouite, 2005). In general, Atlantic *P. elephas* attain larger modal and maximum sizes than in the Mediterranean, and at all fishing grounds reductions in size have been registered over the past four decades. Male *P. elephas* caught in trammel-nets off Scotland and Cornwall in 1965–75 had mean CLs of 145–160 mm compared with 122–134 mm for females (Hepper, 1977; Ansell & Robb, 1977). Later studies (Hunter *et al.*, 1996) showed a decline to 125.6 mm CL in Cornish male *P. elephas*, and concluded that it was caused by the replacement of pots by trammel-nets during the 1970s. Corsican *P. elephas* caught in trammel-nets in 1977 recorded modes of 95.6 mm and 103.7 mm CL (Campillo, 1982), but 8 years later it had declined to 75 mm for both sexes (Marin, 1987). Goñi *et al.* (2003b) showed that pots used in the western Mediterranean exclude and thus protect large *P. elephas* (mostly males) and suggests that trammel-nets removed this component during the late 1970s and early 1980s. Mean size of *P. elephas* of the Columbretes Islands marine reserve after 20 years of protection were 117 and 137 mm CL females and males, compared with 89 and 99 mm respectively in comparable fished populations; the difference in maximum sizes was even more marked with 126 mm CL for both females and males in fished areas compared with 172 and 187 mm respectively in the protected population (Goñi *et al.*, 2011).

Maigret (1978) used commercial data (1972–4) from Mauritania and recorded recruitment of *P. mauritanicus* at 73–82 mm CL, male modal sizes at 96 mm and 119 mm (max. 217 mm) and female modal size at 83 mm (max. 195 mm). Experimental

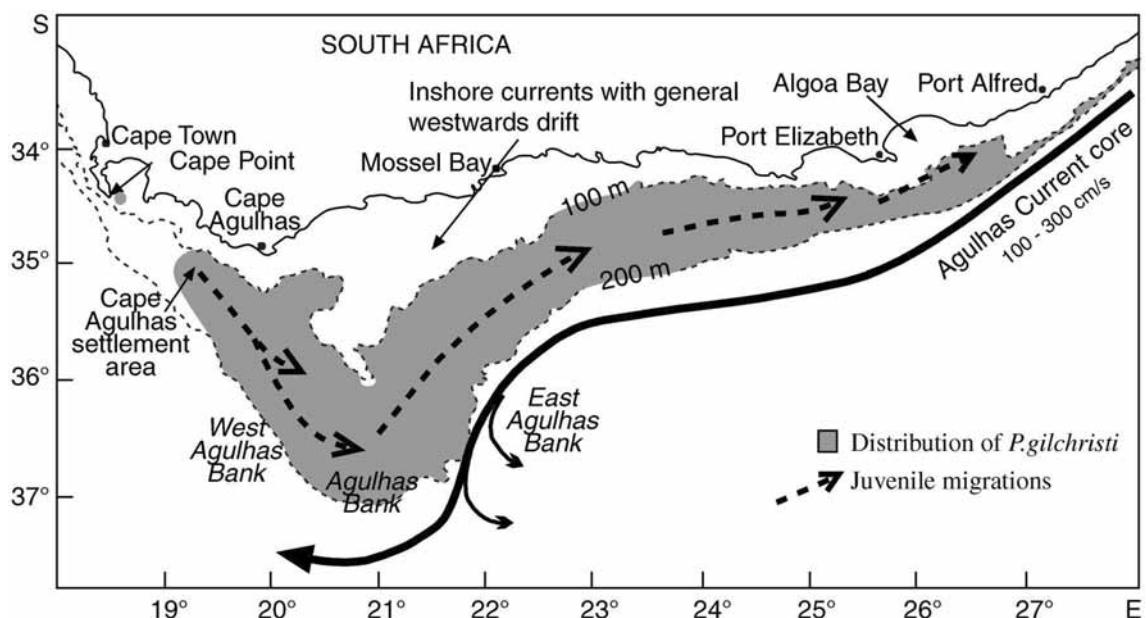


Fig. 11.6 Migration route of *Palinurus gilchristi* juveniles along the south coast of South Africa (Groeneveld & Branch 2002).

catches in 1975 indicated a size range of 77–198 mm CL (males) and 75–197 mm (females). Half of the catches from a sporadic trammel-net fishery in the Bay of Biscay in the 1990s comprise individuals >2 kg (CL >155 mm), with some males weighing up to 7 kg (Latrouite, unpublished data). Sex ratio and size appear to be depth dependent; males are more abundant at 150–250 m depth, whereas large females and juveniles predominate between 250 and 300 m.

The size of *P. charlestoni* caught in commercial traps ranges from 60 to 270 mm CL for males and 60 to 210 mm for females, but males over 220 mm and females over 170 mm represent <5% of landings. The size composition of females is unimodal around 130 mm CL while males exhibit a scattered distribution. Mean lobster weight at landing is around 1.25 kg. The size structure of catches appears not to have changed much over time (Taype de Carvalho, unpublished).

11.3.5 Migrations and movement

Long-term movement patterns of juvenile *P. gilchristi* and *P. delagoae*, against the southwesterly

flowing Agulhas Current, have been shown in tagging studies (Groeneveld, 2002; Groeneveld & Branch, 2002). Over 97% of tagged *P. gilchristi* juveniles at Cape Agulhas migrated >50 km, either southeastwards offshore to the outer reaches of the Agulhas Bank, a mean distance of 154 km, or eastwards alongshore up to Algoa Bay, a mean distance of 461 km (Fig. 11.6). The greatest straight-line distance recorded was 790 km, by a male lobster tagged at Cape Agulhas and recaptured at Algoa Bay. The fastest 5% of migrants moved at 0.43–0.78 km day⁻¹. In general, Cape Agulhas migrants reached the outer Agulhas Bank within 1–2 years, and Algoa Bay within 3 years. No return migrations were observed. The easternmost (upstream) population at Port Alfred is non-migratory and receives no immigrants from elsewhere. The Cape Agulhas area is now considered an important post-larval settlement area, from where juveniles migrate eastwards against the current to recruit to adult habitats.

Juvenile *P. delagoae* tagged near their southern range limit in eastern South Africa (see Fig. 11.1) migrated up to 495 km, northeastwards, alongshore and counter to the Agulhas Current between Durban

and southern Mozambique (Groeneveld, 2002). Some 48.3% of juvenile lobsters ($CL < 65$ mm) but only 2.1% of larger lobsters migrated >20 km, and the fastest 5% of migrants achieved 0.43 km day $^{-1}$. Both *P. gilchristi* and *P. delagoae* appear to have evolved long distance counter-current migrations as a retention mechanism to maintain populations off South Africa and Mozambique.

Apart from the long-shore migration by juveniles, *P. delagoae* exhibits two other migratory life-history strategies (Groeneveld, 2002). Size composition shows that juveniles inhabit deep, offshore waters (400–600 m) and gradually move shallower as they grow larger to recruit to the adult population at depths of 150–350 m (Berry, 1973; Cockcroft *et al.*, 1995). Egg-bearing females tend to concentrate in dense aggregations in shallower strata (150–275 m) in summer, and then move deeper (>300 m) in autumn and winter after their eggs have hatched (Koyama, 1971; Berry, 1972, 1973; Kondritskiy, 1976). These inshore juvenile and reproductive migrations occur over relatively short distances, because of the narrow continental shelf.

Palinurus elephas undertakes a pre-reproductive onshore migration during spring and a reverse post-reproductive offshore migration in late autumn (Mercer, 1973; Ansell & Robb, 1977; Goñi *et al.*, 2000, 2001b). Movements are also motivated by foraging and change of shelter. Tag–recapture studies from the Atlantic and Mediterranean indicate that distances moved by adults are generally 5–20 km after 1–8 years at large (Hepper, 1967, 1970; Marin, 1987; Goñi *et al.*, 2001b); however, there are two reports of movements of 50 and 70 km in the Mediterranean (Relini & Torchia, 1998; Cuccu *et al.*, 1999). Adult *P. elephas* move on average between 2 km and 3.2 km (Goñi *et al.*, 2000; Follesa *et al.*, 2007b), and larger individuals of both sexes tend to be more resident. Ultrasonic telemetry was used to estimate short-distance movements and residence time of *P. elephas* in a marine reserve near Sardinia; tagged individuals moved deeper than the release site over a short term, and shelter availability affected distances moved (Giacalone *et al.*, 2006).

Movements of *P. elephas* post-pueruli (8.5–16 mm CL) were documented by underwater visual

census (Díaz, 2010). The average home range was estimated as 7 m 2 and 89.5% of the individuals returned to the same hole after foraging at night. Acoustic tracking was used to approximate movements of larger juveniles (59–67 mm CL); nocturnal activity started <1 hour after sunset and ended >1 hour before sunrise; lobsters spent on average 20% of the night outside the shelter and movements continued through 80% of the night; and lobsters remained passive and sheltered during the day. Both post-pueruli and larger juveniles exhibited a capacity to orientate, and could find original or similar shelters upon returning from foraging forays over a home range of <20 hectares.

Palinurus mauritanicus migrates during several life-history stages. Off Mauritania, the mean size composition is smaller north of Cape Blanc (20°45'N) than in the south, suggesting a northern nursery area created by northward drift of larvae on bottom currents, followed by juvenile migrations southward (Maigret, 1978). Other migrations are linked to moulting and reproduction – large groups concentrate in autumn along canyon edges and then disperse over the shelf. Females undergo migrations in late autumn, linked to spawning in August to January.

Seasonal movements of *P. charlestoni* have been inferred from catch rates, which indicate that the bulk of the population occurs at 100–200 m depth in summer, compared to 150–250 m in winter (Carvalho & Latrouite, 1992).

11.3.6 Predators, defence and natural mortality

Natural mortality in *Palinurus* is primarily because of predation on larvae, during juvenile stages and during moulting. *Palinurus mauritanicus* post-pueruli are common in the stomachs of demersal fishes, including *Raja clavata*, *Mullus surmuletus*, *Scyliorhinus canicula*, *Helicolenus dactylopterus*, *Lepidorhombus boscii* and *Aspitrigla cuculus* (Valls *et al.*, 2011). *Palinurus gilchristi* is sometimes found in the stomachs of Cape fur seals (*Arctocephalus pusillus*) (Berry, 1971), and *Octopus magnificus* regularly enter traps and predate on captured lobsters (Groeneveld *et al.*, 2006c). Predators of *P. delagoae* include dogsharks *Dalatius licha*

and *Cephaloscyllium sufflans* (Berry, 1973). Both *Octopus vulgaris* and dusky grouper (*Epinephelus marginatus*) are known predators of *P. elephas* in the western Mediterranean (Quetglas *et al.*, 2001), and other fish predators of juveniles in the region are *Labrus* spp., *Scorpaena* spp., and *Serranus* spp. (Marin, 1987).

Palinurus elephas post-pueruli and small juveniles are asocial and shelter in empty date mussel holes and crevices along the shadow faces of rocks to minimize predation; on average, shelters are <1 m from the bottom to allow for easy access to the benthos (Díaz *et al.*, 2001; Díaz, 2010). Semi-circular and subvertical dens are preferred, and optimal shelter size is correlated to lobster size (Gristina *et al.*, 2009), and is also the most important parameter for increasing survival rates (Díaz *et al.*, 2005). Artificial collectors designed according to optimal shelter features were tested by Díaz *et al.* (2004).

Palinurus elephas defended itself against fish predators by pointing or trapping the attacker between the two antennae, where they could whip and lunge at the fish to scrape or scratch it (Barshaw *et al.*, 2003). In addition to ‘point and whip’, Buscaino *et al.* (2011) described an ‘alert’ phase, where a lobster points towards a predator with both antennae while raising its telson and stretching its legs. The lobster remains still, apart from flicking its antennules. Stridulation (sound emission) has been reported when lobsters are threatened by octopus or conger eel, the number of emissions increasing linearly with the number of predator attacks (Buscaino *et al.*, 2011).

Natural mortality (M) estimates for *P. delagoae* are 0.09–0.15 year⁻¹ (Groeneveld, 2000) and 0.1 year⁻¹ for *P. gilchristi* (Pollock & Melville-Smith, 1993). These low values reflect a long-lived, slow growing life strategy. Goñi *et al.* (2010) used a tagging model with a decade of tag–recapture data to estimate mean M of a population of *P. elephas* after 10–20 years of protection in an MPA, obtaining higher values for males (0.20 year⁻¹) than for females (0.16 year⁻¹). Bevacqua *et al.* (2010) used an explicit stochastic model to estimate M at 0.27 year⁻¹ for *P. elephas*, corresponding to an annual survival probability of 76% inside a MPA, and 50% in exploited areas. Loss of T-bar anchor tags

inserted dorso-laterally in *P. elephas* was estimated at 6% year⁻¹ for males and 4.4% year⁻¹ for females (González-Vicente *et al.*, 2009).

11.3.7 Diet

Palinurus elephas preys nocturnally on a variety of benthic organisms, including molluscs, echinoderms and crustaceans (Mercer, 1973; Goñi *et al.*, 2001a). Food preference appears to change according to prey abundance, and decapod crustaceans, ophiuroids or coralline algae are consumed when molluscs and echinoderms are scarce (Goñi *et al.*, 2001a). No cannibalism has been observed under natural conditions, but it has in captivity (Marin, 1987; S. Mallol, pers. obs.). *Palinurus mauritanicus* feeds primarily on fish carrion, molluscs (bivalves and gastropods), crustaceans, polychaetes and echinoderms (ophiuroids and echinoids) (Maigret, 1978). The gastric mills of *P. delagoae* contained 46% (by volume) cephalopod remains that could be matched to a single common, but unidentified cuttlefish (Berry, 1973). Teleost remains (33%) and crustaceans (6%; largely brachyuran exoskeletons) made up the remainder.

11.4 Molecular phylogeny and evolution

Over the past 6 years, much research effort has gone into developing molecular tools for testing hypotheses on speciation and population fragmentation in *Palinurus*. Mitochondrial markers (mainly for the *COI*, 16S rRNA, and the control region genes) and nuclear markers for microsatellites were developed by several laboratories in Europe and South Africa, and analysed to examine genetic variability at both the intra- and interspecific level.

Statistical reconstruction methods on 16S rRNA and *COI* sequences provided strong support for the monophyly of each of the *Palinurus* species (Groeneveld *et al.*, 2007). *Palinurus elephas* appears to be the ancestral species based on fossils and morphology, and was placed as the most basal taxon and used to root trees. The sequence divergence between the two most distantly related species, *P. elephas* in the Atlantic and *P. barbareae* in the

Indian Ocean, was 8.24%, whereas 3.32% separated the two closest relatives, *P. delagoae* and *P. barbareae*. Some of the nuclear coding gene sequences were unable to discriminate between all the species (Palero *et al.*, 2008).

Two alternative theories have been proposed for speciation of *Palinurus* lobsters in the northeast Atlantic/Mediterranean and the southwest Indian Ocean. Groeneveld *et al.* (2007) suggested a pre-Miocene allopatric divergence, with two main lineages (an Indian Ocean clade and an Atlantic clade) separating due to the closure of the marine gateway between the Mediterranean Sea and Indian Ocean after the northward collision of Africa with Eurasia (11.2–23 Mya). In this analysis, *P. charlestoni* from the Cape Verde islands appeared to group within the Indian Ocean clade, closest to *P. gilchristi* from southern South Africa, and this close relationship between the two species was also apparent from nuclear sequences (Cannas *et al.*, unpublished). It suggests that *P. charlestoni* may have diverged from the Indian Ocean clade, possibly after the closure of Tethyan seaway, and invaded the Atlantic from the south by rounding the Cape of Good Hope (South Africa). Based on short branch lengths of parsimony trees, it is also possible that incipient *P. charlestoni* originated during several speciation events that occurred contemporaneously around the time of the closure of the Tethyan seaway, thus remaining in the Atlantic/Mediterranean basin. The theory implies that the *Palinurus* mtDNA evolved no faster than 0.18–0.36% per lineage per million years, one of the slowest mtDNA mutation rates reported to date, and it is supported by the fossil record, which shows that *Palinurus* was present as early as the Cretaceous (100 Mya) and that it was widely distributed then, extending to Madagascar and East Africa, and to North America where it is now extinct (George & Main, 1967, Vega *et al.*, 2006).

Alternatively, Palero *et al.* (2009) suggested a rapid radiation of *Palinurus* spp, also based on short branch lengths shown by classic distance-based and approximate Bayesian computation (ABC) analysis. These authors contend that most *Palinurus* species originated in the past 2 million years (Pleistocene), and that speciation was driven by recent climate-change related oceanographic

processes (i.e. recent glaciation events). A north-to-south pattern of speciation was proposed, with all Indian Ocean species forming a monophyletic clade. Accordingly *P. elephas* and *P. mauritanicus* originated from a common ancestor approximately 2 Mya, *P. mauritanicus* and *P. charlestoni* split 1 Mya, southern Africa was colonized only 0.5 Mya, and *P. delagoae* and *P. barbareae* appeared about 0.2 and 0.1 Mya, respectively. Standard decapod mutation rates were assumed for the analysis.

11.5 Harvest of wild populations

11.5.1 *Palinurus elephas*

Palinurus elephas has been fished for centuries and reports of commercial activity exist at least since the 19th century (e.g. Von Salvador, 1895; Santucci, 1926). Traditionally it was captured by means of traps/pots and sometimes by diving (Hepper, 1977; Hunter *et al.*, 1996; Secci *et al.*, 1999; Goñi *et al.*, 2003a; Cristina & Gagliano, 2004) but a major change in the exploitation strategy occurred in the 1960s and 1970s with the progressive introduction of tangle- and trammel-nets that virtually replaced other fishing methods (Goñi & Latrouite, 2005) (Fig. 11.7). This change, along with the expansion of new gear materials and modern hauling and electronic equipment, increased effec-



Fig. 11.7 *Palinurus elephas* caught in a trammel-net. These nets gradually replaced pots as the gear of choice after the 1960s and 1970s.

tive fishing effort and marked the decline of *P. elephas* populations (Goñi *et al.*, 2003c).

Given its high unit value (e.g. sold fresh at first-sale prices of €40–120 per kg in the Mediterranean) and relative scarcity, *P. elephas* has been heavily harvested throughout its range and is generally considered to be overexploited, although long-term catch per unit effort data (CPUE) is not available for most fisheries (Ceccaldi & Latrouite, 1994, 2000). In the Atlantic, catch rate data from the Welsh fishery showed a decline of 92% between 1980 and 1997 (Hunter, 1999). A sevenfold decline in CPUE was also registered in the southwest Irish fishery between 1972 and 1999 (Tully, 2011). In the Mediterranean, lobster CPUE in the Corsican fishery declined by 25% between 1984 and 1999, associated with a 38% increase in effort (fewer boats but more nets fished) (Ruitort, 1999). In northwest Sardinia, CPUE declined by 70%, associated with a 60% increase in the number of boats between 1976 and 2001. In contrast, during the last decade, catch rates of two Spanish Mediterranean fisheries have remained stable, although at levels about eight times lower than in a population protected in a MPA (Goñi *et al.*, 2010).

Official landing statistics for 2009 sourced from the FAO Global Capture Production summary (<http://www.fao.org>) for the Atlantic fisheries for *P. elephas* and *P. mauritanicus* combined show dramatic declines from 900 t in 1966 to 56 t in 2009. For the Mediterranean, the two species are reported separately. Landings of *P. elephas* peaked in the 1960s and 1970s at near 1000 t, declined to 165 t in 2000, but increased to 404 t in 2009. Unfortunately, irregular reporting by most countries, and the mistaken inclusion of *P. mauritanicus* in some records, complicate the interpretation of the data. Also, in fisheries where *P. elephas* is sold locally (e.g. southern Europe and the Mediterranean) a potentially significant proportion of the catch may go unrecorded. A recent reconstruction of Corsican landings (1950–2008) suggested that 16 times more lobster were landed than are reflected in the data reported to the FAO (Harper & Zeller, 2011). Nevertheless, a decline from 300 t in 1954 to 80 t in 2008 was still apparent.

A recent assessment of the Balearic, Corsican and Sardinian fisheries (LANCONNECT project;

<http://www.ba.ieo.es/lanconnect/>) showed that fleets of 170–220 boats target *P. elephas* in each region with trammel nets during the 5–8-month fishing season. The estimated annual landings of each of these fisheries in 2009 ranged between 60 and 100 t, amounting to a total of 280–300 t, or 70% of the official FAO landings (404 t) for the entire Mediterranean in 2009. Tunisia has a reliable series of landing statistics because nearly all catches of *P. elephas* are exported for foreign consumption. Annual landings between 1990 and 2002 peaked at 74 t in 1993 and declined gradually to 33 t in 2002 (Quetglas *et al.*, 2004).

Irish lobster exports fluctuated from a high of 271 t in 1959 to current landings of around 20 t by 30 boats (Tully, 2011). French Atlantic fisheries landed up to 1000 t in the 1950s, but only 25 t in 2010 (Laurans *et al.*, 2011). Presently, *P. elephas* is considered to be a bycatch of some 100 finfish netting vessels. Portuguese stocks (mainly along the southwest coast) are also overfished with consistent declines in abundance, and present landings are down to 10% of those in the late 1980s and 1990s (Galhardo *et al.*, 2006). In combination, and despite under-reporting, the trends shown above reflect a drastic and real decline of lobster stocks in both the Atlantic and Mediterranean, primarily due to fishing mortality with nets, even if these nets do not always target spiny lobsters.

11.5.2 *Palinurus mauritanicus*

Commercial fishing for *P. mauritanicus* originated along northwest Africa when Spanish and Portuguese trawlers incidentally discovered stocks as shallow as 40 m depth. From 1955 onwards, a French fleet operated along the Mauritanian coast (see Fig. 11.3), expanding to >40 boats (length 25–38 m) in the 1960s, and using cylindrical baited traps and bottom trawls along the shelf edge at 150–300 m depth and occasionally down to 600 m (Maignret, 1978). French landings peaked at 3600 t in 1961 but the fishery shrank to 200 t year⁻¹ in 1970. Reduced effort allowed stocks to recover, and by 1986 landings had increased to 900 t (10 boats). In a 1987 agreement with Mauritania, the European Commission allocated lobster-netting rights to Portugal and an escalation of poaching

rapidly led to a new collapse. French boats abandoned the fishery in 1990. After 1995, *P. mauritanicus* was reduced to a bycatch of boats trawling or netting for demersal fish and cephalopods (M. Diop, pers. comm.).

In the Bay of Biscay sporadic netting for *P. mauritanicus* by one or two boats occurs on coral grounds at 300–400 m depth, but low catch rates have made targeted fishing uneconomical. Trawlers occasionally land *P. mauritanicus* as a bycatch. In the Western Mediterranean, *P. mauritanicus* is also taken by bottom trawlers as bycatch (Holthuis, 1991), and is occasionally targeted with trammel nets or epibathyal fixed nets (Addis *et al.*, 1998); however, as in the Atlantic, yields have declined substantially.

11.5.3 *Palinurus charlestoni*

Fishing for *P. charlestoni* started in 1963 when three French vessels involved in the fishery for *P. mauritanicus* off Mauritania prospected Cape Verde waters (Forest & Postel, 1964). French involvement ceased in 1966 when the Portuguese administration extended its territory to 12 nm offshore; however, Portuguese vessels continued fishing even after 1975, when the Cape Verde archipelago became independent. No data are available on landings of *P. charlestoni* up to 1982, except for an estimate of 50 t in 1976 (Moal, unpublished). Sources differ on actual landings after 1982, and the statistics are therefore indicative: 20–60 t year⁻¹ between 1982 and 1990; a maximum of 85 t in the 1991/92 fishing season, followed by a downward trend with 14 t in 1996/97, and 35 t in 1998/99 (Medina *et al.*, 2003). *Palinurus charlestoni* is fished exclusively with traps (mainly top-entry Cape Verdian traps; 1.5–2 m long; 1.15–1.5 m wide; 0.5 m high; metal frame covered by a wire netting) set singly and baited with mackerel and horse mackerel (Carvalho & Latrouite, 1992). Currently five vessels (12–22 m long), rather old and with no onboard storage facility, are active (Medina, pers. comm.). Standardized fishing effort expressed as the number of Cape Verdian traps hauled annually was around 10,000 at the end of the 1980s, 67,000 in 1992/93 and 20,000 in 1998/99 (Medina *et al.*, 2003).

11.5.4 *Palinurus gilchristi*

Commercial quantities of *P. gilchristi* were first discovered in 1974, and the species now supports the second largest lobster fishery in South Africa, with commercial landings of approximately 1000 t year⁻¹ (Fig. 11.8a). Fishing takes place between Cape Point (19°E) and East London (28°E), where strings of 100–200 plastic top-entry traps baited with hake-heads are set along bottom long-lines on rocky patches between 50–200 m depth. The fishery is capital-intensive, requiring large ocean-going vessels (30–60 m length) capable of staying at sea for up to 35 days at a time. Some vessels supply live lobsters to shore-based facilities, whereas others process and pack whole frozen lobsters or frozen lobster tails – all products are exported.

After 1974, fishing effort and catches increased rapidly above sustainable levels, followed by a collapse of the resource by 1980 (Pollock & Augustyn, 1982; Fig. 11.8a). Much lower fishing effort over the following years resulted in a recovery of the fishery, up to 1984 when a total allowable catch (TAC) was first introduced. Despite this measure, fishing effort (numbers of traps set, and trap soak-times) increased gradually up to 1999. Catch rates in three fishing areas declined concurrently (Fig. 11.8b), by approximately 5–10% per year, or by a cumulative 70% (Groeneveld *et al.*, 2003). Systematic under-reporting of catches was uncovered in 2001, and a large fishing company was prosecuted and subsequently disbanded, leading to a sudden decline in fishing effort in 2001. The number of fishing vessels was reduced by 30% (to nine vessels), and the lower fishing effort and smaller catches resulted in an initial 9% per year increase in catch rates. At present the fishery is considered to be stable (Groeneveld, 2003; Anon., 2010).

11.5.5 *Palinurus delagoae*

Exploratory trawling in 1920 first revealed spiny lobster populations off eastern South Africa (Gillchrist, 1920), and large catches of several tonnes per trawl were sporadically reported up to the 1960s (Berry, 1972) (Fig. 11.9). These catches became rare, and the lobster-directed trawl fishery gradually diversified to catch deep-water prawns,

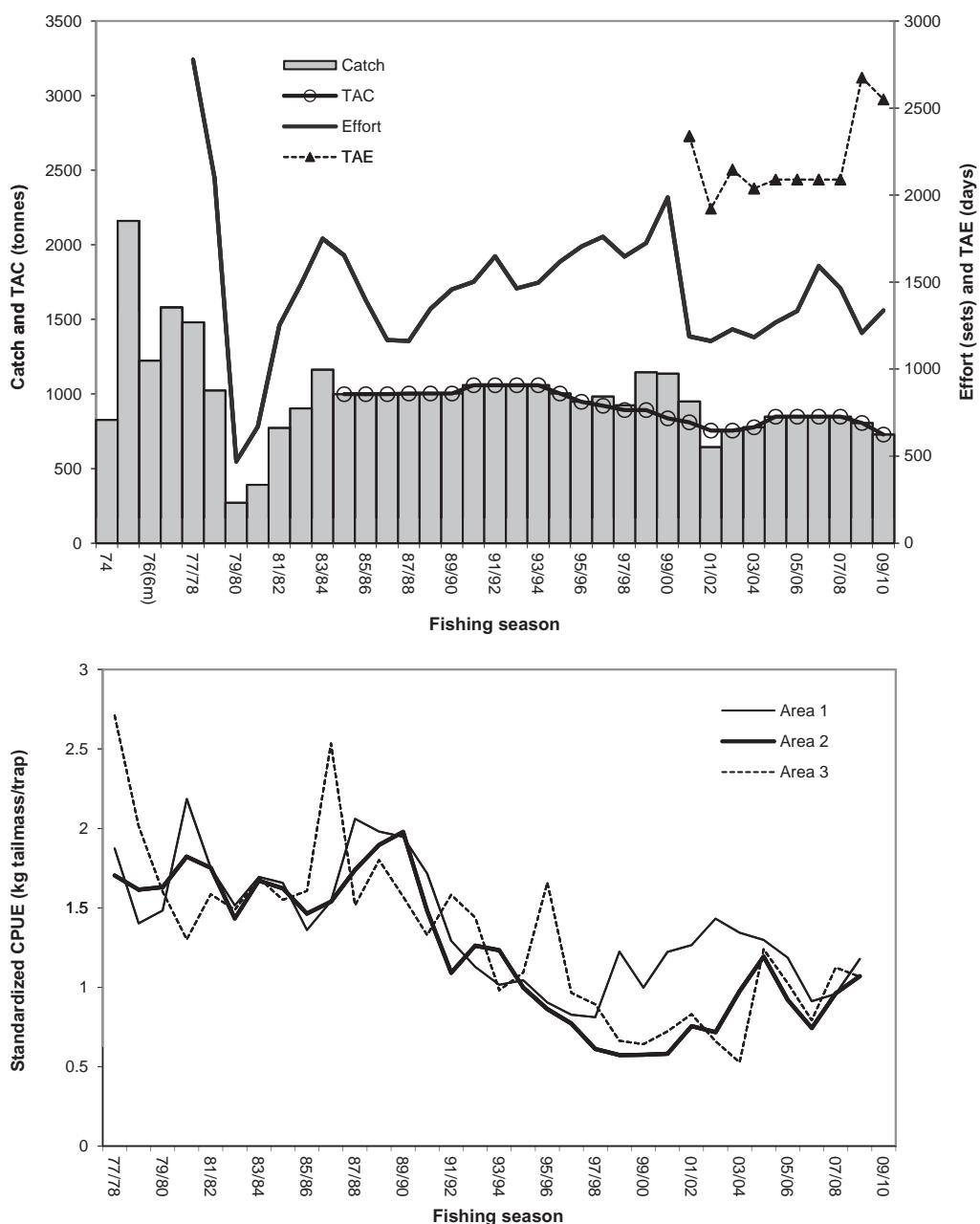


Fig. 11.8 Long-term trends in the commercial trap-fishery for *Palinurus gilchristi* showing: (A) Catch and effort (including TAC and TAE levels); and (B) standardized CPUE trends (kg tailmass/trap) for three fishing areas – Area 1 = East of 25°E; Area 2 = Central South Coast; Area 3 = Agulhas Bank. Data obtained from Anon. (2010) and Groeneveld (2003).



Fig. 11.9 Jackpot catches of up to 5 t of *Palinurus delagoae* per trawl were made during the 1960s (Berry, 1972).

langoustines, geryonid crabs and several fish and cephalopod species (Groeneveld & Melville-Smith, 1995; Fennessy & Groeneveld, 1997). Small quantities of 5–10 t year⁻¹ of *P. delagoae* continue to be landed by deep-water trawlers. A similar multi-species trawl fishery in Mozambique has been active since at least 1960, attracting fishing vessels from South Africa, Japan, Spain, Russia and East Germany (Berth *et al.*, 1984; Torstensen & Pacule, 1992; Palha de Sousa, 1998). Much of the catches have gone undeclared.

Trap-fishing for *P. delagoae* commenced in 1980 in Mozambique and rapidly expanded to cover extensive fishing grounds between Inhaca (27°S) and the Bazaruto archipelago (21°S) (see Fig. 11.1) (Palha de Sousa, 1992, 1998). Initial catches of >300 t year⁻¹ decreased to 100–200 t year⁻¹ by 1994, whereafter increased effort resulted in rapid declines (102–48 t) by 1999. Catch rates declined from 0.74 to 0.33 kg/trap haul, and the fishery was curtailed in 2000 (Palha de Sousa, 2001).

Experimental trap-fishing in South Africa was undertaken between 1994 and 1997, recording initial catches of 89.5 t of *P. delagoae* and ~30 t of slipper lobster *Scyllarides elisabethae* (Groeneveld *et al.*, 1995). Catches declined sharply to 7.8 t in 1997, and catch rates also declined by ~75% relative to 1994 (Groeneveld, 2000). No trapping was undertaken over the next 6 years, but between 2004

and 2007 renewed trapping captured 103 t of target species (65% *P. delagoae*, 28% *S. elisabethae* and 7% red crabs *Chaceon macphersoni*) at depths of 90–462 m (Groeneveld, *et al.*, 2012). Catch rates of *P. delagoae* declined by 42% over the 4 years, and the average CL declined by 4%. The renewed trapping rapidly eroded the gains made over the 6-year period between 1998 and 2003, and the fishery was suspended after 2007.

11.5.6 *Palinurus barbareae*

Sporadic trapping surveys to Walters Shoals (Madagascar Ridge) and submerged seamounts further east on the South West Indian Ridge recorded occasional good catches of *P. barbareae* and *Jasus paulensis*, but not commercially viable quantities (Romanov, 2003; Groeneveld *et al.*, 2006b).

11.6 Protection and enhancement

11.6.1 Marine Protected Areas

Marine reserves or MPAs may provide an alternative for recovery of overexploited spiny lobster populations, by permanently closing fishing or spawning grounds, or proclaiming areas in which fishing mortality is restricted. In the Mediterranean, the MPAs of Columbretes Islands, Nord de Menorca, Medes Islands, and Cabo de Palos in Spain, Banyuls and Bouches de Bonifacio in France and Su Pallosu in Italy are closed or limit lobster fishing within their boundaries. In the Atlantic, at least three MPAs afford protection to *P. elephas*; two in Ireland are closed to net fishing (O. Tully, pers. comm.); one in Brittany is a no-take zone (Laurans *et al.*, 2011).

However, in only a few of the MPAs have the responses of *P. elephas* to protection been studied. A 2-year sampling programme of the artisanal fisheries around the Cabo de Palos and Banyuls MPAs showed an increase in lobster fishing effort and CPUE near the MPA boundaries, thus indicating spillover benefits (Goñi *et al.*, 2008). In the Columbretes MPA, a 20-year no-take area of 55 km² off eastern Spain, lobster abundance, biomass and demography were monitored over a decade (Goñi

et al., 2006, 2008, 2010) during which abundance declined slightly, but biomass increased gradually. Abundance and biomass in the MPA were on average eight and 14 times greater than in the adjacent fished areas. The mean emigration rate of *P. elephas* from the MPA has been estimated at 6% per year and the net contribution of the spillover to the local fishery has increased yields by 13% per year. The Columbretes MPA study showed a marked demographic recovery of *P. elephas*, evidenced by the continued increase in its mean and maximum size over two decades of protection (Goñi *et al.*, in preparation). The regional reproductive output was six times greater than it would have been without the MPA. Long-term studies have also been conducted in the Sou Paloussu MPA, a 3.8-km² no-take area in Sardinia. Restocking and a tag–recapture programme between 1997 and 2005 showed an increase of spiny lobster abundance over time inside the MPA, and movement of lobsters to adjacent fishing grounds, where they become susceptible to capture (Follesa *et al.*, 2007b, 2008, 2009), and repopulation of *P. elephas* in the Gulf of Asinara has been investigated (Cannas *et al.*, 1998).

11.6.2 Enhancement

Complete larval culture from egg stage to puerulus of *P. elephas* was first achieved in 1988 (nine instars, 132 days; Kittaka & Ikegami, 1988), and subsequently repeated in 1996 (seven instars, 65 days; Kittaka, 1997) and in 1999 (six instars, 65–72 days; Kittaka *et al.*, 2001). These studies showed that *P. elephas* phyllosomas hatch at an advanced stage and are generally larger than in *Jasus* and *Panulirus*. More important, however, is that *P. elephas* under culture conditions has an exceptionally short larval cycle (65–72 days) compared to *Jasus* (205–319 days) and *Panulirus* (306–341 days) (Kittaka *et al.*, 2001), a factor that would circumvent a major constraint on commercial cultivation of lobster larvae. *Palinurus elephas* is therefore a good candidate for aquaculture because of its short larval life, rapid growth from the puerulus (Archer & Nickell, 1997; Díaz, 2010) and high market value. Nevertheless, obtaining large quantities of pueruli from the wild is problematical, and

precludes most enhancement strategies based on grow-out and restocking.

11.7 Monitoring and management

11.7.1 Northeast Atlantic and Mediterranean fisheries

Except for a minimum landing size (MLS) decided at the European Community level, all *P. elephas* fisheries are managed at national or regional level. No TAC or quotas exist as the reliability of landing statistics in most countries makes this strategy unfeasible. Hence, regulations are based on technical measures such as MLS, protection of berried females and/or effort limitations, and more recently on spatial management measures, such as MPAs.

Recent information on the poor status of some European fisheries has led to the implementation of new regulations, such as increasing the European MLS from 80 to 90 mm CL in the Mediterranean. Whereas in the Mediterranean the MLS of 90 mm is above the 50% size at functional maturity (SAM) (Goñi *et al.*, 2003a), this is not the case in the Atlantic where the SAM of 103 mm in Ireland is larger than the European MLS of 95 mm CL for Atlantic waters (Tully, 2011). Consequently Ireland (Tully, 2011), England and Wales (A. Lawler, pers. comm.) and France (Laurans *et al.*, 2011) have increased national MLS limits to 110 mm CL.

Fishing effort in *P. elephas* fisheries is mainly limited by an annual seasonal closure, which covers all or part of the egg-bearing period and varies nationally and regionally (e.g. 7 months in the Balearic Islands and Corsica, 5 months in Sardinia and Tunisia). Seasonal closures are also applied in some Atlantic fisheries, such as France (2–3 months; Laurans *et al.*, 2011) but not in others, such as Ireland. Landing berried females is also forbidden in most Mediterranean fisheries, but not in the Atlantic, where it is being considered in some countries.

Finally, MPAs are becoming part of the management toolbox for *P. elephas* fisheries in Europe. In most cases the MPAs tend to be small and provide research sites where unfished populations may be studied. Two large MPAs in the Western

Mediterranean are the Columbretes MPA, essentially a no-take area of 55 km² in Spain, and Les Bouches de Bonifacio in France, comprising 800 km² where lobster fisheries are zoned, including a 13 km² no-take zone and a 130 km² restricted fishing zone. Other smaller MPAs that exclude or reduce *P. elephas* fishing in the Mediterranean and Atlantic are listed in Section 11.6. Spatial management in the Atlantic has been implemented in Ireland, where two MPAs are closed to tangle nets (Tully, 2011) and France, with a small experimental no-take area (Laurans *et al.*, 2011).

Despite the multiplicity of controls imposed in some fisheries, many of the regulations are difficult to enforce. *P. elephas* is targeted by a large number of artisanal vessels, typically distributed in many ports along the coastline, or is a bycatch of bottom trawl or finfish netting. Therefore, at-sea effort control is problematical and regulations are sometimes ignored. Fishermen contend that some of the regulations cannot be adhered to without making fishing uneconomical, and therefore socio-economic considerations are essential for developing workable management plans (Galhardo *et al.*, 2006; A. Pere, pers. comm.). Facilitating stock recovery is urgent and should include the identification of essential habitats for post-larvae and juveniles. Programmes to promote the reintroduction of trap/pot fishing are being considered in some areas (e.g. Balearic Islands, Corsica, Ireland, Brittany) not only because they are more selective but also because their introduction would translate into an effective reduction of effort (Galhardo *et al.*, 2006).

It is not yet possible to discriminate between fishing mortality and environmental factors as responsible for the depleted status of *P. elephas* fisheries. As a high value commodity, it continues to be pursued despite low yields, and rapidly growing prices maintain viable fisheries. Temporal closures appear to be the most effective management measure at present, because they are easy to enforce, reduce the loss of catch due to long soak times, eliminate injuries to undersized specimens returned to the sea, and allow for recovery of the benthic environment.

Palinurus mauritanicus exploitation is managed through an MLS, which is 95 mm CL in the Atlantic and 90 mm in the Mediterranean, and temporal

closures in some fisheries (e.g. December to May in the Balearic Islands).

11.7.2 Southwest Indian Ocean fisheries

The fishery for *P. gilchristi* is managed through a combination of TAC and total allowable effort (TAE) control – this strategy was introduced in 2000 to counteract poor compliance in the fishery at that time (Groeneveld, 2003). The fishery is limited to South African fishing vessels, which may only use plastic top-entry traps set along bottom long-lines. Fishing vessels may operate year-round (1 October to 30 September of the following year), but are restricted to a predetermined number of days that they can be at sea. No MLS is enforced, but egg-bearing females must be returned to the sea – although this does not always happen. Days at sea are monitored using global satellite positioning technology, and fisheries compliance officers at landing points weigh all catches and reconcile them against individual quotas.

Annual numerical assessments of *P. gilchristi* rely on an age-structured production model (ASPM) which projects abundance for management purposes (Johnston & Butterworth, 2001, 2004). The most important inputs to the model are population size structure (collected by observers at sea), total catches, somatic growth rate and a relative abundance index obtained by standardizing daily catch rates reported on catch–return sheets completed by skippers of fishing vessels. The standardization accounts for the influences of vessel characteristics, trap-soak-times, month, year, location and depth of trap-sets on catch rates (Glazer, 1999).

An Operational Management Procedure (OMP; pre-agreed formula which uses resource monitoring data such as total catches, standardized catch rates, length composition) to provide a TAC recommendation was implemented in the fishery for the first time in 2008. The output is tuned to achieve medium term goals through trading-off of high catches with low risks of resource depletion, and small year-to-year changes to the fishery (i.e. stability). The present stock status is considered to be stable with recent estimates putting spawning biomass at some 40% of pre-exploitation levels. Nevertheless some declines have been shown over

the past decade and the management objective is to increase spawning biomass by 20% between 2006 and 2026 (Anon., 2010).

11.8 Conclusions

One of the most interesting aspects of the *Palinurus* genus is its present-day geographic distribution, with three species (*P. elephas*, *P. mauritanicus* and *P. charlestoni*) occurring only in the northeast Atlantic and Mediterranean, far removed from the other three species (*P. barbareae*, *P. delagoae* and *P. gilchristi*) which are restricted to the southwest Indian Ocean. Comparisons of the biological characteristics between these widely geographically distant counterparts offer interesting parallels. (i) The Atlantic and Mediterranean species appear to grow faster, reach sexual maturity at a larger size and attain a much larger maximum size than their southern counterparts. (ii) Conversely, fecundity is much higher in the two Indian Ocean species, possibly as an adaptation to high loss of larvae in the strong Agulhas Current regime, which dominates oceanographic features along southeastern Africa. (iii) Adults moult once per year over a protracted period, and females generally produce a single batch of eggs per year, incubation lasting for 4–10 months. This differs from the frequent moulting episodes and multiple broods produced by warmer water genera. (iv) An exceptionally short larval cycle of *P. elephas* of 65–72 days during culture may make it a good choice for commercial cultivation. (v) Juvenile *P. gilchristi* and *P. delagoae* undertake long-distance counter-current migrations; *P. elephas* and *P. mauritanicus* undertake shorter reproductive- and short-distance ontogenetic migrations. (vi) We suggest that the differences in biological characteristics (size, fecundity and migrations) between the Indian and Atlantic

Ocean species is partially as a result of the adaptations that *P. gilchristi* and *P. delagoae* had to undergo to maintain their populations alongside the strong unidirectional Agulhas Current. (vii) *In situ* post-larval ecology and early growth rates have now been described for *P. elephas* at Majorca – a first for this genus.

Population genetic studies over the past 6 years have contributed much to the understanding of larval dispersal patterns, gene flow and metapopulation structure relative to ocean processes. Key findings from the southwestern Indian Ocean were the description *P. barbareae* from Walters Shoals and other seamounts, and identifying a shallow genetic partitioning between *P. delagoae* populations along the boundary of the Mozambique channel eddies with the upper Agulhas Current. In the northeast Atlantic and Mediterranean basins several metapopulations of *P. elephas* have now been identified – possibly opening the door for defining separate management units. Population expansions over the past 100,000 years have been shown for several *Palinurus* species, and these expansions appear to be relatively consistent with climatic and sea-level changes wrought by late Pleistocene events, particularly the impacts of glacial and interglacial intervals. Furthermore, the shallow water species *P. elephas* and *P. gilchristi* have larger historical effective population sizes than the deep water species, *P. mauritanicus*, *P. delagoae* and *P. barbareae*, thus confirming the trends from commercial fisheries that the deep-water species are more sensitive to overfishing.

MPAs are now part of the management toolbox for heavily exploited *P. elephas* populations, mainly in the Mediterranean, and several studies have shown the benefits of conservation of reproductive potential, even in small areas, and also of the spillover effects of increasing abundance in reserves to adjacent fisheries.

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Chapter 12

Nephrops Species

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Abstract

Nephrops norvegicus (L.) is widely distributed in the north-east Atlantic and Mediterranean. The species forms burrows in muddy sediments and is found wherever conditions are suitable. Important fisheries for *Nephrops* have developed since the 1950s, and it is now one of the most valuable demersal species in the north-east Atlantic. Research into the biology of *Nephrops* dates back over at least a century, and this chapter reviews the current state of knowledge of its biology, ecology and fisheries. The chapter also reviews research into the biology of similar *Metanephrops* species that are also becoming the focus of important fisheries in New Zealand, Australia and elsewhere.

Key Words: *Nephrops*; *Metanephrops*; Norway lobster; fisheries; biology

12.1 Introduction

The Norway lobster, *Nephrops norvegicus* (L.), continues to support the most valuable commercial crustacean fisheries in Europe, with annual landings amounting to over 70,000 t in recent years, worth in the order of US\$270 million. The biology, fisheries and management of the species have been reviewed previously by Farmer (1975), Chapman (1980), Dow (1980), ICES (1982), Sardà (1995), Graham & Ferro (2004) and most recently by Bell *et al.* (2006). This chapter is an update of that most recent review, highlighting developments in our knowledge of the species' natural history, popula-

tion dynamics, exploitation and management over the last 6 years. The species *N. norvegicus* is the only representative of its genus and we will follow the usual custom of referring to it simply as *Nephrops*. While this review will focus on *Nephrops*, reference will be made to other similar species where further information is available.

12.2 Species and distribution

Nephrops norvegicus (Linnaeus, 1758), is a member of the family Nephropidae, sub-family Nephropinae, and has the typical physiognomy of a clawed

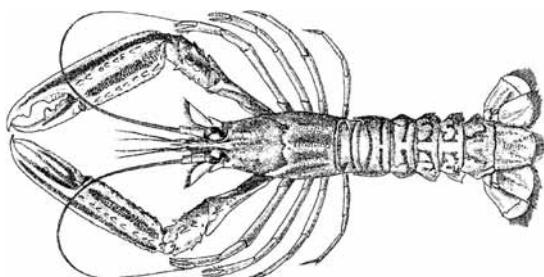


Fig. 12.1 General appearance of the Norway lobster, *Nephrops norvegicus* (L.) (after Holthuis, 1950).

lobster, albeit with a slenderer body shape and longer claws than the ‘true’ lobsters *Homarus americanus* and *Homarus gammarus* (Fig. 12.1). Other distinguishing characteristics include a carapace with a distinct post-cervical groove and longitudinal spinose keels; a long and spinose rostrum; an abdomen with transverse grooves; and large, well-pigmented and kidney-shaped eyes (hence the genus name *Nephrops*, which means ‘kidney-eye’). Its colour is pale to reddish orange (Holthuis, 1950; Hayward & Ryland, 1990).

Nephrops from the Mediterranean Sea is sometimes referred to as *Nephrops norvegicus* var. *meridionalis* (e.g. Zariquey Alvarez, 1968), the distinction with the type species being based on a small difference in morphology of the second maxilliped, but the validity of this sub-species is controversial (Holthuis, 1945; Crnkovic, 1969) and this form is now considered a synonym of *N. norvegicus*. Passamonti *et al.* (1997) found very low genetic divergence between Scottish and eastern Mediterranean populations of *Nephrops* on the basis of allozyme characterization.

Nephrops is widely distributed on the continental shelves and upper continental slopes of the north-east Atlantic and the Mediterranean, from Iceland and Norway in the north, to Morocco and Greece in the south, at depths from 20 to 800 m (Fischer *et al.*, 1987; Holthuis, 1991; Ardizzone *et al.*, 1999; Abello *et al.*, 2002), although the main populations are generally at locations more shallow than 200 m. The species is absent from the Baltic Sea, the Black Sea and the Levantine coast. Occasional records of *Nephrops* have been reported outside its main distributional area (e.g. Canary Islands, Greenland;

Farmer, 1975; Barquin *et al.*, 1998), but these should be considered incidental.

In addition to *Nephrops norvegicus*, the family Nephropidae comprises another 40 similar species. Species of the genera *Eunephrops* and *Metanephrops* are mostly found on the upper part of the continental slope, at depths between 200 and 600 m, while species of the genera *Acanthacaris*, *Nephropides*, *Nephropsis*, *Thymopides*, *Thymops* and *Thymopsis* are mostly found in deeper waters, between 400 and 1000 m (Holthuis, 1991). Of these, only a few are of importance to the commercial fisheries: *Metanephrops armatus* (Taiwan), *M. andamanicus*, *M. australiensis*, *M. velutinus* (NW Australia), *M. challengerii* (New Zealand), *M. formosanus* (Taiwan), *M. japonicus* (Japan), *M. mozambicus* (SE Africa) and *M. thomsoni* (Korea, Taiwan) (Holthuis, 1991; Ingle, 1997). While their catches (a few hundred tonnes each, at the most), are by no means comparable to those of *Nephrops norvegicus* (70,000 tonnes annually), some of these species support valuable national fisheries. Their generally greater depth of occurrence, shorter fishing history and lower overall commercial value has meant they have been less intensively studied than *Nephrops* and research has mostly been limited to the more commercially important species.

Nephrops is fished wherever it is found in exploitable quantities and is one of the commercially most important demersal species in the north-east Atlantic. Table 12.1 and Fig. 12.2 give an overview of the major *Nephrops* populations and fishing grounds, their average landings figures for the years 2006–10, and the countries that take most of the catches. Figure 12.3 shows the steady increase in landings from less than 10,000 t in 1950 to around 70,000 t in recent years. The increase has principally been seen in the Atlantic fisheries, and the present-day landings of around 5000 t from the Mediterranean represent a considerable decrease from the peak of up to 16,000 t in the early 1990s. Recent landings by fisheries for *Metanephrops* species are listed in Table 12.2. Since 2005, landings have only been reported for fisheries off New Zealand, Mozambique and Australia.

Since *Nephrops* and similar species are dependent on muddy seabeds (see below), their overall geographical distribution are highly discontinuous.

Table 12.1 *Nephrops* landings by fishing area and stock (averages for 2006–10), and countries taking most of the landings.

Stock/fishing area ^{1,2}	Landings 2006–10 (tonnes) ³	Principal countries ⁴
Iceland (1)	2100	Iceland
Faeroes (2)	50	Faeroes
Northern North Sea	14600	
Noup (3)	120	UK
Moray Firth (4)	1500	UK
Fladen Ground (5)	12200	UK
Norwegian Deep (6)	700	Denmark, Norway
Central & Southern North Sea	8800	
Firth of Forth (7)	2400	UK
Farn Deeps (8)	2600	UK
Botney Gut – Silver Pit (9)	1000	UK, Netherlands, Germany
Off Horn Reef (10)	1200	Denmark, Netherlands, Germany, Belgium, UK
Skaggerak and Kattegat	4700	
Skagerrak (11)	2800	Denmark, Sweden, Norway
Kattegat (12)	1800	Denmark, Sweden
West of Scotland	14100	
N Minch (13)	3500	UK
S Minch (14)	4700	UK
Clyde (15)	5500	UK
Irish Sea	9800	
W Irish Sea (16)	7100	UK, Ireland
E Irish Sea (17)	700	UK, Ireland
North, West & South of Ireland	2700	
Aran Grounds (18)	800	Ireland
Porcupine Bank (19)	1400	Ireland, Spain, UK, France
S and SW Coast of Ireland (20)	800	Ireland
Celtic Sea (21)	5600	Ireland, France, UK
Bay of Biscay	3200	
N Bay of Biscay (22)	2900	France
S Bay of Biscay (23)	300	France
Northern Spain	80	
Cantabrian Sea (24)	14	Spain
N Galicia (25)	45	Spain
Iberia Atlantic coast	300	
W Galicia & N Portugal (26)	34	Spain
S and SW Portugal (27)	170	Portugal
Gulf of Cadiz (28)	160	Spain
Morocco Atlantic coast (29)	35	Morocco
Western Mediterranean	1000	
Catalan Sea (30)	560	Spain
Ligurian & N Tyrrhenian Sea (31)	370	Italy
Adriatic Sea (32)	1700	Italy, Croatia
Eastern Mediterranean	2600	
Ionian Sea (33)	2200	Italy
Aegean Sea (34)	500	Greece
Grand total NE Atlantic	65700	
Grand total Mediterranean	5400	
Grand total all areas combined	71000	

¹Numbers in brackets refer to location of fishing ground as shown in Fig. 12.2.

²Shaded rows represent distinct stocks (or groupings of stocks, in the case of the Mediterranean) within preceding larger sea areas. Note that landings figures for the larger areas may exceed the sum of the figures for the distinct stocks, owing to landings taken within the larger areas but outside the individual stocks.

³Average annual landings for 2006–10 for most areas, sourced from FAO for Morocco and the Mediterranean and from ICES for all other areas; landings for individual areas within the Mediterranean are averages for 2006–08; some pro-ration of Italian landings was necessary to estimate 2006–10 totals for Western, Eastern and Adriatic areas of the Mediterranean.

⁴Countries taking at least 100 t of total international landings annually, in order of importance, or the country with the largest share of landings for stocks supporting less than 100 t annually.



Fig. 12.2 *Nephrops* stocks and fishing grounds in European waters (see Table 12.1 for details).

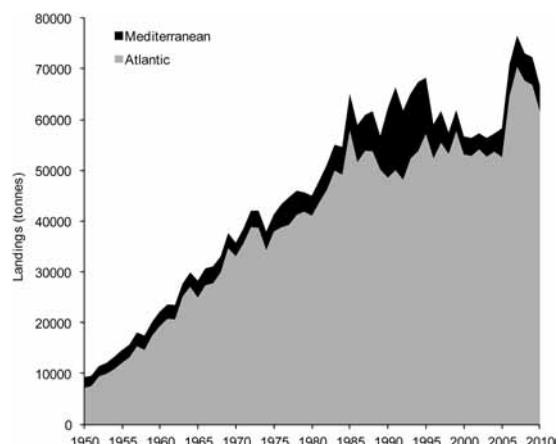


Fig. 12.3 Trend in *Nephrops* landings from the Atlantic and Mediterranean since 1950 (data from FAO).

In European waters, there are more than 30 different *Nephrops* populations, which are all physically isolated from each other, most often by large stretches of unsuitable sediment (coarse sand, gravel, bedrock, etc.). *Metanephrops* around New Zealand are divided into five distinct main and other smaller populations (Tuck, 2009). *Nephrops* is also very sedentary and only rarely migrates over distances longer than a few hundred metres (Jensen, 1965; Chapman, 1982).

Even within areas that are considered to be inhabited by the same unit stock, the distribution of *Nephrops* can be very heterogeneous, depending on sediment characteristics such as grain size and redox potential (Tully & Hillis, 1995; Maynou *et al.*, 1996; Maynou & Sardà, 1997). A stock may thus be divided into a (large) number of smaller 'stocklets', with different population densities, size

Table 12.2 Landings of *Metanephrops* species by FAO fishing areas (tonnes, averages for 2005–09).

Area	<i>Metanephrops australiensis</i> ¹	<i>Metanephrops mozambicus</i>	<i>Metanephrops challenger</i>
Eastern Indian Ocean	40		
Western Indian Ocean		107	
Southwest Pacific			
Western Central Pacific	18		744

¹Catches in Australian NW shelf trawl fishery mostly *M. australiensis*, but also includes *M. andamanicus*, *M. boschmai* and *M. velutinus*.

and sex compositions, and also different biological features (growth rate, size at first maturity, etc.).

Nephrops has a preference for muddy seabed sediments, with >40% of silt and clay. In areas where sediment composition and *Nephrops* densities have been studied in detail (e.g. around the British Isles and in the Adriatic Sea), there is a close relation between the distribution of *Nephrops* and the nature of the bottom deposits (Alfirević, 1968; Farmer, 1975; Bailey *et al.*, 1993; ICES, 2001). This knowledge, combined with the introduction of instruments for seabed detection and classification on commercial fishing vessels, has led to the rapid expansion of *Nephrops*-directed fisheries in areas of ‘suitable’ sediment that were formerly unexploited or only lightly exploited. This has notably been the case on the Fladen Ground (northern North Sea), where the landings steadily increased from about 1000 t in the mid-1980s to 12,000 t or more since 2007, and in both the Horn Reefs area (southeastern North Sea) and the Norwegian Deep, where they rose from less than 50 t in the late 1980s to over 800 t 10 years later (ICES, 2011c). The Devil’s Hole, south of the Fladen Ground, is one of the most recent new fishing grounds to be identified, with landings increasing to around 1,000 t between the late 1990s and the late 2000s.

12.3 Life history

12.3.1 Growth

Moulting

In common with all arthropods, growth in *Nephrops* is the combined effect of moult frequency and

size increment at moult. Growth rates vary widely between and even within stocks (see later), there is a general pattern of moult frequency that applies to most. After having passed to the benthic stage and up to the autumn of their first year of life, juvenile *Nephrops* grow very rapidly, moulting around once per month (Conan, 1978). Moult frequency gradually decreases to three or four moults annually during the second and third years, usually occurring in late winter or spring, in summer and in autumn. After the onset of sexual maturity moult frequency is further reduced to one or two moults per year in males (usually in late winter or spring, and in late summer or autumn) and no or one moults per year in females (in late winter or spring, after the hatching of the eggs) (e.g. Hillis, 1971a; Farmer, 1973; Charauau, 1975; Conan, 1975, 1978; Sardà, 1991; Talidec & Reyss, 1993). There is no evidence of terminal anecdisis in *Nephrops* (Farmer, 1973).

Increments at moult typically range between 1.0 and 2.5 mm carapace length (CL) (which corresponds to a relative size increment of 3–12%), but considerably larger and smaller values have been recorded in many populations and relative size increments are usually inversely related with pre-moult size (Farmer, 1973; Charauau, 1975, 1977; Bailey & Chapman, 1983; Sardà, 1985; González-Gurriarán *et al.*, 1998; Verdoit *et al.*, 1999). Scottish studies, which covered the full size range of both immature and mature *Nephrops*, show evidence of a change in growth pattern at the onset of sexual maturity (Bailey & Chapman, 1983). In a laboratory study using wild-caught *Nephrops* from the south coast of Portugal, Castro *et al.* (2003) found no systematic relationship between moult

increment and pre-moult size. They concluded instead that moult increment could be modelled as a random Normal variable, with mean values not significantly different between the sexes.

Actual moulting takes 20–30 min (Sardà, 1983) and is a laborious process during which the animals are very vulnerable to predation and cannibalism. The period between successive moults can be subdivided into four main stages, which can be recognized from morphological alterations in the setae of the pleopods (Charauau, 1973; Sardà 1983). According to Sardà's sub-division of the intermoult period, there are two post-moult stages, a so-called 'resting stage' and a pre-moult stage, the relative duration of which changes as the animals grow older (Sardà, 1983).

Size at age

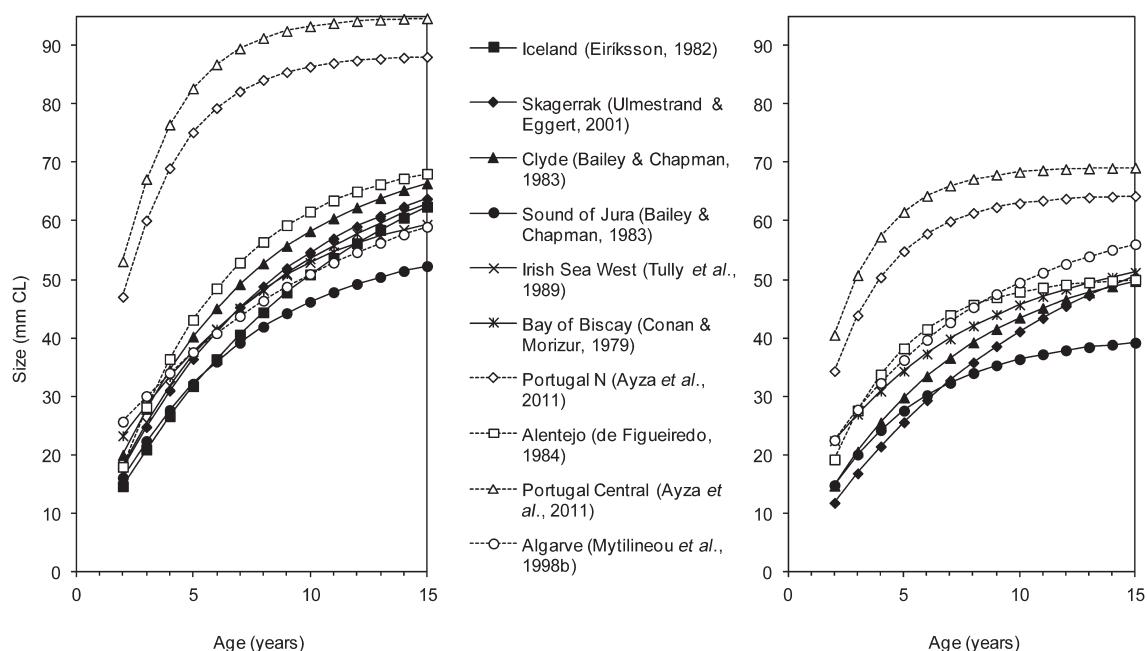
Direct determination of age in *Nephrops* is not routinely possible. There has been some progress in calibrating age with concentration of the 'age pigment' lipofuscin in neural tissues (Tully, 1993; Belchier *et al.*, 1994), but this has not yet been developed into a reliable method that can routinely be applied in growth studies of *Nephrops*. Following the progression of size modes interpreted as age cohorts can allow inferences about growth patterns from size-frequency data. However, unambiguous identification of age cohorts is often problematic, particularly for ages after sexual maturity when reduced growth rates and variability of growth between individuals means that successive age-classes are not clearly separable in terms of size modes. The modal progression method has nevertheless been commonly used, often employing computer-aided methods (such as ELEFAN, MIX and MULTIFAN) for resolving distribution mixtures into individual components (e.g. Mytilineou & Sardà, 1995; Castro *et al.*, 1998; Ayza *et al.*, 2011). Tagging studies probably remain the most reliable approach to collecting growth data on adult *Nephrops*, but large-scale tagging projects are costly and recapture rates are usually low, in the order of 2–20% (Jensen, 1965; Chapman *et al.*, 1989; de Figueiredo, 1989; Cryer & Stotter, 1997; Tuck *et al.*, 2009). Information on growth patterns also comes from growth increments and intermoult

periods observed for individuals kept in captivity (e.g. Hillis, 1971a, 1979; Farmer, 1973; Charauau, 1975; Sardà, 1983, 1985). Latrouite *et al.* (1991) developed a radiometric method for determining intermoult periods, and this has been applied in a growth model incorporating individual variability by Verdoit *et al.* (1999) (see also Talidec & Reyss, 1993). Shelton & Chapman (1995) developed a histological moult-recording tag for *Nephrops* based on implantation of living tegument tissue into the abdominal haemocoel, successfully demonstrating that it could be used to record the number of moults between implantation and recapture. Neither radiometric nor histological methods have yet seen wide application, however, and information on growth largely comes from historical tagging studies and modal progression analyses.

Although growth is a discontinuous process in *Nephrops*, continuous growth curves such as the von Bertalanffy growth function are generally used as a mathematically convenient description of the relationship of average size with age for the purposes of stock assessment and other population analyses. The main parameters of the function are L_∞ , asymptotic maximum size, and K , the rate at which this size is approached; a third parameter t_0 , the theoretical age at zero size, scales the growth curve to absolute rather than relative ages and cannot always be estimated. As can be seen from Fig. 12.4, growth curves estimated for different stocks vary widely. There is no obvious geographical pattern in these estimates, but it is worth noting that growth relationships may depend on local environmental conditions (see below) and that differences in fishing pressure between stocks may affect sizes at age through the effects of size-selective fishing mortality (Tuck *et al.*, 1997a; Sánchez Lizaso *et al.*, 2000; Fig. 12.5). Further, there must be uncertainty associated with some estimates, particularly those based on interpreting size modes as age cohorts. The growth parameters for Portuguese stocks determined by Ayza *et al.* (2011) are markedly at variance with results for other stocks in the region (e.g. de Figueiredo, 1984), but it is unclear whether this is due to local conditions (environment, fishing pressure and stock structure) or to uncertainties in identifying age cohorts.

A

Atlantic stocks



B

Mediterranean stocks

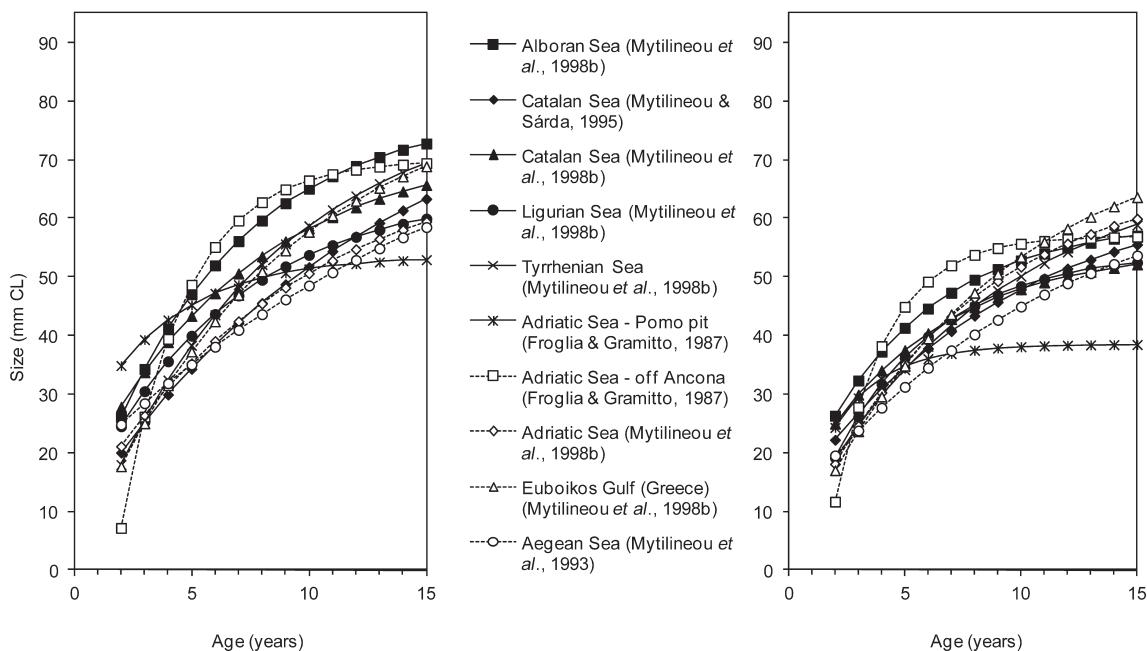


Fig. 12.4 (A) Growth curves of male (left) and female (right) *Nephrops* – Atlantic stocks. (B) Growth curves of male (left) and female (right) *Nephrops* – Mediterranean stocks.

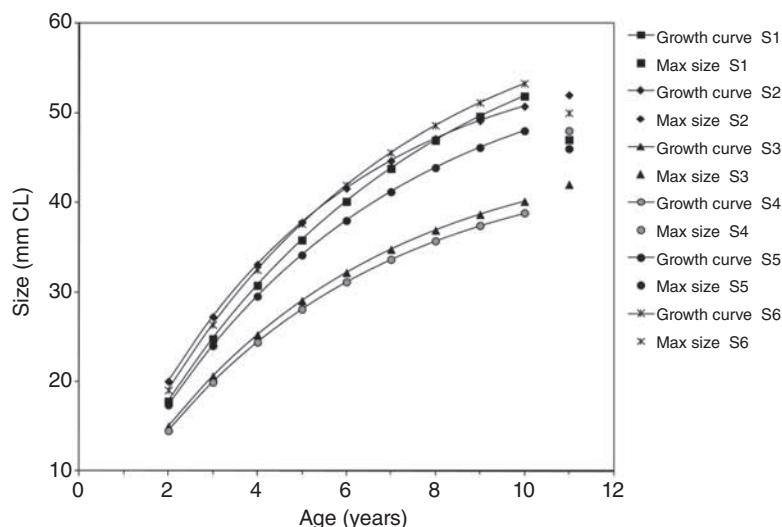


Fig. 12.5 Growth curves of male *Nephrops* at different locations in the Firth of Clyde (S1–S6), and corresponding maximum sizes in the catches. Tuck, I.D., Chapman, C.J. & Atkinson, R.J.A (1997a). Reproduced with permission of Oxford University Press.

Differences in growth rates can occur over quite small spatial scales. Within the same biological population, there may be major differences in the size structure and growth parameters of patches of *Nephrops* inhabiting smaller areas with different environmental and/or population characteristics (de Figueiredo, 1984; Tully & Hillis, 1995; Tuck *et al.*, 1997a; Thompson *et al.*, 1998). In the Clyde (West Scotland), the K values for male *Nephrops* were found to range between 0.16 and 0.22 year $^{-1}$, and the values of L_{∞} between 45.5 and 65.5 mm CL (Tuck *et al.*, 1997a; Fig. 12.5), on the Portuguese south and south-west coast, they were in the range 0.21–0.28 year $^{-1}$ and 61.5–71.5 mm CL (de Figueiredo, 1984), and Ayza *et al.* (2011) reported values of 0.38–0.41 year $^{-1}$ and 88.3–94.9 mm CL for north and central Portuguese stocks. These ranges are wider than the reported differences in growth parameters between, for example, the Icelandic and the Bay of Biscay *Nephrops* stocks. The exact reasons for the variability in growth rates are difficult to establish, since they are likely to be the combined effect of several driving forces (temperature, sediment particle size, food availability, population density, fishing pressure, etc.), each of which may have different and possibly interactive effects.

In view of the above, it is impossible to draw firm conclusions on the reasons why size at age

differs – or seems to differ – between *Nephrops* stocks on a wider geographical scale. Some of the growth curves reported in the literature may not be representative for the stock as a whole, and may well have appeared different if the underlying data had been obtained from another location within the same stock, with other environmental and/or population characteristics. The high level of intra-population variability also poses a problem for the analytical stock assessments where growth relationships are used to set the time scale in analyses based on size data.

12.3.2 Reproduction

Sexual maturity

Estimates of the size at 50% maturity (L_{50}) are available for many *Nephrops* stocks, albeit mostly for females only. Estimates of the L_{50} for female *Nephrops* differ between stocks but also depend on the method used: ovary maturation stage, the presence of spermatophores, or ovigerous (berried) condition (Table 12.3). Estimates of L_{50} derived from data on the proportions of berried females are usually larger than those based on the other criteria. Berried females are much less likely to emerge from their burrows after spawning (or at least their

Table 12.3 Size (mm CL) at 50% maturity of female *Nephrops*.

Stock/fishing area	Method used					Source
	A	B	C	D	E	
Iceland					25	Eiríksson (1982) in ICES
All Scottish stocks	25–27					Afonso-Dias & Bailey (1998)
Clyde	27–28					Bailey (1984)
Clyde	22–34					Tuck <i>et al.</i> (2000)
Sound of Jura	23					Bailey (1984)
Irish Sea West			25–26			Hillis (1979)
Irish Sea West			23.5			Briggs (1988)
Irish Sea West	22.9	21.2		23–28		McQuaid <i>et al.</i> (2006)
Botney Gut – Silver Pit	27.5					Redant (1994)
Bay of Biscay	24–25					Fontaine & Warluzel (1969)
Bay of Biscay	23–24	22–23				Morizur (1983)
North Portugal			50.7			Ayza <i>et al.</i> (2011)
Central Portugal			46.9			Ayza <i>et al.</i> (2011)
Algarve	29					de Figueiredo (1982)
Algarve	30					Orsi Relini <i>et al.</i> (1998)
Algarve			29.5			Arrobas (1982)
Alboran Sea	36					Orsi Relini <i>et al.</i> (1998)
Catalan Sea	30–31		32.5			Sardà (1991)
Catalan Sea	30					Orsi Relini <i>et al.</i> (1998)
Ligurian Sea	32					Orsi Relini <i>et al.</i> (1998)
Tyrhenian Sea	32					Orsi Relini <i>et al.</i> (1998)
Strait of Sicily			30–32			Bianchini <i>et al.</i> (1998)
Adriatic Sea	30					Orsi Relini <i>et al.</i> (1998)
Adriatic Sea – Pomo Pit				≈26		Froglio & Gramitto (1981)
Adriatic Sea – off Ancona				≈32		Froglio & Gramitto (1981)
Euboikos Gulf (Greece)	33					Orsi Relini <i>et al.</i> (1998)
Pagasetikos Gulf (Greece)	28.1					Mente <i>et al.</i> (2009)

A = Ovary maturation stage (plus ovigerous condition).

B = Presence/absence of spermatophores.

C = Ovigerous condition.

D = Morphometrics.

E = Unknown or not specified.

range and duration of emergence is reduced) and therefore their true proportions are likely to be underestimated, especially in samples that are collected by trawling. This results in a shift of the maturity ogive to the right and an overestimate of the size at 50% maturity (Redant, 1994). Generally speaking, female *Nephrops* mature at a size between 23 and 30 mm CL in the relatively shallow-water populations of north-western and northern Europe, and at a size between 28 and 36 mm CL in the deep-water populations off Portugal and in the Mediter-

ranean (Table 12.3; but note much larger sizes at maturity in Portuguese stocks estimated by Ayza *et al.* (2011) based on proportions of berried females, corresponding to large maximum sizes in the populations). The corresponding age at 50% maturity, 3–4 years, however, is roughly the same in all areas. In some populations, there is evidence of a decrease in the proportions of mature females in the largest size classes, which suggests that not all of the older females spawn every year (Sardà, 1991; Redant, 1994).

As with growth, there can be major differences in sexual maturity parameters within the same biological population. In the Clyde (west Scotland), L_{50} estimates for female *Nephrops* (based on oocyte counts) were found to vary between 22.5 and 33.5 mm CL (Tuck *et al.*, 2000), i.e. over a range that is wider than the overall range of L_{50} estimates reported for all north-western and northern *Nephrops* stocks combined (Table 12.3). In all parts of the population concerned however, females appeared to mature at the same age (3–3.5 years), which seems to confirm that maturation is age dependent rather than size dependent (Tuck *et al.*, 2000).

Male sexual maturity has been studied for Irish Sea *Nephrops*, using both primary (presence of spermatophores in the vasa deferentia) and secondary sexual characteristics (allometric changes in the morphology of the appendix masculina and the cutter claw) (McQuaid, 2002; McQuaid *et al.*, 2006). Although in the Irish Sea, 50% of the males are capable of producing spermatophores at a size of 15 mm CL, they only develop a fully grown appendix masculina – and hence become physically capable of mating with a female – at a size of 24–27 mm CL and an age of 3 years (Farmer, 1974a; McQuaid, 2002; McQuaid *et al.*, 2006). Based on changes in morphometric allometry, McQuaid *et al.* (2006) estimated male size at maturity at 26–31 mm CL on Irish Sea grounds, similar to the 26 mm CL estimated by Farmer (1974a). Morphometric estimates by Tuck *et al.* (2000) for Clyde *Nephrops* ranged from 29–46 mm CL. Mouat (2004) also used morphometrics to give estimates of 23–45 mm CL for male size at maturity on various Scottish grounds, with as much variability within as between grounds, probably related to local differences in growth rates.

Maturity has been examined in female *Metanephrops* through examination of ovary stages and the presence of eggs on the pleopods, and for males through examination of the testes. In the early 1970s in New Zealand, macroscopic condition stages were developed for ovary, egg and testes development (Fenaughty, 1989). These stages for ovary and egg development are still used on research surveys, and an adaptation has been developed for Ministry of Fisheries observers. This work

also used the size of the smallest ovigerous female as an indicator of the size at onset of maturity (Fenaughty, 1989). Size at maturity varies between areas (Tuck & Dunn 2011).

Reproductive cycle

An overview of the geographical differences in the reproduction cycle of *Nephrops* is given in Table 12.4. The periods of hatching and spawning, and the length of the incubation period vary with latitude, and the breeding cycle changes from annual to biennial as one moves from south to north.

In populations where the reproduction cycle is essentially annual (such as in the Mediterranean, around the Iberian peninsula, in the Bay of Biscay, the Irish Sea and most of the North Sea), it can be summarized as follows. Mating takes place in winter or spring, while the females are still in the soft, immediate post-moult condition (Farmer, 1975). Throughout the spring and summer months, the ovaries mature – a process that is associated with marked changes in the biochemical composition of the ovaries and the hepatopancreas (Tuck *et al.*, 1997c; Rosa & Nunes, 2002) – and egg-laying takes place in late summer or early autumn. It is generally assumed that berried females remain in their burrows until the next hatching period in late winter or early spring. A recent study by Aguzzi & Sardà (2007), however, indicates that burrow emergence is not inhibited in berried females, but rather that there is a reduction in the range and duration of emergence. Shortly after hatching, the females moult and mate again, and the cycle resumes.

Incubation of the abdominal eggs is strongly temperature dependent, and increases from approximately 5.5 months at 15°C to approximately 10 months at 8°C (Dunthorn, 1967). As the average temperature decreases, the duration of the incubation period increases, hatching is delayed until it starts to overlap with the spawning season (which means that there is insufficient time left for the females to take part in that year's reproduction cycle), and the breeding cycle becomes biennial (Table 12.4). Biennial breeding cycles are typical for the cold-water *Nephrops* stocks around Iceland and the Faeroe Islands (Andersen, 1962; Eiríksson,

Table 12.4 *Nephrops* spawning and hatching periods.

Stock/fishing area	J	F	M	A	M	J	J	A	S	O	N	D	Source
Iceland													Eiríksson (1970)
Faeroe													Andersen (1962)
Scotland (all stocks)													Thomas & de Figueiredo (1965)
Farn Deep													Symonds (1972)
Botney Gut – Silver Pit													Redant (1987)
Irish Sea West													O'Riordan (1964)
Bay of Biscay													Fontaine & Warluzel (1969)
Bay of Biscay													Conan (1978)
North Galicia													Fariña (1989)
Portugal													de Figueiredo & Barraca (1963)
Catalan Sea													Sardà (1991)
Ligurian Sea													Orsi Relini & Relini (1989)
High Adriatic													Karlovac (1953)
Adriatic													Froglio & Gramitto (1981)
Hatching period													
Spawning period													

1970, 1993; Nicolajsen & Eiríksson, 1990). Also in warmer temperature regimes however, there is evidence that not all females reproduce annually (Bailey, 1984; Sterk & Redant, 1989; Sardà, 1991; Redant, 1994). As a female grows older, spawning is delayed by the combined effects of recovery from moulting and then ovary maturation, until a point is reached where ovary resorption occurs and the female misses out a year of egg carrying (Bailey, 1984). Whether reproduction proceeds biennially from then onwards is not clear.

It is tempting to view temperature as the regulatory factor of the breeding cycle, and most observations seem to confirm this assumption. The fact, however, that also in isothermal environments the breeding cycle of *Nephrops* is closely phased, with clear-cut spawning and hatching seasons (Orsi Relini & Relini, 1989), suggests that there may be other driving forces as well, although there is no indication what these forces might be.

Fecundity

Potential and effective fecundity have been studied in many *Nephrops* stocks. Estimates of potential fecundity are derived from oocyte counts in the ovary, and estimates of effective fecundity from the numbers of eggs close to hatching (so-called stage D). The latter, however, should be treated cautiously, especially when the samples are collected by trawling, since this may cause abrasion of the abdominal egg clump and hence additional loss of eggs, in the order of 10–20% (Chapman & Baltynne, 1980).

Potential fecundity is exponentially related to female body size (Fig. 12.6), and increases from 600–1200 oocytes in females of 25 mm CL, to 3200–4800 oocytes in females of 45 mm CL. Effective fecundity is substantially lower than potential fecundity in all *Nephrops* stocks (Fig. 12.7), but the level of egg loss differs widely between areas. In

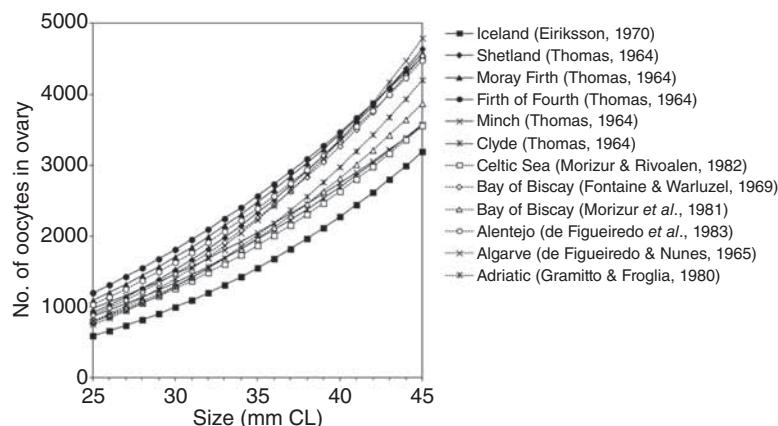


Fig. 12.6 Potential fecundity of female *Nephrops* in different areas or stocks.

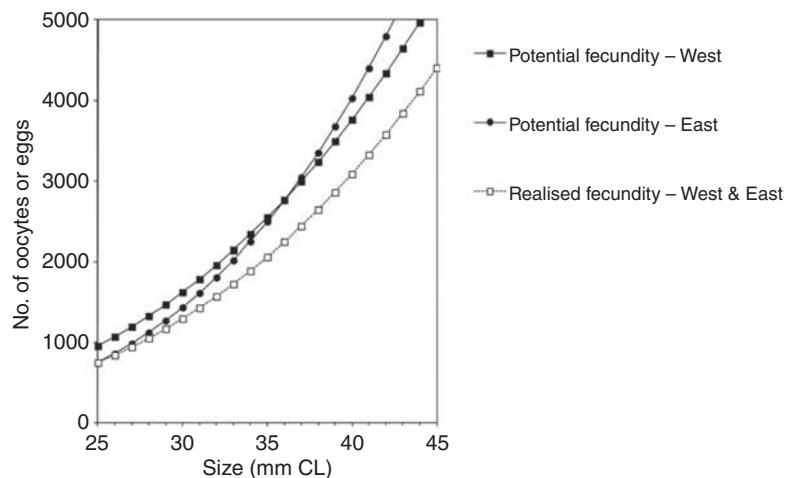


Fig. 12.7 Potential and realized fecundity of female *Nephrops* in the Irish Sea (after McQuaid et al., 2009).

the Bay of Biscay and the Mediterranean, the loss of eggs from ovary to stage D is 40–50% (Gramitto & Froglio, 1980; Morizur, 1981; Morizur *et al.*, 1981; Mori *et al.*, 1998), while on the Portuguese coast it is as high as 70–75% (de Figueiredo & Barraca, 1963; de Figueiredo *et al.*, 1983). In Irish Sea stocks, McQuaid *et al.* (2009) estimated egg losses between extrusion and egg maturity of 40% at 25 mm CL increasing to 65% at 40 mm CL, and noted that as few as 20% of oocytes survive to become free-swimming larvae. Extrusion failure and failure to adhere to the pleopods have been put forward as the main reasons for the loss of eggs

between ovary and first abdominal stage, and unsuccessful embryonic development, predation and cannibalism (on the abdominal egg clumps) as the main reasons for the loss of eggs during the actual incubation period (de Figueiredo & Nunes, 1965; Morizur *et al.*, 1981).

Metanephrops challengeri fecundity is considered to be low, and only between 11 and 790 eggs have been recorded on pleopods at the end of the incubation period for females ranging in size from 35–56 mm CL (Wear, 1976; Fenaughty, 1989). Choi *et al.* (2008) noted similar levels of fecundity for *M. thomsoni*. Studies in Australia also support

the suggestion that *Metanephrops* fecundity is somewhat lower than that for *Nephrops* (Phillips, 1992). However, given that the eggs are incubated on the pleopods, eggs are subject to loss throughout the incubation period, and also during the collection process, particularly by trawl sampling. Egg size appears to be larger in *M. challengereri* (Wear, 1976) than *Nephrops* (Farmer, 1975), which may partly explain the lower fecundity.

12.3.3 Food and feeding

Nephrops is an opportunist predator and scavenger (Thomas & Davidson, 1962), making short foraging excursions in the vicinity of its burrow (Chapman & Rice, 1971; Chapman *et al.*, 1975). Foraging mainly occurs during periods of subdued light, although it is likely that larger individuals spend a greater proportion of their time in foraging (Chapman, 1980). A study by Aguzzi *et al.* (2009a) indicated that in conditions of subdued light on the continental slope in the western Mediterranean other burrowing species co-occurring with *Nephrops* timed their emergence to minimize encounters with this predator. Descriptions of feeding methods are given by Yonge (1924) and Thomas & Davidson (1962), based on aquarium observations. Active prey are captured by grasping with chelipeds and walking legs, and the walking legs are also used to close around passive food items. Food is conveyed to the mouth using the anterior walking legs assisted by the maxillipeds.

Similar to many other decapods, *Nephrops* possesses a ‘gastric mill’ – a set of calcareous ossicles operated by gastric muscles in the cardiac-foregut (stomach). The actions of the mouthparts and gastric mill, breaking up food and grinding into a fine powder, are described in detail by Yonge (1924) (see also Farmer, 1974c). As noted by Höglund (1942), this vigorous mastication of the food makes it difficult to identify food items from examination of stomach contents. Despite this difficulty, several studies have described the diet of *Nephrops* in various parts of its range, relying on fixing with formaldehyde to prevent further digestion of stomach contents before examination (Parslow-Williams *et al.*, 2002). Organisms with hard parts are likely to be slightly over-represented in the

stomach samples, partly for reasons of identifiability, but also because of shorter digestion times for soft tissues. Sardà & Valladares (1990) calculated that soft prey items such as polychaetes are likely to be underestimated by about 10%. For the purposes of drawing broad conclusions about diet composition, this source of bias can probably be ignored.

The results of stomach contents analyses indicate that *Nephrops* is an unselective feeder, and representation of different items in the stomach appears to be governed by prey abundance rather than any feeding preference. Daily rations of 0.40–1.76 g stomach content dry weight per 100 g individual wet weight have been estimated for *Nephrops*, which is high compared with other decapods crustaceans occupying a similar niche, perhaps because of its low trophic diversity (Cristo & Castro, 2005). Crustaceans, polychaetes, molluscs and, to a lesser extent, echinoderms appear to make up the bulk of the diet. In Scottish samples Thomas & Davidson (1962) found 67% of *Nephrops* stomachs to contain crustaceans, 66% to contain polychaetes, 64% to contain molluscs and 50% to contain echinoderms. A wide range of species were represented within each of these groups. For example, the most abundantly represented crustacean groups were ostracods, amphipods and decapods up to the size of *Nephrops* itself. For *Nephrops* in the Firth of Clyde, Parslow-Williams *et al.* (2002) showed that up to half of the total weight of ingested items comprised crustaceans. Crustaceans in the diet appear to give a lower energetic return than soft-bodied prey items such as polychaetes, but do serve as a source of essential minerals such as calcium (Parslow-Williams *et al.*, 2002).

Generally similar results have been obtained in various other parts of the geographical range: Andersen (1962) lists various polychaetes and molluscs in *Nephrops* stomachs from the Faeroes; Fontaine (1967), Fontaine & Warluzel (1969) and Lagardère (1977) list molluscs, crustaceans, polychaetes and some other groups from the Bay of Biscay; Gual-Frau & Gallardo-Cabello (1988), Cristo (1998) and Cristo & Cartes (1998) list crustaceans, molluscs, polychaetes, echinoderms, fish and some other groups from the south of Portugal and in the Mediterranean. Comparison at the higher taxonomic levels between the studies of Thomas &

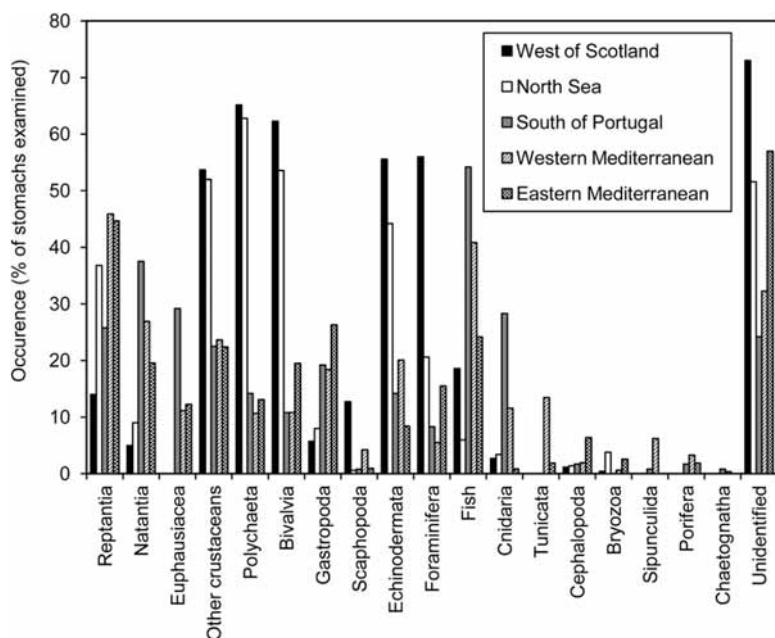


Fig. 12.8 Diet of *Nephrops* in different parts of its range: occurrence of food items identified in the contents of the gastric-foregut (stomach). Data for west of Scotland and the North Sea from Thomas & Davidson (1962); data for Portugal and the Mediterranean from Cristo & Cartes (1998).

Davidson (1962) and Cristo & Cartes (1998) shows similar diet composition in Scottish, Portuguese and Mediterranean samples (Fig. 12.8). Some differences are also apparent, such as the absence of Euphausiacea and greater importance of echinoderms in the Scottish samples, but the overall picture is one of relatively constant diet composition. Cristo & Cartes (1998) came to similar conclusions with regards to different areas of the Mediterranean and southern Portugal, and also confirmed the previous finding by Gual-Frau & Gallardo-Cabello (1988) (for southern Portugal) that the diet does not vary seasonally. As would be expected, the similarity across geographical areas does not extend to the level of species. Whereas, for example, *Crangon* spp. were found in the stomachs of Scottish *Nephrops* (Thomas & Davidson, 1962), the closest counterparts in southern European samples would be species of *Aristeus*, *Sergestes* and *Solenocera* (Lagardère, 1977; Gual-Frau & Gallardo-Cabello, 1988; Cristo, 1998; Cristo & Cartes, 1998).

Suspension feeding appears to be rare in larger decapods, and Thomas & Davidson (1962) sug-

gested that *Nephrops* does not ingest particles below 1 mm in diameter. Farmer (1974c) noticed that the exopodites of the mouthparts in *Nephrops* are continuously waving, and speculated that the function of their plumose setae might be to remove suspended food particles that might otherwise foul the mouthparts during feeding. The results of Loo *et al.* (1993) suggest instead that *Nephrops* are capable of active suspension feeding by this method. In experiments where *Nephrops* were offered planktonic food items, these authors found evidence that *Nephrops* are able to retain particles down to a size of 200 µm. Both *Nephrops* and European lobster (*Homarus gammarus*) were able to clear water of brine shrimp nauplii, about 600 µm in size, and *Nephrops* appeared also to ingest rotifers averaging 200 µm in size. Haemocyanin concentration in the blood (an index of nutritional state) declined more slowly in *Nephrops* held in unfiltered sea water than in those held in filtered sea water, indicating a significant nutritional gain from suspension feeding. It has been suggested that this may contribute to maintaining high production of *Nephrops* in the Skagerrak and Kattegat stocks.

owing to high organic enrichment in this area (ICES, 2011c).

No account of feeding behaviour in *Nephrops* would be complete without mentioning cannibalism. Sardà & Valladares (1990) found that mortality due to cannibalism in groups of *Nephrops* held in laboratory tanks was 12% over 16 days if the animals were provided with other sources of food, and 36% in starved *Nephrops*. It is not known how significant a contribution cannibalism makes to the feeding of *Nephrops* in the wild, but it is widely considered that it acts as a factor constraining the recruitment of juveniles to the stock under conditions of high adult stock density.

A preliminary investigation into *Metanephrops* feeding was conducted from samples collected during exploratory research fishing in the early 1970s (Hine, 1976). Stomach contents included fish, molluscs, crustaceans, annelid worms, foraminifera and unidentified material. No differences in feeding were identified between size, sex or locality. A similar apparently indiscriminate pattern of feeding has been described for *M. andamanicus* (Berry, 1969). Choi *et al.* (2008) described the diet of *M. thomsoni* in the East China Sea, finding crustaceans and polychaetes to be the predominant food items found in the foregut, along with small quantities of fish bones and scales. Wassenberg & Hill (1989) found differing proportions of fish, crustaceans and squid in the foregut contents of three *Metanephrops* species around Australia: equal proportions of fish and crustaceans in *M. andamanicus*, mainly fish and seldom squid in *M. boschmai* and mainly crustaceans in *M. australiensis*. They suggested that these species scavenged or attacked mobile fauna, tearing off appendages.

12.3.4 Activity patterns

Burrowing behaviour

Activity patterns, and specifically burrowing and emergence behaviour, are a strong determinant of diurnal and seasonal variability in catch rates (e.g. Aguzzi & Sardà, 2008a). It was not until the mid-1960s that evidence was produced of the existence (Priestley & Thomas, 1964) and the semi-permanent

nature (Dybern & Höisæter, 1965) of *Nephrops* burrows. *Nephrops* burrows vary in structure and size, from simple U-shaped tunnels with a main entrance and a narrow rear-opening, to complex structures with three or more large openings and several small vertical shafts. Typical *Nephrops* burrows are 20–30 cm deep and have a distance between main entrance and rear-opening of 50–80 cm (Rice & Chapman, 1971; Hillis, 1974). Newly settled post-larvae and early juveniles do not seem to make their own burrows, but to live in association with larger animals (Tuck *et al.*, 1994).

Burrow densities have been studied with underwater TV cameras on various Atlantic and Mediterranean *Nephrops* grounds (ICES, 2003, 2011a,b; Smith *et al.*, 2003; Smith & Papadopoulou, 2003; Aguzzi *et al.*, 2004a; Tuck *et al.*, 2004; Morello *et al.*, 2007). Mean densities generally range between 0.1 and 1.6 m⁻² (Table 12.5), but much lower densities (0.004–0.1 m⁻²) have been recorded in the Aegean Sea (Smith *et al.*, 2003).

Several studies indicate that *Nephrops* burrow density is related to sediment particle size. In Scottish *Nephrops* populations, high burrow densities are usually seen on coarse muds with high proportions of sand, and low burrow densities on fine muds with a low sand content (Chapman & Bailey, 1987). Similar studies in the Irish Sea, albeit on a different range of sediment types, found the converse (Hillis, 1987, 1988; Tully & Hillis, 1995), suggesting that the relationship between *Nephrops* burrow density and sediment particle size is not simply linear. Afonso-Dias (1998) (cited by Campbell *et al.*, 2009b) suggested a dome-shaped relationship, with highest densities in medium-grained muds which are cohesive enough to allow *Nephrops* to construct stable burrows (Fig. 12.9). Burrow collapse in less cohesive sediments leads to lower density in coarser muds, while the construction of more extensive burrow systems in the finest muds leads to larger areas of individual occupancy and hence greater competition for space and lower densities. Campbell *et al.* (2009b) confirmed the existence of a dome-shaped relationship between burrow density and percentage of silt and clay in the sediment for the North Minch stock, but noted a departure from this relationship on an isolated

Table 12.5 *Nephrops* burrow densities for different stocks, estimated by underwater TV surveys.

Area	Stock	Range of mean burrow density (m ⁻²)	Reference
Sweden/Denmark	Kattegat/Skagerrak	0.28–0.32	ICES (2011c)
North Sea	Fladen Ground	0.17–0.35	ICES (2011c)
	Noup	0.15–0.63	ICES (2011c)
	Moray Firth	0.14–0.48	ICES (2011c)
	Firth of Forth	0.38–1.14	ICES (2011c)
	Farn Deep	0.25–0.67	ICES (2011c)
West of Scotland	North Minch	0.25–0.80	ICES (2011b)
	South Minch	0.26–0.67	ICES (2011b)
	Stanton Bank	0.24–0.27	ICES (2003)
	Sound of Jura	0.50–1.34	ICES (2011b)
	Firth of Clyde	0.33–1.13	ICES (2011b)
Irish Sea	Western Irish Sea	0.88–1.16	ICES (2011b)
	Eastern Irish Sea	0.33–0.43	ICES (2011b)
West of Ireland	Aran Grounds	0.56–1.43	ICES (2011b)
	Galway Bay	0.42–1.61	ICES (2011b)
	Slyne Grounds	0.40–0.85	ICES (2011b)
Celtic Sea	Smalls Ground	0.47–0.63	ICES (2011b)
Western Mediterranean	Catalan coast	0.81	Aguzzi <i>et al.</i> (2004a)
Adriatic Sea	Pomo Pit	0.58–0.69	Morello <i>et al.</i> (2007)
Aegean Sea	Mytilini	0.046	Smith <i>et al.</i> (2003)
	Limnos	0.025	Smith <i>et al.</i> (2003)
	Thasos	0.014	Smith <i>et al.</i> (2003)
	Skyros	0.019	Smith <i>et al.</i> (2003)
	Skiathos	0.017	Smith <i>et al.</i> (2003)
	Pagasetikos	0.12	Smith <i>et al.</i> (2003)
	Evoikos	0.004	Smith <i>et al.</i> (2003)

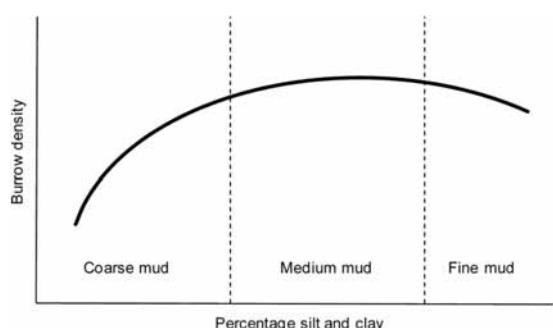


Fig. 12.9 Relationship of *Nephrops* burrow density with sediment composition. Campbell, N., Allan, L., Weetman, A. & Dobby, H. (2009b). Reproduced with permission of Oxford University Press.

mud patch, presumably owing to local environmental factors. They also found a linear relationship on the Fladen Ground, variable between years but always with highest densities on the finest sediments. Possibly this is a consequence of generally lower densities on this ground compared with North Minch, reducing the scope for spatial competition to constrain density. Other plausible hypotheses to account for this pattern could be advanced, however, and it seems likely that the relationship between burrow density and sediment composition is variable between stocks.

Nephrops spend most of their time inside their burrow or laying at its entrance, and only leave the safety of their shelter to forage, for moulting and for social interactions such as mating and agonistic behaviour (Farmer, 1974b; Chapman & Howard, 1979; Chapman, 1980). There is some evidence of

homing behaviour in *Nephrops*, but also of shifts from one burrow to another, and fighting over the possession of burrows is a common feature, particularly among larger males (Chapman & Rice, 1971). Katoh *et al.* (2008) described fighting behaviour in male *Nephrops* and demonstrated the important role of chemical signals in the urine in mediating dominance behaviour.

Metanephrops species are also known to burrow, and burrow counts are used as an index of abundance for *M. challengereri* in New Zealand. Burrow densities observed for these populations at the lower end of the range observed for *Nephrops* (typically 0.03–0.13 m⁻²), and burrow systems generally appear to be relatively short, simple U-shaped tunnels, although the depth in which *Metanephrops* occurs (300–500 m) has prevented the scuba-based techniques employed to investigate burrow structure to some European *Nephrops* stocks.

Diurnal activity patterns

A considerable part of our initial knowledge on diurnal activity patterns in *Nephrops* was based on observed patterns in trawl catch rates, in both the commercial fisheries and research vessel surveys (primarily in north-western European waters). In addition, there also was substantial evidence from direct *in situ* investigations, albeit mostly in shallow waters, by means of underwater TV and scuba diver observations. The combined data show that the diurnal activity patterns are clearly depth related (Table 12.6). In shallow waters (<30–40 m), peak emergence occurs during night time, and catch rates are at their lowest during daytime (e.g. Chapman & Rice, 1971; Hillis, 1971b; Chapman

et al., 1972; Chapman & Howard, 1979). At intermediate depths (40–100 m), the single night peak splits into two periods of peak emergence, one around dawn and the other around dusk, which gradually move from the nightly into the day-time hours as depth increases (e.g. Höglund & Dybern, 1965; Simpson, 1965; Hillis, 1971b; Chapman *et al.*, 1972; Farmer, 1974b; Chapman & Howard, 1979; Redant & De Clerck, 1984). In deeper waters (100–200 m), the two peaks merge into a single peak during day-time, and catch rates are at their lowest during night-time (e.g. Höglund & Dybern, 1965; Simpson, 1965; Hillis, 1971b). The patterns described here are generalized patterns, and there are many examples of datasets where single or successive 24-hour cycles depart from the general pattern, for reasons which are not always clear.

In the 1970s, it was assumed that hunger state and light intensity were the triggering factors for the circadian activity rhythm in *Nephrops*, with hunger state being the driving force and light intensity – or changes in light intensity – being the regulatory factor for the actual emergence from the burrows (Chapman, 1980). At depths between 20 and 200 m, maximum emergence was observed at light intensities between 10⁻⁵ and 1 lux (Hillis, 1971b; Chapman *et al.*, 1972), and this was considered to be the ‘optimum light intensity range’ to allow foraging and avoid predation, while at the same time avoiding retinal damage due to exposure of the highly sensitive eye to excessive light (Chapman, 1980).

However, since then increasing evidence has shown that the regulatory mechanisms of emergence and hiding behaviour are much more complex, and probably not entirely exogenous.

Table 12.6 Periods of peak emergence of *Nephrops* from burrows.

Depth	Time of day		
	Night	Day	Night
Shallow waters <30–40 m			
Intermediate depths 40–100 m			
Deep waters 100–200 m			

Firstly, observations on animals held in captivity suggested the existence of endogenous activity rhythms (Atkinson & Naylor, 1973, 1976; Naylor & Atkinson, 1976; Hammond & Naylor, 1977). Secondly, observations on Mediterranean deep-water stocks of *Nephrops* revealed the existence of diurnal activity patterns that did not match the above-mentioned ‘optimum light intensity range’, which suggests that (i) *Nephrops* may be sensitive to changes in the intensity of particular wavelengths (probably around 480 nm), rather than to light intensity as such, and (ii) other external factors than light (e.g. the availability of nyctheremal prey species) may play a role as triggering factor of the diurnal emergence behaviour (Froglio, 1972; Froglio & Gramitto, 1981, 1985; Aguzzi *et al.*, 2003, 2009d). Behavioural and physiological rhythms in *Nephrops* have recently been reviewed by Aguzzi & Sardà (2008a). Recent research, particularly into *Nephrops* activity patterns on the shelf continental slope of the Mediterranean has done much to elucidate the complex and interactive roles of depth, light intensity, current fluctuations, satiety, haemolymph melatonin levels, sex and ovigerous state on diel and other rhythms of burrow emergence and feeding activity (Aguzzi & Sardà, 2008b; Aguzzi *et al.*, 2004b, 2007, 2008, 2009a,b,c; Chiesa *et al.*, 2010).

Emergence has been inferred from catch rates in New Zealand *Metanephrops* fisheries (300–500 m) and is consistently highest during the hours of daylight, and lowest during the hours of darkness (Tuck, 2010), and there is some suggestion that the relative rates of emergence over the dawn and dusk period vary seasonally and spatially. Australian studies (Ward & Davis, 1987) suggest that *M. australiensis* has peak emergence at dawn and dusk, while *M. andamanicus* shows no detectable diel pattern. Work by Paramo & Saint-Paul (2012) at depths of 200–550 m in the Caribbean indicates nocturnal burrow emergence in *M. binghami*.

Acoustic tagging of *Metanephrops* has been trialled in New Zealand as a technique to investigate emergence patterns, following Chapman *et al.* (1974, 1975). Shallow water tests indicated that the acoustic signal from the tags used would be obscured when a lobster was in a burrow, and the signal from animals released at 420 m

showed strong evidence of a 12.6-hour cycle in emergence, and also greater emergence during hours of daylight.

Seasonal activity patterns

Seasonal activity patterns are most pronounced in female *Nephrops*, and are closely related to the reproductive cycle. Shortly after spawning, the berried females retreat in their burrows (but see below), and they mostly stay there for the entire duration of the incubation period (in the majority of stocks, from late summer or autumn until late winter or spring). Reduced commercial catch rates of immature females and males during the winter in some areas (e.g. southern North Sea, Celtic Sea, Bay of Biscay), suggests that these also tend to spend more time in their burrows during winter than during the rest of the year, but this pattern is much less pronounced than in berried females. As a combined result of these seasonal activity patterns (i) fishery catch rates are usually lower in winter than in summer; (ii) winter catches predominantly consist of males, certainly in the larger, adult size classes; and (iii) berried females are virtually absent from the winter catches (e.g. Thomas & de Figueiredo, 1965; Arrobas, 1982; Redant, 1987; Sardà, 1991; Briggs, 1995).

In late winter or spring, the females re-appear from their burrows, to hatch their eggs. In some areas, there is a small dip in female catch rates shortly afterwards, which may be associated with the spring moult (Redant, 1987). After the hatching and mating season, the females spend at least as much of their time as the males and maybe more, foraging outside the burrows. This results in (i) increased overall fishery catch rates throughout the summer and (ii) sex ratios in the catch close to 1 : 1 or in favour of the females up to the next spawning period in late summer or autumn (same references as above).

Work by Aguzzi *et al.* (2007) suggests that feeding burrow emergence is not inhibited in ovigerous female *Nephrops*. They describe instead a pattern of reduced duration and range of emergence, characterized as ‘doorkeeping’ behaviour. This finding is consistent with the observation that ovigerous females are more commonly caught in

baited traps than trawls, suggesting that they will take advantage of the opportunity of food sources close to burrow entrances.

The seasonal patterns described here apply to populations where spawning is essentially annual. In populations where spawning is biennial, the female part of the stock falls into two fractions, spawning in alternate years. Each fraction will show the typical hiding behaviour when berried, but since this affects only half (or thereabout) of the adult female population, the associated changes in, for example, sex ratios in the fishery catch will be much smaller than in stocks where the majority of adult females spawn every year (ICES, 1982). Another striking exception to the general pattern is the Farn Deep stock (south-western North Sea), where female catch rates peak during the winter months and are at their lowest in the summer (Symonds, 1972a; ICES, 2003).

Metanephrops populations show seasonal patterns in catch rate and sex ratio in catches related to patterns of moulting (generally being less available to trawl gear when moulting), but unlike *Nephrops* ovigerous females do not appear to show a reduction in availability to fishing.

Hypoxia

Hypoxic conditions, occasionally observed, for example in the Kattegat and the Adriatic (Froglio & Gramitto, 1982; Bagge, 1988; Hallbäck & Ulmestrond, 1990), can cause severe disruption of the natural emergence patterns and even mass mortality in *Nephrops* populations. When oxygen saturation in the bottom water layers drops below about 50%, *Nephrops* are forced up from their burrows in search of oxygen (Bagge & Munch-Petersen, 1979). Under moderate hypoxia, locomotory activity declines and the animals raise their bodies on stilted legs to increase oxygen availability. Eriksson *et al.* (2006) showed that berried females exposed to hypoxic conditions irrigated their brood using their pleopods, thereby enhancing their survival. Oxygen saturation levels below about 25% are lethal within 24 hours, particularly in juveniles which are more sensitive to hypoxia than adults (Eriksson & Baden, 1997). Moderate hypoxia and its associated behavioural responses makes *Neph-*

rops much more vulnerable to trawling, and the increased catch rates may, at least in the beginning, give the false impression that stock density is increasing. Severe hypoxia can wipe out entire *Nephrops* populations, and it may take years before the stock recovers to the pre hypoxia situation (Hallbäck & Ulmestrond, 1990; ICES, 1990).

Baden & Neil (2003) showed that manganese accumulation on the appendages is a biomarker for exposure to hypoxia in *Nephrops*, and that manganese interferes with chemoreception. Krång & Rosenqvist (2006) found that exposure to manganese significantly affected food search behaviour in *Nephrops*, reaction times to food odour stimuli being more than doubled compared with individuals that had not been exposed.

12.4 Population dynamics

12.4.1 Population structure

Larval dispersal

The planktonic larvae of *Nephrops* pass through three developmental stages (first, second and third zoea) before they acquire their post-larval benthic life-form and move to the seabed (Farmer, 1975). Larval development is temperature dependent, and takes from approximately 7 weeks at 8°C to approximately 3 weeks at 18°C (Farmer, 1975; Dickey-Collas *et al.*, 2000b).

Larval settlement is a critical phase in the life history of *Nephrops*, especially since the larvae need to settle in areas of suitable sediment to be able to survive (Bailey *et al.*, 1995). When dispersion of the larvae is high, or when the area inhabited by the parental stock is very small, it may not be possible to sustain a self-regenerating population against the losses during the planktonic larval stages (Hill & White, 1990). In the western Irish Sea, hatching of the *Nephrops* larvae was found partly to coincide with the formation of a cyclonic near-surface gyre, centred on the mud patch of their parental population. The gyre retains the larvae over the area of suitable sediment and thus provides a mechanism that helps to reduce the loss of larvae when they return to the seabed (Brown *et al.*, 1995; Hill *et al.*, 1996). There are indications of similar

retention mechanisms in several other areas, including the Kattegat and Skagerrak (between Denmark and Sweden), the North Sea, the Minches (on the west coast of Scotland) and the Celtic Sea (Bailey *et al.*, 1995; Brown *et al.*, 1995; Hill *et al.*, 1997; Øresland, 1998). The existence of such retention mechanisms however, also has important implications for stock management, since it means that the stocks concerned are physically isolated from each other, and that the chances for replenishment of a depleted stock with larvae from a neighbouring stock are virtually non-existent (Brown *et al.*, 1995). A modelling study by Marta-Almeida *et al.* (2008) suggests a high level of advection of larvae from hatching areas in southern Portugal, most being lost to deeper waters where successful settlement is unlikely, others likely to recruit to adjacent stocks. Only 0.2–0.5% of hatching larvae were estimated to self-recruit to the Algarve stock, but the extent to which this limits recruitment to the adult stock is uncertain.

In contrast with *Nephrops*, for which the period between hatching and moulting to the megalopa stage is in the order of one month, larval development in *Metanephrops* species is extremely brief. Wear (1976) found what appeared to be only one larval stage in *M. challengeri*, although the study was only able fully to examine the first larval stage, with the conclusion that the second instar was post-larval in nature made from observations through the cuticle of first stage zoea larva about to moult. Similarly short larval durations have been recorded for *M. thomsoni* and *M. sagamiensis* (Uchida & Dotsu, 1973; Iwata *et al.*, 1992; both studies cited by Okamoto, 2008). Okamoto (2008) showed larvae of *M. japonicus* hatched at a pre-zoeal stage and moulted to megalopae within a few hours with no intervening zoeal stage. Based on these studies, the potential for larval dispersal in *Metanephrops* appears to be much more limited than for *Nephrops*, with presumably a strong linkage between natal and settlement areas.

Stock genetics

Exchange of adult *Nephrops* between neighbouring stocks are likely to be virtually non-existent, but, as noted above, the extent to which larvae are con-

tained over their natal areas or transported between grounds appears to be variable between stocks depending on local hydrography. Modelling by Marta-Almeida *et al.* (2008) indicated larval transport over distances of 100–200 km along the south and south-west Atlantic coasts of the Iberian peninsula, raising the possibility of genetic connections between stocks separated by these distances. Evidence so far suggests little systematic geographical pattern in genetic structure over the range of *Nephrops*. Passamonti *et al.* (1997) used allozymic characterization to compare Aegean and west of Scotland populations. Despite some significant genotypic variation among populations, no geographical pattern was apparent and the overall conclusion was that there is a low level of genetic divergence between geographically distant populations. On the basis of another allozyme analysis, Maltagliati *et al.* (1998) similarly concluded that, although some genetic sub-structuring was apparent within the Mediterranean, local variability appeared to be as high as long-distance variation. Their characterization of Mediterranean populations was that *Nephrops* ‘appears fragmented in groups, or islands, which replace a fraction of their residents with individuals migrating at random from a large collection of local populations’. Stamatis *et al.* (2006) reached similar conclusions about Atlantic and Mediterranean *Nephrops* populations based on an allozymic study.

Pampouli *et al.* (2011) used microsatellite loci to examine the possibility that *Nephrops* populations contained within troughs and banks around Iceland are genetically isolated. No significant genetic differentiation was found in this study, either among Icelandic populations or between *Nephrops* from Iceland and the west of Scotland. Dispersal of larvae was suggested as one possible cause for the lack of genetic structure. The authors also suggested as an alternative hypothesis that recent population expansion from refuge areas occupied by *Nephrops* during the last glacial maximum 21,000 years ago may have resulted in a low level of genetic differentiation among present day populations. A similar suggestion of recent divergence was made by Stamatis *et al.* (2004), who found low levels of differentiation among Atlantic and Mediterranean populations based on

mitochondrial DNA. The conclusion that there was unlikely to have been a separate Mediterranean refuge for *Nephrops* during the last glaciation was also supported by later allozymic studies (Stamatis *et al.*, 2006).

Preliminary electrophoretic analyses (Smith, 1999) suggest that *Metanephrops challenger* are genetically distinct in some offshore stocks from those in other areas around New Zealand, and there is substantial heterogeneity in samples from other fisheries. The abbreviated larval phase of this species may lead to low rates of gene mixing.

12.4.2 Mortality

As with many other species, there is considerable uncertainty about rates of natural mortality in *Nephrops* populations, despite the instantaneous rate coefficient M being an important parameter in fisheries stock assessments. The value of M is usually treated as being constant, although sources of natural mortality including predation, parasites and diseases (see below) are likely to be density-dependent and to vary from year to year. Despite attempts at joint modelling of *Nephrops* stocks together with those of major predators (Brander & Bennett, 1986, 1989), there is no real evidence of significant changes in natural mortality levels, e.g. as a result of stock declines of North Sea or Irish Sea cod (although, as suggested by Engelhard & Pinnegar (2008), some recent increases in *Nephrops* abundance in northern areas could be related to depletion of major whitefish stocks such as cod).

The value of M is sometimes estimated from generalizations about the relationships between natural mortality, growth parameters and environmental temperature (Pauly, 1980). This method was used by Sardà & Lleonart (1993) to arrive at estimates for annual M of about 0.4 (33%) for both males and females in the Catalan Sea, and by de Figueiredo (1984) to obtain annual M of 0.5–0.6 (39–45%) for females and 0.3–0.4 (26–33%) for males in Portuguese waters. Maynou *et al.* (2003) report various other estimates for Mediterranean stocks, varying from 0.25 to 0.82 (22–56%) for females and from 0.25 to 0.65 (22–52%) for males. Natural mortality is sometimes assumed to decline rapidly with age over the first few years of life;

assessments of Mediterranean stocks sometimes use a method based on stock productivity to estimate a vector of M at age (Abella *et al.*, 1997). A recent assessment of the Catalan Sea (Balearic) stock was based on M declining from 1.004 at age 0 to 0.166 at ages 9+ [General Fisheries Commission for the Mediterranean (GFCM) stock assessment documents].

Some of these estimates are rather higher than is plausible, particularly for stocks which also support exploitation. Morizur (1982) used length distributions from ‘quasi-unexploited’ stocks to obtain estimates for annual M of 0.2–0.3 (18–26%). The values most commonly assumed for assessment of *Nephrops* stocks in the Atlantic are 0.3 for males and immature females, and 0.2 for mature females (assumed less vulnerable to predation during the ovigerous period). Based on the lower limit of overwinter depletion of burrow densities in the Farn Deep stock, at locations inferred to be unvisited by fishing vessels, Bell *et al.* (2005) considered these values to be plausible. Similar values of M were assumed for Mediterranean stocks by Sardà *et al.* (1998).

For *Metanephrops challenger*, estimates of M have been made based on scaling relationships with the growth parameter K (Cryer & Stotter, 1999). In current assessments of this species, annual M is fixed at 0.2.

Predators

Cod (*Gadus morhua*) is generally identified as the most important predator of *Nephrops* in the northern parts of its range (e.g. Farmer, 1975). Symonds & Elson (1983) estimated that cod accounted for 88% of the predation on *Nephrops* by fish in the western Irish Sea, and concluded that this was the only species to exert significant predation mortality. Other studies have confirmed the importance of cod as a predator of *Nephrops* in areas to the north of the English Channel (e.g. Thomas, 1965; Rae, 1967a,b, 1968; Warren, 1976; Björnsson & Dombaxe, 2004). Brander & Bennett (1986, 1989) modelled the interactions between cod and *Nephrops* in terms of predation and fishing mortality, and suggested that maximum fishery yield of *Nephrops* would be achieved with fishing pressure

increased on cod and decreased on *Nephrops*. Brander & Bennett (1989) noted that catch rates of *Nephrops* in the Irish Sea were negatively correlated with cod stock biomass, but there is little evidence that *Nephrops* stocks have benefited from the declines in cod stocks observed over recent years (Bennett & Lawler, 1994). This may be because the alleviation of cod predation pressure is offset by increased predation of juvenile *Nephrops* by small fish that are themselves preyed upon by cod (Armstrong *et al.*, 1991). The importance of *Nephrops* to cod can, perhaps, be overstated. Bromley (1991) found that the rate of energy intake by cod was six times higher while feeding on sprat than while feeding on *Nephrops*. Björnsson & Dombaxe (2004) also noted the poor quality of *Nephrops* as food for cod, and suggested that the predation of cod on *Nephrops* in Icelandic waters could be reduced by increasing stocks of alternative prey species such as capelin (*Mallotus villosus*).

Despite the undoubted primacy of cod in northern areas, many other species are known at least occasionally to prey upon *Nephrops*. Thomas (1965) found *Nephrops* in the stomachs of 13 species of fish trawled from Scottish waters, of which the most important are summarized in Fig. 12.10. *Nephrops* has even been recorded in the stomachs of giant squid (*Architeuthis* sp.) off the west of Ireland (Lordan *et al.*, 1998), although there is no suggestion that this is a major *Nephrops* predator. See Farmer (1975) for a comprehensive list of fish species for which *Nephrops* has been recorded as prey. Armstrong (1982) examined the stomachs of cod and two smaller gadoid species in the Irish Sea and found a strong positive relationship between fish length and the size of *Nephrops* taken (Fig. 12.11A). *Nephrops* constituted 5% of the average daily intake of poor cod (*Trisopterus minutus*), 16% of the intake of pouting (*T. luscus*) and 43% of the intake of cod (weighted averages calculated from tables in the Appendix of Armstrong, 1982). Warren (1976) reported a similar predator–prey size relationship for *Nephrops* taken by cod in the North Sea and Irish Sea (Fig. 12.11B). The size distribution of *Nephrops* in cod stomachs was similar to that observed in a small-mesh trawl, but with a slight bias towards more small and fewer large individuals taken by cod.

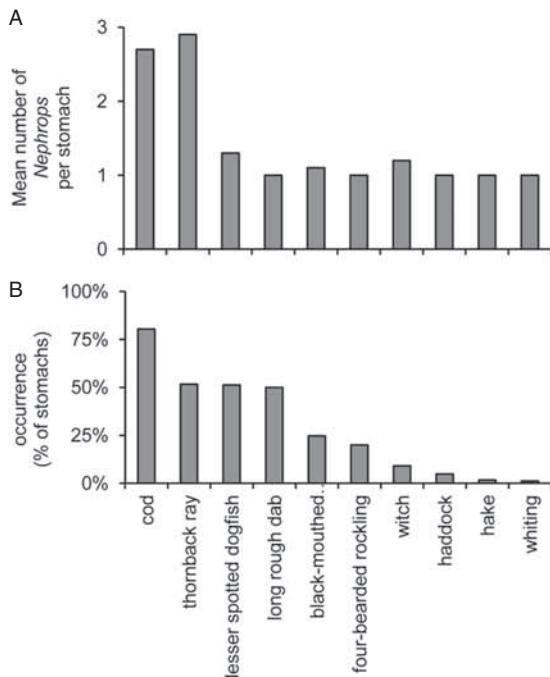


Fig. 12.10 Predators of *Nephrops* in Scottish waters, from Thomas (1965). (A) mean number of *Nephrops* per stomach; (B) percentage of stomachs examined that contained *Nephrops*.

Information on the predators of *Nephrops* in the southerly parts of its distribution is more scanty, but it is presumed that cod is replaced by other large demersal fish species that co-occur with *Nephrops*. Gauss-Garady (1912, 1913) (cited by Farmer, 1975) reported a range of fish species as major predators of *Nephrops* in the Adriatic Sea, including anglerfish (*Lophius* spp.), various elasmobranchs, hake (*Merluccius merluccius*), weevvers (*Trachinus* spp.), gurnards (*Trigla* spp.), scorpionfish (*Scorpaena* spp.) and small gadoids. The gadoid species included Mediterranean poor cod (*Trisopterus minutus capelanus*), which has also been reported as an important predator of *Nephrops* off the east coast of Spain (Planas & Vives (1952) and in the Euboikos Gulf, eastern Greece (Politou & Papaconstantinou, 1994). Presumably, this species accounts for predation only of the smaller size-classes of *Nephrops* (c.f. Fig. 12.11A). Gauss-Garady (1912, 1913) also reported the harbour crab (*Liocarcinus depurator*) and the musk octopus (*Eledone mos-*

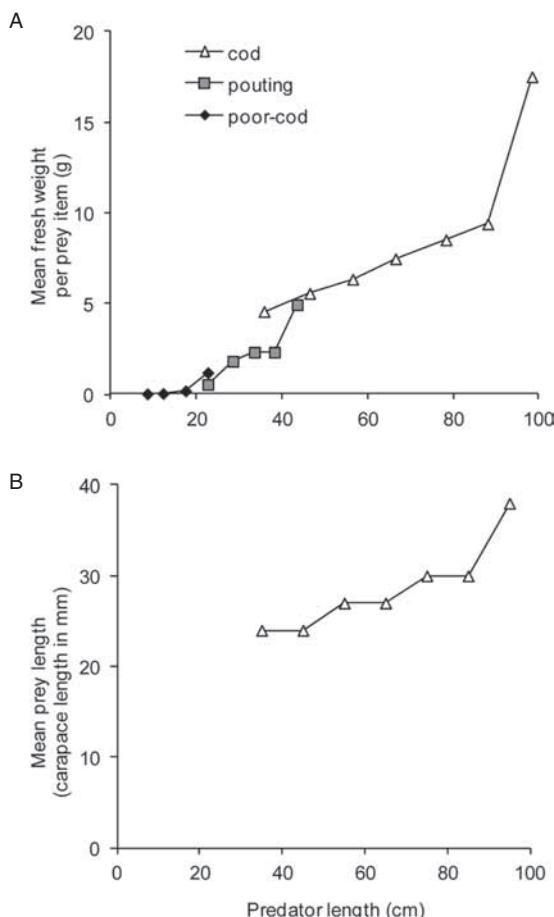


Fig. 12.11 Relationship between predator size and mean size of *Nephrops* recorded in stomachs: (A) mean fresh weights of *Nephrops* recorded in stomachs of poor-cod (*Trisopterus minutus*), pouting (*Trisopterus luscus*) and cod (*Gadus morhua*) in the Irish Sea by Armstrong (1982); (B) mean carapace lengths of *Nephrops* recorded in stomachs of cod in the North Sea and Irish Sea by Warren (1976).

chata) as feeding on *Nephrops*, although neither is likely to be a major predator. Quetglas *et al.* (1999) found a very low incidence (<1%) of *Nephrops* in the stomachs of the European flying squid (*Todarodes sagittatus*) in the western Mediterranean.

Fish predation on *Metanephrops* in New Zealand waters was also briefly examined in the exploratory research fishing in the early 1970s (Hine, 1976). This work found *Metanephrops* in the stomachs

of dogfish (*Squalus acanthias*), school shark (*Galeorhinus galeus*), carpet shark (*Cephaloscyllium isabellum*), sea perch (*Helicolenus* spp.) and hake (*Merluccius australis*). Ling (*Genypterus blacodes*) has also been reported as a predator of *Metanephrops* (Cryer & Stotter, 1999). More recent studies on the Chatham Rise have identified ling and smooth skate (*Dipturus innominatus*) as regular predators (Dunn *et al.*, 2010a), but *Metanephrops* was also recorded in the stomachs of Bollon's rattail (*Caelorinchus bolloni*), pale ghost shark (*Hydrolagus bemisi*), lookdown dory (*Cynoscion traversi*), red cod (*Pseudophycis bachus*) and sea perch (Dunn *et al.*, 2009; Dunn *et al.*, 2010b; Stevens & Dunn, 2011). Sea perch and carpet sharks have also been identified as predators of *M. andamanicus* (Berry, 1969).

Parasites and diseases

A comprehensive review of the diseases of both *Nephrops* and *Metanephrops* has recently been published by Stentiford & Neil (2011). Stewart (1984) noted that the list of parasites and diseases known to afflict lobsters is not extensive, and this is certainly true of *Nephrops*. Epizoa including polychaetes, bryozoans, hydrozoans, molluscs, cirripedes, sessile stanges of a cyclophoran and, exceptionally, Foraminifera have been noted on the exoskeleton of *Nephrops* (Barnes & Bagenal, 1951; Farmer, 1977; Stentiford & Neil, 2011), but individuals in commercial and survey catches are generally very clean shelled. The extent to which this is due to grooming, burrowing behaviour or relatively high moult frequency is unknown, but heavy epibiont loads are seen only rarely, usually in exceptionally large individuals which presumably moult with less than annual frequency.

'Shell disease' caused by fungal and bacterial agents and characterized by chitinolysis and necrosis of the exoskeleton has been recorded in a number of decapod crustacean species (Rosen, 1970; Stewart, 1984), but its incidence in *Nephrops* appears to be extremely low. A brown-coloured necrosis of the exoskeleton is frequently observed where *Nephrops* has been injured, which Farmer (1975) considered to be the result of chitinoclastic bacteria destroying the exoskeleton at the site of

the injury. Ziino *et al.* (2002) found only 1% of *Nephrops* sampled from Italian fish markets showed signs of shell disease. This was manifested as lesions on the chelae (sometimes with bacterial colonization), consistent with intra-specific conflicts. Possibly the low incidence of shell disease is related to the relatively high frequency of moulting, although shell disease has been reported in some small species of peracarid crustacean with much higher moult frequency (Rosen, 1970).

A rapid onset abdominal muscle necrosis was first noted in creel catches of *Nephrops* taken from the west coast of Scotland in the summer and autumn of 1999 (Stentiford & Neil, 2000). Individuals were reported to be dying or moribund during vivier transport, and the opaque appearance of the tail meat caused some catches to be refused at market. Stentiford & Neil (2000) found that 8% of individuals in a trawl-caught sample from the Firth of Clyde showed signs of necrosis in at least one abdominal muscle fibre immediately after capture, this proportion rising to 29% after 4 hours. Death of the affected individuals occurred within days. The condition is characterized by degeneration and disruption of muscle fibre organization, infiltration with damaged muscle with granulocytes and a loss of contractile proteins from affected tissues. No causative agent has been identified, although Stentiford & Neil (2000) noted the presence of unidentified bodies in some severely damaged muscle tissues which may have been viruses. They suggested that the condition is most likely to be idiopathic (host-induced), caused by a combination of damage to the exoskeleton and stress during and immediately after capture. This was confirmed by Ridgway *et al.* (2007), who identified idiopathic muscle necrosis as being connected with stressful conditions experienced by *Nephrops* and involving no pathogenic agents. Bacterial infection following the condition further contributes to degradation of muscle tissues. Similar conditions caused by microsporidians in other species are characterized by much slower progression (e.g. Breed & Olsen, 1977). The overall incidence of the condition in *Nephrops* populations is unknown, but Stentiford & Neil (2000) speculated that it may well contribute to the high mortality of fishery discards returned to the sea after trawl capture.

A microsporidian infection was recently discovered by Stentiford *et al.* (2010) in *Metanephrops challengereri* off New Zealand. The parasite *Myospora metanephrops*, which causes destruction of the skeletal and heart muscles of infected individuals, is the first known example of such an infection in a clawed lobster species. Infected lobsters in trawl catches were characterized by lethargy and changes in cuticle pigmentation and translucency. The infection has only been positively identified from one fishery to the south of New Zealand, but animals showing similar external characteristics have been observed elsewhere around New Zealand (Ian Tuck, pers. obs.). Stentiford & Neil (2011) emphasize that further work is needed to determine the consequences of this parasite for population level mortality and commercial marketability of catches.

Studies over the past two decades have highlighted the importance of dinoflagellates as parasites of crustaceans, including many species of commercial importance (Shields, 1994). Syndinid dinoflagellates of the genus *Hematodinium* have been identified as the causative agents for a number of crustacean diseases, such as 'Bitter Crab Disease' in some majid crabs (Meyers *et al.*, 1987; Taylor & Khan, 1995) and 'Pink Crab Disease' in the edible crab *Cancer pagurus* (Stentiford *et al.*, 2002). In the early 1980s, a low incidence of lethargic, abnormally coloured *Nephrops* was observed during routine biological sampling off the west coast of Scotland. Affected individuals were characterized by an opaque, yellow/orange coloration, milky-white haemolymph and low haemolymph pressure. Field *et al.* (1992) examined the haemolymph of affected individuals and discovered the presence of a parasitic dinoflagellate resembling *Hematodinium perezi*. A background prevalence of 10–15% appeared to apply over much of the west coast of Scotland, but with incidences up to 70% in the Clyde Sea area.

In view of poor meat quality and the possibility of increased mortality in economically important stocks of *Nephrops*, a considerable amount of research into the aetiology, diagnosis, pathology and incidence of *Hematodinium* infections in *Nephrops* has been undertaken over recent years. A key element in this research has been the development

of diagnostic tools. External assessment of coloration and opacity has been found to underestimate the prevalence (Tärnlund, 2000; Stentiford *et al.*, 2001b), and the most commonly used method is the microscopic examination of pleopods where the parasite is visible in the haemolymph. Field & Appleton (1995) developed a 4-point scale for the pleopod method which allows the progression of the disease to be monitored. Sophisticated immunoassay and polymerase chain reaction (PCR) assay methods have been developed to allow detection of low-level (sub-patent) and tissue-based (latent) infections that cannot be identified by the pleopod method (Field & Appleton, 1996; Stentiford *et al.*, 2001d; Small *et al.*, 2002; 2006). Tank studies have shown that patent infection development can take up to 9 months (Beavers, 2010, cited by Stentiford & Neil, 2011). Despite its limitations, however, the pleopod method remains a useful technique for the detection and monitoring of advanced infections of the haemolymph (patent infections). Both the body colour and pleopod methods have been used to identify *Hematodinium* infections in *Nephrops* populations from east and west Scottish coasts, the southern North Sea and the Skagerrak and Kattegat (Field *et al.* 1992; Field & Appleton, 1995; ICES, 1996; Tärnlund, 2000; Stentiford *et al.*, 2001b; Briggs & McAliskey, 2002).

The prevalence of *Hematodinium* infections in *Nephrops* stocks shows marked seasonal patterns. The most common pattern is for peak prevalence in spring and lowest prevalence in autumn. This pattern is evident in stocks on the west coast of Scotland (Field *et al.*, 1998; Stentiford *et al.*, 2001b) and in the Irish Sea (Briggs & McAliskey, 2002). Studies in Swedish waters using the body colour method indicated the highest prevalence in autumn during the early 1990s (ICES, 1996), but Tärnlund (2000) found no difference between spring and autumn 2000 using the same method, and using the pleopod method found higher prevalence in autumn. Various other patterns of prevalence have been described in relation to size, sex, moult stage and ovary stage, and prevalence within some individual stocks can also be quite variable between years (Field *et al.*, 1998; Stentiford *et al.*, 2001b; Briggs & McAliskey, 2002).

Conclusions about *Hematodinium* prevalence based on trawl-caught samples are complicated by the effect of the parasite on burrow emergence and swimming behaviour, both of which affect catchability. Laboratory studies have shown infected *Nephrops* to remain outside the burrow for 19.4% of the day compared with 1.7% in uninfected *Nephrops* – a more than 10-fold increase (Stentiford *et al.*, 2001c). Infected animals also show a progressive decline in swimming performance as the infection severity increases (Stentiford *et al.*, 2000b). Both responses will increase the exposure of infected animals to trawling and predators, and reduce the ability to escape.

Modes of transmission of *Hematodinium* remain uncertain. Moult ing is assumed to be important in infection, but the long period of sub-patency makes it difficult to associate infection with any specific period (Stentiford & Neil, 2011). Other suggested transmission mechanisms include ingestion of spores during suspension feeding, cannibalism, intermediate or reservoir hosts such as benthic amphipods, and sexual transmission (reviewed by Stentiford & Neil, 2011). Stentiford & Neil (2011) highlight that the long-term persistence of a seasonal cycle of patent infection levels in catch samples from the Clyde area over the past two decades, with peaks of 20–25%, is indicative of mechanisms and a reservoir to perpetuate the infection between years.

Reduced muscle performance in the earlier stages of the infection appears to be due to the parasite drawing on carbohydrate reserves, perhaps compounded by increased oxygen demand, while in the final stages of infection the structure of the muscle is damaged as the parasite depletes amino acids and proteins (Stentiford *et al.*, 2000a, 2001a). The culmination of infection is inevitably death, either through exposure to predators and fishing, or through sporulation (Appleton & Vickerman, 1998). The consequences of this mortality for *Nephrops* population dynamics are uncertain, but there is at least potential for natural mortality to be elevated beyond the values usually assumed. There is at least circumstantial evidence of enhanced population-level mortality of *Nephrops* from Field *et al.* (1998) who noted that reductions in burrow densities and catch rates coincided with the highest

prevalence of *Hematodinium* on the west coast of Scotland. Stentiford & Neil (2011) review the evidence that ‘emergence’ of the disease in a fishery may be associated with fishery-induced changes in population structure increasing the proportion of susceptible hosts within the population rather than sudden environmental change or appearance of the pathogen. These authors also highlight the possibility of disrupted recruitment caused by parasitic castration, typically a feature of dinoflagellate infections of crustaceans. This has not been specifically examined in *Nephrops*, but Briggs & McAliskey (2002) showed that infection prevented maturation or destroyed gonads in female *Nephrops* from the Irish Sea. Clearly, further work on the population consequences of *Hematodinium* infections is a high priority.

Stewart (1980) lists some of the larger parasites that have been recorded on lobsters, including some on *Nephrops*. The immature stage of the aspidobothrid trematode *Stichocotyle nephropis*, which in its adult form is a parasite of skates and rays, has frequently been found encysted in the stomach and intestinal wall of *Nephrops*, but its incidence appears to be very variable in time and space. Symonds (1972b) reported incidences between zero and 20% in samples taken from the coasts of Britain during the early 1960s. In samples taken about the same time, Mackenzie (1963) found the parasite to be absent from populations on the east coast of Scotland, including the Firth of Forth (the type locality), where Cunningham (1887) had described it as ‘fairly common’ during the late 19th century. Other parasites recorded in *Nephrops* include the gregarine protozoan *Porospora nephropis* from the digestive tract, a lernaeopodid copepod found in the vas deferens, a eunicid polychaete worm in the branchial chamber and egg mass, and a systemic infection by a *Mesanophrys*-like ciliate species (references in Sinderman, 1970; Farmer, 1975; Stewart, 1980; and Stentiford & Neil, 2011). In none of these cases is there information on the pathology in *Nephrops*, but the impact is generally assumed to be small (Stewart, 1980). Cymothoid isopods have been found associated with *Nephrops* in the eastern Mediterranean, but it is uncertain whether or not the association is truly parasitic (Ateş *et al.*, 2006).

Conniostomatid copepods of the genus *Nicotöhöe*, which includes the ‘gill maggot’ of *Homarus gammarus*, have been found on the gills of several *Metanephrops* species (Sinderman, 1970; Kabata, 1966, 1967). *Metanephrops velutinus* is the type host for the parasitic bopyrid isopod *Pseudione nephropis*, but although infection is known to cause growth reduction and physiological castration in other decapod species, there is no information on the likely impact on *M. velutinus* (Stentiford & Neil, 2011).

12.4.3 Population regulation

Little is known about how the recruitment of juvenile *Nephrops* to a stock depends on the population of adults. Estimates of stock biomass and recruitment levels from analytical stock assessments based on size data for *Nephrops* are now considered not to represent the true range of inter-annual variability, but Bell (1999) attempted to estimate the form of stock-recruitment relationships for *Nephrops* in the North Sea by combining data from several stocks, thus widening the range of contrast in relative stock biomass and recruitment. A stock-recruitment function fitted to the data showed a negative relationship between stock size and recruitment over the range of ‘observed’ stock sizes, i.e. a compensatory, density-dependent relationship (Shepherd, 1982).

Stock-recruitment relationships were examined for a wider range of Atlantic stocks by ICES (2000). Recruitment and stock indices were constructed from commercial catch rate data for ranges of length-classes corresponding to recruits and sexually mature adults in the fished stocks. No relationship at all was apparent for some stocks (western Irish Sea, Firth of Clyde), possibly because the range of observed variation was too narrow. For one stock (south-east Iceland), the relationship appeared to be linear and positive, a result hard to explain on biological grounds for a sustainably exploited stock. Negative relationships were apparent for several North Sea stocks and possibly for the south and south-west Portugal stock.

Further exploration using catch rate indices has failed to corroborate these patterns (ICES, 2002), but there are theoretical grounds for supposing that

stock-recruitment relationships in *Nephrops* might indeed be density dependent, with reductions in the numbers of juveniles recruiting to the stock at high adult densities. These are set out by ICES (2000), and include: (i) physical constraints on the distribution of a stock defined by the extent of available muddy habitat; (ii) the probable dependence of newly settled pre-recruits on the presence of adult burrows; (iii) the territorial behaviour of adults, which constrains the number of burrows per unit of area; (iv) the likely density-dependence of predation and cannibalism, which may increase the mortality of juveniles at high stock densities; (v) the possibility of density-dependent constraints on growth rates at high densities, which might prolong the exposure to heavy predation. Concerns about sperm limitation are sometimes expressed for fisheries that are strongly concentrated on the male portion of the stock. This has been cited as a reason to explain recent declines in the Farn Deeps *Nephrops* stock and a reference point for fishery management has been formulated to protect male spawning potential (ICES, 2011c).

More research is needed into the form of stock-recruitment relationships in *Nephrops*, particularly since this is potentially an extremely important factor for fishery management. More information is also needed on the role of climate and other environmental factors in determining recruitment. González Herraiz *et al.* (2009) linked long-term population variability of *Nephrops* on the Porcupine Bank with the North Atlantic Oscillation (NAO) index, a synoptic variable describing the state of the large-scale climatic system which exerts highly correlated effects on local weather (e.g. Post & Forchhammer, 2002). Minima in catch rate trends were related with positive phases of the NAO lagged by 6–7 years. The exact reasons for this relationship are unclear and likely to be complex, but the authors suggest that they could be driven by general biomass declines at lower trophic levels linked to changes in temperature and winter storms occurring at NAO positive phases and to factors concerning the containment of larvae over suitable ground for settlement. Zuur *et al.* (2003) found no evidence that trends in catch rate in northern stocks of *Nephrops* were related with the NAO or sea surface temperature.

In contrast with most northern stocks of *Nephrops*, which have generally been stable or increasing over recent years, several southern Atlantic stocks of the species have shown significant declines since the early 1990s (Fariña & González Herraiz, 2003). Engelhard & Pinnegar (2008) examined climate change, differences in fishing pressure, trends in targeted fishing effort or effects of fishing on the abundance of predators as possible reasons for this north-south contrast. These four hypotheses are complementary and each was considered to be plausible, but the most likely explanation was considered to be a combination of reduced predation following cod declines in northern areas, temperature changes possibly leading to a mismatch between the availability of suitable substrates and water temperatures in southern areas, and changes in the targeting of fishing effort (see also Rijnsdorp *et al.*, 2008).

12.5 Harvest of wild populations

12.5.1 Fishing methods

Nephrops is commercially exploited throughout its geographic range, and is subject to a variety of different fishing practices. *Nephrops* habitat is readily accessible to trawling, and this method of fishing dominates the landings in most areas. Static gears are, however, important locally in some inshore areas around Scotland and Sweden, and is the only method of fishing currently used in the Faeroese *Nephrops* fishery.

The types of gear generally vary on a regional basis, and in relation to the nature of the *Nephrops* fishery. *Nephrops* is taken in fisheries both as the target species, and as a valuable bycatch. The species caught alongside *Nephrops* vary considerably in relation to the fishery being exploited and the gear used. On the northern European continental shelf the fisheries tend to be specifically targeted at *Nephrops*, or are mixed fisheries with cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*) or plaice (*Pleuronectes platessa*) as the other target species. In the deeper water to the west of Scotland and south and west of Ireland, megrim (*Lepidorhombus*

whiffagonis) and monkfish (*Lophius* spp.) are the dominant fish in the mixed fisheries, with hake (*Merluccius merluccius*) becoming more important further south. Off the Atlantic coast of the Iberian peninsula, the fisheries target hake, with *Nephrops* as a small but economically important bycatch, while in the Mediterranean *Nephrops* is the target species in fisheries operating at depths around 400 m, within the framework of more general multi-species fisheries in this area. A range of the issues relating to trawl fisheries for *Nephrops* are reviewed by Graham & Ferro (2004).

Nephrops trawl fisheries

Prior to the 1950s, *Nephrops* were largely landed as bycatch in a number of European trawl and seine fisheries, but were also discarded as unwanted bycatch in others. The majority of landings at this time were made by France, principally from the Irish Sea, Celtic Sea and Bay of Biscay, with about 80% of all landings coming from the north-east Atlantic, 20% from the Mediterranean. Targeted trawling for *Nephrops* on a wider commercial scale is considered to have begun in the late 1950s, as markets developed further. Trawls used to target *Nephrops* were generally wide, with a low headline height, reflecting the lack of both herding and prolonged swimming ability of the species. These were initially adaptations of existing gear, but dedicated *Nephrops* trawls were rapidly developed, particularly for the waters around the UK and Ireland. The traditional *Nephrops* trawl has a low headline, typically less than 2 m, with short wings, constructed from single polyethylene, 70 or 80 mm mesh throughout, although some trawls are constructed with a larger mesh size in the upper sections. Although fish are taken using this type of trawl, they are predominantly designed for the capture of *Nephrops*. The initial trawl fisheries for *Nephrops* were conducted in fine, muddy areas, and trawl ground-gear was light, often made of natural fibre (grass rope). The introduction of rubber discs threaded onto the footropes, and ultimately larger heavier discs (up to 250 mm in diameter) allowed fisheries to develop close to increasingly 'hard' or rocky ground. This design was the precursor to what is known as a 'scraper' trawl, which has

extended wings and a heavier construction. The extended wings increase the herding efficiency of groundfish species such as plaice and monkfish. These trawls are often preferred for more mixed fisheries and typically have a larger codend mesh size (>100 mm), to comply with catch regulations. The dual-purpose trawls are similar in design to the scraper trawl but have an increased headline height to enhance the capture of finfish such as haddock and whiting.

The introduction of multiple trawl rigs in the mid-1980s led to further development in *Nephrops* fisheries. This method of trawling was introduced to *Nephrops* fisheries by Danish vessels, towing two conventional long-winged, low headline trawls, and has expanded since the late-1980s to become commonplace throughout the European *Nephrops* fleet in the Atlantic. The use of twin or multiple rig trawls means that the effective spread of a single large trawl can be obtained with multiple smaller trawls (with less hydrodynamic drag), and up 20–30% greater overall trawl width can be achieved for the same vessel power when compared to a single trawl. When fishing for species such as *Nephrops*, monkfish and flatfish, the increased spread associated with multiple rig trawls can increase the catching efficiency considerably.

Around the UK, *Nephrops* trawl fisheries can be divided into two main groups on the basis of landings: a very clean *Nephrops* fishery, often on inshore grounds, and a more mixed fishery usually taking place on more offshore grounds where commercial fish are more prevalent (Kunzlik *et al.*, 2003). Further south in the North Sea the fishery is mixed, with plaice as the main fish bycatch. In the Irish Sea cod, whiting and plaice are taken in *Nephrops* fisheries, while to the south and west of Ireland and in the Bay of Biscay, hake, monkfish and megrim are more important as bycatch. Off the Iberian peninsula, *Nephrops* is itself a minor (although valuable) bycatch in fisheries targeting horse mackerel (*Trachurus trachurus*) and blue whiting (*Micromesistius poutassou*) (ICES, 2003). There is also a crustacean trawl fishery in Portuguese waters, where *Nephrops* is taken alongside species such as deepwater pink shrimp (*Parapenaeus longirostris*) and rose shrimp (*Aristeus antennatus*) (Monteiro *et al.*, 2001).

In *Nephrops* fisheries the legal minimum mesh sizes required are often smaller than for most finfish species (with the exception of the Mediterranean), and bycatches and discarding rates of undersize fish and invertebrates can be high (Stratoudakis *et al.*, 2001; Catchpole *et al.*, 2005). Detailed studies of the composition of bycatch in *Nephrops* trawl fisheries have been undertaken in stocks within English (Evans *et al.*, 1994; Catchpole *et al.*, 2005), Scottish (Wieczorek *et al.*, 1999; Bergmann *et al.*, 2002) and Italian waters (Wieczorek *et al.*, 1999). Levels and composition of discards vary considerably with location, even over short distances (Bergmann *et al.*, 2002). Bell *et al.* (2008) examined trawl catch composition on the Farn Deep ground and concluded that catch rates of haddock, whiting and lemon sole (*Microstomus kitt*) were unrelated to those of *Nephrops*, while catch rates of cod and plaice were inversely related. These results suggested that spatial and temporal targeting of *Nephrops* fishing could be used to minimize bycatches of some fish species.

A detailed review of recent developments of trawl gear in *Nephrops* fisheries is beyond the scope of this chapter, but there is an extensive literature describing the results of gear trials aimed at reducing bycatches, particularly of juvenile whitefish. Given stock declines in species such as cod, maintaining fishing opportunities for *Nephrops* has been strongly dependent on dissociating *Nephrops* trawling from catches of other species occurring on the same ground. This has partly been achieved by adaptive spatial exclusion of fishing from locations where catch rates of juvenile cod and other whitefish species are high, but a great deal of effort has been directed towards the use of square-mesh panels, separator panels, grids and other methods of improving fish escapement and selectivity for *Nephrops* (e.g. Catchpole *et al.*, 2006b, 2007; Graham & Fryer, 2006; Loaec *et al.*, 2006; Revill *et al.*, 2006, 2007; Krag *et al.*, 2008; Valentinsson & Ulmestrond, 2008; Frandsen *et al.*, 2009; Drewery *et al.*, 2010; Sala & Lucchetti, 2010).

According to Sardà (1998), three types of otter trawl gear are used to exploit *Nephrops* in the Mediterranean, used mainly by Spain (western areas), Italy (central areas) and Greece (eastern areas). The types differ in net size and proportions, width of

mouth opening and size of otter doors, reflecting local conditions and vessel types and the multi-species nature of the fisheries. The Italian trawl is the smallest type, considered best adapted to *Nephrops* fishing (Sardà, 1998; Maynou *et al.*, 2003). Mesh size in the codend is 40 mm in most areas, but smaller meshes (28–32 mm) may be used by Greek trawlers (Sardà, 1998; Maynou *et al.*, 2003).

A variety of fish species are taken alongside *Nephrops* in the Mediterranean trawl fisheries, including blue whiting, Mediterranean poor cod (*Trisopterus minutus capelanus*), megrim (*Lepidorhombus boscii*) and grey gurnard (*Eutrigla gurnardus*) (Mytilineou *et al.*, 1998a). Other important species caught alongside *Nephrops* in the Mediterranean include blue whiting (*Micromesistius poutassou*), greater forkbeard (*Phycis blennoides*), hake and silver scabbardfish (*Lepidopus caudatus*), crustaceans such as rose shrimp (*Parapenaeus longirostris* and *Aristeus antennatus*) and red shrimp (*Aristaeomorpha foliacea*) and cephalopods, including flying squid (*Todaropsis eblanae*), short-finned squid (*Illex coindetti*) and curled octopus (*Eledone cirrhosa*). Discards of undersized fish and non-commercial fish and crustaceans have been estimated at 20% of the catch in the northern Tyrrhenian Sea and 40% of the catch in Greek waters (Maynou *et al.*, 2003).

In addition to mortality of target and bycatch species, trawling activities also have implications for other components of marine ecosystems. Muddy sediments suitable for *Nephrops* accumulate in high depositional areas where disturbance from currents and storms are uncommon. The effects of trawling disturbance on a muddy sealoch habitat was investigated by Tuck *et al.* (1998), and wider effects on other *Nephrops* habitats were considered by Ball *et al.* (2000). The most obvious effects were the tracks left by the trawl doors, which may last up to 18 months in some areas. Effects on infauna included a reduction in the abundance of large-bodied fragile organisms, and an increase in the abundance of opportunists, which would ultimately lead to a community with reduced species abundance and faunal diversity (Ball *et al.*, 2000). Recovery from experimental disturbance was observed, but is thought to take longer than in other habitats (Tuck *et al.*, 1998), where communities in

more dynamic environments may be more adapted to natural disturbance. With the exception of seapens, epifauna are generally scarce in muddy habitats, and direct effects are likely to be limited, and less than for harder substrates. Return of dead discards to the sea represents another potential interaction of trawl fishing activities with benthic communities. Catchpole *et al.* (2006a) estimated that on the Farn Deeps ground discards from the fishery could contribute up to 37% of the energy requirements of benthic scavengers during the fishing season.

Metanephrops trawl fishery

A targeted trawl fishery in New Zealand developed for *Metanephrops challenger* during the late 1980s. The first landings were recorded in 1986–87, with the fishery rapidly increasing and expanding into new areas. By 1990–91, total landings exceeded 450 t, with 11 vessels involved in the fishery at this time, and while most landings came from two areas off North Island, exploratory fishing was also taking place elsewhere around the coast.

By 1991–92 total landings had increased to almost 900 t, with the increase in landings associated with newly developed fisheries to the south of New Zealand and on the Chatham Rise. The landings have been maintained around this level since this time, declining slightly in recent years, with the fishery based on four main areas. Although *Metanephrops* are likely to be distributed widely on the muddy slopes around New Zealand, only very small landings have been made from other areas to date. The New Zealand Quota Management System (QMS) limits access to the *Metanephrops* fishery, and the fleet currently comprises nine vessels, using either twin or triple rig bottom trawls.

Bycatch in the New Zealand *Metanephrops* fisheries has been the focus of a number of studies (Anderson, 2004; Ballara & Anderson, 2009). Bycatch accounts for a relatively high proportion of the total catch, with total annual bycatch estimates ranging from 3,000 to 8,000 t, compared to total landed trawled *Metanephrops* catches of 800–1,000 t. Main bycatch species include ling (*Genypterus blacodes*), hoki (*Macruronus novaezealandiae*),

sea perch (*Helicolenus* spp.), red cod (*Pseudophycis bachus*), silver warehou (*Seriolella punctata*) and giant stargazer (*Kathetostoma giganteum*). Total annual discard estimates range from about 1500 to 5000 t, dominated by rattails (Macrouridae), javelinfish (*Caelorinchus australis*), skates and crabs, ling, red cod, hoki, spiny dogfish (*Squalus acanthias*) and sea perch. Discarding of *Metanephrops* is minimal at 0.3% of total discards and discards averaging 2.5 kg of total discards per kilogram of lobster caught.

In New Zealand fisheries, seabird captures in *Metanephrops* target tows have been examined over a number of years (Baird & Smith, 2007). Observed captures ranged from six to 17 per year, although total seabird captures have not been estimated for any *Metanephrops* fishery because low observer coverage would result in unreliable estimates (Bradford, 2002). Model based estimates of the nationwide seabird bycatch by *Metanephrops* trawlers for the fishing years 1997–98 to 2003–04 have been produced (MacKenzie & Fletcher, 2006). Median annual captures ranged from 13 to 93 seabirds, but the confidence intervals around these estimates are large. Capture estimates include only those seabirds landed (alive, injured or dead) on fishing vessels. Seabird ‘warp strike’, where seabirds are struck by trawl warps as they forage on offal or discarded fish near the vessel, has not been quantified in scampi fisheries but is a generic problem in fisheries where offal is discarded while trawling. Legislation requires that vessels over 23 m employ tori lines to scare birds away from the warps, and although most scampi vessels are smaller than this, they employ the lines on a voluntary basis. The main quota holder has developed its own code of practice in accordance with the New Zealand government’s *Code of Practice Guidelines for the National Plan of Action to Reduce the Incidental Catch of Seabirds in New Zealand Fisheries*. Birds killed or injured as a result of such interactions may not be recovered aboard the vessel, in which case they will not be included in capture estimates. *Metanephrops* trawlers occasionally catch marine mammals, including fur seals and sea lions (Baird, 2005; Baird & Doonan, 2005).

Examination of the invertebrate bycatch of research trawls in New Zealand (Bay of Plenty) in

relation to the distribution of previous trawling effort for *Metanephrops* and finfish (Cryer *et al.*, 1999) led to conclusions that bottom trawling has impacts on benthic community structure that are similar to those frequently observed in coastal fisheries (Cryer *et al.*, 2002, 2005b). Both species richness (observed number of species) and a diversity index were negatively correlated with an index of historical *Metanephrops* fishing effort. Many species of benthic invertebrates were substantially less common in heavily trawled areas, although some species, including *M. challengerii*, were more common in heavily trawled areas.

Discarding from trawl fisheries

Discarding of undersize or poor quality (soft post-moult) *Nephrops* occurs in most northern European *Nephrops* fisheries, and discarding rates can be high in some areas (Evans *et al.*, 1994; Redant & Polet, 1994; Bergmann *et al.*, 2002). Mortality rates of discarded individuals have been estimated at 75% under typical commercial trawl fishery conditions (Sangster *et al.*, 1997), although recent simulation experiments suggest that mortality rates may be higher in the Kattegat and Skagerrak, where the discarded animals are exposed to low salinity surface waters (Harris & Ulmestrand, 2004). In some cases discards are left on deck for considerable periods before being thrown overboard, and probably suffer 100% mortality. Evans *et al.* (1994) considered that very little of the catch of *Nephrops* and bycatch species from the Farn Deep fishery was returned to the seabed, most of it being removed for human consumption or eaten by seabirds at the surface of the sea. Physiological stress is very high in trawl discards (Harris & Andrews, 2005a,b; Lund *et al.*, 2009) and can also damage both retained and discarded *Nephrops* (Milligan *et al.*, 2009). Macher *et al.* (2008) examined the potential benefits of reducing discards of undersized *Nephrops* in the Bay of Biscay fishery by improving trawl selectivity. Simulations indicated large gains in biomass, but the authors warned that ecosystem carrying capacity may in practice limit the extent of potential increase. They also noted that regulating access to the fishery would also be needed for long-term sustainability.

As already noted, behavioural and selectivity factors result in very low catches of undersized *Nephrops* in creel fisheries, and any discarding is related to marketing (or local agreements) rather than minimum landing size. Discard survival of creel-caught *Nephrops* is high (Sangster *et al.*, 1997). Bernasconi & Uglov (2008) examined physiological and immunological variables in *Nephrops* catches and identified a significantly lower intensity of stress in individuals caught in creels compared with trawl-caught individuals.

Within the New Zealand QMS, management is on the basis of catches rather than landings, and there is minimal discarding of *Metanephrops*.

Baited traps

Crabs and lobsters have traditionally been fished with baited traps (creels). A perceived benefit of creeling for *Nephrops* is that it maintains the captured target species in good condition and discard survival is high (Sangster *et al.*, 1997). Some concerns have been expressed about high representation of ovigerous females in creel catches from some Scottish sea lochs (see Section 12.5.2), but the population level consequences of this have not been investigated in detail. ‘Ghost fishing’ of lost gear is a common concern about trap fisheries, but an investigation by Adey *et al.* (2008) on the west coast of Scotland indicated that once the bait has been consumed lost creels effectively cease to fish.

As already noted, all landings of *Nephrops* from Faeroe Islands waters are now taken by creels. With the development of the UK *Nephrops* trawl fishery, fishermen also used creels to target *Nephrops* in more inshore areas on the west coast of Scotland, either where trawling was banned through legislation or impractical owing to the patchiness of suitable seabed. With the recent development of markets for live *Nephrops* in southern Europe with high market prices, the Scottish *Nephrops* creel fishery has attracted extra effort, and contributes 15–20% of the total landings from some stocks. Aside from the west coast of Scotland, there is creel fishing for *Nephrops* at various other locations around the coasts of the UK, but significant quantities are rarely taken. In Sweden, a creel fishery for *Nephrops* has developed since the mid-1980s

in inshore areas where trawling is prohibited. Up to 20% of Swedish *Nephrops* landings from the Skagerrak are taken in creels, and there is also a small Swedish creel fishery in the Kattegat. Historically, there has been some trap fishing of *Nephrops* by Portugal, but catches by this method have been insignificant in recent years. Trap fishing has been trialled for *Metanephrops* in New Zealand, but has not proved successful.

Investigations into *Nephrops* creel fisheries are largely limited to the Scottish west coast, where fish bycatch varies seasonally and includes poor cod (*Trisopterus minutus*) and the lesser spotted dogfish (*Scyliorhinus canicula*), and more occasionally, cod, haddock, whiting, conger eel (*Conger conger*) and ling (*Molva molva*). Other crustaceans (small edible crab (*Cancer pagurus*), swimming crabs (*Liocarcinus* spp.), squat lobsters, shrimps, hermit crabs (*Pagurus* spp.)), starfish and gastropods also feature in catches. This bycatch is largely discarded, and survival in the invertebrates is generally considered to be high, although high levels of seabird predation have been observed in some areas (Adey, 2007). Teleost fish often suffer swim bladder damage when creels are lifted, and mortality can be high. Morello *et al.* (2009) undertook fishing trials with various creel designs in the Adriatic Sea and found a generally similar bycatch composition to Scottish creel fisheries, including conger eel, swimming crab, squat lobsters and curled octopus.

Although not specifically targeting *Nephrops*, incidental bycatch is made in some gill net fisheries in the Aegean Sea, where *Nephrops* is attracted by the fish catch, and then entangled in the netting (Smith & Papadopoulou, 2003). Traps and trammel nets may also be used by small-scale fishermen in areas of the northern Aegean and Adriatic Sea where trawling is prohibited (Maynou *et al.*, 2003).

The effects of *Nephrops* creeling on what are considered to be the more fragile components of muddy habitat seabed communities have been examined by Kinnear *et al.* (1996). Three seepen species present in a Scottish sea loch (*Pennatula phosphorea*, *Virgularia mirabilis* and *Furniculina quadrangularis*) were found to be resilient to smothering, dragging and uprooting by creels, and each of the species was able to recover in terms of orientation in the sediment and feeding activity fol-

lowing disturbance. Seepen mortality throughout the investigations was very low.

12.5.2 Catchability

The catchability of *Nephrops* in trawls and creels is strongly influenced by the behaviour of the animal, through either availability on the seabed for trawling (related to burrow emergence) or factors affecting entry into creels (related to feeding patterns and agonistic behaviour). These factors vary considerably over time, and also between sex and individual size, which means that the two fisheries exploit different components of the stock, and show different seasonal patterns (see Section 12.3.4).

Since *Nephrops* spend the majority of their time in their burrows (Chapman, 1980), emergence rates are the main factor influencing catchability in trawl fisheries. The burrows extend 20–30 cm below the mud surface, and animals within burrows are unlikely to be caught by a passing trawl. Emergence varies on a daily basis with ambient light level, in relation to the lunar tidal cycle, and also on a seasonal basis in relation to moulting (both sexes, although at different times) and reproductive state (females). Catch rates are known to vary in relation to all of these factors.

On a daily basis, emergence rates (and hence catch rates) are generally considered highest at dawn and dusk in northern European populations, although this varies with depth and peak emergence timing ranging from midday in deep water to during the night in very shallow populations (Table 12.6). Seasonal patterns of light level also influence this, and fisheries have responded accordingly, with activity in some Scottish inshore fisheries starting operations much earlier in the morning or even concentrated over night in the summer, but only fishing during the day in winter. Over the lunar cycle, emergence appears to be higher on neap tides, when tidal strengths are lower, and it has long been recognized that catch rates are highest at these times (Storrow, 1912).

Ovigerous female *Nephrops* are thought to emerge only rarely from burrows, since they are poorly represented in trawl catches during the egg incubation period (Table 12.4). This is assumed to be related to reduced foraging outside the burrow

during this time. However, a noteworthy feature of creel catches is that they include much larger proportions of ovigerous females than trawl catches, indicating that they are attracted at least to immediately available food items. In the Scottish creel fisheries ovigerous females may comprise 20–30% of the catch during the latter half of the year, while they are largely absent from the trawl catches. Males dominate in trawl catches during the ovigerous period, with the result that fishing mortality on mature males is far higher than on mature females, particularly in winter fisheries (e.g. ICES, 2003).

Catchability in the creel fishery is related to bait attraction, and interactions between animals. Behavioural interactions may mean that smaller individuals tend not to enter creels (c.f. Miller, 1990; Addison, 1995; Miller & Addison, 1995, for *Homarus* spp.). Escape of smaller individuals may also be greater in creels than in trawls, owing to the open nature of the mesh. *Nephrops* selectivity in trawls is generally poor below mesh sizes of 100 mm (Anon., 2002).

Studies investigating the seasonal and longer term patterns in the creel fisheries on the west coast of Scotland have consistently observed a bi-modal pattern in monthly landing rates (Tuck & Bailey, 2000; Fig. 12.12). Although this pattern may be influenced by discarding practices, the data appear to reflect availability to creels. A peak landing rate in March is associated with large catches of males, and is followed by a reduction in May and June which may be linked to moulting. The smaller peak in July–August is associated with increased catches

of females, which appear to become more available to fishing between egg hatching and the spawning of the next brood. The subsequent decline in landing rates is associated with sharply decreased availability of females after spawning, but masks increases in landing rates of small males, possibly entering the fishery after an autumn moult.

12.5.3 Catches

The high unit value of *Nephrops* means that although total landings are relatively low (around 70,000 t total annual landings, worth around \$270 million first sale value (see Table 12.1, Fig. 12.3); compared with many fish species, they have been the most valuable demersal species landed into the UK and Ireland since the late 1990s, and are also important in a number of other European countries.

Although they have their own fisheries for *Nephrops*, the main importers for both frozen and fresh product are Italy, Spain and France, with net *Nephrops* imports of \$118 million, \$96 million and \$82 million, respectively (FAO data for 2009). The main exporters of *Nephrops* are the UK, Denmark, Ireland, the Netherlands and Spain (\$177 million, \$71 million, \$28 million, \$28 million and \$12 million in 2009, respectively), and the Netherlands, Sweden, Morocco and Portugal also export significant amounts.

New Zealand *Metanephrops* catches are graded and frozen at sea for export to Europe and Asia, with an export value of about \$9 million.

12.6 Monitoring and management

12.6.1 Management measures and structures

Various technical measures are in place for the management of *Nephrops* fisheries. Minimum legal sizes (MLS) are 20 mm CL, 70 mm total length (TL) in the Mediterranean, Irish Sea, west of Scotland, Bay of Biscay, Portugal and Spain, 40 mm CL, 130 mm TL in the Kattegat and Skagerrak and 25 mm CL, 85 mm TL in most other areas. Relatively high mortality of discards (Symonds & Simpson, 1971; Guégen & Chareau, 1975; Section

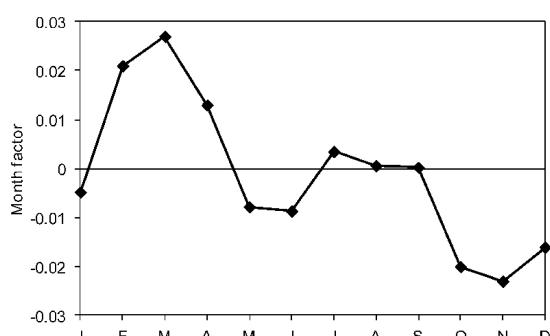


Fig. 12.12 Contribution of month to variations in *Nephrops* landing rate (kg creel^{-1}) in a Scottish west coast creel fishery (Tuck & Bailey, 2000).

12.5.1), however, means that the selective properties of the fishing gear are the primary determinant of mortality at size.

The regulations on gear and mesh size specifications are too complex and extensive to summarise here, but in most areas of the north-east Atlantic 80 mm diameter meshes or larger are specified for the cod-ends of trawl gear, often with square-mesh panels and larger diameter diamond mesh headline panels to allow the escapement of young fish. Traditional trawlers in the Mediterranean use a relatively unselective 40 mm mesh. Most of the gear regulations are aimed at limiting bycatch and mortality of fish rather than improving the size-selectivity of the gear for *Nephrops*. See Section 12.5.1 for further information on recent gear developments.

The primary tool used to manage *Nephrops* fisheries in the north-east Atlantic is the Total Allowable Catch (TAC). Many of the fisheries in this area are shared between different nations, and advice on appropriate levels for annual TACs is given by the International Council for the Exploration of the Sea (ICES). ICES assessments and advice for *Nephrops* are based on Functional Units which represent individual stocks. Current management within the EU is based on aggregating these into TAC areas, which often are much larger. This leads to potential problems when stocks of differing exploitation status exist within the same TAC area, although in practice the structure of fleets in terms of vessel size and other factors may act to limit movement of fishing effort between areas. Advice on TACs is based on the previous history of catches that have been supported without resulting in adverse stock trends, on various stock indicators such as catch per unit effort (CPUE) and mean size, and increasingly on the results of underwater television (UWTV) surveys of burrow densities.

Following the introduction of the ‘MSY’ (maximum sustainable yield) approach to EU fishery management, ICES has been developing reference points for *Nephrops* fisheries at a Functional Unit level – a target reference point representing the exploitation rate at which MSY is achieved, and a stock biomass limit above which there is considered to be a low risk of impaired recruitment. For *Nephrops* stocks, the target exploi-

tation rate is based on length-based yield per recruit (YPR) and spawning stock biomass per recruit (SPR) analyses, which provide proxies for fishery yield and spawning potential respectively. Depending on risk factors identified for an individual stocks (based on average burrow densities, harvest levels, variability of stock abundance, knowledge of biological parameters and the nature of the fishery – see ICES, 2010), the target reference point for exploitation rate is set at the value of F_{\max} (fishing mortality at which YPR is maximized), $F_{0.1}$ (fishing mortality at which the slope of the YPR curve is reduced to 10% of its value at the origin, being precautionarily less than F_{\max}) or $F_{35\% \text{ SPR}}$ (fishing mortality at which SPR is at 35% of its unexploited potential). F_{\max} is the least precautionary choice (highest value) and $F_{35\% \text{ SPR}}$ the most precautionary (lowest value). Target reference points are estimable for most stocks, needing only data on the size composition of landings and biological parameters for growth and sexual maturity. For stocks assessed by UWTV, the target reference point is couched in terms of a harvest ratio, which is the ratio of catch numbers to the UWTV estimate of overall stock abundance. The biomass limit reference point depends on the existence of a reliable index of abundance or biomass and is frequently not available for any given stock. For stocks with a sufficiently long time-series of UWTV surveys, the lowest abundance estimate of the series is often selected as the limit, unless there has been evidence of stock declines. For the Farn Deeps stock, the limit has been set at the lowest UWTV abundance estimate seen prior to a stock decline. In the case of the western Irish Sea, trawl survey indices scaled to recent UWTV abundance estimates have been used to provide the historical perspective necessary for identifying a meaningful limit.

TACs are not set for Mediterranean *Nephrops* fisheries, but stock assessments are regularly undertaken for the main stocks and reference points such as F_{\max} and $F_{0.1}$ are estimated from length-based analyses in a similar way to Atlantic stocks. The Scientific Advisory Committee of the GFCM provides advice on management measures (e.g. GFCM, 2011).

New Zealand *Metanephrops challengeri* stocks have been managed within the QMS since 1 October

2004. Prior to this the stocks were managed with a mixture of individual quotas and competitive catch limits. The QMS allocates Individual Transferrable Quota to companies or individuals, on the basis of catch history. TACs are maintained at or above a level that can produce MSY. There is no MLS for *Metanephrops*, and although minimum mesh sizes are set at 80 mm for the body of the trawl, and 55 mm for the cod end, the fishery uses larger mesh sizes. All bycatch of quota species must be reported and landed, and fishers without appropriate quota pay deemed values for excess catch.

12.6.2 Stock assessments

The term ‘stock assessment’ is often used in its narrowest sense to mean the application of mathematical methods to estimate the abundance or biomass of an exploited stock, its rate of exploitation and often other statistics such as levels of recruitment of juveniles to the fishable stock (e.g. Hilborn & Walters, 1992). Such assessments are generally based on combinations of commercial fishery, survey and biological sampling data. The outcomes are usually compared against criteria for overexploitation and used to determine likely prospects for future stocks and fisheries. Assessments of this type are currently carried out on many exploited *Nephrops* stocks (e.g. Eiriksson, 1992; Sardà *et al.*, 1998; ICES, 2011a,b,c).

At its simplest, stock assessment can involve straightforward examination of trends in commercial catches or catch rates. *Nephrops* stock assessments of this type have been performed for a century or more. For example, Storrow (1912) examined trends in landings data for the *Nephrops* fishery off the north-east coast of England (Farn Deep ground) for 1895 onwards, and used monthly catch rate data to separate the effects of fishing effort and changes in the availability of *Nephrops* in determining seasonal patterns of landings. Basic summaries of trends in landings, catch rates, sex ratio, mean size in the catch and other fishery statistics continue to form an important part of the regular assessments of exploited *Nephrops* stocks in the north-east Atlantic, and for some stocks this is the only source of information on stock status (ICES, 2011a,b,c).

Trends in fishery statistics

Mean size in catch samples can be informative about changes in some population processes. Increases in mean size could reflect either declines in recruitment, i.e. decreased numbers of small individuals in the population, or decreased mortality, i.e. increased numbers surviving to attain the larger size-classes, and the opposite interpretations could apply to decreases in mean size. Clearly, changes in mean size can only be interpreted alongside other sources of information. Mean size can also be affected by changes in discarding practices and the size-selective properties of the fishing gear, e.g. brought about by an increase in the minimum legal mesh size. Mean size is often calculated for just the size-classes unaffected by discarding (typically 35 mm CL and larger).

CPUE landings per unit effort (LPUE) are often treated as indices of stock abundance. This requires the assumption that catchability (proportion of the population captured by a unit of fishing effort) remains constant over time. Typical units would be kg per hour of trawling, but adjustments for vessel power are sometimes used. CPUE and LPUE are most reliably measured from catch returns supplied by a standard ‘reference’ fleet of commercial vessels. Fariña & González Herraiz (2003) used CPUE data from several fleets to show declining trends in *Nephrops* stocks around northern Spain and Portugal. Eiriksson (1999) examined spatial correlations in CPUE trends to determine geographical stock units for *Nephrops* around the southern coast of Iceland. Changes in the efficiency of fishing operations can cause problems for interpretation of CPUE and LPUE. For example, the introduction of ‘rock-hopper’ trawl gear and more precise geographical positioning systems (GPS) during the 1990s allowed *Nephrops* fishers in the Bay of Biscay to exploit previously inaccessible grounds and to locate their operations more precisely. The result was that LPUE statistics for *Nephrops* vessels remained stable at relatively high values whilst the stock biomass in the Bay of Biscay declined by almost a third between the late 1980s and the late 1990s (ICES, 2003). Bell *et al.* (2005) showed that spatial targeting of fishing effort at a sedentary *Nephrops* stock also creates

the potential for CPUE and LPUE to be maintained at misleadingly high levels during a stock decline. There is no information about whether this has actually occurred in practice, but there has been some evidence of concentration of fishing effort on the remaining centres of concentration in a heavily depleted Portuguese *Nephrops* stock.

Some of the problems in interpreting commercial LPUE and CPUE data can be addressed using statistical methods such as generalized linear modelling to account for sources of variation in catch rates such as vessel size, gear type and seasonal factors (e.g. Hilborn & Walters, 1992). Sbrana *et al.* (2003) used cluster analysis of commercial trawl catch data from the Tyrrhenian Sea (western Mediterranean) to identify ‘metiers’, or fishing tactics, corresponding to different assemblages of species in the catch, vessel characteristics and fishing areas, and applied generalized linear modelling to isolate an annual *Nephrops* abundance signal adjusted for vessels and months.

Trawl surveys

Besides being used to infer stock trends from commercial fishery data, CPUE is also commonly used as an index of abundance from trawl surveys directed at various species. Scientific surveys have the advantage over commercial statistics in that they are directed fully at a target species and undertaken in controlled circumstances. However, limits on time and resources mean that the host of factors which affect catch rates (e.g. Maynou & Sardà, 2001), cannot be expected to be averaged out as they might be in the multiple trawl tows underlying commercial data. Bell *et al.* (2008) found that only 19% of the variance in trawl catch rates on the Farn Deep ground could be accounted for by variations in abundance measured by UWTV surveys of burrow densities. Short-term variation in *Nephrops* catch rates, such as the greater catches on neap than on spring tides, have long been recognized (Storrow, 1912), and factors such as weather conditions and sea state are also known to be important (Maynou & Sardà, 2001). Much recent research into activity patterns by *Nephrops* is shedding light on the extent to which these may affect availability to be sampled by trawl surveys (e.g. Aguzzi & Sardà, 2008a,b;

Aguzzi & Bahamon, 2009). Trawl surveys clearly have their limitations, but nevertheless Tuck *et al.* (1997b) showed that under carefully controlled circumstances, survey catch rates could provide a useful index of local abundance. Catch rates in trawls timed to coincide with times of peak burrow emergence were strongly correlated with underwater TV estimates of burrow densities (see below) at the same locations (see also Smith & Papadopoulou, 2003). Trawl surveys have also successfully been used to describe spatial patterns in *Nephrops* stocks and to provide point estimates of stock biomass (Fariña *et al.*, 1994; Maynou *et al.*, 1998).

Larval production method

Another fishery-independent method of stock assessment is based on measuring larvae abundance and back-calculating the female stock biomass required to produce this. This involves using estimates of weight-specific fecundity of females and accounting for mortality of larvae between hatching and measuring their abundance. In the most rigorous application of this method to *Nephrops* so far, Briggs *et al.* (2002) used a combination of field and laboratory studies to obtain robust larval mortality and fecundity estimates for the Irish Sea stock. A mortality curve fitted to estimates of the total abundance of three larval stages was extrapolated to age zero to obtain an estimate of 425 billion larvae produced at hatching (Fig. 12.13). Fecundity was measured at 10,000 eggs per g of female, of which 35% was estimated to be lost during the incubation period, giving an effective fecundity of 68 eggs per g of female. This resulted in an estimate of female spawning stock biomass in the Irish Sea of 6,288 t, which compared well with a contemporary estimate of 7,750 t from analytical assessment of commercial fishery data (ICES, 2001). The larval production method has previously been applied in the Irish Sea by Thompson *et al.* (1986) and Nichols *et al.* (1987), giving female biomass estimates in the range 8000–12,000 t, and in the Firth of Clyde by Tuck *et al.* (1997b), who also noted a reasonable correspondence between larval production and analytical assessment estimates.

The larval method appears to work well in providing fishery-independent estimates of *Nephrops*

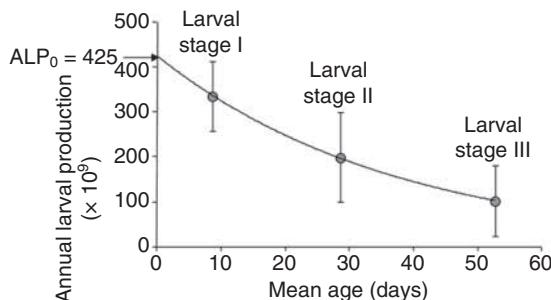


Fig. 12.13 Calculation of annual larval production for *Nephrops* in the Irish Sea from estimates of abundance at three larval stages. A mortality curve through the estimates is extrapolated to age zero to obtain an estimate of ALP_0 , the annual larval production at hatching. Error bars represent two standard errors. Briggs, R.P. & McAliskey, M. (2002). Reproduced with permission of Oxford University Press.

stock biomass, but its heavy demands on labour and resources means that it is unlikely ever to be used as a routine monitoring tool. Opportunities to apply the method are most likely to arise as a result of plankton surveys directed at other or additional aims, as was the case for Briggs *et al.* (2002) who used *Nephrops* larvae data from cruises directed at sampling fish eggs and larvae in the Irish Sea (Fox *et al.*, 1997; Dickey-Collas *et al.*, 2000a).

Underwater television and photographic surveys

The fishery-independent survey method that is now seeing widespread use in *Nephrops* assessments is the survey of burrow densities by UWTV. Work by Chapman (1979, 1985) showed that it is possible to measure *Nephrops* burrow densities by underwater photographic and TV surveys of the grounds. The underwater television approach has been developed into a full stock assessment method (Bailey *et al.*, 1993; Marrs *et al.*, 1996), and has been applied to various stocks in the north-east Atlantic and Mediterranean (Table 12.5). Considerable attention has been paid to accounting for edge effects, detection rates, species identification and occupancy (Campbell *et al.*, 2009a) and bias-corrected density estimates are now used to provide absolute estimates of stock abundance for calculating harvest ratios and limit reference points (see above) for many north-east Atlantic stocks.

The method typically involves slowly towing a sledge-mounted TV camera over the ground, and counting the number of burrow systems over a measured distance. Identification of *Nephrops* burrows, and determining which burrow entrances correspond to the same burrow system is a skilled task which inevitably involves some degree of subjectivity, but there is generally good agreement between counters, both between and within laboratories (Marrs *et al.*, 1996; Addison *et al.*, 2000). Marrs *et al.* (1996) noted a significant correlation between the diameter of burrows and the size of the occupants, and it has been suggested that UWTV surveys potentially could use measurement of burrow sizes to obtain indices of recruitment as well as of stock size (Addison *et al.*, 2000). Correia *et al.* (2007) have shown that it may be possible to develop automated counting of burrows in video images, which could reduce the human time and resources needed for image processing following UWTV surveys.

In New Zealand, development of photographic techniques, including surveys, has been underway since 1998, using a high resolution still camera rather than video. Survey series are being developed for each of the main stocks, with tri-annual surveys forming the core of *Metanephrops* stock monitoring within the New Zealand Ministry of Fisheries Deepwater 10 year plan. Two indices are calculated from the surveys: the density of visible lobsters (as a minimum estimate of absolute abundance), and the density of major burrow openings. The use of high resolution still images for the surveys allows accurate estimation of the area viewed (for calculation of density) and also the taking of measurements from the images (particularly for animal and burrow size). Although the number of animals observed on photographs is low (typically 10% about of the number of burrows), a relationship between animal size and burrow size has been observed, and from a size distribution of major burrow openings from each survey, the size distribution of the population generating the burrows has been estimated. Sex ratio at length (from research trawl catches) is used to partition numbers at length into sexes, and a stock biomass estimate is then made using sex-specific length-weight relationships.

Both the major burrow openings and visible animal indices have been used as a relative index of *Metanephrops* abundance within the length based model (Tuck & Dunn, 2006, 2011), and also used in conjunction with information on the size distribution of the population to estimate stock biomass. The length distribution estimated from the burrow size distribution is also used within the model to estimate the photo survey selectivity ogive.

Analytical assessment methods

Fishery-independent techniques, particularly UWTV burrow counting, are now the principal method of stock assessment for *Nephrops* in the north-east Atlantic, but analytical assessments based on commercial fishery data are still undertaken to provide information on biological reference points, and in some instances to form the main basis for inferences about stock status.

A major problem for analytical assessments is that there is no routine method of age-determination of *Nephrops*, so that inferences about the age-structures of stocks and catches are drawn from size-frequency distributions. Some of the first analytical assessments for *Nephrops* stocks were performed by Jones (1979) using length cohort analysis (LCA), a length-based analogue of Pope's (1972) cohort analysis. The method uses data on the length composition of the catch, together with values for natural mortality and von Bertalanffy growth parameters, to estimate stock size and fishing mortality at size, and using weigh-at-age data can generate information on the state of exploitation in relation to growth overfishing. The relatively modest data demands led to the method being widely used to assess *Nephrops* stocks in the north-east Atlantic (e.g. ICES, 2001) and in the Mediterranean (Sardà *et al.*, 1998). For many years this was the main assessment method for *Nephrops* used by ICES, and it is still commonly applied in Mediterranean stock assessments carried out under the aegis of GFCM. A major drawback of the method is that it is applicable only to steady-state (equilibrium) stocks, i.e. to stocks showing no overall trend in abundance or level of exploitation. Length composition data are often averaged over several years of no overall trend to approximate the steady state

assumption. LCA and similar length-based pseudo-cohort analyses are still applied by ICES to provide information on fishery selectivity at length in estimating target reference points based on YPR and SPR (see Section 12.6.1).

Abella *et al.* (1999) considered that a steady-state assumption was justified for *Nephrops* stocks in the Ligurian and Tyrrhenian Seas (western Mediterranean), but nevertheless failed to fit equilibrium surplus production models to time-series of mortality estimates. Attempts to fit similar models, but in a dynamic context (biomass dynamic models – Hilborn & Walters, 1992), have also not been successful for *Nephrops* stocks, probably because of the lack of ‘contrast’ in the data (ICES, 2000). Surplus production models are sometimes applied to Mediterranean stock assessments by GFCM, but have not been used as the main source of inferences on stock status. The SURBA (Survey-Based Assessment) method (Beare *et al.*, 2005), based on estimating year-class and fishing mortality values from trends in survey indices, has also been applied to trawl survey data for *Nephrops* in the Mediterranean, but again has not been used as the main assessment method.

The most successful applications of dynamic stock assessment methods to *Nephrops* have used age-based virtual population analysis (VPA). The main input to VPA is a time series of catch-at-age data. The problem of age determination has been overcome by deterministic ‘slicing’ of length compositions into age-classes using von Bertalanffy growth parameters (ICES, 2004). This has been criticized on the grounds that it ignores variations in growth between individuals and between year-classes, thus ‘smearing’ the year-class signal in the data (ICES, 2004). Inappropriate growth parameters, or spatial and temporal variations in growth rates, can also cause biases, and it is often difficult to trace unequivocal year-classes in ‘age’-composition data generated by slicing. VPA tuned to commercial CPUE (and sometimes to fishery-independent abundance indices from trawl or UWTV surveys) succeeded LCA as the main form of stock assessment for *Nephrops* used by ICES, but has now largely been abandoned in favour of UWTV assessments and simple interpretation of fishery statistics. However, VPA is still successfully

applied in the assessment and management of Icelandic *Nephrops*, and for the Bay of Biscay stocks it is used to provide information on relative trends in recruitment and biomass (although the status of this stock is officially classed as ‘unknown’ in ICES advice) (ICES, 2011b).

Explicitly length-based dynamic methods have also been applied to *Nephrops* with some success (Dobby, 2004; ICES, 2004), and there has also been some use of methods which make fewer demands on the necessity to determine age (ICES, 2002; Mesnil, 2003). The results have provided rather similar results to comparable VPA assessments, although rather more variability in stock trends was apparent from the length-based methods (Dobby, 2004).

New Zealand *Metanephrops* stocks are assessed using a Bayesian length-based assessment model (Cryer *et al.*, 2005a; Tuck & Dunn, 2006, 2009, 2011). The current model is implemented using the CASAL (C++ algorithmic stock assessment laboratory) framework (Bull *et al.*, 2008), and fits to trawl and photographic survey abundance indices and commercial CPUE within a spatial and seasonal model structure.

12.6.3 Status of stocks

The recent status of assessed *Nephrops* stocks falls into three main categories: (i) stocks to the north of the Bay of Biscay, which are largely stable or increasing; (ii) north-east Atlantic stocks to the south of the Bay of Biscay, which have shown severe declines over the last two decades; and (iii) Mediterranean stocks, which tend to be overexploited in the sense of growth overfishing, but which have not shown signs of recruitment failure. A summary of recent quantitative stock assessment outcomes is given in Table 12.7.

The first category of stable or increasing northern stocks includes a number with a long history of exploitation, particularly in inshore areas such as the Firth of Clyde and the Firth of Forth (ICES, 2011b,c). Some of these are at least fully exploited in the sense that exploitation rates are at levels above which growth overfishing would be occurring. The English Farn Deeps stock showed signs of decline after the mid-2000s, possibly owing to

recruitment failure from sperm-limitation following strongly male-biased fishing mortality, but the fishery is now considered to be at sustainable levels (ICES, 2011c). The overall tendency for stability or increases in northern stocks has been attributed *inter alia* to declines in cod stocks, an important predator of *Nephrops* (e.g. see Engelhard & Pinnegar, 2008), but it is also true that there has been opening up of opportunities by expansion into new areas, particularly offshore. The Fladen Ground in the northern North Sea is now the largest of all *Nephrops* fisheries, and this is an offshore ground which has been developed since the 1980s. Other offshore areas have been targeted more recently, including the ‘Devil’s Hole’ to the south of the Fladen Ground and deep water areas to the west of Ireland.

Southern stocks, particularly those around the Atlantic coasts of Spain and Portugal, have shown marked declines over at least two decades (ICES, 2011a). Given an absence of fishery-independent abundance indices and reference points for these stocks, their status is classed as unknown (hence these stocks are not included in Table 12.7), but on the basis of CPUE and other indicators abundance is qualitatively assessed as being at very low levels compared with historic levels. Changes in targeting behaviour in the mixed fisheries taking *Nephrops* may account for some of the declines in landings, but it seems likely that large-scale climatic processes linked to the North Atlantic Oscillation may have had a profound influence on recruitment processes in the Iberian stocks (see Section 12.4.3).

Recent stock assessments for Mediterranean stocks of *Nephrops* have indicated exploitation rates in excess of target levels represented by $F_{0.1}$ (see Section 12.6.1), but the risk of stock collapses is considered to be low (assessments by GFCM). Sardà *et al.* (1998) has previously inferred that fishing may be endangering recruitment in several Mediterranean stocks for which spawning potential was estimated to be below 30% of its unexploited value.

The two New Zealand *Metanephrops challengeri* stocks for which assessments have been accepted are both considered to currently be at about 40% of unexploited levels, the target level for these stocks within the QMS.

Table 12.7 Status of exploited *Nephrops* stocks in the north-east Atlantic and Mediterranean in 2010 and 2011.

Stock ¹	Assessment method ²	Exploitation rate ³		Basis for reference point ⁴	Stock size ⁵	Stock threshold ⁶
		Current level	Reference point			
Iceland (1)	VPA	$F = 0.17$			16000 t	
Moray Firth (4)	UWTV	HR = 11.2%	HR = 11.8%	$F_{35\% \text{ SPR}}$	406 million	262 million
Fladen Ground (5)	UWTV	HR = 9.8%	HR = 10.3%	$F_{0.1}$	2767 million	5224 million
Firth of Forth (7)	UWTV	HR = 18.4%	HR = 16.3%	F_{\max}	682 million	292 million
Farn Deeps (8)	UWTV	HR = 8.3%	HR = 8.0%	$F_{35\% \text{ SPR males}}$	892 million	879 million
Skagerrak & Kattegat (11, 12)	UWTV	HR = 6.4%	HR = 7.9%	$F_{35\% \text{ SPR}}$		
N Minch (13)	UWTV	HR = 7.6%	HR = 12.5%	$F_{35\% \text{ SPR}}$	1115 million	465 million
S Minch (14)	UWTV	HR = 7.4%	HR = 12.3%	$F_{35\% \text{ SPR}}$	2076 million	1016 million
Firth of Clyde (15)	UWTV	HR = 17.5%	HR = 16.4%	F_{\max}	1750 million	579 million
Sound of Jura (15)	UWTV	HR = 1.1%	HR = 14.5%	$F_{35\% \text{ SPR}}$		
W Irish Sea (16)	UWTV	HR = 15.0%	HR = 17.1%	F_{\max}	5000 million	3000 million
E Irish Sea (17)	UWTV	HR = 5.8%	HR = 9.8%	$F_{0.1}$	469 million	
Aran Grounds (18)	UWTV	HR = 8.3%	HR = 10.5%	$F_{35\% \text{ SPR}}$	827 million	
Celtic Sea (21)	UWTV	HR = 10.9%	HR = 10.9%	$F_{35\% \text{ SPR}}$	1483 million	
Catalan Sea (30)	LCA	$F = 0.446$	$F = 0.295$	$F_{0.1}$		
Ligurian & N Tyrrhenian Sea (31)	LCA	$F = 0.350$	$F = 0.210$	$F_{0.1}$		
N Adriatic Sea (32)	LCA	$F = 0.685$ (females) $F = 0.870$ (males)	$F = 0.246$ (females) $F = 0.200$ (males)	$F_{0.1}$	1253 t (females) 744 t (males)	

¹Numbers in brackets refer to location of fishing ground as shown in Fig. 12.2. Information on status sourced from Information Centre of the Icelandic Ministry of Fisheries and Agriculture (Icelandic stock), the International Council for the Exploration of the Sea (other north-east Atlantic stocks) and the General Fisheries Commission for the Mediterranean (Mediterranean stocks). All assessments are from 2011, except for Catalan Sea and N Adriatic Sea which are from 2010.

²Assessment methods: VPA, age-based virtual population analysis; UWTV, underwater television surveys of burrow densities; LCA, length cohort analysis.

³Exploitation rate: F , annual rate of fishing mortality averaged over reference ages or lengths; HR, harvest ratio, which is the ratio of catch numbers to stock abundance estimated by UWTV. Shaded cells indicate exploitation rates that exceed the target reference point.

⁴Target fishing mortality estimated from yield or spawner per recruit analyses: $F_{35\% \text{ SPR}}$, fishing mortality at which spawning stock biomass per recruit is at 35% of its value for an unexploited stock; F_{\max} , fishing mortality at which yield per recruit is maximised; $F_{0.1}$, fishing mortality at which the slope of the yield per recruit curve is at 10% of its value at the origin.

⁵Most recent estimate of stock biomass or abundance: values in tonnes are analytical estimates from VPA or LCA; values in millions are based on UWTV surveys of burrow densities.

⁶The stock threshold is the abundance below which there is considered to be a risk of impaired recruitment.

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Chapter 13

Commercial Scyllarids

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Abstract

Among the 20 genera and at least 88 species constituting the four subfamilies of Scyllaridae, only members of four genera, *Thenus* (Theninae), *Scyllarides* (Arctidinae), *Ibacus* and *Parribacus* (Ibacinae), form any kind of significant fishery because of the large size of individuals. Although scientific knowledge on commercial slipper lobsters has increased considerably in the recent few decades, it is still limited compared with that for commercially valuable spiny and clawed lobsters and is based on studies from a handful of species. The present chapter presents the current available knowledge on the taxonomy, anatomy, distribution, ecology, life history, behaviour, and fisheries of commercial scyllarids belonging to the above four genera. While some advances had been made in aquaculture of one species (*Thenus orientalis*) insufficient information on slipper lobster biology and ecology, lack of fisheries regulations and trends of reduced annual production of several exploited taxa call for the need for focused studies on these lobsters.

Key Words: slipper lobsters; *Scyllarides*; *Thenus*; *Ibacus*; *Parribacus*; taxonomy; ecology; life history; behaviour; fisheries

13.1 Introduction

Slipper lobsters, family Scyllaridae (Latireille, 1825), are a taxon of lobsters for which limited scientific information is available, compared with that for commercially valuable lobsters in the Nephropidae and Palinuridae families. Slipper lobsters have been known of and described since the late 1700s with numerous species being discovered after 1852 (Holthuis, 2002). They are found within the superfamily Palinuroidea that consists of spiny

lobsters (Palinuridae), furry lobsters (Synaxidae), blind claw-footed lobsters (Polychelidae) and slipper, shovel-nosed or bulldozer lobsters (Scyllaridae) (Holthuis, 1991; Lavalli & Spanier, 2010). The Scyllaridae are organized into four subfamilies (Ibacinae, Arctidiane, Scyllarinae and Theninae) and comprise 20 genera with at least 88 species that have been recognized to date (Holthuis, 2002; Webber & Booth, 2007; Burton & Davie, 2007). Webber & Booth (2007) stated that further species would inevitably be described, particularly in

the subfamily Scyllarinae, which are distributed throughout a greater range of latitudes and depths than the other three subfamilies of scyllarids and already include well over half of the species in the family.

Only four genera, *Scyllarides* (Arctidinae), *Ibacus* and *Parribacus* (Ibacinae), and *Thenus* (Theninae) form any kind of significant fishery because individual species tend to be large in size (Mikami & Kuballa, 2007, Spanier & Lavalli, 2007). Of these four, the largest body of knowledge exists for *Scyllarides* (Gill, 1898). This is due, probably, to the large number (14) of species known in this genus (Holthuis, 1991), their wide geographical distribution in tropical and subtropical habitats around the world, the large size they attain as adults [up to 50 cm total body length (TL) in *S. haanii*, according to Holthuis (1991)], and their economic importance as edible crustaceans. Considerable knowledge is also available for species within the genus *Thenus* because of some importance to certain fisheries and the success in rearing them in aquaculture (e.g. Mikami & Kuballa, 2007; Rogers *et al.*, 2010; Jeffs, 2010; Vijayakumaran & Radhakrishnan, 2011). Otherwise, information has been gleaned when overfishing of one or more species of spiny lobsters in an area results in increased fishing pressure on local slipper lobsters. For example, the depletion of the local spiny lobsters *Panulirus penicillatus* and *P. gracilis* in the Galápagos Islands brought about increased fishing pressure on *Scyllarides astori* (Hearn, 2006; Hearn *et al.*, 2007) with a concomitant increase in research on *S. astori*. Likewise, a 50% drop in recruitment to fisheries of *Panulirus marginatus* in Hawaii since 1989 resulted in subsequent overexploitation of the Hawaiian slipper lobsters (*S. squamosus*, *S. haanii*, *Parribacus antarcticus*) (Polovina *et al.*, 1995). Research on such species always lags behind exploitation, which is problematic for the creation of sustainable slipper lobster fisheries.

The present review is an attempt to summarize the somewhat patchy information available in the scientific literature on the commercial species of the above four genera. Although there is minor commercial interest in some scyllarid species in the recreational fisheries and the aquarium industry (e.g. Spanier & Lavalli, 2007), the present review

is focused solely on the slipper lobster species fished for human consumption.

13.2 Taxonomy and systematic hierarchy

13.2.1 Features of the genera

Scyllarides

The genus *Scyllarides* belongs to the subfamily Arctidinae and is typified by a dorsoventrally compressed body with a highly vaulted carapace that may or may not have a small, shallow, cervical incision. The mandibular palp is typically tri-segmented. There are only two genera in this subfamily, *Arctides* and *Scyllarides* (Holthuis, 1991, 2002; Chan, 2010). The genus *Scyllarides* is characterized by a first abdominal somite that lacks a transverse groove dorsally and a carapace that lacks a postorbital spine. The abdomen shows no dorsal sculpturing, apart from a median ridge (Holthuis, 1991).

Ibacus and *Parribacus*

The genera *Ibacus* and *Parribacus* belong to the subfamily Ibacinae (together with *Evibacus*). The carapace is strongly dorsoventrally compressed with a deep cervical incision along the lateral margin of the carapace. The mandibular palp, in contrast with Arctidinae, is simple or bi-segmented. *Ibacus* and *Parribacus* are typified by eye orbits that are open anteriorly and possess a well-defined open cervical incision. The dorsal surface of *Ibacus* is smooth and punctuate with pubescence, while it is coarsely squamose-tuberculated in *Parribacus*. The fifth abdominal segment is spined in *Ibacus* and spineless in *Parribacus* which also has bi-segmented mandibular palp compared with a single segment in *Ibacus* (Holthuis, 1991, 2002; Lavalli & Spanier, 2007b; Chan, 2010).

Thenus

The genus *Thenus* belongs to the monogeneric subfamily Thenidae. The body is strongly dorsoventrally compressed. No flagellum is present on the exopod of the first and the third maxilliped (similar to Scyllarinae). The eye orbit is located in

the extreme anterolateral extent of the carapace and the eyes are extremely small. The lateral margin of the carapace lacks teeth and only has the cervical incision, an anterolateral tooth and a postcervical tooth. The fifth leg of female is achelate (Holthuis, 1991, 2002; Lavalli & Spanier, 2007b; Chan, 2010).

13.2.2 Species and distribution

All distribution patterns presented here refer to adult specimens only.

Scyllarides species

Scyllarides species are illustrated in Fig. 13.1.

Scyllarides aequinoctialis (Lund, 1793) (Fig. 13.1A; English FAO name – Spanish slipper lobster) is also the type species of the genus. In this species, the carapace is less highly vaulted, the cervical incision is nearly absent and pregastric and gastric teeth are barely set off from the surface. However, the dorsal surface of the first abdominal somite bears three well-defined and highly distinctive spots: a horseshoe shaped middle spot, and two rounded sub-medial spots. These lobsters are found

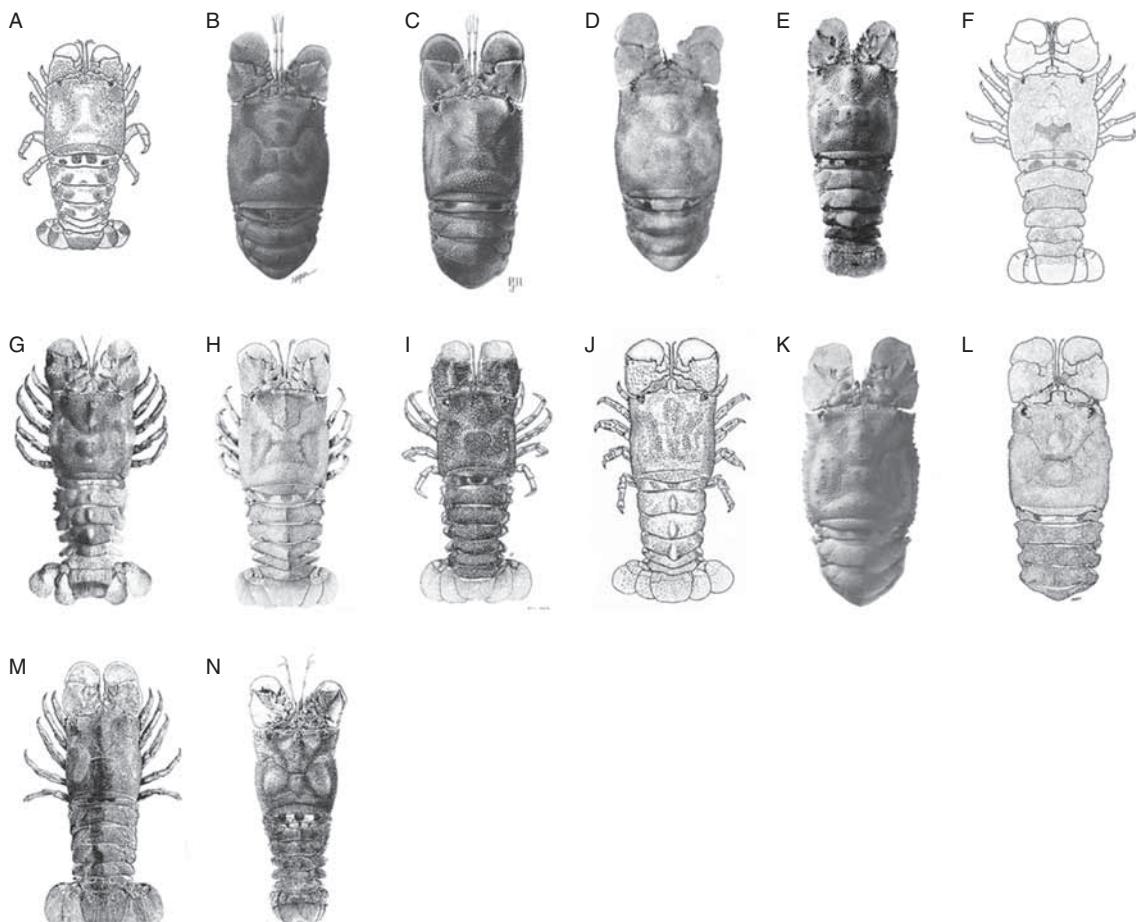


Fig. 13.1 Lobsters within the *Scyllarides* genus. (A) *Scyllarides aequinoctialis*; (B) *S. astori*; (C) *S. brasiliensis*; (D) *S. deceptor*; (E) *S. delfosi*; (F) *S. elisabethae*; (G) *S. haanii*; (H) *S. herklotsii*; (I) *S. latus*; (J) *S. nodifer*; (K) *S. obtusus*; (L) *S. roggeveeni*; (M) *S. squammosus*; (N) *S. tridacnophaga*. (A–J, L–N) Modified from Holthuis, 1991, used with permission from the Food and Agricultural Organization of the United Nations and (K) modified from Holthuis, 1993, used with permission from NCB Naturalis on behalf of Zoologische Mededelingen.

in the Western Atlantic from South Carolina, USA and Bermuda via the West Indies, including the Gulf of Mexico and the Caribbean, to southern Brazil. The maximum TL is over 30 cm and carapace length (CL) is about 12 cm. Their depth distribution is from less than 1 m to 180 m, but usually not deeper than 64 m. These lobsters prefer substrates of sand or rock that are often found on outer reefs. They prefer shelters located with complex, high-relief, coral habitats (Holthuis, 1991, Sharp *et al.*, 2007).

Scyllarides astori Holthuis, 1960 (Fig. 13.1B; English FAO name – Galápagos slipper lobster) has a carapace that is characterized by the gastric and pregastric teeth forming broad elevations. The first abdominal somite bears two distinct lateral spots, between which are numerous small spots that may fuse together. The geographical range of this species is unclear. Holthuis & Loesch (1967) and Hickman & Zimmerman (2000) suggest that it may be endemic to the Galápagos Islands, while Reck (1983) states that the occurrence of larvae around the Cocos Islands (as per Johnson, 1971a) may indicate the existence of breeding populations elsewhere in the eastern Pacific. According to Holthuis (1991) and Gotshall (1998), *S. astori* is also found in the Gulf of California, so its status as an endemic species may require revision. This typically reddish-brown coloured lobster generally reaches a TL of 30 cm, although the maximum recorded size is 37.8 cm (Hearn, 2004). Hearn *et al.* (2007) estimated the following parameters of the von Bertalanffy growth function: CL_∞ for males = 163.8 mm, for females = 175.3 mm, and *k* = 0.124 and 0.145 for males and females respectively (where *k* is the rate at which the asymptotic total length, *L*_∞, is approached) and 0.145 for males and females respectively. It is found on rocky substrates, preferring vertical walls with caves and crevices (Barr, 1968; Martínez *et al.*, 2002; Hearn *et al.*, 2007), where it shelters during the day. Reck (1983) observed individuals from shallow depths (0–5 m) to at least 40 m, while Gotshall (1998) suggested a depth range up to 90 m. According to Martínez *et al.* (2002) and Hearn *et al.* (2003), it is less abundant in the immediate subtidal zone, the preferred habitat for the red spiny lobster *Panulirus penicillatus* that shares similar habitats with *S. astori* in the Galápagos Islands.

Scyllarides brasiliensis Rathbun, 1906 (Fig. 13.1C; English FAO name – Brazilian slipper lobster) is characterized by the presence of a cervical incision along the lateral margin of the carapace and tubercles on the surface of the carapace near the gastric tooth. The first abdominal somite bears only two red lateral spots dorsally. There is very limited information on the distribution of this species. Its TL is about 20 cm with a CL of up to 12 cm. It is found in 22–38 m of depth in the Western Atlantic off Brazil, from Maranhão to Bahia (Holthuis, 1991). There is also a record of this species from Dominica in the West Indies (Holthuis, 1991) on sand, gravel and rock bottoms (Coelho & Ramos-Porto, 1983/1985, 1998).

Scyllarides deceptor Holthuis, 1963 (Fig. 13.1D; English FAO name – hooded slipper lobster) has distinct grooves on its carapace with well-defined gastric and pregastric teeth; however, the cervical incision while wide is not very distinct. The dorsal surface of the first abdominal somite bears two very distinct and sharp spots. This species reaches a TL between 13–27 cm and a CL of 5–12 cm. It is found in the Western Atlantic from southern Brazil to northern Argentina in depths from 40 to 220 m (Williams, 1986; Melo, 1999; Duarte *et al.*, 2010) and on substrates similar to *S. brasiliensis* (Coelho & Ramos-Porto, 1983/1985, 1998) such as shallow rocky bottoms with patches of gravel and sandy sediments (Oliveira *et al.*, 2008) or steep morphologies covered with shells and slabs of sandstone (Duarte *et al.*, 2010).

Scyllarides delfosi Holthuis, 1960 (Fig. 13.1E; English FAO name – three-spot slipper lobster), like *S. deceptor*, has distinct grooves on its carapace and well-defined gastric and pregastric teeth. Its cervical incision is distinct, but narrow. The first abdominal somite bears one circular central spot and two irregularly shaped lateral spots on its dorsal surface. The TL of this species reaches up to 25 cm and the CL is typically 6–9 cm. It is found in the Western Atlantic along the north coast of South America from Venezuela to Brazil in depths between 42 and 80 m on muddy substrates (Opresko *et al.* 1973).

Scyllarides elisabethae (Ortmann, 1894) (Fig. 13.1F; English FAO name – Cape slipper lobster) has distinct cervical and postcervical incisions along the lateral margin of its carapace. The TL of this species exceeds 25 cm and its CL reaches 9 cm.

It is found only in the Indian Ocean along southeast Africa in substrates of fine sand or mud and at depths ranging from 37 to 380 m (usually at less than 100 m) (Williams, 1986).

Scyllarides haanii (De Haan, 1841) (Fig. 13.1G; English FAO name – Aesop or ridgeback slipper lobster) has a distinct dorsal groove on the carpus of the first pereiopod, and a large medial hump on the fourth abdominal somite. The first abdominal somite bears two small but distinct lateral spots and a large, irregular median spot (Holthuis, 1991). The TL of this species reaches 50 cm and the maximum CL thus far reported is 17 cm. It is found in the Indo-West Pacific around Japan, Korea, China, Indonesia, Australia, and Hawaii, and in the Red Sea and western Indian Ocean in depths ranging from 10–135 m on rocky substrates (Holthuis, 1991). DiNardo & Moffitt (2007) reported this species in the Hawaiian Islands at depths ranging from 60 to 200 m, with the greatest concentrations between 100 and 150 m. They also reported that this species was caught in low abundance in the north-western Hawaiian Islands until the fishery was closed in 2000.

Scyllarides herklotsii (Herklots, 1851) (Fig. 13.1H; English FAO name – red slipper lobster), like *S. haanii*, has the dorsal groove on its first pereiopod, but its fourth abdominal somite does not bear a large hump. Its first abdominal somite bears three circular or irregularly shaped red spots that are widely separated. The maximum TL reported for this species is about 32 cm, but usually they are not more than 25 cm. It is found in West Africa from northern Senegal to southern Angola on sand and rocky substrates, but sometimes on mud, and mostly at depths between 5 and 70 m. There are reports of this lobster in deeper waters beyond 200 m (Holthuis, 1991).

Scyllarides latus (Latreille, 1802) (Fig. 13.1I; English FAO name – Mediterranean slipper lobster) is similar to both *S. haanii* and *S. herklotsii*, in that it too bears a dorsal groove on its first pereiopod. Like *S. herklotsii* it lacks a large hump on its fourth abdominal somite. The first abdominal somite bears a large central, circular spot that is separated from the lateral spots by a narrow yellow ring-like zone. The carapace is covered in conspicuous and high tubercles.

There is a considerable body of knowledge on this species due to studies done in the Azores Islands, Israel, and Italy. It is found mainly on hard substrates at depths of 4 to 100 m (Holthuis, 1991) in the Mediterranean Sea and Eastern Atlantic from the coast of Portugal to Senegal, Madeira, the Azores, the Selvagens, and the Cape Verde Islands (Maignet, 1978; Fischer *et al.*, 1973, 1981; Campbell, 1982; Martins, 1985a; Holthuis, 1991; Pessani & Mura, 2007). However, in many areas, and especially along the Mediterranean coasts of Europe, this species is rare due to overfishing (Spanier, 1991; Pessani & Mura, 2007). It is also found on artificial reefs (Spanier *et al.*, 1990; Spanier & Lavalli 1998, 2007; Spanier *et al.*, 2010, 2011a). Holthuis (1991) reported the maximum TL of this species to be about 45 cm, with a CL of up to 12 cm. However, the studies of Martins (1985a) in the Azores, Bianchini *et al.* (1996) in Italy, and Spanier *et al.* (1988) and Almog-Shtayer (1988) in Israel indicate that the present sizes are smaller due most likely to selective fishing pressure on larger specimens. Spanier & Lavalli (1998) reported that females tended to be larger than males and Atlantic specimens seem to be heavier than those from the southeastern Mediterranean. However, a genetic comparison of *S. latus* from Israel, Italy and the Azores Islands indicated very little variability between these populations (Bianchini *et al.*, 1998). Bianchini & Ragonese (2007) obtained in the laboratory the following parameters of the seasonalized von Bertalanffy growth function, $CL_{\infty} = 127.2$ mm, $k = 0.20$, $C = 1.0$, $t_s = 0.83$ (where C is the seasonal oscillation amplitude and t_s is the start of the oscillation with respect to t_0 , the hypothetical age when the length should be zero), which were in agreement with data from long-term recaptures in the wild and similar to those of *S. astori* from the Galápagos Islands.

Scyllarides nodifer (Stimpson, 1866) (Fig. 13.1J; English FAO name – ridged slipper lobster) bears a large swollen hump in the upper basal part of the carpus of the first pereiopod, and three distinct red spots on the first abdominal somite. All pereiopods have conspicuous red bands on the propus, merus and carpus. The posterior margin of the second abdominal somite bears a prominent tooth. The TL of this species typically reaches about 35 cm and its

CL ranges from 11 to 13 cm (Holthuis, 1991; Sharp *et al.*, 2007). Sharp *et al.* (2007) suggested that *S. nodifer* appeared to be less specific in its sheltering preference than *S. aequinoctialis*. It occurs in depths of up to 42 m on sandy substrate or sand mixed with mud, shells, coral, coralline algae or sponge, and is also found on limestone block ridges (Shipp & Hopkins, 1978) and artificial reefs or the undersides of drilling platforms (Moe, 1991). It may bury into sediment. Its colouration is cryptic on limestone ledges and rocky outcroppings (Lyons, 1970; Ogren, 1977; Fischer, 1978; Hardwick & Cline, 1990; Holthuis, 1991).

Scyllarides obtusus Holthuis, 1993 (Fig. 13.1K; local name – stump) is a recently described species from the waters off Saint Helena (Holthuis, 1993). Previously this species was identified with various *Scyllarides* species from the Atlantic Ocean and the waters off East Africa. It is closest in form to the West African *S. herklotsii* and South American *S. delfosi*, but differs from the former in having a swollen base of the carpus of the first pereiopod, more pronounced ridges on all pereiopods, a wider and flatter carapace with more prominent gastric and pregastric teeth, and closer placed spots on the first abdominal somite. It differs from the latter in having a flatter carapace with a more distinct and rough postcervical groove and larger, more distinct lateral margin teeth, and more closely spaced and equally sized spots on the first abdominal somite. The largest specimen reported had a CL of 106 mm (Holthuis, 1993). This species is endemic to the area surrounding Saint Helena and occurs on hard substrates at depths between 5 and 75 m. It supports a local fishery, and has done so since early times; the earliest reference to this lobster is from 1646 (Holthuis, 1993).

Scyllarides roggeveeni Holthuis, 1967 (Fig. 13.1L; English FAO name – Easter Island slipper lobster) has distinct gastric and pregastric teeth, a deep cervical groove on the carapace, three distinct spots on the first abdominal somite and distinct humps or medial ridges on the second through fourth abdominal segments. The TL of this species is about 30 cm, with a CL of 11 cm. It is only found off Easter Island but is poorly understood because no regular fishery exists for it (Holthuis, 1991).

Scyllarides squamosus (H. Milne Edwards, 1837) (Fig. 13.1M; English FAO name – blunt slipper lobster and also known locally as the scaly slipper lobster) bears a cervical incision along the lateral margin of its carapace, and two pointed teeth on the inner orbital margin. The orbit is almost closed due to the presence of a toothed lobe along the inner orbital angle that nearly touches the outer orbital angle. The first abdominal somite bears three red spots: a poorly defined medial spot and two well-defined lateral spots. The maximum TL of this species is about 40 cm and its CL reaches up to 15 cm. It is found in the Indo-West Pacific from Japan, Hawaii, Melanesia, New Caledonia, and Australia to the eastern coast of Africa on reefs and rocky substrates of a few meters depth to about 80 m (Holthuis, 1991). It is most common at depths between 20 and 50 m (Fischer & Bianchi, 1984). This species was a major target of the lobster fisheries in the north-western Hawaiian Islands (DiNardo & Moffitt, 2007) until the fishery was closed in 2000 due to dramatic declines in the catch. O’Malley (2011), who studied the population ecology of this species in Hawaii using tag/recapture information, stated that somatic growth of this species differed from its congeners. He found that it growth abruptly declined at maturity and that the growth at length was better described using the Schnute model as opposed to the more commonly von Bertalanffy growth model.

Scyllarides tridacnophaga Holthuis, 1967 (Fig. 13.1N; English FAO name – clamkiller slipper lobster), like *S. roggeveeni*, has distinct gastric and pregastric teeth, sharp median ridges on the second to fourth abdominal somites, and three distinct spots on the first abdominal somite. It differs from *S. roggeveeni* in that its pregastric tooth is two-topped, its cervical groove is shallow, and the central spot on the first abdominal somite is sharply defined rather than being indistinct. The TL of this species reaches 30 cm and its CL ranges from 6 to 12 cm. It is found in the Indo-West Pacific throughout the Red Sea (up to Eilat, in the northern tip of the Gulf of Aqaba), along the eastern Africa coast (Somalia, Kenya), in the Gulf of Aden, and along Pakistan and the western coast of Thailand. This lobster is found mainly on or close to reefs and other hard substrates at depths between 5 and 112 m (Holthuis, 1968, 1991).

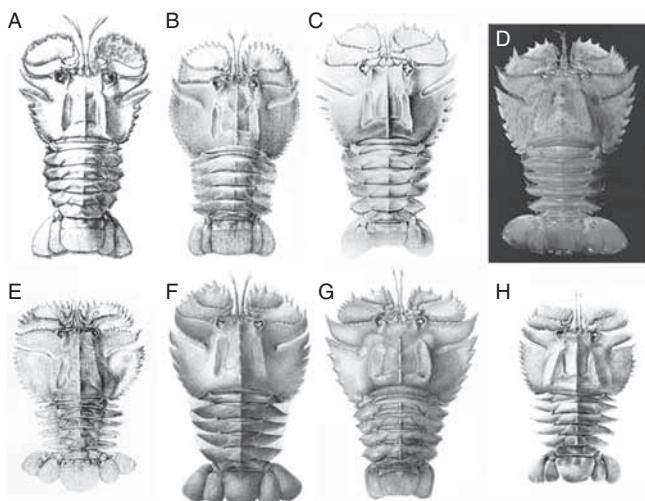


Fig. 13.2 Lobsters within the *Ibacus* genus. (A) *Ibacus alticrenatus*; (B) *I. brevipes*; (C) *I. brucei*; (D) *I. chacei*; (E) *I. ciliatus*; (F) *I. novemdentatus*; (G) *I. peronii*; (H) *I. pubescens*. Holthuis, L.B. (1991) Marine lobsters of the world. FAO Fisheries Synopsis No. 125, Vol. 13. FAO, Rome, with permission from FAO, and Brown, D.E. & Holthuis, L.B. (1998). The Australian species of the genus *Ibacus* (Crustacea: Decapoda: Scyllaridae) with the description of a new species and addition of new records. *Zoologische Mededelingen*, Leiden 42, 281–301, with permission from Naturalis.

Ibacus species

Ibacus species are illustrated in Fig. 13.2. At present there are eight recognized species of *Ibacus*. All are found at relatively great depths in the Indo-West Pacific region (Holthuis, 1991, Brown & Holthuis, 1998; Haddy *et al.*, 2007, Chan, 2010).

Ibacus alticrenatus Bate, 1888 (Fig. 13.2A; English FAO name – velvet fan lobster) has a short, woolly pubescence on its dorsal surface. The fourth segment of antenna is slender and lacking in lateral teeth, and narrows from its base to tip (Holthuis, 1991). The merus of the third maxilliped is flat to concave on its posterior surface (Webber & Booth, 2007). This species is distributed in Australia [New South Wales (NSW), Bass Straits, Tasman Sea, Victoria, South Australia] from northeast Queensland (Latitude 20°S), around the southern Australian coastline, to North West Cape (Latitude 22°S) in Western Australia. It is also found around most of New Zealand (North Island, South Island and the Chatham Islands). It has an overall depth range between 80 and 700 m, but is most commonly caught on the upper continental slope between 200 and 400 m. Holthuis (1991) reported that the CL of this species ranges from 1.5 to 3 cm with a maximum TL of 6.3 cm. Recently Haddy *et al.*, (2007) reported

that maximum size and weight for males was *c.* 55 mm CL and 85 g, and for females *c.* 65 mm CL and 140 g. Length-weight relationships (sexes combined) were total weight = $0.0007 \times \text{CL}^{2.9365}$ ($R^2 = 0.955$; $n = 513$).

Ibacus brevipes Bate, 1888 (Fig. 13.2B; English FAO name – serrate fan lobster) bears 12–18 teeth on lateral margins of its carapace behind the cervical incision (Brown & Holthuis, 1998). The merus of the third maxilliped is enlarged and swollen with deep transverse incisions similar to *Evibacus* (Webber & Booth, 2007). Inner margin of the merus has short, deep incisions that do not reach the middle of the segment, while the outer meral margin has a broad, wing-like expansion or keel that is strongly toothed along its entire length. The CL in this species ranges from 2 to 5 cm and the maximum TL is about 12 cm (Holthuis, 1991). This species is found in the Indo-West Pacific region: South China Sea, Philippines, Indonesia, Moluccas, New Caledonia and north-eastern Australia (Coral Sea) from 186–457 m (Brown & Holthuis, 1998).

Ibacus brucei Holthuis, 1977 (Fig. 13.2C; English FAO name – glabrous fan lobster) has microscopically small, scattered setae on the dorsal surface of its carapace, such that it appears una-

dorned to the naked eye. The fourth segment of the antenna is not slender, at first widening in a lateral direction before narrowing into the apex, and has a distinct lateral margin that is provided with well-developed teeth (Holthuis, 1991). The merus of the third maxilliped is as in *I. alticrenatus* (Webber & Booth, 2007). These lobsters are found along Australia's east coast mainly between central Queensland (latitude 20°S) and central NSW (latitude 32°S) with a few isolated records as far south as latitude 35°S. The species has also been recorded from northern New Zealand waters off the Kermadec Islands and on the West Norfolk Ridge. Its overall depth range is between 80 and 560 m, but it is most abundant near the continental shelf break in depths between 150 and 250 m. Holthuis (1991) reported CL of this species ranging from 2 to 5.7 cm with a maximum TL of about 13 cm. Recently Haddy *et al.* (2007) reported that the male maximum size and weight was *ca* 65 mm CL and 130 g, and for females was *c.* 74 mm CL and 190 g. Length-weight relationship (sexes combined): total weight = 0.0003 × CL^{3.1712} ($R^2 = 0.982$; $n = 1544$).

Ibacus chacei Brown & Holthuis, 1998 [Fig. 13.2D; common names in eastern Australia- smooth bug, Balmain bug, and garlic bug (Haddy *et al.*, 2007)] is a recently described species that was previously confused with *I. brevipes* because of similarity of size and appearance and overlapped geographic and depth distributions (Webber & Booth, 2007). However, *I. chacei* is confined to eastern Australia between northern Queensland (latitude 17°S) and southern NSW (latitude 36°S), although it is rarely caught south of Sydney (latitude 34° S). Its overall depth range is between 20 and 330 m, but it is most abundant on the mid-continental shelf between 50 and 150 m. The merus of the third maxilliped is as in *I. brevipes* (Webber & Booth, 2007). Male maximum size and weight is *c.* 73 mm CL and 250 g, and for females *c.* 83 mm CL and 325 g. Length-weight relationship (sexes combined): total weight = 0.0004 × CL^{3.0702} ($R^2 = 0.992$; $n = 7597$) (Haddy *et al.*, 2007).

Ibacus ciliatus (Von Siebold, 1824) (Fig. 13.2E; English FAO name – Japanese fan lobster) has a naked adult carapace that bears 10–12 (usually 11)

posterolateral teeth along the lateral margin (Holthuis, 1991). The maximum TL of this species reaches about 23 cm and its CL ranges from 4 to 7.6 cm in males and 4 to 8 cm in females (Holthuis, 1991). The merus of the third maxilliped is as in *I. alticrenatus* (Webber & Booth, 2007). This species is found in the Indo-West Pacific region, along Japan (southward of Nigata on the west coast (*c.* 38°N) and from Tokyo Bay on the west coast (*c.* 35.5°N)) as well as along the south coast of Korea to Hainan Island (S. China), in the South China Sea, off Taiwan, on east coast of the Philippines, and along Thailand (Holthuis, 1991).

Ibacus novemdentatus Gibbes, 1850 (Fig. 13.2F; English FAO name – smooth fan lobster) has a naked but pitted (glabrous) carapace with a narrow cervical incision. The lateral margin behind the cervical incision bears seven or eight teeth. The posterior branchial carinae of the carapace are straight or only slightly convex diverging slightly distally; they lay in one line with the anterior branchial carinae. The posterior incision of the orbit lacks prominent tubercles. The merus of the third maxilliped is as in *I. brevipes* (Webber & Booth, 2007) in that it is swollen, with deep incisions on inner margin, many of which reach past the middle of the segment; there is also a wing-like expansion or keel of the outer margin strongly toothed from the top to bottom. Anterior teeth of the epistome are directed forwards (Holthuis, 1991). The TL of this species reaches 19 cm and its CL ranges from 3 to 7 cm (Holthuis, 1991). This species is distributed in the Indo-West Pacific region: East Africa (Kenya-Cape Province), Western Indian Ocean (north-west Madagascar, Mauritius-Seychelles Ridge), Korea, Japan, South China Sea, Taiwan, Vietnam, Philippines, Indonesia, north-western Australia, and in the Northern Territory (Timor Sea and Arafura Sea). Depth ranges between 37 and 400 m (Brown & Holthuis, 1998).

Ibacus peronii Leach, 1815 (Fig. 13.2G; English FAO name – butterfly fan lobster) is the type species of the genus. The posterior branchial carinae of the carapace are strongly convex, and do not lay in one line with the anterior branchial carinae. The posterior incision of the orbit bears a distinct tubercle. The lateral margin of the carapace

bears six or seven (rarely eight) posterolateral teeth. The merus of the third maxilliped is as in *I. brevipes* (Webber & Booth, 2007). The anterior teeth of the epistome are directed ventrally. This species is the best known of the Australian fan lobsters and is widely distributed around the southern half of the continent from about the Queensland–NSW border (latitude 28°S) to central Western Australia (latitude 29°S), including the east coast of Tasmania and Bass Strait. The species is also reported from southeast Queensland (Brown & Holthuis 1998) but none was found in trawl samples during recent studies (Courtney, 2002). With an overall depth range of 4–288 m, *I. peronii* has the shallowest minimum depth reported for any *Ibacus* spp. and is mainly found close to shore in waters less than 80 m deep. Holthuis (1991) reported that the CL of this species ranged from 2 to 8 cm with a maximum TL of about 23 cm. Recently Haddy *et al.* (2007) reported that the maximum size and weight of males is c. 79 mm CL and 290 g, and for females it is c. 89 mm CL and 375 g. Length-weight relationship (sexes combined): total weight = $0.0004 \times \text{CL}^{3.0886}$ ($R^2 = 0.995$; $n = 425$) (Haddy *et al.*, 2007).

Ibacus pubescens Holthuis, 1960 (Fig. 13.2H) has a thick cover of velvety pubescence on the adult carapace. The lateral margin of carapace bears 11–13 (usually 12) posterolateral teeth (Holthuis, 1991). The merus of the third maxilliped is as in *I. alticrenatus* (Webber & Booth, 2007). As with *I. brevipes*, *I. ciliatus* and *I. novemdentatus*, this species has a broadly tropical distribution between the South China Sea and Northern Australia (Haddy *et al.*, 2007).

Paribacus species

This genus contains six species (Fig. 13.3), all of which are used locally as human food (Holthuis, 1991; Chan, 2010). All *Paribacus* species have a carapace that is covered dorsally with coarse squamose tubercles and that lacks post-rostral or branchial carinae. All lack a posteromedian spine on the fifth abdominal somite and have a two-segmented mandibular palp (Holthuis, 1991).

Paribacus antarcticus (Lund, 1793) (Fig. 13.3A; English FAO name – sculptured mitten

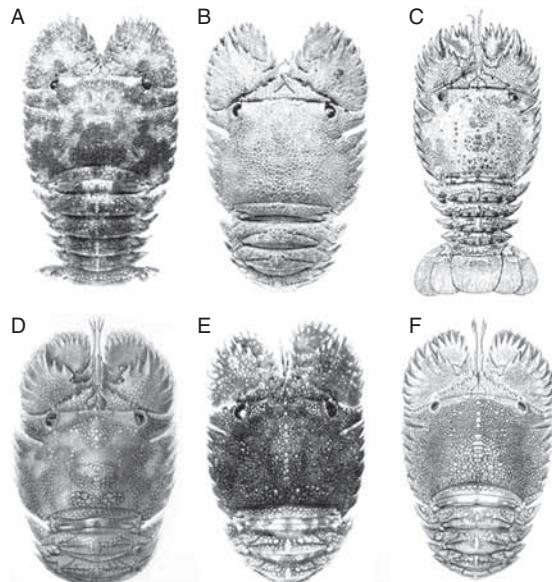


Fig. 13.3 Lobsters within the *Paribacus* genus. (A) *Paribacus antarcticus*; (B) *P. caledonicus*; (C) *P. holthuisi*; (D) *P. japonicus*; (E) *P. perlatus*; (F) *P. scarlatinus*. Holthuis, L.B. (1991). Reproduced with permission of FAO.

lobster) is distinguished by the presence on its abdominal somites of a wide and naked transverse groove separating the anterior part of the somite from the posterior, bearing, at most, a few hairs and tubercles medially. The anterior part of the second to third abdominal somites, situated before the transverse groove, bears distinct tubercles. The median carinae of the second and third abdominal somites are distinct and elevated. At the lateral margin of the carapace, the two lateral teeth before the cervical incision are of almost equal size. The lateral margin of the fourth segment of the antenna bears six teeth (excluding the apical tooth). Holthuis (1991) reported that the CL of this species ranges from 2 to 9 cm and its maximum TL reaches c. 20 cm. This species has a wide distribution range and is found in both the western Atlantic region from Florida to north-eastern Brazil (Bahia), including the West Indian islands and the mainland coast of the Caribbean Sea, and in the Indo-West Pacific region from eastern/south eastern Africa to Hawaii and Polynesia. It is found at shallow depths

(0–20 m) in coral or stone reefs with a sandy bottom (Holthuis, 1991).

Parribacus caledonicus Holthuis, 1960 (Fig. 13.3B; English FAO name – Caledonian mitten lobster) has blunt and oppressed squamiform tubercles on its carapace. Two lateral teeth are present before the cervical incision on the margin of the carapace, but they are unequal in size, with the posterior being larger than the anterior. The fourth segment of the antenna bears seven teeth along the outer margin (apical tooth not included). The legs are short and robust. The transverse groove separating the anterior part of the abdominal somites from the posterior is narrow and filled with many short hairs; the anterior part of the second to fifth abdominal somite carries distinct tubercles. The median carinae of the second and third abdominal somites generally do not project beyond the surface. Holthuis (1991) reported that the CL of this species ranged from 4.5 to 8 cm with a maximum TL of c. 18 cm. This species is found in shallow water on reefs, usually on the exposed side, often in surge channels. During the day, it is frequently attached to the ceilings of caves and is found in large groups (Coutures & Chauvet, 2003). It is distributed in the Indo-West Pacific region along Queensland, Australia; New Caledonia and Loyalty Islands, the New Hebrides, Fiji Islands and Samoa (Holthuis, 1991, 1985).

Parribacus holthuiisi Forest, 1954 (Fig. 13.3C; English FAO name – red-spotted mitten lobster) has two lateral teeth along the carapace margin and before the cervical incision, the posterior of which is smaller. The distance between the orbit and the anterolateral angle of carapace is more than two-fifths the distance between the two orbits. The outer margin of the second segment of the antenna generally bears five teeth (apical tooth not included). The walking legs are relatively slender. The transverse groove separating the anterior and posterior parts of the abdominal somites is narrow and filled with many short hairs. The first abdominal somite has five red and sharply defined spots on the posterior margin, and a row of smaller spots that is placed more anteriorly. The anterior part of second to fifth abdominal somites is smooth, without a reticulate pattern of shallow and narrow grooves. Holthuis (1991) reported that the CL of this species ranges

from 2.5 to 6.5 cm with a maximum TL of c. 14 cm. The species is only found in the Society, Tuamotu and Gambier Islands in the southern Pacific. A larva, possibly belonging to this species, was reported at 14°13.6'S 126°00'W in the Pacific Ocean. Adults are found in shallow water on the sandy bottom of coral reefs (Holthuis, 1991).

Parribacus japonicus Holthuis, 1960 (Fig. 13.3D; English FAO name – Japanese mitten lobster) lacks a dorsal tooth on its rostrum. The carapace bears two lateral teeth before the cervical incision, the posterior one of which is slightly smaller than the anterior. The outer margin of second segment of the antenna generally has five teeth (apical tooth not included). The distance between the orbit and the anterolateral angle of carapace is two-fifths or less than the distance between the two orbits. The transverse groove that separates the anterior and posterior portions of the abdominal somites is narrow and filled with many short hairs. The first abdominal somite bears three to five spots that are not well defined on the posterior margin. The median carinae of second and third abdominal somites are not raised much above the surface. In the second to fifth abdominal somites, the anterior part bears a reticular pattern of shallow and narrow grooves. Holthuis (1991) reported that the CL of this species ranges from 4 to 7.4 cm and the maximum TL is c. 16 cm. This species is found on shore reefs in shallow waters up to 20 m around Japan (north-west coast, west of Maizuru, 135°15'E; Pacific coast from Tokyo Bay, 140°E, south-westward to Ryukyu Islands) (Holthuis, 1991).

Parribacus perlatus Holthuis, 1967 (Fig. 13.3E; English FAO name – Easter Island mitten lobster) bears pointed squamiform tubercles on the upper surface of the carapace. The carapace bears two lateral teeth before the cervical incision anterior the posterior is smaller than the first. The fourth segment of the antenna bears six teeth on the outer margin (apical tooth not included). Legs are short and robust. The transverse groove that separates two parts of the abdominal somites is narrow and filled with many short hairs. The median carinae of the second and third abdominal somites are almost level with the surface of the somites. The anterior part of the second to fifth abdominal somites carries

distinct tubercles. Holthuis (1991) reported that the CL of this species ranges from 4 to 5 cm and the maximum TL is c. 11 cm. This species is only found at Easter Island in the Pacific where it is found in shallow water among rocks or hiding in caves and crevices during daytime (Holthuis, 1991).

Parribacus scarlatinus Holthuis, 1960 (Fig. 13.3F; English FAO name – marbled mitten lobster) bears a dorsal tooth on its rostrum. The posterior of the two lateral teeth of the carapace before cervical incision is smaller, but not very much smaller than the anterior tooth. The outer margin of the second antennal segment generally bears six teeth (apical tooth not included). Distance between the orbit and the anterolateral angle of carapace is two-fifths or less the distance between the two orbits. The transverse groove that separates the two parts of the abdominal somites is narrow and filled with many short hairs. The first abdominal somite bears a single row of three to five not sharply defined spots on the posterior margin. The median carinae of the second and third abdominal somites is almost level with the surface of somites, while the anterior part of second to fifth abdominal somites bears a reticular pattern of shallow and narrow grooves. Holthuis (1991) reported that the CL of this species ranges from 2.5 to 7 cm and reaches a maximum TL of c. 15 cm. This species is found in shallow waters, in or near reefs in central Pacific Ocean from Kapingamarangi through the Marshall, Gilbert and Phoenix Islands to the Marquesas.

Thenus species

The *Thenus* spp. are illustrated in Fig. 13.4. This monotypic genus was recently revised by Burton & Davie (2007), and the name *Thenus indicus* Leach, 1816 was revived. Burton & Davie (2007) used three techniques to analyse differences among the species: morphometrics/morphology, starch gel isozyme electrophoresis and mitochondrial DNA sequencing of 16S and *COI* genes. All three investigations supported the recognition of five species. Despite significant genetic divergence, several sympatric species are morphologically similar and identification can be difficult. All *Thenus* spp. have a dorso-ventrally compressed carapace that

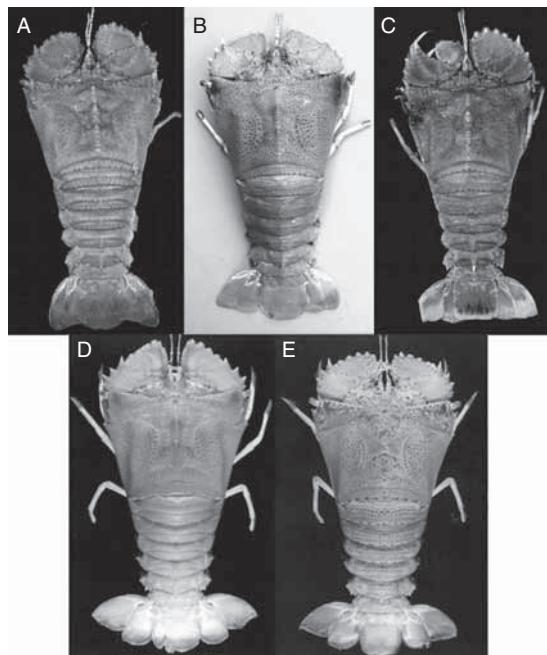


Fig. 13.4 Lobsters within the *Thenus* genus. (A) *Thenus australiensis*; (B) *T. unimaculatus*; (C) *T. parindicus*; (D) *T. orientalis*; (E) *T. indicus*. Modified from Burton & Davie, 2007. © Magnolia Press.

is broader than long, with an upward, broadly expanding anterolateral border. All have a broad and acute tooth behind the orbit, an elevated median dorsal ridge on the carapace and the first five abdominal segments and a telson that is longer than broad (Burton & Davie, 2007).

Thenus australiensis Burton & Davie, 2007 (Fig. 13.4A) has obvious spots or large patches present on some or all segments of the legs. The outer face of the second pereiopod propodus has an upper longitudinal groove that bears obvious setae over at least the proximal half of that surface. The merus of the third maxilliped bears a small spine proximally on its inner ventral margin, while the inner margin of the ischium is prominently dentate along its entire length. No single morphometric ratio has been isolated that will exclusively identify this species, but only *T. australiensis* can have ratios that fall outside the following maximum and minimum values: carapace width (width of widest

section: width of carapace with calliper arms sitting on left and right postorbital spines) is less than 1.13 times the CL; length of antenna 1 (between first and second internal anterior spines to the articulation notch on posterior margin) is greater than 0.74 times the width (width of antenna 1: internal margin to external margin); length of antenna 2 (articulation notch on posterior margin of antenna 2: trough between first anterior and second external spines of antenna 2) is greater than 0.67 the width (width of antenna 2: from internal spine to last external spine); length of antenna 2 is greater than 0.37 times the CL. This species is found Northern Australia south to Hervey Bay, south-eastern Queensland and Shark Bay, Western Australia, and probably north to Singapore (Burton & Davie, 2007).

Thenus indicus (Leach, 1816) (Fig. 13.4E) has no spotting on its legs. The outer face of the second pereiopod propodus has an uppermost longitudinal groove that bears obvious setae over at least the proximal half. The merus of the third maxilliped bears a small spine proximally on the inner ventral margin and the inner margin of the ischium is prominently dentate along its entire length. No single morphometric ratio has been isolated that will exclusively identify this species, but only *T. indicus* can have ratios that fall outside the following maximum and minimum values: first pereiopod's merus width (MW1) is less than 0.07 of the CL; third pereiopod's merus length is more than 0.45 the CL. This species is found in south-east Asia, including the coastal waters of Pakistan, India, the Gulf of Thailand, Singapore and Taiwan (Burton & Davie, 2007).

Thenus orientalis (Lund, 1793) (Fig. 13.4D) has obvious spots or large patches present on some or all segments of the legs. The outer face of the propodus of the second pereiopod has an uppermost longitudinal groove bearing obvious setae over at least the proximal half. The merus of third maxilliped bears a small spine proximally on the inner ventral margin and the inner margin of the ischium is prominently dentate along its entire length. No single morphometric ratio has been isolated that will exclusively identify this species, but only *T. orientalis* can have ratios that fall outside the fol-

lowing maximum and minimum values: telson length more than 0.31 times its width (from left to right latero-posterior spine); width of merus of pereiopod 2 less than 0.079 times the CL. Specimens were collected in the coastal regions of Okinawa in southern Japan, southern Vietnam, the Philippines, Taiwan, the Singapore region, and in the Indian Ocean from south-western Indonesia and the United Arab Emirates (Burton & Davie, 2007).

Thenus parindicus Burton & Davie, 2007 (Fig. 13.4C) has no spotting on the pereiopods. The outer face of the propodus of the second pereiopod has an uppermost longitudinal groove with setae reduced to a thin short line near the base or completely lacking. On the first pereiopod the setae in the uppermost groove extend only over the proximal half. The merus of the third maxilliped lacks a small spine proximally on the inner ventral margin and the inner margin of the ischium is distally dentate, but smoother and only slightly molariform proximally. This species has been recorded in Australia from Darwin, the Gulf of Carpentaria, and south to the Clarence River, NSW, eastern Australia; it is also found from waters off Karachi, Pakistan, indicating a much wider distribution in the Indian Ocean. It appears to be common only as far south as Moreton Bay (Burton & Davie, 2007).

Thenus unimaculatus Burton & Davie, 2007 (Fig. 13.4B) has a purple to black pigmentation blotch on the inner face of the merus of the second and sometimes third legs; this blotch is usually large, but can vary in extent and may be reduced to a narrow streak. Often there is purple pigmentation surrounding the eye socket. The outer face of the propodus of the second pereiopod has an uppermost longitudinal groove bearing obvious setae over at least the proximal half. The merus of the third maxilliped bears a small spine proximally on its inner ventral margin and the inner margin of the ischium is prominently dentate along its entire length. No single morphometric ratio has been isolated that will exclusively identify this species, but only *T. unimaculatus* can have ratios that fall outside the following maximum and minimum values: carapace width greater than 1.29 times the CL; length of the propodus of pereiopod 1 less than

0.23 times the CL; length of the propodus of pereiopod 2 greater than 0.39 times the CL; width of propodus of pereiopod 1 greater than 0.35 times the length. This species is apparently confined to the Indian Ocean as specimens examined came from Mozambique, United Arab Emirates and southwestern Thailand (Burton & Davie, 2007).

13.3 Anatomy

The anatomy of adult slipper lobsters follows the general decapod body plan of having a segmented body divided into three regions: the head (cephalic region), thorax, and abdomen. The cephalic and thoracic regions are fused into a cephalothorax, which is covered dorsally and laterally by the carapace. As with most malacostracans, the cephalic region consists of five segments, each of which bears a pair of appendages – in this case, the first and second antennae and the true mouthparts (mandible, first maxillae, and second maxillae). These appendages are primarily sensory in function and are involved in feeding. The thoracic region consists of eight segments, each of which bears paired appendages that serve feeding (including sensory) and locomotory functions. Those appendages include the first, second and third maxillipeds and the first through fifth pereiopods. The abdominal region, often misnamed the ‘tail’, consists of six segments, the first five of which bear a pair of biramous pleopods (aka ‘swimmerets’), and the last of which bears pleopods that are modified into broad flattened appendages called uropods. The telson or true tail is not a segment (Schram, 1986) and forms the central axis of the tail fan, which is then flanked by the uropods.

As in nephropid and palinurid lobsters, the thoracic appendages consist of inner (endopodite) and outer (exopodite) branches that emerge from a basal segment called the protopodite (Phillips *et al.*, 1980). Each of these parts is also segmented to provide flexibility via seven joints, all of which act as a simple hinge flexing in only one plane (Macmillan, 1975). Moving proximally to distally, the protopodite is divided into the coxa and basis; the endopodite is divided into the ischium, the merus, the carpus, the propus and the dactyl. The exopodite

is divided into the proximal basal region and the distal multiarticulate flagellum.

Adult slipper lobsters differ from clawed and spiny lobsters in several important respects. Their carapace is dorso-ventrally flattened and bears numerous blunt tubercles on its surface, which contrasts with the spines borne upon less-flattened spiny lobster carapaces and the barrel-like, smooth carapaces of nephropid lobsters. The structure of these tubercles (Fig. 13.5) confers a strength advantage to slipper lobsters – each tubercle acts as a ‘blunt-cracking’ device that prevents a crack from running the length of the carapace (Barshaw *et al.*, 2003; Tarsitano *et al.*, 2006). The carapace is also significantly thicker and thus stronger than either clawed or spiny lobster carapaces (Barshaw *et al.*, 2003).

All segments of the legs of spiny lobsters and clawed lobsters are covered in a ‘bottlebrush’ setal tuft pattern comprises fine chemo- and mechanosensory hairs that support probing and exploratory behaviour. The segments of the pereiopods of slipper lobsters, in contrast with the general arthropod pattern (shared even with insects), are much less setose. Additionally, slipper lobsters lack any chelae on their first or second pereiopods – instead, the first through fourth pereiopods end distally in a distinctly sharpened dactyl nail, covered in a tough cuticle that lacks setae, which presumably is an adaptation to opening their preferred molluscan prey (Malcom, 2003; Fig. 13.6). The dactyl of the fifth pereiopod is sexually dimorphic: in males it follows the typical pattern of forming a blunt nail, but in females, the dactyl and propus segments articulate to form a small, false chela with which the female grooms and ventilates the eggs attached to her pleopods (Moe, 1991; Malcom, 2003; Fig. 13.7).

Slipper lobster antennules (first antennae) are foreshortened to ~0.05% of their body length – in clawed lobsters, antennules represent 0.1 body lengths, and in spiny lobsters they can reach 1.5 body lengths (Grasso, unpublished data). These antennules bear four segments, the most distal of which branches into a lateral and medial flagellum (Fig. 13.8). Each flagellum is composed of smaller segments called annuli. The lateral flagellum bears numerous types of sensory hairs on the annuli that

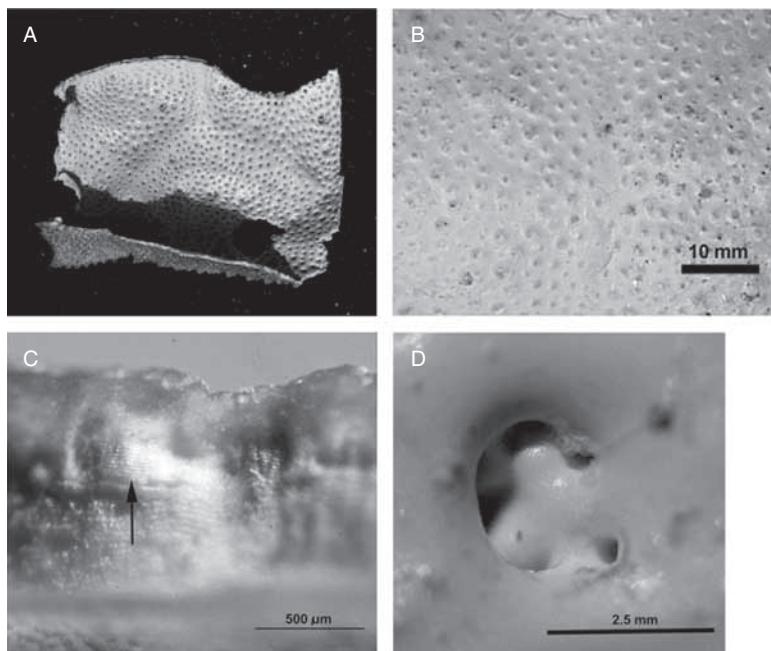


Fig. 13.5 (A) Tuberculate surface of a slipper lobster carapace; (B) inner surface of carapace showing the pits formed by tubercles; (C) histological section of the exoskeleton, showing numerous laminate layers; (D) single tuberculate pit, showing inner strut structure that confers added strength to carapace. Tarsitano, S.F., Lavalli, K.L., Horne, F. & Spanier, E. (2006) Reproduced with permission of S. Tarsitano.

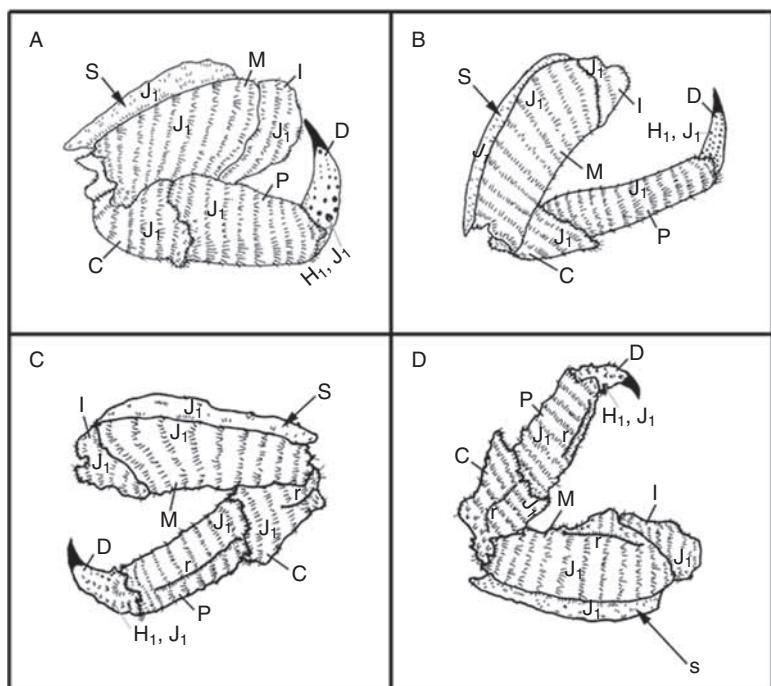


Fig. 13.6 Outer, or aboral, views of walking legs of *Scyllarides* spp. (A) left first pereiopod; (B) left second pereiopod; (C) right third pereiopod; (D) right fourth pereiopod. D-dactyl; P, propus; C, carpus; M, merus; I, ischium; s, meral shield; J₁, cuspidate setae; H₁, simple setae, •, stripped dactyl setal pit. Malcom, C. (2003) Texas State University at San Marcos, San Marcos, Texas.

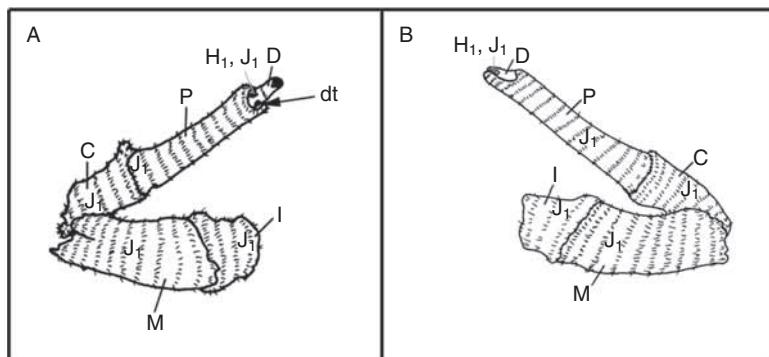


Fig. 13.7 Inner, or oral, views of the left 5th pair of walking legs of *Scyllaride* spp. (A) male; (B) female, showing false chelae formed by dactyl and propodus segments. D, dactyl; P, propodus; C, carpus; M, merus; I, ischium; s, meral shield; J₁, cuspidate setae; H₁, simple setae; dt, dactyl tuft. Malcom, C. (2003) Texas State University at San Marcos, San Marcos, Texas.

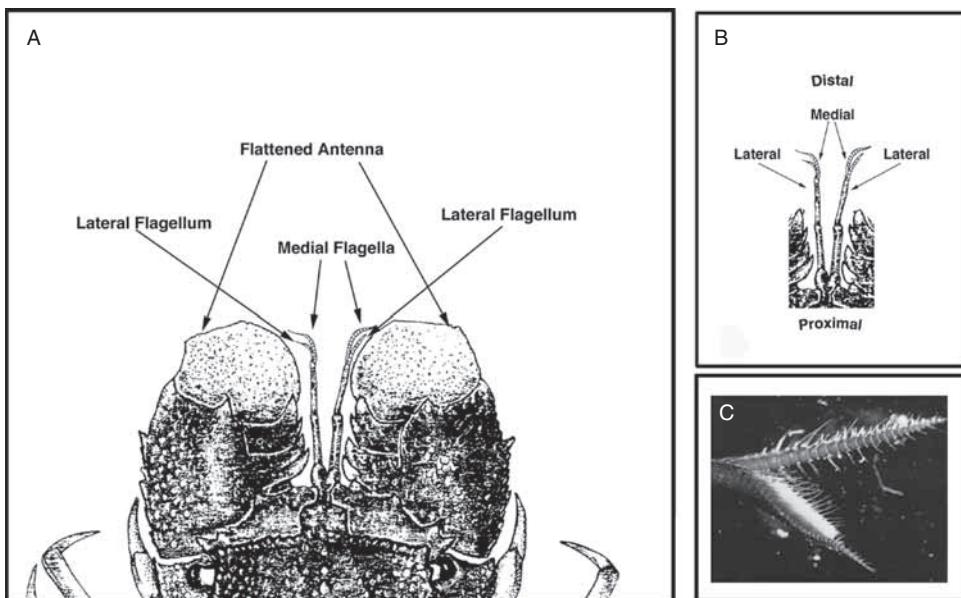


Fig. 13.8 Anterior aspect of a slipper lobster (*Scyllarides* spp.). (A) paired second antennae, erroneously dubbed 'shovels' or 'flippers', have six segments and are shortened and flattened dorsoventrally; (B) paired first antennae, or antennules, have four segments, the most distal of which branches into a lateral and medial flagellum; (C) flagella are composed of smaller segments (annuli) upon which setae are borne. Weisbaum, D. & Lavalli, K.L. (2004). Reproduced with permission of John Wiley & Sons. Holthuis, L.B. (1991). Reproduced with permission of FAO.

most likely have chemo- and mechanosensory functions (Weisbaum & Lavalli, 2004). The second antennae, which are slender and rod-like in clawed and palinurid lobsters, become shortened and flattened dorso-ventrally to the point where they are hard to recognize as antennae. They comprise six

segments, but these are all severely reduced in length and are flattened into plate-like structures. The sixth segment forms a plate with a wide range of movement in the dorso-ventral plane that seems important in controlling the pitch of swimming, and is also used in intraspecific aggression (see

Sections 13.5.1 and 13.5.5). This appearance of the second antennae is responsible for the names for these lobsters, such as ‘shovel-nosed’ or ‘bulldozer’ lobster (Holthuis, 1991).

Internally, the alimentary tract is divided into the foregut, midgut and hindgut. The foregut and hindgut are lined with chitinous cuticle that is shed at each moult, while the endodermal midgut lacks such a cuticular lining (Johnston, 2007). The foregut comprises a short oesophagus that leads into the two-chambered proventriculus (anterior cardiac and posterior pyloric stomachs). In clawed and spiny lobsters, the cardiac stomach typically bears a gastric mill with distinct ossicles (teeth) for grinding the food; however, these ossicles are severely reduced or even absent in slipper lobsters, reflective of the soft nature of the animal’s diet (Johnston & Alexander, 1999). In phyllosoma larvae, the proventriculus is simply a non-divided tube that lacks ossicles; instead, it bears brush-works of setae on its posterior lateral edges and spines and other setae on its dorsal and ventral surfaces that serve to sort fine particles (Mikami & Takashima, 1993; Mikami *et al.*, 1994; Johnston, 2007). The midgut comprises a small dorsal caecum and a large bi-lobed digestive gland (hepatopancreas). The hindgut is a simple tube terminating at the anus on the telson (Johnston, 2007).

As in other decapods, the circulatory system is open. While open circulatory systems have been considered to be low pressure and sluggish, higher malacostraca have highly regulated and efficient systems with flow patterns that rival vertebrate closed systems (McMahon & Burnett, 1990). In contrast to nephropids, no work has been done on scyllarid circulatory systems.

13.4 Life history

The life history of scyllarids parallels that of palinurids and can be divided into a series of developmental phases. These lobsters typically begin their pelagic lives as phyllosoma larvae, i.e. flattened, leaf-like, transparent planktonic forms with long appendages and cephalic shields that are very long and wider than the thorax (Phillips *et al.*, 1981).

However, some scyllarids hatch as a naupliosoma (pre-larva; Fig. 13.9A), which is a short-lived form (a few hours) that bears only the first three pairs of cephalic appendages (Booth *et al.*, 2005; Sekiguchi *et al.*, 2007). In such primitive forms, the antennae bear natatory setae and the TL of the animal reaches 1–2 mm (Booth *et al.*, 2005). Three species of *Scyllarides* apparently hatch as this early form: *S. aequinoctialis* (Robertson 1968, 1969), *S. herklotsii* (Crosnier, 1972) and *S. latus* (Martins, 1985a). Several *Ibacus* species also hatch in this form: *Ibacus alticrenatus* (Lesser, 1974) and *I. ciliatus* (Harada, 1958 although according to Holthuis, 1985 the observed individuals may have been *I. novemdentatus*). Others hatch as a phyllosoma (Fig. 13.9B–D) with the full suite of cephalic and thoracic appendages. Abdominal appendages are typically absent or rudimentary in early phyllosoma, but appear in later stages (Booth *et al.*, 2005; Sekiguchi *et al.*, 2007).

All thoracic appendages bear an exopodite until the larvae undergo their metamorphic moult into post-larvae. At that time, exopodites are lost from all thoracic appendages except the maxillipeds, where they are retained and used for generating currents around the mouth region (Lavalli & Factor, 1995, 1992). However, scyllarid phyllosoma deviate from other decapod larvae in that they are missing an exopod on the third maxilliped (but see Phillips *et al.*, 1983 who assert that the third maxillipeds bear a conspicuous exopod bud in *S. haani* and/or *S. squamosus*). Whether this indicates a phylogenetic separation of feeding strategy or swimming requirements is unknown (Booth *et al.*, 2005).

The developmental period for scyllarid phyllosoma is far more variable than that for palinurids, and can last from a few weeks to at least nine months (Booth *et al.*, 2005; Sekiguchi *et al.*, 2007, Table 4.2 and references therein). All scyllarids metamorphose into a nisto phase (=to the pueruli in spiny lobsters). This nisto phase is responsible for making the transition from a planktonic to a benthic life. The nisto settles and moults and the lobster then begins its benthic life as a young juvenile and eventually matures into the adult, reproductive phase.

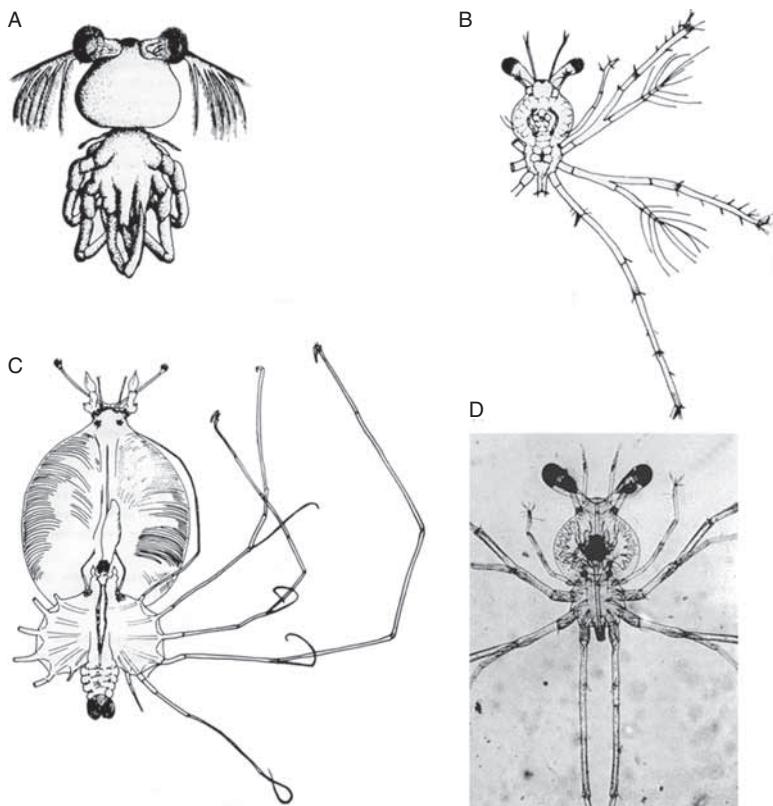


Fig. 13.9 Larvae of *Scyllarides latus*. (A) naupliosoma ($\times 50$); (B) phyllosoma stage I ($\times 20$); (C) phyllosoma stage IX ($\times 2.2$); D) phyllosoma stage I, hatched in the laboratory on 19 June 1994. Martins, H.R. (1985a). © Brill. Bianchini, M.L. & Raisa, P.F. (1997). © MiRAAF.

13.4.1 Phyllosoma

Dispersal of phyllosoma varies among species and depends largely on whether the parental stock is found within lagoons formed by coral island barrier reefs or in deeper waters (Baisre, 1994; Johnson, 1971a,b; Yeung & McGowan, 1991; Coutures, 2000). Those hatched in coastal lagoons tend to remain there, while those hatched in deeper water gradually move shoreward, such that final-Stage phyllosoma of some scyllarids are found much closer to shore than is typical of palinurid phyllosoma (Sekiguchi *et al.*, 2007). *Scyllarides aequinocialis*, *S. astori*, *S. herklotsii*, *S. nodifer* and *S. squamousus* all have oceanic distributions of their phyllosoma and are presumed to be dispersed in a

manner similar to that for palinurids, since few mid- to late-stage larvae are found in inshore regions (Robertson, 1969; Johnson, 1971b; McWilliam & Phillips, 1983; Phillips *et al.*, 1981; Yeung & McGowan, 1991; Coutures 2000; see Table I in Booth *et al.*, 2005). Late-stage phyllosoma of *Ibacus* spp. and *Thenus* spp. are not widely dispersed, appearing to remain coastal or intermediate in the extent of offshore distribution (Sekiguchi *et al.*, 2007, Table 4.2 and references therein). The larvae undertake diel vertical migrations, but data are limited as to the extent of these migrations and the species-specific preferences for various depths (Minami *et al.*, 2001; Sekiguchi *et al.*, 2007) as well as the efficacy of their swimming behaviour. It is likely that smaller instars vertically migrate

less than later, larger instars (Yeung & McGowan, 1991). Those species or instars that do exploit this strategy may use passive transport by occupying vertical strata that move them in specific directions (Sekiguchi *et al.*, 2007). Some phyllosoma even travel attached to the aboral surface of jellyfish medusae or siphonophores (e.g. Shojima, 1963; Thomas, 1963; Herrnkind *et al.*, 1976; Ates *et al.*, 2007), which may affect larval dispersal or allow them to remain relatively near shore (Booth *et al.*, 2005; Sekiguchi *et al.*, 2007).

Duration of the planktonic larval period in Scyllaridae varies from several weeks to months (Table 4.2 in Sekiguchi *et al.*, 2007, and references therein). In the genus *Scyllarides*, only a few species have been studied, and for these, the planktonic larval development period appears to last between 6 and 10 months, with the number of instars ranging from 11 to 13 (Robertson, 1969; Crosnier, 1972). The TL reached during the phyllosoma phase ranged from 25 to 48 mm (Michel, 1968; Robertson, 1969; Crosnier, 1972; Johnson, 1971a; see Table I in Booth *et al.*, 2005, and Table 4.2 in Sekiguchi *et al.*, 2007). In *P. antarcticus* larval development appears to last ~9 months with more than 11 larval Stages, and the size of the final phyllosoma ranges from 75 to 83 mm TL (Johnson, 1971b; Baisre, 1994). In several species of *Ibacus* the larval development period ranges from 2 to 6 months with six or seven Stages, and the size of the final phyllosoma ranges from 25 to 46 mm TL (Dotsu *et al.*, 1966; Ritz & Thomas, 1973; Shojima, 1973; Takahashi & Saisho, 1978; Atkinson & Boustedt, 1982; Mikami & Takashima, 1993; Marinovic *et al.*, 1994). The estimated length of larval life in *Thenus* spp. is much shorter and lasts between 27 and 45 days, which is one of the reasons this taxon was successful in aquaculture attempts (e.g. Mikami & Kuballa, 2007; Vijayakumaran & Radhakrishnan, 2011). Additionally, there are fewer larval stages (only four instars) the size of the final Stage phyllosoma ranges from 13 to 20 mm TL (Barnett *et al.*, 1984; Mikami & Greenwood, 1997a,b).

Phyllosoma are feeding forms and appear to be predatory, using their pereiopods to hold onto food items, which are then shredded by the maxillipeds and masticated by molar processes of the mandi-

bles (Mikami & Takashima 1993). Mostly fleshy foods are ingested; such food types are more readily available in coastal waters than in offshore, oligotrophic waters (Mikami *et al.*, 1994; Booth *et al.*, 2005; Sekiguchi *et al.*, 2007). Some scyllarid larvae have been observed holding hydromedusae, but it was not known if these were subsequently ingested (Shojima, 1963). However, a recent report of a videotaped scyllarid lobster phyllosoma swimming while dragging a prayid siphonophore behind it suggests that gelatinous forms have importance as food and/or defence against predation (by ingestion of the nematocysts) and refutes the idea that riding these forms is energy saving due to passive transportation (Ates *et al.*, 2007). Recently, molecular techniques using the central domain of the 18SrDNA gene have identified food items of some species of scyllarid and palinurid phyllosoma larvae, and suggest that these forms feed on appendicularians, salps and cnidarians (Suzuki *et al.*, 2006). Ctenophores fed to larvae of *Thenus orientalis* are accepted readily and provide nutritional support (Gopakumar *et al.*, 2008).

13.4.2 Nistos

The final-stage phyllosoma moults into the nisto, or post-larval stage, which, like spiny lobster pueruli and clawed lobster post-larvae, recruit into the benthic environment. The nistos are neither completely planktonic nor completely benthic – they are caught in plankton tows demonstrating that they are pelagic at least part of the time (Booth *et al.*, 2005). In many species of scyllarids, the nisto appears to bury into soft substrates during the day and swim actively at night; some species even change colouration daily between these two habitats to remain cryptically coloured in both (Booth *et al.*, 2005). Some scyllarid nistos are excellent swimmers (using their abdominal pleopods), while other species are poor swimmers; some are also capable of executing tail flips (backward swimming) as a means of escape (Lyons, 1970). Webber & Booth (2001) suggest that these swimming differences exist due to marked differences in the size of pleopods among different species. However, this suggestion has not been adequately tested.

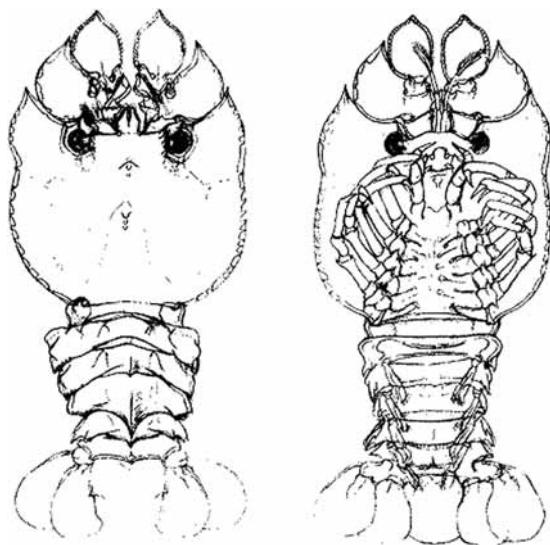


Fig. 13.10 Nisto of *Scyllarides nodifer* (redrawn from Lyons, 1970 by Rachel Pollak); used with permission.

Like the phyllosoma, the scyllarid nisto is completely transparent, which makes it cryptic in the water column and, no doubt, helps it to avoid predation. It has a large, flattened, disc-shaped carapace and a small abdomen (e.g. nisto of *S. nodifer*, Fig. 13.10) and may more closely resemble adult *Ibacus* and *Parribacus* forms than adult *Scyllarides* forms. As such, scyllarid nistos have been referred to as a ‘pseudibacus’ (Chace, 1966; Crosnier, 1972; Holthuis, 1993). No information is currently available on the duration of the nisto stage for *Scyllarides*, *Parribacus* or most *Ibacus* species; that of *Thenus* species is approximately a week in culture conditions while it is 2–3 weeks in *Ibacus peronii* (Ritz & Thomas, 1973; Sekiguchi *et al.*, 2007). The size of nistos varies widely depending on species: a few *Scyllarides* species studied ranged from 9 to 15 mm CL (Barnard, 1950; Johnson, 1968; Michel, 1968; Lyons, 1970; Crosnier, 1972; Holthuis, 1993; Mikami & Takashima, 1993), while nistos of *Parribacus* spp. typically are larger, ranging from 20–21 mm CL (Johnson, 1971b; Holthuis, 1985; Coutures *et al.*, 2002). *Ibacus* spp. nistos range in size from 11 to 20 mm CL (Dotsu *et al.*, 1966; Ritz

& Thomas, 1973; Shojima, 1973; Takahashi & Saisho, 1978; Atkinson & Boustead, 1982; Holthuis, 1985; Mikami & Takashima, 1993; Marinovic *et al.*, 1994), while those of *Thenus* spp. are the smallest sizes, ranging from 8 to 9 mm (Barnett *et al.*, 1984; Mikami & Greenwood, 1997a,b). Haddy *et al.* (2007) state that *Ibacus peronii* larvae develop through six to eight Stages over 2–4 months before metamorphosing into transparent nisto larvae. During this period, the nisto becomes increasingly pigmented before moulting into juveniles after 17 to 24 days (mean = 19 days), at an average size of 12.2 mm CL (Marinovic *et al.*, 1994).

As with spiny lobster pueruli, the nisto appears to rely on energy reserves, rather than to actively feed (Sekiguchi *et al.*, 2007). However, its proven-triculus has features that are transitional between the phyllosoma and the juvenile (Johnston, 2007) suggesting that the ability to process and sort ingested food particles is more advanced than it is in the phyllosoma. While the phyllosoma lacks a cardio-pyloric valve that divides the anterior cardiac chamber from the posterior chamber, the nisto has this feature. But, like the phyllosoma, the nisto lacks a gastric mill, suggesting that food, if consumed, is similar in softness to that of the phyllosoma, and is primarily masticated by the mouth-parts prior to ingestion (Johnston, 2007).

Nistos are morphologically similar to juveniles and, like juveniles and adults, have flattened second antennae. The structure of the abdominal pleopods is the main morphological difference between the nisto and the juvenile, with nisto pleopods bearing swimming (natatory) setae (Williamson, 1969). The colouration pattern also differs: transparent for the nisto and reddish-brown coloured for the juveniles.

13.4.3 Juveniles

In contrast to an ever-increasing body of knowledge of the juvenile life of clawed and spiny lobsters, almost nothing is known about the juvenile habits of slipper lobsters. Knowledge of all life history stages is available only for some soft bottom scyllarids such as *Thenus* species that have been successfully reared in the laboratory (e.g. Mikami

& Kuballa 2007) or *Ibacus* species (Atkinson & Boustead 1982; Stewart & Kennelly 1997).

This primarily is the result of a problem in sampling and not knowing where juvenile grounds lay. For example, in *S. latus* no live juvenile has been sampled recently (Spanier & Lavalli 1998). The smallest individual commercially fished off the Israeli coast weighed 100 g. Almog-Shtayer (1988) reported that the smallest male in her biological sample was 64 mm CL (200 g) and the smallest female was 69 mm CL (252 g). Off the coast of Italy, the smallest animals caught by Bianchini *et al.* (1996) weighed 100 and 103 g. Two small exuviae were recorded in the coast of Israel – one of 38 mm CL at 15 m depth and the other of 47.5 mm found washed ashore. Romeo *et al.* (2004) recorded a rare small male of 39 mm CL (81 mm TL) (21.33 g) among 200 *S. latus* collected in the Straits of Messina at a depth between 15 and 60 m along a jagged coastline with steep bottom topography and a mixture of rocks, sand, and coraliferous biotic community. Surveys of invertebrate collections in various museums revealed a small specimen of *S. latus* (36 mm CL) collected in spring 1987 using a 20 mm mesh scientific trawl net at depth of 450–700 m in front of Leghorn (Livorno) on a soft and muddy bottom at least 40 km offshore and an even smaller specimen of 11.7 mm CL collected in Reggio Calabria at a depth of >850 m (Italy) (Fig. 13.11). This juvenile – or possible nisto – had body proportions similar to those described for the nistos of *S. nodifer* by Lyons (1970) (Fig. 13.11) and a size similar to the nisto sizes of several species of *Scyllarides* (*S. aequinoctialis*, *S. astori*, *S. nodifer*, *S. elisabethae*, *S. herklotsii*, *S. squamosus*) that ranged from 9 to 15 mm CL (Spanier & Lavalli, in press). Without knowing habit information, the only inference that can be made is that these juveniles settle in deep water, mostly likely in muddy habitats, and then migrate to shallower grounds used by adults. Similar suggestions have been made for other scyllarids. For example, *Ibacus* juveniles appear to migrate shoreward from offshore waters to recruit into adult grounds (Stewart & Kennelly, 1997). Hearn (2004) and Hearn *et al.* (2007) suggest that juveniles occupy a different spatial niche from adults and are



Fig. 13.11 Early benthic juvenile stage of the Mediterranean slipper lobster, *Scyllarides latus* from Reggio Calabria (Photo by J. J. Gottlieb, used with permission; scale numbers are in centimeters.)

far more cryptic than adults because few individuals are found that are smaller than 20 cm TL. It is clear that in order to obtain sufficient numbers of small individuals, specific sampling techniques must be developed which target the juveniles, that may prove difficult if many of the species have juvenile development in deep, oceanic waters.

Because juveniles are rarely sampled in the wild, growth rate determination is difficult in these lobsters. Data mainly come from rearing studies of the few species that survive well in the laboratory or from grow-out studies where sufficient numbers of juveniles have been captured. Rudloe (1983) reared juveniles of *S. nodifer* from a CL of 23 mm to 73 mm and predicted that approximately 18 months and 9–10 moults were required to reach the adult size (for details see Section 13.8). Other fast growing species include *Ibacus* spp. that reach sexual maturity after four to six moults (Haddy *et al.*, 2007). Cultured *Thenus orientalis* take about 400 days (19 moults) to grow to a size of c. 250 g (Mikami & Kuballa, 2007). In contrast, Hearn (2004) suggested that 7–8 years are necessary for juvenile *S. astori* to recruit fully into the adult population. Hence, from what little data we have on juvenile life history, it appears that many, but

not all, of the commercially important scyllarids are capable of rapid growth.

13.4.4 Adults

Arctidinid adults (e.g. *Scyllarides* spp.) are typically large. Sex ratios are close to unity in those species that have been adequately sampled (*S. latus*, Martins, 1985a; Spanier & Lavalli, 1998; *S. astori*, Hearn, 2004). Females generally exceed 90–100 mm CL, although sexual maturity can be reached at smaller sizes for some species (e.g. *S. squammosus*, 65–81 mm CL, DeMartini & Kleiber, 1998). Shortly after mating, they extrude a large number of eggs (conservative numbers range from 140,000–356,000), based on TL of the individual, with those eggs ranging from 0.6 to 0.7 mm diameter (Martins, 1985a; DeMartini & Williams, 2001; Hearn *et al.*, 2007). Such high fecundity rates may be an adaptation to oceanic loss of larvae and variable recruitment of nistos due to cyclic changes in oceanic climate (Booth *et al.*, 2005). The eggs are brooded for 4–8 weeks before release over a number of days (*S. latus*, Bianchini & Ragonese, 2003) although Almog-Shtayer (1988) reported that *S. latus* females carried eggs for only an average of 16.5 days. Ovigerous females are more commonly sampled in colder to warm, but not hot months (Hearn *et al.*, 2007). There is some evidence that they may return to inshore reefs earlier than males in the autumn and leave sooner after shedding eggs in the mid-summer, possibly to maximize thermal regimes for developing embryos (Spanier *et al.*, 1988). Most species appear to move to colder, deeper waters when inshore water temperatures rise steeply in the summer or, for those species that remain in lagoons, have higher abundances at locations where thermal regimes are less than 25°C (Hearn, 2004).

Growth has not been well studied for most *Scyllarides* spp. and is primarily inferred from recapture studies and/or laboratory experiments. In some species, mean CL is larger for females than for males (*S. latus*, Martins, 1985a; Almog-Shtayer, 1988), while in others, males exceed females in size (*S. astori*, Hearn *et al.*, 2007). Tag–release studies suggest that lobsters moult annually (*S. latus*, Bianchini *et al.*, 2001), although data from *S.*

astori populations suggest that moults occur every 18–24 months (Hearn, 2004; Hearn *et al.*, 2007). In laboratory settings, slipper lobster growth increments can be regressive, a circumstance due possibly to holding conditions (Almog-Shtayer, 1988; Bianchini *et al.*, 2003). Moulting typically occurs at night and in cooler to warmer months (Chessa *et al.*, 1996; Spanier & Lavalli, 1998; Bianchini *et al.*, 2003). Death at moult is generally infrequent, ranging from 8–22% (Chessa *et al.*, 1996; Spanier & Barshaw, 1993). The old exoskeleton starts softening some 10–22 days pre-moult, while the new shell is fully hardened 3 weeks post-moult. The entire process takes approximately 7 hours, with lobsters remaining shelter-bound for 5–9 days post-moult (Almog-Shtayer, 1988). Exuviae are left outside of shelters, and there is no evidence that slipper lobsters consume them as do clawed lobsters (Spanier & Lavalli, 1998).

Adults of the subfamily Ibacinae are usually smaller than those of the subfamily Arctidinidae and rarely exceed 20 cm TL (Holthuis, 1991). The sex ratios of the four commercially caught species of *Ibacus* off eastern Australia are approximately 1:1. Females grow to larger sizes and reach sexual maturity at a larger size apparently because males, after attaining sexual maturity, moult less frequently than females. Females initiate ovarian maturation at CLs of 38 mm for *I. alticrenatus*, 44 mm for *I. brucei*, 50 mm for *I. chacei* and 48 mm for *I. peronii*, and attain 50% physiological maturity at CLs of 39, 47, 55 and 50 mm, respectively (Haddy *et al.*, 2007). Size of *I. alticrenatus* and *I. brucei* after being recruited to the fishery but before attaining sexual maturity is 39 and 47 mm CL, respectively (Haddy *et al.*, 2007). Mating occurs when the female is hard-shelled (Section 13.5.4.). The number of eggs is much lower than in members of the subfamily Arctidinidae and it is highly variable both within and among the eight species of *Ibacus*. It increases with the size of the animal, ranging between c. 1700 and 14,800 eggs for *I. alticrenatus*, 2000 and 61,300 eggs for *I. brucei*, 2100 and 28,800 eggs for *I. chacei* and 5500 and 36,700 eggs for *I. peronii* (Haddy *et al.*, 2007). The main reasons for these differences relate to life-history strategies and the sizes of eggs produced. For example, *I. brucei* produces a small egg (0.73–

1.01 mm) and, as a result, the brood fecundity of *I. brucei* is relatively high. In contrast, *I. alticrenatus*, *I. chacei* and *I. peronii* produce relatively large eggs (1.0–1.4 mm in diameter) and possess a relatively lower fecundity than *I. brucei* (Haddy *et al.*, 2007). Egg incubation times have been estimated to vary between approximately 2–3 months for *I. brucei* and 3–4 months for *I. alticrenatus*, *I. chacei* and *I. peronii*. Incubation periods in the species are likely to be temperature dependent with longer incubation in cooler water (Stewart & Kennelly, 1997.). Moult frequencies of captive *I. peronii* suggest that after maturation, moulting is a seasonal event (October to January) with males moulting slightly earlier than females. However, moulting may not necessarily occur annually since tagged lobsters were caught repetitively in consecutive years without having increased in size (Haddy *et al.*, 2007). The growth models for *I. peronii*, determined by Stewart & Kennelly (2000), suggest the potential for this species to live for more than 15 years with a maximum size reached after 5–8 years.

Very little information is available on adults of *Parribacus* species and it is mainly on *P. antarcticus*. Sharp *et al.* (2007) captured two females of this species during summer (July) that bore evidence of reproductive activity (for details see Section 13.5.4).

Holthuis (1991) reported that the maximum TL of *Thenus* spp. was 250 mm though this appears to be an underestimate. Growth is quite rapid and for *T. indicus* and *T. orientalis* a CL of 40 mm (approximately 40 g total weight) is reached within the first 12 months and approximately 80% of maximum size is reached by 2 years of age. Maximum age for *T. indicus* is between 2 and 4 years, and between 4 and 8 years for *T. orientalis*. Females appear to attain larger sizes than males as evidenced by fishery sampled size ranges in both Indian and Australian waters: in Mumbai *T. orientalis* males typically range from 41 to 277 mm TL, while females range from 55 to 275 mm TL (Kagwade & Kabli, 1996a), while in Sakthikulangen males range from 111 to 115 mm TL and females range from 101 to 180 mm TL. Similar trends exist in the *T. orientalis* fishery off Chennai (Subramanian, 2004) and off Australia (Jones, 2007) in both the *T. indicus* and *T. orientalis* fisheries. Sex ratios in the *T. orientalis*

fisheries of India appear to be 1:1 (Subramanian, 2004), but are skewed towards males off Australia (Jones, 2007) with a ratio of 0.57. In contrast, the sex ratio of *T. indicus* is typically constant at 1:1 throughout the year (Jones, 2007). Jones suggested that increased abdominal dimensions explained the greater weight of females, while maximization of reproductive efficiency via larger size and the ability to carry more eggs explains the greater mean size of females. However, for *T. orientalis* in India, Radhakrishnan *et al.* (2007) argued that there is a lack of a pronounced difference in the morphometric relationship between TL and CL due to a less convoluted vas deferens in *T. orientalis* males and fewer eggs being carried on the pleopods of females; thus, the two sexes grow to a similar size in this species. Such differences between Indian and Australian populations of thenids may reflect differences between sub-species or even between different species in view of the recent taxonomic revision of the genus by Burton & Davie (2007).

As with all lobsters, fecundity of scyllarids scales with length. Kagwade & Kabli (1996b) showed a linear relationship between TL and the number of eggs in *T. orientalis* and estimated that a female of 165 mm TL produces 22,050 eggs, while a specimen of 240 mm TL produces 53,280 eggs. Females above 130 mm TL were generally mature. Jones (2007) reported that age at maturity of *T. orientalis* in Australia was 1 year; mean fecundity was 32,230 for *T. orientalis* (compared to 12,455 eggs for *T. indicus*), ranging from 10 to 30,000 eggs (compared to a fecundity range of 20,000 to 50,000 eggs reported for this species in India by Radhakrishnan *et al.*, 2007). Egg size was c. 1.12 mm; and eggs required an incubation of 40 days (35 days in India according to Radhakrishnan *et al.*, 2007). Jones (2007) reported that sexual dimorphism in *Thenus* spp. was very subtle and that mating (during intermoult) was believed to involve a brief encounter.

Various studies in India showed at least two annual spawning periods; however, only a single spawning period was reported for *T. orientalis* off the Tokar delta in the Red Sea (Radhakrishnan *et al.*, 2007). Jones (2007) also reported two or more spawnings per season for this species in Australia. Radhakrishnan *et al.* (2007) stated that *T. orientalis*

is a slow-growing species and the females appeared to grow more slowly than males after attaining sexual maturity. However Jones (2007) reported for both *T. orientalis* and *T. Indicus* in Australia that growth was quite rapid, with maximum size for *T. indicus* in Australia being reached between 2 and 4 years, and that for *T. orientalis* being reached between 4 and 8 years. The possible differences in growth between India and Australia may stem from different environmental conditions (e.g. temperature regime, availability of food, fishing pressure) or from genetic variations between populations.

13.5 Behaviour

Slipper lobster behaviour, like so many other aspects of their biology, has also not been well studied. Those studies that exist focus mainly on two species, *Scyllarides latus* and *Thenus orientalis* with occasional others being examined. Because these animals are held readily in laboratory settings, there is potential for understanding many kinds of behaviour, as has been done for nephropid lobsters, *Homarus americanus* and *H. gammarus*, and for several spiny lobster species.

13.5.1 Feeding behaviour

Feeding behaviour depends greatly on the structures with which lobsters can macerate their food and differs with life history stage as these structures gain more substance and size with age. The feeding habits of only some species of spiny lobsters are known and these are primarily for the adults of *T. orientalis* (Johnston & Alexander, 1999) and *I. peronii* (Suthers & Anderson, 1981).

As in clawed and spiny lobsters, the oesophagus of slipper lobsters is short, presumably to allow for rapid ingestion (Johnston, 2007). It leads into the proventriculus, which is divided into the anterior cardiac stomach and the posterior pyloric stomach. In clawed and spiny lobsters, the cardiac stomach has three large ossicles that make up the gastric mill (one medial and two lateral ‘teeth’); however, in slipper lobsters, these teeth are reduced in size and less calcified (Johnston & Alexander, 1999). This

difference is likely due to the diet specialization that has occurred in slipper lobsters – that of primarily consuming bivalve flesh, or other fleshy items, compared with clawed and spiny lobsters that consume both flesh and shell fragments. The overall effect of the reduction in ossicular size and additional folding of the proventricular wall is to expand the volume capacity of the cardiac stomach (Suthers & Anderson, 1981; Johnston & Alexander, 1999). Food proceeds from the cardiac stomach to the pyloric stomach through a cardio-pyloric valve, which lacks the spines and accessory teeth seen in other decapods (Johnston & Alexander, 1999). The pyloric stomach possesses dense mats of setae that provide filtering of the semi-digested, masticated food particles entering from the cardiac stomach, such that only the smallest particles pass into the digestive gland while larger particles pass into the midgut caecum and then into the hindgut (Johnston & Alexander, 1999). Little is understood about the digestive enzymes involved in food breakdown (Johnston, 2007).

Some slipper lobsters (e.g. *Scyllarides* spp.) have become specialized for feeding on bivalves or clams, mussels, and oysters. Bivalves have existed since the pre-Cambrian era and have colonized much of the world’s marine and aquatic environments. Given their specialization for feeding on bivalves, it seems almost certain that the radiation of slipper lobsters followed the beds of bivalves around the world. Where clawed lobsters crush small bivalves with their claws and spiny lobsters use their mandibles to crack and chip away at small bivalve shells to access the meat, slipper lobsters have evolved an elegant feeding mechanism that involves using the physics of the bivalve shell to their advantage, while, at the same time, overcoming the disadvantage of the extremely effective adductor muscles that keep molluscan valves closed. To get around this energetic cost, slipper lobsters have evolved a bivalve opening mechanism that employs delicate manipulation and mechanical advantage for prying. In essence, they shuck bivalves (Lau, 1987; Spanier, 1987), using tactile and olfactory senses, as well as a guided mechanical advantage, to avoid the cost that a ‘brute’ force mechanism would require. In contrast, clawed lobsters use repetitive loading via their

crusher claw to cause fracture lines in the rigid shell of bivalves (Moody & Steneck, 1993). This works because there is little organic matrix that would blunt the cracks created by repetitive loading. Spiny lobsters lack claws but have, in their place, strong mandibles, which they use to bite cracks into the valve edges of bivalves (Lavalli, personal observations). Once a sufficiently large hole is bitten into the edge, the lobster can dig molluscan flesh out of the shells. In the case of both claw-loading and biting of bivalves, the process to crack the shell takes some time; probably, this time exceeds that needed by slipper lobsters to ‘shuck shells’. Slipper lobsters, like spiny lobsters, lack claws, and apparently also lack strong mandibles; thus, they resort to using their legs – and specifically their dactyl tips – to open bivalves (Lau, 1987; Spanier, 1987).

During the feeding sequence, slipper lobsters typically approach a bivalve with their antennules down near the substrate. Upon encountering the mollusc, the lobster picks up the shell with the first two to three pairs of walking legs and repetitively probes the outer valves with its antennules, as though ‘smelling’ and assessing the shell for its possible value (Malcom, 2003). This behaviour contrasts with that of clawed and spiny lobsters that

do not use their antennules for such probing activities, but instead use them to distantly chemo-orient to the food source (Devine & Atema, 1982; Zimmer-Faust & Spanier, 1987; Moore & Atema, 1991; Moore *et al.*, 1991a,b; Derby *et al.*, 2001; Beglane *et al.*, 1997; Nevitt *et al.*, 2000). In clawed and spiny lobsters, the setose walking legs are used for initial assessment of the penetrability of the shell (Derby & Atema, 1982). After an initial assessment of the shell by the antennules, the slipper lobster then holds it firmly with either the first, third and fourth pairs of walking legs, or the second, third and fourth pairs of walking legs, and uses dactyl tips of either the second or first pair of walking leg to repetitively probe the edges of the valves (Figure 13.12A,B; Malcom, 2003). By such repetitive probing, they eventually wedge the dactyl tips into the shell edge and then insert the tips further and further into the shell – a process known as ‘wedging’ (Lau, 1987). Once one pair of pereiopod dactyls is inserted, another pair – usually those of the second and/or the third pereiopods – is used to cut the mantle tissue along the pallial line (line of attachment to the valve). Then the lobster uses a ‘scissoring’ motion of the first two pairs of walking legs to increase the opening angle and to provide access to the adductor muscles (Fig. 13.12C,D; Malcom,

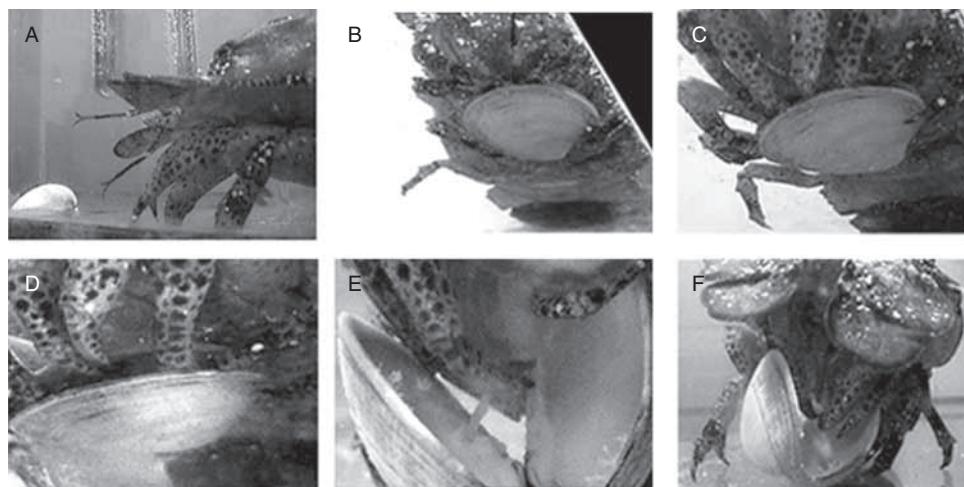


Fig. 13.12 The feeding process of scyllarid lobsters. (A) investigative behavior, using the antennules; (B) probing of the shell by the first two sets of pereiopods; (C) insertion of the pereiopods into the shell; (D) wedging and subsequent cutting of the adductor muscles; (E) opening of the shell and removal of the bivalve flesh; (F) scraping of the empty shell. Malcom, C. (2003) Texas State University at San Marcos, San Marcos, Texas.

2003). The second walking legs cut the adductor muscles, so that the valves open freely. With the valves open, the meat is repetitively scraped out of the valves and passed directly to the third maxillipeds (Fig. 13.12E,F; Lau, 1987; Malcom, 2003). These appendages are used to stretch the flesh and pass the strands back to the subsequent five pairs of mouthparts for ingestion. Until the molluscan flesh is actually passed back to the third maxillipeds, the antennules make repeated downward motions to probe inside the valves, to touch the flesh and to touch the shell as the legs scrap the flesh from it (Malcom, 2003).

The sensory-motor mechanisms that slipper lobsters use in shucking are unknown at this time. Visual cues can be excluded because the shucking process takes place beneath the animal and is outside the field of view of its dorsally placed eyes. Touch, proprioceptive and chemosensory modalities are candidates and there is evidence to suggest that each is involved. The touch and proprioceptive senses that could control this task are located in the legs. For manipulation, the positions of each leg segment, as well as each leg in its entirety, informed by proprioception, are likely to signal the size, orientation and location of the bivalve shell through signalling of joint angles. Points of contact for application of manipulative forces may be sensed through tactile sensors on the dactyl tips or through the tension in muscle organs. The legs do bear numerous tufts of setae (Malcom, 2003), but most are placed on the more proximal segments of the propus, carpus, merus, and ischium, rather than the distal dactyl (see Fig. 13.6A,D; Fig. 13.13A). Those that are present on the proximal edge of the dactyl segment are usually damaged, most likely due to the abrasive action they suffer while shucking. However, the remaining setae may pick up information from the surrounding water as the flesh of the bivalve is exposed to that water after valve opening. Setal types present consist mostly of simple, cuspidate, teasel-like, connate, and miniature simple (Fig. 13.13B,F) (Malcom, 2003). Simple setae have been demonstrated to have both chemo- and mechano-receptive functions in clawed (Derby, 1982) and spiny lobsters (Cate & Derby, 2001).

Perhaps the most interesting aspect of the feeding process is the role of the chemosensors. It is unclear how slipper lobsters detect buried food items, as they lack setal tufts on the tips of their pereiopod dactyl segments. In the few tracking tests that have been conducted, *S. aequinocialis*, *S. notifer* and *S. latus* performed poorly in locating food source odours over 2 metre distances compared to *H. americanus* and *Panulirus argus* (Grasso, unpublished observations as reported in Lavalli *et al.*, 2007). Nevertheless, they are capable of somehow locating and digging bivalves out from 3.5 cm of sediment (Almog-Shtayer, 1988), and increase flicking rates of the antennules while doing so, or when bivalves are deposited in their holding tanks (Lavalli, personal observations). Obviously, the antennules, acting as distance chemoreceptors, play some role in the detection process, but that role is not understood. Once a bivalve is located and the lobster engages in shucking behaviour, leg motions are suspended several times while the lobster brings its distance chemoreceptor organs (antennules) beneath the carapace and into contact with the bivalve (Malcom, 2003). This is surprising for two reasons. First, the chemosensory maxillipeds are better positioned to reach the shell. Second, as mentioned above, the tactile and proprioceptive sense from the legs should be sufficient to provide feedback information during opening. But, because slipper lobsters are unique in lacking distally placed dactyl setal tufts, they may not be able to obtain sufficient sensory feedback without using the antennules. Thus, the antennules may be used as both a contact and distance chemoreceptive mechanism. The annuli of the lateral flagella are covered with a variety of different types of setae (Weisbaum & Lavalli, 2004; Fig. 13.13H,I); many of these have already been identified as chemoreceptors and/or mechanoreceptors in clawed and spiny lobsters. The positioning of the setae places them in a position where stimuli carried by currents, possibly generated by the exopodites of the mouthparts, can reach them and provides an assessment of the shell and flesh within.

While the preferred food is molluscan bivalves, slipper lobsters are also known to take sea urchins, crustaceans, sponges, gastropods, barnacles, sea

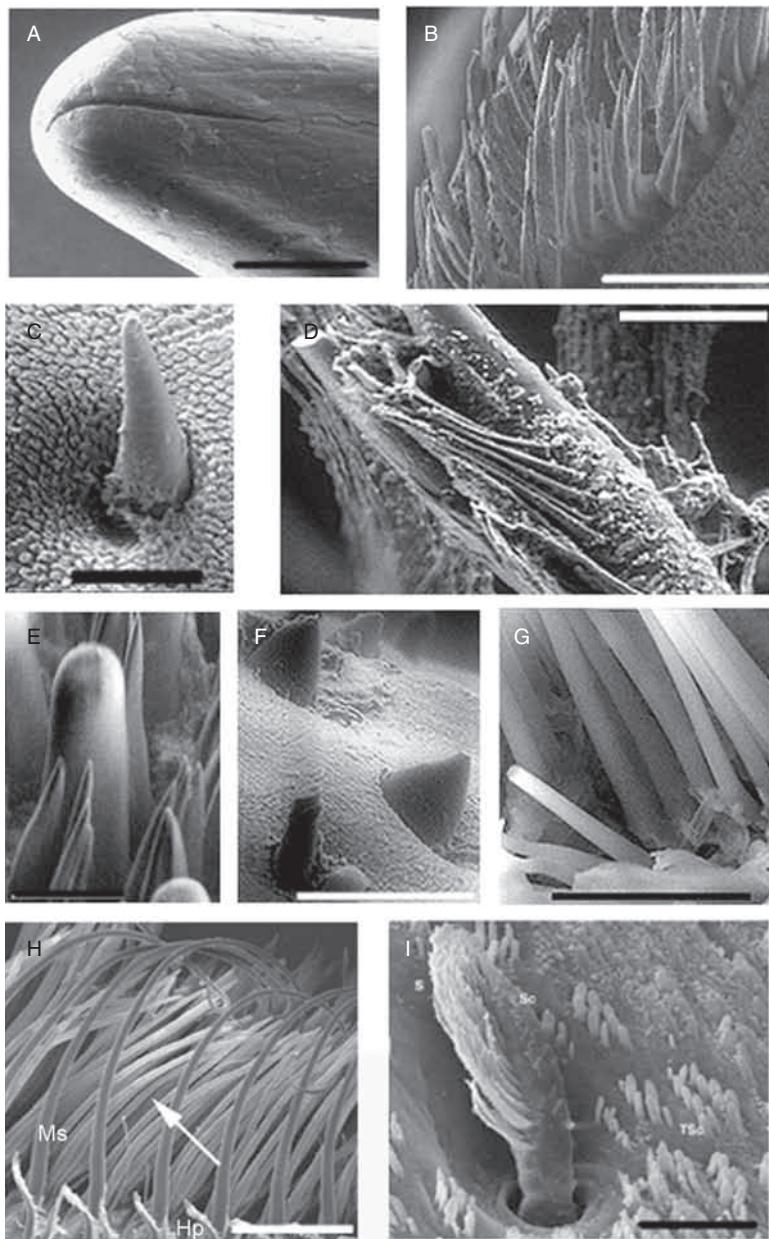


Fig. 13.13 Setal types found on scyllarid pereiopods and antennules. (A) dactyl tip of left second pereiopod of *S. aequinoctialis*; (B) simple setae set in groove on oral surface of left fifth pereiopod propus of *S. nodifer*; (C) cuspidate seta of right oral surface of 3rd pereiopod propus of *S. aequinoctialis*; (D) teasel-like seta with setules from left 1st pereiopod, aboral surface of *S. aequinoctialis*; (E) cuspidate and simple setae of female's right 5th pereiopod dactyl, oral surface of *S. aequinoctialis*; (F) conate setae on merus shield of third right pereiopod, oral surface of *S. nodifer*; (G) miniature simple setae covering the cuticular surface of the aboral surface of propus of *S. aequinoctialis*; (H) aesthetasc (arrow), modified simple setae (Ms) and hemi-plumose setae (Hp) found on the ventral surface of the antennular flagellum; (I) tooth-brush setae found on the dorsal surface of the antennular flagellum showing scale (Sc), setules (S) and textured scaling on flagellar surface (TSc). Scale bars: A, 200 µm; B, 200 µm; C, 200 µm; D, 20 µm; E, 50 µm; F, 250 µm; G, 350 µm (box, 20 µm); H, 273 µm; I, 20 µm. Malcom, C. (2003) Texas State University at San Marcos, San Marcos, Texas. Weisbaum, D. & Lavalli, K.L. (2004). Reproduced with permission of John Wiley & Sons.

squirts, algae (*Ulva* spp.) and fish flesh. Different species may well prefer different food items; for example, *S. latus* prefers bivalves to all other food items, and *S. astori* prefers white sea urchins, *Tripneustes depressus* (Martínez, 2000, Hearn *et al.*,

2007), yet both display a varied diet as evidenced by stomach content analyses (Martínez, 2000). Very few studies have been made of the gut contents of wild slipper lobsters (e.g. Martínez, 2000 and Lau, 1988 are two of the few), so individual

species preferences remain largely unknown. Laboratory preference tests with *S. latus* show a preference of soft flesh to crabs, and bivalves to soft flesh or snails, while no preference was shown between choices of oysters, clams, and limpets (Almog-Shtayer, 1988).

Thenus spp. employ a tactic more similar to clawed lobsters to locate food – they nocturnally explore an area of soft sediment by repetitive probing of their first two pairs of pereiopods (the setae of which are likely chemosensitive), while continuously moving their antennules up and down and flicking the lateral filaments (Jones, 2007). Radhakrisnan *et al.* (2007) also reported that *T. orientalis* in India actively swam for nocturnal feeding, something that would be advantageous for search behaviour in an environment characterized by low densities of preferred food species. Once food is located and captured, often by a swift lunge, there is a fine coordination among the mouthparts, pereiopods, and antennules during the consumptive phase (Jones, 2007). Radhakrisnan *et al.* (2007) reported that gut contents of commercially fished *T. orientalis* in India included a high proportion of molluscs (27.7%) followed by bottom sediments (24.1%), fishes (22.9%), crustaceans (10.7%), polychaetes (4.2%) and miscellaneous food items (10.4%). Although cephalopods, abundant in the habitats of *T. orientalis* in India, and fish were identified in the contents of the guts, Radhakrisnan *et al.* (2007) suggested that *T. orientalis* was an opportunistic scavenger, rather than an active predator. The fact that *T. orientalis* is a slow-moving crustacean compared with fast-swimming squids, cuttlefishes and fish decreases the likelihood that these lobsters are actively capturing such fast prey. Jones (2007) reported that scallops, goatfish and shrimps were always consumed when offered under laboratory conditions. Radhakrisnan *et al.* (2007) stated also that the mud and sand that formed an important constituent of the food of these burrowing animals, suggesting that they might feed on detritus. Thus, based on the stomach contents, Radhakrisnan *et al.* (2007) inferred that *T. orientalis* was an opportunistic, omnivorous, benthic feeder that burrows in soft and sandy mud, engulfs sediments consisting of sand and mud, and then preys on organisms that it encounters in this way.

From observations on species that are gregarious (e.g. *S. latus*, Barshaw & Spanier, 1994a), there is intraspecific competition over food items. The least aggressive of such encounters is the ‘approach/retreat’ sequence common to all lobsters (Atema & Cobb, 1980) – one lobster walks towards the other which responds by walking away or otherwise avoiding the approaching lobster. A more aggressive encounter involves use of the flattened second antennae and is called a ‘flip’. Here the lobster jerks up its flattened second antennae under the opponent’s carapace, attempting to dislodge it. In the most intense aggressive behaviour, the attacking lobster grabs the anterior portion of the opponent and holds on with the dactyl nails of the walking legs. The opponent usually tail flips, as does the attacking lobster, which causes the opponent to end up on its back. Often after this ‘face grab’ manoeuvre, both lobsters are holding onto the same food item, ventral side to ventral side, and they continue in this fashion until one lobster finally relinquishes its hold on the food item (Barshaw & Spanier, 1994a).

13.5.2 Sheltering behaviour and substrate preferences

Adult specimens of *Scyllarides* spp. are camouflaged to a certain extent due to their flattened morphology and colouration that blends into hard substrates (e.g. Ogren, 1977; Spanier & Lavalli, 1998). However, in the brightly illuminated water of their shallow habitats, this camouflage provides only limited concealment against diurnal predators. *Scyllarides* spp., therefore, like most other lobsters, are nocturnal. They forage during the night and shelter during the day on the ceilings of caves, in crevices in vertical rocky walls (e.g. Barr, 1968; Martínez *et al.*, 2002 and Hearn *et al.*, 2007 for *S. astori*; Spanier & Lavalli, 1998 for *S. latus*), and in other natural dens, as well in artificial reefs in the field (including ship wrecks Spanier *et al.*, 2010, 2011a), or in man-made shelters in the laboratory. However, in laboratory holding tanks, where predators are not encountered for a long time, they tend to shift to diurnal activity (Spanier *et al.*, 1988; 1990; Spanier & Almog-Shtayer, 1992). Micro-habitat preferences have been determined for *S.*

latus by providing lobsters with a variety of shelter designs in artificial reefs made of used car tires (for a review of such studies, see Spanier & Lavalli, 1998; Spanier *et al.*, 2010, 2011a). *Scyllarides latus* significantly preferred horizontally-oriented dens to vertically-oriented dens where light levels were higher. They also preferred shelters with small, multiple openings, like those between tyres, over those with larger entrances (in the tyres themselves). When additional 'back doors' were experimentally blocked, they stopped using these manipulated dens.

A tendency for gregarious sheltering among *S. latus* was observed in a survey of natural dens where 95% of lobsters cohabited with one or more conspecifics (Spanier & Almog-Shtayer, 1992). This gregarious behaviour was also observed in the laboratory and for very large lobsters (>100 mm CL), which differs from gregarious spiny lobster species where the tendency for cohabitation is greater in smaller and medium-sized animals (e.g. Spanier & Zimmer-Faust, 1988). Similar clustering behaviour was observed among *S. latus* in naturalistic habitats and with artificial shelters in laboratory tanks. In the absence of a predator, freshly caught laboratory-held lobsters significantly preferred and formed clusters under an opaque artificial shelter compared to a transparent shelter of the same shape and size. When they were supplied with no shelter but with shade, the lobsters concentrated under the shade (Spanier & Almog-Shtayer, 1992). When neither shelter nor shade was supplied, they showed distinct gregarious behaviour similar to the defensive 'rosette' observed in migrating Caribbean spiny lobsters under attack by a triggerfish (Herrnkind, 1980; Herrnkind *et al.*, 2001; Kan-ciruk, 1980). Gregarious sheltering of more than 50 *S. latus* individuals was observed by Spanier (personal observation) in a single, large, open cave at a depth of 30 m. However, field predation studies indicate that gregarious behaviour does not confer any advantage on individuals within the group who are under attack by fish predators. They suffer an equal amount of predation as do lone animals exposed to the same fish predators and gain only a small advantage of time, as predatory attack patterns are less focused when lobsters are grouped (Lavalli & Spanier, 2001). Reports of gregarious

behaviour also exist for *S. nodifer* (Moe, 1991), but nothing is known about the function of such behaviour.

The adults of many species are found on hard substrates (refer to Section 13.2.2 above). It is likely that *Scyllarides* species sampled both on hard and soft substrates derive from circumstances where lobsters that usually shelter in hard substrates were collected in soft substrates during their short and long term movements. Nevertheless, a few species of *Scyllarides* have been reported only on soft substrates (e.g. *S. elisabethae* that digs in the mud (Holthuis, 1991), *S. nodifer* that is often caked in mud (Hardwick & Cline, 1990) and *S. aequinoctialis* that has been observed to bury in the sand as well as shelter within coral rock caves and under coral heads (Moe, 1991)). It is assumed that such digging into soft substrates is an anti-predator adaptation, similar to that seen in other lobster genera living long-term or temporarily on soft substrates, such as *Ibacus* and *Thenus* spp.

Parribacus species also inhabit hard substrates or on sandy bottom of reefs and hide during the daytime in crevices and caves, often attached to the ceiling of the caves (Holthuis, 1991). Little is known about the sheltering behaviour and substrate preferences of these species. Sharp *et al.* (2007) infrequently encountered *P. antarcticus* in the Florida Keys and suggested that these lobsters preferred high-relief coral structures, similar to *S. aequinoctialis* and occupied the den wall, rather than the floor. Of the four *P. antarcticus* they encountered, three were found on the reef buttress zone; the remaining individual was captured in a spiny lobster trap along the seaward edge of the reef. They reported that two of these four lobsters were encountered during night-time dives and were apparently foraging on the reef away from their shelters. Holthuis (1991) reported that this species sheltered sometimes in small groups (like *S. latus*, see above). Their flattened morphology and the colourful coloration of their dorsal surfaces enable them to blend into the colourful hard substrates of the reef.

All five species of *Thenus*, and eight species of *Ibacus* inhabit relatively soft sandy or muddy substrates (Burton & Davie, 2007; Haddy *et al.*, 2007) and are well-adapted for digging into the substrate

in terms of their morphology as well as their behaviour. Faulkes (2006) reported that *I. peronii* spent most of the day underneath the sand and that digging was a distinct form of locomotion that possessed different mechanical problems from other locomotory modes common in crustaceans such as walking and swimming. He described *I. peronii* as using a ‘wedge’ strategy to submerge into sand. The lobster penetrated the sand with the walking legs, then extended the abdomen to push sand backwards, then flexed the abdomen while pushing backward with the legs, which slowly drove the body into the sand. This basic sequence repeated for several minutes. Digging often ended with a short series of tail flips. When presented with a choice of substrates, *I. peronii* preferred to dig in sand over shell grit, but individuals showed no preference for different types of sand. Similarly Jones (2007) reported that both *T. indicus* and *T. orientalis* were nocturnally active, with clear peaks in activity at dusk and just prior to dawn. During daylight hours, both species buried themselves in the sediment with only the eyes and antennules exposed. Jones (2007) observed a relatively low frequency of antennular flicking in lobsters in this position. Burying behaviour was essentially the same for the two species and similar to that described for *Ibacus* spp. by Faulkes (2006). Their large plate-like antennae ('shovels') are not involved in burying behaviour contrary to the suggestions by George & Griffin (1972). In sediment choice experiments described by Jones (2007) *T. indicus* displayed a significant preference, for the finest sediment grade offered, dominated by particles of less than 63 µm in diameter while *T. orientalis* displayed a clear preference for sediments composed of moderate to coarse particle size. Jones (2007) assumed that these findings strongly suggested a niche separation between these two species. It is interesting to note that the colour of the dorsal surfaces of *Thenus* spp. that inhabit relatively shallower, and more illuminated habitats (the shallow continental shelf) is yellow-brown (see pictures in Burton & Davie, 2007). These colours may supply some camouflage on the yellow-brown background of their soft shallow habitats. The dorsal surfaces of most *Ibacus* species that inhabit mainly deeper parts of the continental margins

(mid-continental shelf to upper continental slope (Haddy *et al.*, 2007) are, however, more red-purple in colour (see pictures in Brown & Holthuis, 1998) possibly as an adaptation to the substrate and illumination in these depths..

13.5.3 Predators and antipredator behaviour

The response of slipper lobsters to predator attack has been well studied (e.g., by the grey triggerfish, *Balistes carolinensis*) (Spanier *et al.*, 1988; 1991; Spanier & Almog-Shtayer, 1992; Spanier *et al.*, 1993; Barshaw & Spanier, 1994a,b; Lavalli & Spanier, 2001; Barshaw *et al.*, 2003; Lavalli *et al.*, 2007) and consists of three strategies, two of which are typically executed in sequence: (i) the ‘fortress strategy’ in which the animal grasps the bottom and attempts to outlast its attacker’s motivation to penetrate its hard shell (described in Barshaw *et al.*, 2003); (ii) the ‘swimming escape’ response (described in Barshaw & Spanier 1994a, b, and Barshaw *et al.*, 2003; see also Section 13.5.2); and (iii) remaining sheltered in dens (Spanier *et al.*, 1988; Spanier & Almog-Shtayer, 1992; see also Section 13.5.2). Lacking claws (like *Homarus* spp.) or long spinose antennae (like spiny lobsters; see Zimmer-Faust & Spanier, 1987; Spanier and Zimmer-Faust, 1988; Lozano-Alvarez & Spanier, 1997; Herrnkind *et al.*, 2001) with which to fend off swimming predators, slipper lobsters have developed a shell that is twice as thick and more durable to mechanical insult than clawed or spiny lobsters (Barshaw *et al.*, 2003). They use their short, strong legs to grasp the substrate and resist being dislodged (Barshaw & Spanier, 1994a,b). When this ‘fortress defence’ fails, they are exceptionally deft swimmers capable of evasive manoeuvres like barrel rolls (presumably using their flat, broad antennae like reciprocal aileron stabilizers on an airplane wing) en route to a shelter (Spanier *et al.*, 1991; see Section 13.5.2). Also they may suddenly change the direction of their swimming, presumably to confuse the chasing predator. This is an energetically costly response to a threat and is generally used as a last resort. It has been argued that slipper lobsters have matched the energy

invested by clawed lobsters in claws and spiny lobsters in antennae by increasing only moderately the thickness of their shells and bettering their swimming escape behaviour (Barshaw *et al.*, 2003). This strategy appears to support a highly successful lifestyle, as slipper lobsters are the most diverse group of lobsters with at least 88 species distributed worldwide (Booth *et al.*, 2005; Burton & Davie, 2007; Chan, 2010; Lavalli, & Spanier, 2007b,).

Slipper lobsters that live in complex substrates also display a variety of shelter-related behaviours that provide a third highly effective survival strategy (Barshaw & Spanier, 1994a). By combining nocturnal foraging with diurnal sheltering, as well as carrying food to their shelters for later consumption, slipper lobsters may fully minimize their exposure to diurnal predators. Horizontally oriented shelters supply shade and reduce visual detection by diurnal predators. Small shelter openings also supply shade but, in addition, increase physical protection against large diurnal predators, especially fish with high body profiles. Clinging may enable the lobsters to survive an attack inside a den and even in open areas. Multiple shelter openings enable escape through a 'back door' if a predator is successful in penetrating the den. They can then escape by using their fast tail-flip swimming capability (see Section 13.5.2). The tendency for cohabitation with conspecifics (as seen in *P. antarcticus* (Holthuis, 1991; Sharp *et al.*, 2007) or *S. latus* (Lavalli & Spanier 2001) may be adaptive because of collective 'prey vigilance' and defence or concealment among cohorts ('selfish herd' response or the 'dilution effect' *sensu* Hamilton, 1971). If all else fails, their thick carapace, designed to effectively blunt cracks (see Barshaw *et al.*, 2003; Horne & Tarsitano, 2007; Tarsitano *et al.*, 2006 and Section 13.3 for details) may serve them in times of exposure to attacking predators.

Very little is known about the antipredator behaviour of soft bottom species. Jones (2007) described the concealment behaviour of *Thenuis* as an adaptive response to avoid predation. He suggested that unlike hard substrate species, soft substrates species could only achieve concealment by burrowing. He stated that burrowing behaviour typically occurred at the cessation of a period of

activity and was normally completed in less than 2 minutes. Fully buried lobsters are entirely concealed except for the eyes and antennules. During nocturnal activity, lobsters were often observed burying themselves partially, for periods of relatively short duration. Partial burying was clearly distinguishable from normal burying and Jones (2007) suggested that it provided suitable concealment during rest periods.

Ibacus spp. also are found on soft bottom substrates and are known to bury into those sediments, much in the same manner as *Thenuis* spp. (Haddy *et al.*, 2007; Faulkes, 2006) presumably also as antipredatory concealment.

Spanier *et al.* (2011b) compared morphological characteristics of adults of 31 species of slipper lobsters, representing all four subfamilies of Scyllaridae. Their study suggests that slipper lobsters display two main body shapes: triangular (e.g. *T. orientalis*) and rectangular (e.g. *S. latus*) and that genera displaying these shapes also exhibit distinct differences in body thickness that affects the location of the centre of mass. Those that are triangular in shape tend to be thinner and wider, which is likely to positively affect their ability to hydrodynamically lift off substrates and have more effective swimming strokes. This may make them better swimmers as they can invest less energy in getting up in the water column, and move into a faster and longer swim. They also tend to be the softer substrate (sand, mud) genera. Those that are more rectangular tend to be thicker and narrower (cylindrical), which is likely to provide less lift and decrease swimming stroke efficiency. These species tend to be found in complex habitats (coral reefs, rocks) where walking might be a more effective means of locomotion and a better strategy for sheltering in crevices during the day (associated with the possible need for a quick escape swimming from the 'back door of the den', see Section 13.5.5, where a triangular body shape would be a disadvantage). They also suggest that the position of the eyes and their sizes may be significant in antipredator interactions. For example, in *Thenuis* spp., the eyes are at the lateral-most edges of the carapace. These widely spaced eyes could be advantageous in providing a better binocular distance estimation (to

detect predator) and a wide visual periphery (lessened if eyes are small) that can also be useful for predator detection. However, eyes in this position are more susceptible to attack by predators. For other species, such as *Ibacus*, the eyes are medially located, which may suggest the need for better depth perception or for protection against predators. In *Parribacus* and *Scyllarides* spp. the positions of the eyes are intermediate between the above mentioned two extreme positions. Lau *et al.* (2009), in the only study so far of visual capacities of slipper lobsters, suggest that at least in *S. latus*, the eyes seem suited for vision in dimly lit environments, but they are susceptible to attack by predators (Barshaw *et al.*, 2003); hence, positioning on the carapace and sculpturing around the eye orbit area may be adaptations to predation pressures that are balanced against needs for prey detection.

The size of the eye varies amongst scyllarid taxa. Smaller eyes may be typical of shallow water species (like *Thenus* spp.) or diurnal/crespuscular activity (more exposure to light). Smaller eyes may also represent burrowing habits and they can be adaptations to minimize damage to the photoreceptors (whose function would be limited to detect changes in brightness). Eyes are relatively large in *Parribacus* spp., with dimensions that are probably necessary to form images in dim light (Lau *et al.*, 2009). In *Scyllarides* and *Ibacus* spp., eyes are of intermediate size. Lau *et al.*, (2009) proposed that the position of the eyes on the head and the thick cornea in *S. latus* is indicative of a need to protect the eyes against physical damage. Their study of the anatomy and ultrastructural organization of the eye of the Mediterranean slipper lobster (Plate 13.1) also suggest that this lobster possesses polarized-light sensitive photoreceptors. They explain that many fish predators use polarization patterns to orient themselves and that having polarization sensitivity can help enhance contrasts. Thus there could be an advantage to having polarized light sensitive eyes also in the prey – the lobster.

Besides the triggerfish, shark (the spotted gully shark, *Triakis megalopterus* (Smith, 1849) have been reported to feed on *S. elisabethae* in South Africa (Smale & Goosen, 1999), dusky groupers (*Epinephelus guaza*, Linnaeus, 1758) have been

reported as predators of adult and juvenile *S. latus* (Martins, 1985a), and red (*Epinephelus morio*, Cuvier & Valenciennes, 1828) and gag grouper (*Mycteroperca microlepis*, Goode & Bean) have been reported as predators of *S. aequinoctialis* and *S. nodifer* (Lyons 1970). Combers (*Serranus* spp.) and rainbow wrasse (*Coris julis*, Linnaeus, 1758) apparently prey on juvenile *S. latus* (Martins 1985a).

13.5.4 Mating behaviour

Because scyllarids copulate, spawn, and brood readily in the laboratory, some aspects of their reproductive biology are known. However, less is known of the actual mating behaviour or the rituals involved during the mating process. Males of *Scyllarides* spp. produce white, gelatinous spermatophores, which they carry around on the base of their fourth and fifth pereiopods (Almog-Shtayer, 1988; Spanier, personal observations). These are transferred externally to females. It is not clear whether females retain the spermatophores externally and fertilise their eggs externally, or whether they somehow manipulate the spermatophore and store it internally. In some species, females have been observed carrying spermatophores externally 6–10 days or less prior to egg extrusion (*S. latus*, Martins, 1985a; Almog-Shtayer, 1988; Fig. 13.14), while in others, the lack of observable spermatophores prior to egg extrusion has led to a belief that the spermatophore is stored internally and fertilization is internal (*S. nodifer*, Lyons, 1970; *S. squamosus* appear to lack external sperm masses, DeMartini *et al.*, 2005). Females of most species can spawn multiple broods in a season due to short brooding periods (but see Hearn *et al.*, 2007 for a contrasting view, in which *S. astori* broods once annually), and these broods are usually carried during spring and summer months. Only in *S. latus* have both eggs and spermatophores been observed simultaneously (Almog-Shtayer, 1988). It is possible, but so far not known, that different species of *Scyllarides* employ different strategies for fertilization.

Male *Thenus* spp. do not appear to deposit a persistent spermatophoric mass in the process of mating (Jones, 2007). Soft, non-persistent masses



Fig. 13.14 External sperm mass on *S. latus* female (arrows). Bianchini, M.L. & Raisa, P.F. (1997) © MiRAAF.

were observed by Kizhakudan *et al.* (2004) for *T. orientalis* and females oviposited within 8 hours post-mating and lost the spermatophore within 12 hours. Jones (2007) presumed that fertilization occurred soon after mating when the eggs were transported from the genital apertures to the pleopods or a short time afterwards when the eggs were deposited on the pleopods. Kizhakudan *et al.* (2004) reported that oviposition occurred within 5–7 hours post-mating and was completed by 8 hours post-mating. Radhakrishnan *et al.* (2007) reported that the spermatophoric masses of *T. orientalis* were attached to the post-ventral sternite and anterior abdominal region of female in the form of a white, longitudinal, jelly-like mass. Oviposition was completed within 6–8 hours and the spermatophore was lost in about 12 hours after mating; incubation period was 35 days. However, neither pre-copulatory courtship behaviour nor mating has been directly witnessed in *Thenus orientalis* or *T. indicus* in over 2000 hours of remote video observation of captive populations Jones (2007), so it assumed that social interactions are uncommon and mating rituals are extremely simple.

Likewise, mating has not been directly observed in *Ibacus* spp. but observations of *I. chacei* and *I. peronii* in the field and in aquaria indicated that moulting was not a prerequisite and mating apparently occurred when the female was hard-shelled (Haddy *et al.*, 2007). Spermatophoric masses were persistent, gelatinous, an opaque white colour, and

were deposited as two elongated strips, approximately 20–30 mm long close to the genital openings. It is likely then that fertilization occurs externally and relatively soon after mating while the eggs are being transported from the genital apertures to the setae.

Very limited information is available on *Parribacus* spp. Spermatophores seem to persist even after spawning and new spermatophores are deposited atop old ones (Sharp *et al.*, 2007). Thus, spawning occurs without moulting.

13.5.5 Movement patterns

Slipper lobsters demonstrate two modes of movement: (i) slow, benthic walking movements that may be nomadic within a small home range or migratory from inshore, shallower waters to offshore, deep waters; and (ii) swimming movements that can be used for rapid escape or, as some have suggested, for vertical movements in the water column.

Daily and seasonal horizontal patterns

Tagging studies of *S. latus* off the coast of Israel indicate two annual patterns of movement: local nomadic movements made while inshore and migratory offshore movements. During the inshore lobster season (February to June in the south-eastern Mediterranean), lobsters left their shelters at night to make short-term movements to forage and bring back food (mostly bivalves). More than 71% of tagged lobsters were recaptured in the artificial reef site repeatedly during this season. Time between repeat captures was 1–17 weeks (mean 29 days) and this rate probably represents local nomadism (Spanier *et al.*, 1988). In contrast, only 7.2% of the tagged lobsters were recaptured in the same man-made shelter site after more than half a year. Time between these captures ranged between 10–37 months (mean 338 days) and may represent migratory movements. Returning lobsters have to orient and locate the small artificial reef site in the widespread continental shelf.

For several years, these types of seasonal surveys of *Scyllarides* lobsters were conducted in the above-mentioned artificial tyre-reef complex (Spanier

et al., 1988). Lobsters appeared in the reefs in early winter (December to early February), with their numbers peaking in the spring (March to May). From June onward, their numbers decreased in the shallow part of the continental shelf and they disappeared from shallow water in August/September to the beginning of the following winter. This seasonality correlates with water temperature. They appear in the shallow part of the continental shelf (15–30 m depth) when water temperatures are the lowest for the south-eastern Mediterranean region (14.5–16°C) and their numbers decrease when water temperatures increase to 26–27°C (Spanier *et al.*, 1988). A similar trend is seen in the yield of the commercial fisheries off the Mediterranean coast of Israel. However, no migratory inshore-offshore pattern is seen off Sicily where tagged *S. latus* were found in all seasons of the year (Bianchini *et al.*, 2001).

Mobility of *Thonus* spp. in Australia also has been examined through use of tag and recaptures studies and monitoring of commercial catch levels (Jones, 2007). Average time at liberty is 183 days, with most lobsters being recaptured an average of 24 kilometres from the point of release. Thus, it is likely that *Thonus* spp. could be very mobile and capable of moving large distances, but because their movements lack any kind of pattern or directionality, they are not likely to be migratory. Work by Radhakrishnan *et al.* (2007) confirms this in that female *T. orientalis* in India remain in the fishing grounds during the peak spawning period and do not undertake breeding migrations to either shallower or deeper waters.

It is likely that some *Ibacus* species may undertake extensive migrations while others may simply exhibit nomadic movement patterns. Stewart & Kennelly (1998) tagged 3,892 *I. peronii* and 716 *I. chacei* and found that *I. peronii* demonstrated a nomadic pattern of movement – a total of 557 tagged individuals of this species (14.3%) were recaptured close to their place of release (mean of 0.35 km) and with no specific directional movement. In contrast, 94 recaptured *I. chacei* (13.1% of the animals tagged, representing a wide size range) demonstrated a clear northwards migration from their release locations, traveling up to 310 km

in 655 days. The average minimum rate of movement (calculated as the shortest distance between release and recapture location divided by time at liberty) was 0.15 km/day, but ranged up to 0.71 km/day.

What might cause some scyllarid species to migrate large distances while others remain more local? Several traps set offshore, off-season, and at a depth of 48 m in the Mediterranean caught *S. latus* lobsters in October. Water temperature at these trap sites was 23.6°C, while in the much shallower artificial reef site at 18.5 m where no lobsters were detected, it was 27.7°C. Also lobsters were caught during the fall at depths greater than 50 m by a rough bottom trawl (Spanier *et al.*, 1988). This limited information suggests that slipper lobsters off the coast of Israel seasonally move to deeper and more northerly waters (i.e. colder water). By migrating, the colder-water lobsters may avoid the high, and perhaps unfavourable, summer and autumn temperatures in the shallow waters of the Levant basin of the Mediterranean. Today minimum winter water temperatures at these depths have increased to 16.5°C and may rise as high as 32°C in August to September due probably to global climate change. These temperature increases may affect movement patterns of lobsters and may also cause moulting difficulties or abnormalities (also reported by Spanò *et al.*, 2003). Some lobsters kept in the laboratory with ambient water supply (26°C and higher) for over 2 months died in the fall while moulting or only incompletely moulted (Spanier, personal observations). Thus, one possible function of the seasonal shallow-to-deep migration may be to meet physiological and behavioural requirements for moulting. Moulting in deeper habitats may also be a predator avoidance strategy during this vulnerable period, as has been suggested by Berry (1971).

Those species that do migrate and then return to specific local inshore areas seem to be capable of shoreward homing movements. The advantage of a homing ability is obvious, particularly for inshore areas that may have only limited shelter-providing habitat. Thus, it may be advantageous for lobsters to ‘recall’ preferred natural or artificial reef sites and to return to them after short- as well as long-

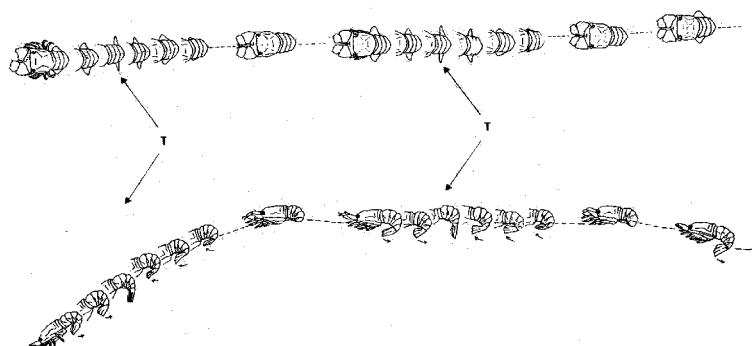


Fig. 13.15 Illustration of the 'burst-and-coast' type of swimming of the Mediterranean slipper lobster, *Scyllarides latus*. A drawing of a swimming sequence, based on video recordings; top view: above, side view: below. Spanier, E., Weihs, D. & Almog-Shtayer, G. (1991). Reproduced with permission of Elsevier.

term movements. However, the mechanism by which some slipper lobsters orient and locate their preferred habitats is completely unknown. They may use some geomagnetic cues or magnetic maps, as has been reported for spiny lobsters (Lohman, 1984, 1985; Boles & Lohman, 2003). Interestingly, those species that live in featureless habitat don't seem to conduct homing movements and are more nomadic in nature.

Swimming behaviour (vertical movements)

In mechanical terms, tail-flip swimming in crustaceans constitutes locomotion in which a single 'appendage' – the abdomen – produces thrust by a combination of a rowing action and a final 'squeeze' force when the abdomen presses against the cephalothorax (Neil & Ansell, 1995). Although the tail-flip response is known in adults and juveniles of all three major taxonomic group of lobsters (e.g. Newland & Neil, 1990; Newland *et al.*, 1992; Jacklyn & Ritz, 1986; Jeffs & Holland, 2000), as well as in other crustaceans, it is best developed in slipper lobsters. Tail flipping is first developed in the nisto phase, where it can vary among species in strength (Robertson, 1968; Lyons, 1970; Barnett *et al.*, 1986; Higa & Saisho, 1983).

The hydrodynamics of swimming in slipper lobsters has been studied in *Ibacus peroni*, *I. alticrenatus* (Ritz & Jacklyn, 1985; Jacklyn & Ritz, 1986; Faulkes, 2004), *Thenus orientalis* (Ritz & Jacklyn, 1985; Jacklyn & Ritz, 1986; Jones, 1988, 2007) and *Scyllarides latus* (Spanier *et al.*, 1991; Spanier &

Weihs, 1992, 2004). *S. latus* uses a 'burst-and-coast' type of swimming (see Weihs, 1974) in response to a predator (triggerfish) or harassment from divers (Fig. 13.15). Large amplitude movements of the tail propel the lobster quickly backwards, with periods of acceleration reaching top velocities of three body lengths per second; these movements are followed by periods of powerless gliding, decelerating to velocities of less than one body length per second. The force per tail beat ranges between 1.25 to more than 3.00 newtons and correlates with body length because additional force is needed to move the greater mass of larger animals, rather than to increase speed and acceleration. The intermittent fast-escape swimming is only of short duration and does not appear to be used for foraging or long-range movements; instead it is an emergency response, whereby the animal invests considerable energy resources to reduce its exposure time in the open area until it can reach safety. Spanier & Weihs (1992) suggested that the flattened second antennae of *S. latus* (mistakenly called 'shovels' or 'flippers'), with their movable joints, play an important hydrodynamic role in controlling the swimming movement. Essentially, they serve as stabilizers and rudders in 'take-off,' acceleration, gliding, turning (e.g. Fig. 13.16), and landing. This adjustment in lift via the second antennae is also seen in *Ibacus* spp. and *Thenus* spp. (Jacklyn & Ritz, 1986).

Significant lift is created during backward tail flips, and articulations of the flattened first antennae (aka 'rudders') alter the distributions of this lift so

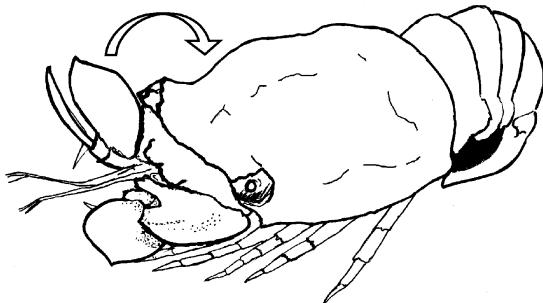


Fig. 13.16 An illustrated example of differential tilting and spreading of the second antennae to produce turning movements during swimming of the Mediterranean slipper lobster, *Scyllarides latus*. Reproduced with permission of Rachel Pollack.

that pitching and rolling movements are possible. In contrast, spiny lobsters found in similar habitats and ranges (e.g. *Jasus edwardsii*), produce a negligible amount of lift during each tail flip and do not possess antennae that were shaped or positioned properly to control any created lift. As a result, spiny lobster tail-flips are not efficient for continuous swimming or manoeuvering (Ritz & Jacklyn, 1985; Jacklyn & Ritz, 1986). Neil & Ansell (1995) compared data of swimming performance for a number of decapod, mysid and euphausiid crustaceans. Maximum velocity of body movement achieved during the tail-flip is similar across the adults in each group, and ranges from 10 mm to 300 mm body lengths, although this represents a 30-fold difference in the velocities expressed as body lengths per second. *S. latus* is ranked as the fastest of those tested, with a maximum velocity of close to 1 m s^{-1} compared with 0.6 m s^{-1} in the clawed lobster *Nephrops norvegicus* (Newland *et al.*, 1988).

In a more recent analysis, Spanier & Weihs (2004) identified the contribution of the tail as propulsor, legs as landing gear and second antennae as control surfaces. They also examined secondary hydrodynamic effects of carapace curvature and the longitudinal ridge along the carapace that is associated with vortex production and control. This ridge may function as a keel, much like the ventral keel (produced by scale armature) of rigid body boxfishes (Bartol *et al.*, 2002), and may sta-

bilize motion, resulting in a smooth swimming trajectory.

In *Thenus* spp., Jones (1988, 2007) distinguished between a locomotory form of swimming that was characterized by a slower speed (29 cm s^{-1}) and the absence of explicit stimulus (e.g. Fig. 13.17), and escape swimming which is much faster (1 cm s^{-1}), similar to the speed seen in *S. latus*) and always involved direct stimulus or threat. In locomotory swimming, lift was generated by the body shape (aerofoil) and by the downward thrust of the abdomen, while drag was reduced by all pereiopods being extended anteriorly (Jacklyn & Ritz, 1986). Lift height was controlled by the second antennae and each flexion helped to maintain the animal above the sediment (Jacklyn & Ritz, 1986; Jones, 1988). In comparison, escape swimming always consisted of an abdominal flexion that was proportional to the magnitude of the stimulus. Faulkes (2004) argued that these two separate responses were not necessarily the result of separate and distinct neural circuitry, but could simply represent two extremes of the non-giant flexor motor neuron affected tail flips.

Ibacus spp. have been examined both for the hydrodynamics of swimming as well as for the neural circuitry controlling swimming. Jacklyn & Ritz (1986) argued that since the abdomen was fully extended before being flexed, and because some flexions occurred with only a partial extended abdomen, these flexion's must be mediated by the lateral giant (LG) interneurons. However, Faulkes (2004) found that *Ibacus* spp. did not respond to sudden tactile stimuli with tail flips, but only tail flipped when turned over. Histological analysis of the abdominal ventral nerve cord showed that *I. peronii* lacked medial giant and LG interneurons, as well as the fast flexor motor giant (MoG) neurons in the abdomen and thorax. These neurons that modulate the fast escape response of crayfish and lobsters have been lost in all members of the infraorder Palinura, which includes spiny and slipper lobsters (Faulkes, 2008). In their place, Faulkes (2004) found that *I. peronii* had fast flexor neurons and flexor inhibitor motor neurons that appeared to mediate the tail flip response. Faulkes (2004) argued that the adaptive value of the giant interneuron-mediated escape tail flip response

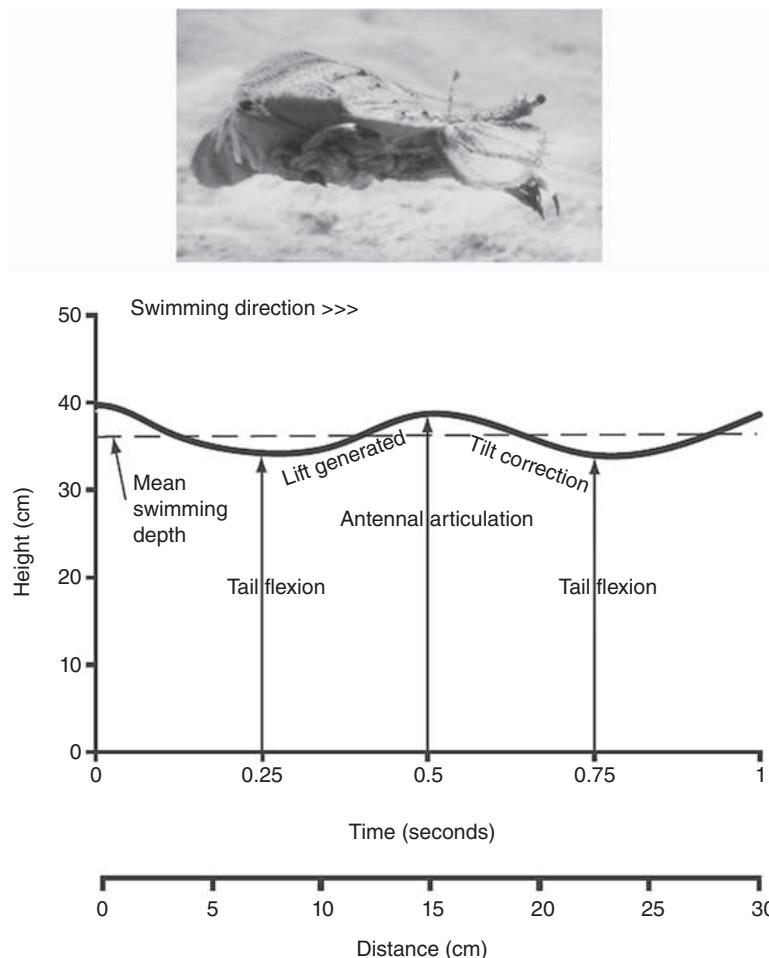


Fig. 13.17 Diagrammatic illustration of locomotion (free) swimming of *Thenus* spp. Jones (2007). Reproduced with permission of Taylor & Francis Group LLC.

should be inversely proportional to the amount of time the abdomen was flexed and, because it was flexed normally in *Ibacus* spp., such a tail flip response would only produce minimal movement and be rather ineffective as an escape mechanism.

The carapace and abdomen of slipper lobsters, like those of other decapod crustaceans, are covered with stiff, presumably mechanosensory hairs (Fig. 13.18). In slipper lobsters, this basic pattern shows two distinct elaborations. First, in *Scyllarides* spp. the hairs are arranged in groups of 7–12 on small islands of hard, protruding cuticle (about 500 islands are present on the carapace, depending on the species) (e.g. Fig. 13.18). Second, this pattern continues out onto the surfaces of the flattened

antennae to the extent that the antennae, when extended, appear to form a continuous surface with the carapace. These structures likely serve a hydrodynamic sensing role during the swimming escape response and may provide important sensory feedback for the lobster while swimming. However, the sensory modalities involved in swimming remain largely unknown.

13.6 Diseases

There are only a few reports on diseases or parasites of slipper lobsters, in general, and of specific species in particular (e.g. Bianchini & Raisa, 1997;

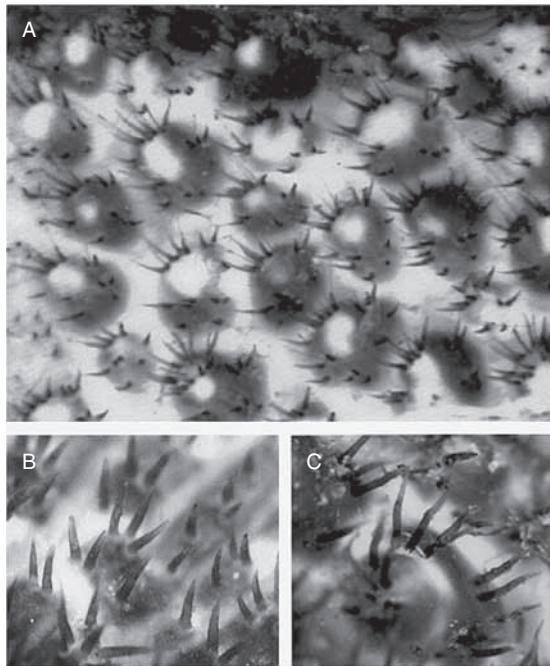


Fig. 13.18 Setal tufts found covering the surface of the scyllarid (*S. latus*) carapace. (A) setal tufts of tubercles; (B) arrangement of setae (likely cuspidate or simple setae) within carapace tufts; (C) single tuft, showing distribution of setae around tubercle.

Newell, 1956). This limited information is covered in Chapter 5. *Scyllarides* specimens become ill occasionally and die in the laboratory from as yet unknown causes. Halacarid mites, *Copidognathus. matthewsi* have been found on the gills of the *P. antarcticus* and apparently cause tissue necrosis (Newell, 1956). The success of pilot-scale aquaculture production of *Thenus* spp. in Australia and the potential of culturing *Ibacus* spp. (see Section 13.8) emphasized the need for more knowledge on pathogens of these species since phyllosoma are very susceptible to microorganisms in the water column (Perry, 2001; Mikami & Kuballa, 2007). Traditionally, a number of antibiotics as well as chemicals have been heavily used for controlling bacterial colonies in the rearing water. Alternative methods are the use of ultraviolet light (UV) and ozone (O_3) sterilizers (for details see Mikami &

Kuballa, 2007; Vijayakumaran & Radhakrishnan, 2011). Disease caused by gram-negative *Vibrio* (Vibriosis) is the main problem in hatchery production of lobster larvae and both phyllosoma and their live feed *Artemia* nauplii, have had high *Vibrio* loads resulting in mass mortality. Other serious problems were fouling with filamentous bacteria (*Leucothrix* sp.) and protozoans (such as *Zoothamnium* sp., *Vorticella* sp. and *Acinata* sp.) (Vijayakumaran & Radhakrishnan, 2011). They added that the live feed *Artemia* nauplii could introduce bacteria almost continuously to the culture system.

13.7 Harvest of wild populations

Slipper lobsters contributed annually only 1924 t (less than 0.75%) to the reported global fisheries production of lobsters (257,532 t) in 2009 (FAOSTAT, August 10, 2011). This is a considerable reduction from a 2006 report where slipper lobsters contributed 4185 t (~1.7%) to the reported global fisheries production of lobsters (252,111 t) in 2006. The most economically important taxon is *Thenus* spp. with reported annual fisheries production in 2009 at 1083 t; this is largely the result of it being by-catch in many commercial trawl fisheries off the tropical coasts of the Indian and Pacific oceans (Jones, 2007; Vijayakumaran & Radhakrishnan, 2011). Four species of *Ibacus* (*I. alticrenatus*, *I. brucei*, *I. chacei*, *I. peronii*) support a small fishery in Australia. They are caught mostly off eastern Australia (southern Queensland and northern NSW waters) also as a by-product in the demersal trawling fishery for king prawns (Haddy *et al.*, 2007). The total annual landings for all *Ibacus* species is approximately 200 t (Haddy *et al.*, 2007). In contrast, landings of *Scyllarides* spp. (maximum 1–2 t per species) and *Parribacus* spp. are generally small compared with *Thenus* and *Ibacus* species. While *Scyllarides* spp. are large, and thus preferable for human consumption, only a few species support trap fisheries (Holthuis, 1991; Williams, 1986). *Scyllarides astori* (Holthuis & Loesch, 1967), *S. deceptor* (Ramos, 1951), *S. delfosi* (Opresko *et al.*, 1973), *S. elisabethae* (Fischer & Bianchi, 1984), *S. roggeveeni* (Holthuis, 1972), and *S. tridacnophaga* are usually consumed

if caught, but they are fairly rare and support no commercial fisheries. Those that are captured are typically taken as by-catch of trawling operations (Rudloe, 1983; Sharp *et al.*, 2007), in trammel nets (Holthuis, 1991) or by diving (Spanier & Lavalli, 2007); some are also caught as by-catch of other pot fisheries, especially those targeting spiny lobsters (Fausto Filho *et al.*, 1966; Fischer *et al.*, 1981; Fischer & Bianchi, 1984; Holthuis, 1991; Moe, 1991; Freitas & Santos, 2002). Part of the problem in fishing these less commonly taken species lies in understanding the effects of various trap configurations (shape/design, weight, presence of floats, movability in stormy weather, etc.) on the catchability of the lobsters, particularly if they regularly engage in both horizontal and vertical movements (O'Malley, 2004). Until more work is conducted on trap design specifically for slipper lobsters, it is likely that most species will continue to be caught as by-catch of other fisheries.

13.7.1 *Thenus* spp. fishery

Vijayakumaran & Radhakrishnan (2011) argued that in the western and central Pacific 75–94% of slipper lobster catches belonged to *Thenus* spp., most from the single species of *T. orientalis*. However, in view of the recent revision of this genus and the recognition of five species (see Section 13.2.2), this assumption should be re-examined. The exploitation of *Thenus* spp. in Australia and most of Southeast Asia is mainly the result of by-catch (up to 2.5% by weight) of trawl fisheries (Holthuis 1991); although a diver-based fishery for *Thenus* spp. was reported from the Red Sea in the 1960s by Ben-Tuvia (1968). In Northern Australia penaeid shrimp and scallops constitute the target species of the trawl fishing industry and more than 90% of the Australian *Thenus* catch comes from Queensland waters (Jones, 2007). The catch per unit effort (CPUE) in this fishery had been stable over the past two decades, although total catch had diminished with reductions in fishing effort. While a maximum catch of 755 t was recorded for Queensland in 1997, more recently that has declined to ~400 t.

Radhakrishnan *et al.* (2007) reported that *T. orientalis* was the only slipper lobster of commercial

significance in India and, although catch rates were low, they constituted the most important part of lobster fisheries on the northwest, southwest, and southeast coast of India. However, the 2009 FAO reported global annual fisheries production of *Thenus orientalis* in 2009 is only 34.5% of the maximum production in this century (2003) (FAOSTAT, 2011).

13.7.2 *Ibacus alticrenatus* fishery

Haddy *et al.* (2007) reported that the annual landings of this species in Queensland, NSW, Victoria, and south Australia (based on commercial catch databases in 2000 to 2004) was 5.5 t. They are fished as by-product on upper-continental slope grounds by prawn trawlers or fish trawlers targeting mixed catches. Although catch rates as high as 60 kg per hour were achieved during exploratory trawling on unfished grounds (Gorman & Graham, 1978), Haddy *et al.* (2007) reported that typical commercial catch rates were ~5–10 kg per hour with peak catch rates (12–36 kg per hour) at depths of 300–360 m. This deep water species did not exhibit a marked nocturnal behaviour and many lobsters were caught during the day (Haddy *et al.*, 2007).

13.7.3 *Ibacus brucei* fishery

This is also a deep water species and the annual landings of it in Queensland, NSW, Victoria and South Australia were 2.5 t (Haddy *et al.*, 2007). As with *I. alticrenatus*, this species did not exhibit nocturnal behaviour and, although catch rates as high as 50 kg per hour were achieved for this species during exploratory trawling on unfished grounds (Gorman & Graham 1978), reported normal catches were ~5–10 kg per hour (Haddy *et al.*, 2007).

13.7.4 *Ibacus chacei* fishery

The reported annual landings in Queensland and NSW of 159 t make this species the prime contributor (77%) of the fisheries yield of *Ibacus* in Australia (Haddy *et al.*, 2007). This relatively

shallow water species demonstrated a marked nocturnal behaviour with night tows bringing up to ~20 times higher landings than daytime tows. Haddy *et al.*, (2007) suggested that they are largely inactive during daytime, probably burying in the seabed, and thus less vulnerable to trawls.

13.7.5 *Ibacus ciliatus* fishery

This species, like its congeners, is mostly caught by trawlers and sold on the fish markets of Japan, Korea, Taiwan, Philippines, Thailand, and Vietnam (Holthuis, 1991). A considerable reduction in the global annual fisheries production of this species was indicated in the 2009 FAO report of 599 t which is only 36.6% of the maximum annual production in this century (2003) (FAOSTAT, 10 August 2011).

13.7.6 *Ibacus peronii* fishery

This is also a relatively shallow water species that yields the second largest annual landings (39 t or ~19%) of the fisheries yield of *Ibacus* in Australia (Haddy *et al.*, 2007). As with *I. chacei*, this species exhibits marked nocturnal behaviour, with average numbers per night-time tow being almost double that from daytime tows (Haddy *et al.*, 2007).

13.7.7 *Parribacus* spp. fisheries

Several *Parribacus* species are fished in various locations, primarily in the Pacific, but never in high numbers. These include *P. antarcticus*, *P. caledonicus*, *P. holthuiisi*, *P. japonicus*, *P. perlatus*, and *P. scarlatinus*. In Indonesia, *P. antarcticus* are caught in nets, along with targeted spiny lobsters, during the north-east monsoon period and while there is a commercial market, they represent only 11% of the catch and fetch a price that is significantly lower (one-tenth) than that for spiny lobsters (Tewfik *et al.*, 2009). Elsewhere, they are captured by hand either by diving or at some locations by walking on reefs at low tides and pulling them out of dens (e.g. *P. caledonicus*) (Coutures & Chauvet, 2003). In these circumstances, the CPUE of *Parribacus* sp.

is similar to that of spiny lobster species and often these lobsters are similarly priced.

13.7.8 *Scyllarides aequinoctialis* fishery

Although the meat of this species was not considered of high quality (see Section 13.7), the FAO reported an increase in the global annual production of this species from 0 for the years 2000 to 2008 to 1 t in 2009 (FAOSTAT, 2011). It is considered among the five species of lobster that are both commercially and recreationally harvested in US waters (together with *H. americanus*, *Panulirus interruptus*, *P. argus* and *P. marginatus*) (Anonymous, 2008). *S. aequinoctialis* and *S. nodifer* landings are typically reported together, since these species co-occur throughout their range (Sharp *et al.*, 2007). The majority of landings occur along the Florida coast, although Alabama has routinely reported landings during 1999–2009; most landings in the Gulf of Mexico are in federal waters rather than state waters, whereas in the Atlantic, most landings are in the state waters (Anonymous, 2011). Landings increased significantly in federal Gulf waters from 1999 to 2004 to approximately 14,000 lbs (~7 t) and then have steadily declined to around 6000lbs (~3 t) by 2008. Currently only Florida state provisions prohibit the landing and possession of ovigerous females or females that have had their pleopods clipped (implying removal of egg masses), as the federal fisheries management plan for spiny lobsters has been amended to remove slipper lobsters from its oversight (Anonymous, 2011). This species is also fished in Central and South America, but perhaps mainly for the consumption by poor people as suggested by Holthuis (1991).

13.7.9 *Scyllarides astori* fishery

Although Holthuis (1991) reported that there was no traditional fishery in the Galápagos targeting *S. astori*, it is currently exploited at a local scale, and caught incidentally in the spiny lobster fishery for personal consumption and sale on the local market. Thus it only constitutes a small portion of the total lobster catch (Sonnenholzner *et al.*, 2009, Hearn *et al.*, 2007). Recorded catch increased from two

(1990s) to 13 t (2003) (Murillo *et al.*, 2003; Sonnenholzner *et al.*, 2009) and then declined slightly to 12.8 t (Molina *et al.*, 2004) live weight. Also the CPUE, expressed in terms of live weight removed per diver day, was 19 kg/diver day in 2002, but declined to 10.7 kg/diver day in 2003 (Hearn *et al.*, 2007). Since the creation of the Galápagos Marine Reserve in 1998, fishing activity in Galápagos has been limited to the local fishing sector, which is organized into four fishing cooperatives – one each on the islands of Santa Cruz and Isabela, and two on the island of San Cristobal (Hearn *et al.*, 2007). Fishing activity is restricted by law to the local artisanal fleet, which is made up of approximately 1000 fishermen operating from small fiberglass and wooden vessels with outboard engines. Lobsters are caught by hand, usually at night, by divers. Hearn *et al.* (2007) reported that there was no closed season or minimum landing size for *S. astori*, but there was a ban on the capture and landing of ovigerous females. They added that this species was defined as a product for local consumption and its export was limited to 10 lbs (~4.5 kg) of lobster tail or 12 individuals per person each time that person left the islands. Approximately 3 t of tails (corresponding to 8.4 t live weight) are exported annually to continental Ecuador.

13.7.10 *Scyllarides deceptor* fishery

Scyllarides deceptor is captured off the Southern Brazilian coast by otter trawlers fishing for shrimp within a limited area that is 40–70 m deep (Perez *et al.*, 2001, 2003). Oliveira *et al.* (2008) reported that the catches of this lobster were profitable and had increasingly attracted trawlers that landed 296 t in Santa Catarina state between 2000 and 2009, peaking at 70.8 and 72.1 t in 2001 and 2002, respectively. Since then, landings have decreased, dropping to 10.9 t in 2003; annual production has not exceeded 25 t since 2002, and 18.5 t is the last annual production published (2009) (UNIVALI/CTTMARMar, 2010). This is partial data since this species is distributed and fished in other coastal areas in southern Brazil and Argentina, as well as captured along rocky coastlines by snorkelers to supply local restaurant needs (Oliveira *et al.*, 2008). Recently, Duarte *et al.* (2010) reported a significant

decrease in the relative abundance of lobsters (both *S. deceptor* and *S. brasiliensis*) in the Santos region while monitoring 856 landings of shrimp trawlers and 28 landings of the octopus fleet. As a result, they recommended protecting the area of the ‘Farol do Boi’ (60–135 m deep) as an exclusion zone for trawl fleets, especially since this area is characterized by a bottom topography that supplied natural shelters providing protection for lobsters against diurnal predators (see Section 13.5.2).

13.7.11 *Scyllarides latus* fishery

Scyllarides latus has been exploited throughout its range in both the Mediterranean and Atlantic for some time (Spanier & Lavalli, 1998), with negative repercussions for the size structure of the population and the population sizes (Maigret, 1978; Martins, 1985a; Lewinsohn & Holthuis, 1986; Spanier, 1991; Bianchini *et al.*, 1996). Atlantic populations have suffered the greatest decline in both population numbers and size structure – at one time lobsters captured typically weighed 1–3 kg (Saldanha, 1979; Bianchini *et al.*, 1996); now they range in weight from 200 g to 1.5 kg (Bianchini *et al.*, 1996). Both pots baited with bivalves (Anonymous, 1983), and diving (with hand collection or spearing) are used as capture methods (Spanier & Lavalli, 1998). Although the FAO reported a drop in the global annual production of this species from 2 t in 2000 to 1 t thereafter until 2009 (FAOSTAT, 10 August 2011), the estimation of the annual yield off the Israeli coasts alone is 1.5 t (Oren Sonin, Israel Department of Fisheries, personal communication) and one has to add to this the (as yet unknown) yield of the fisheries of this species off Turkey and some north African countries.

13.7.12 *Scyllarides nodifer* fishery

The fishery for *S. nodifer* began in the 1980s and is basically a trawl fishery in the Gulf of Mexico in ‘hang-free’ corridors where trawls are less likely to be caught on rocks and damaged (Hardwick, 1987). Most of the fishers involved in this fishery are shrimpers (Sharp *et al.*, 2007). In the 1980s approximately 500 lobsters could be taken each night during spring and summer months, which

corresponded to this species' spawning season (Moe, 1991). These hang-free corridors support repetitive trawling, leading Hardwick (1987) to estimate the population of these lobsters as 6.14 million individuals. Additional fisheries for this species have opened in the Florida Keys, where they are conducted by divers for the aquarium trade (Bill Sharp, personal communication). *Scyllarides nodifer* is also taken as by-catch in *P. argus* pots in the Florida Keys, but not in great numbers. Because *S. aequinoctialis* is sympatric with *S. nodifer*, it is often taken as by-catch of the ridge slipper trawl lobster fishery, but is not nearly as numerous (Moe, 1991). Landings of these two species are typically reported together as a result (Sharp *et al.*, 2007). Most landings occur in the federal waters of the Gulf of Mexico, along the Florida coast. However, in the Atlantic where landed, most are caught in state waters (Anonymous, 2011). Currently federal and Florida state provisions prohibit the landing and possession of ovigerous females or females that have had their pleopods clipped (implying removal of egg masses) (Anonymous, 2011). Despite these protections, significant decreases in landings of slipper lobsters have occurred in both Gulf of Mexico and Atlantic waters from highs in 1999–2004 of approximately 14,000 lbs (~7 t) to a low in 2008 of 6000 lbs (~3 t). While this decrease in landings would suggest the need for more stringent management for slipper lobsters, the US Gulf of Mexico Fisheries Management Plan for spiny lobsters removed slipper lobsters (which would remove the prohibition of landing/possessing ovigerous females or clipped and stripped females) and urged other state agencies to take over management protection (Anonymous, 2011).

13.7.13 *Scyllarides obtusus* fishery

Scyllarides obtusus has been misidentified and confused with *S. latus*, *S. elisabethae*, and *S. herklotsii* (Holthuis, 1993), but it is a species endemic to St Helena where it has sustained a fishery for over 400 years. The fishery is mostly active between November and March and is accomplished with traps baited formerly with albacore (*Thunnus alalunga*) and currently with fish (typically tuna, *Thunnus* spp., or skipjack, *Katsuwonus pelamis*) set at about

27 m depth (Edwards, 1990). Catches average about 1.3–2.2 kg per pot, with an average live weight of 1.15 kg (Edwards, 1990).

13.7.14 *Scyllarides squammosus* fishery

Currently there is an effort underway to develop a fishery in Queensland, Australia targeting both *S. squammosus* and *S. haanii*. A trial fishery comprising only a few licensed boats has been operating since 1998, has landed less than 5 t annually and has been collecting fishery-dependent data which are not currently available to the public due to agreements between the government and the fishing industry (Sumpton *et al.*, 2004). Whether this fishery develops more fully or, if developed, remains sustainable, is not predictable as little biological data are available for these species. For example, in Hawaii, the lobster fishery for *Panulirus marginatus* also captured *S. squammosus* in equal numbers (Polovina *et al.*, 1991). As a result, minimum harvestable sizes were established for *S. squammosus* (based on spiny lobster parameters) and several studies were conducted on the shape of trap vents to reduce the capture of sublegal adults (Everson *et al.*, 1992; Parrish & Kazama, 1992). Nevertheless, the fishery for *S. squammosus* in Hawaii was closed in 2000 because it was not sustainable (DeMartini *et al.*, 2005).

13.7.15 Fishery concerns

Unfortunately, and because of the limited numbers of slipper lobsters taken around the world compared with spiny lobsters, very few regulations exist for exploited slipper lobster populations. Although the FAO statistics (FAOSTAT, 2011) are not complete and probably lack some information from small, remote, and artisanal fisheries, as well as fisheries by divers, the trend of reduced annual production of several taxa of Scyllaridae (see Section 13.7) is alarming. Jones (2007) reported that the fishery for *Thenus* in Australia was managed and regulations included a total ban on the taking of berried females and a minimum size of 75 mm CL. For *Ibacus* spp. in Australia, Haddy *et al.* (2007) reported that fishery management regulations banned the retention of egg-bearing females

of all species. Minimum legal sizes of 100 mm carapace width (CW, equivalent to approximately 50–55 mm CL) existed for *I. peronii* and *I. chacei* in NSW, but there were no minimum size regulations for the other species. A minimum legal size of 90 mm CW existed for *I. peronii* in Victoria, and a minimum CW of 100 mm CW existed for all species of *Ibacus* in Queensland. By-catch reduction devices in trawls were also mandatory in the NSW and Queensland prawn fisheries but they released few, if any, small *Ibacus* specimens (Haddy *et al.*, 2007).

Where regulations exist for *Scyllarides* spp., they protect berried females, or females that have had their eggs stripped or the pleopods clipped to remove egg masses (e.g. Florida for *S. nodifer* and *S. aequinoctialis*) and may impose minimum legal sizes (e.g. Hawaii for *S. squammosus*; Galápagos Islands for *S. astori*; Queensland, Australia for *S. squammosus* and *S. haanii*). However, imposition of these minimum legal sizes is often based on no data, or as in the Hawaiian fishery for *S. squammosus*, is based on spiny lobster size parameters rather than slipper lobster size parameters (DeMartini & Kleiber, 1998, DiNardo & Moffitt, 2007). Little work has been done to determine size at sexual maturity, taking into account the difference between physiological maturity (where a lobster might be capable of reproduction, but does not reproduce) and functional maturity (where the lobster is reproductively active) (DeMartini *et al.*, 2005). Because unberried but mature slipper lobster females may be indistinguishable from immature females on the basis of gross morphological features such as those used for assessing spiny lobster maturity (e.g. changes in the number of pleopod setal number, relative length of abdominal and thoracic segments, or proportional lengths of pereiopod segments at the pubertal moult), a tool needs to be developed to assess maturity in the field. Thus far, only in *S. squammosus* has such a tool been developed (DeMartini *et al.*, 2005) – a relative pleopod (exopod) length to tail (abdomen) width relation that is verified as highly accurate with histological examination of ovary condition. Without knowledge of the population's size structure and the size at maturity, any population targeted for a fishery is at risk of over-exploitation. Such overex-

ploitation has occurred with *S. squammosus* in Hawaii and with *S. latus*, such that fishing bans are now in effect and/or marine parks/reserves have been declared in specific areas. Similar overfishing could occur in species that have limited ranges and spawning grounds (e.g. *S. astori*, *S. nodifer*, *S. obtusus* and *S. squammosus*). Recognizing these problems, developing fisheries for other *Scyllarides* species are attempting to address issues of seasonal closures and minimum landing sizes before problems arise (e.g. *S. astori* fishery, Hearn *et al.*, 2007; *S. squammosus* and *S. haanii* fisheries in Queensland, Sumpton *et al.*, 2004).

For species where catches are so low that no real commercial fishery exists, but artisanal fisheries operate, very little information is known about sexual maturity, sex ratios, population numbers, size at maturity and basic life history patterns. This lack of knowledge puts these species at risk of overexploitation. Hence, more work needs to be directed towards understanding slipper lobster biology.

13.8 Aquaculture and restocking

Few scyllarid species have been cultured from larvae to nisto (Sekiguchi *et al.*, 2007). Vijayakumaran & Radhakrishnan (2011) argued that *Thenus* spp. and *Ibacus* spp. might be fast emerging candidates of aquaculture interests since adults females were relatively large and produced larger eggs that completed development in about a month (*Thenus*) or 2–4 months (*Ibacus*). They suggested that these shorter larval life histories and the hardy nature of the larvae had aided in the development of large-scale aquaculture of *Thenus* in recent years, especially in Australia (Mikami & Kuballa, 2007) with mass production and high survival of larvae and post-larvae. The slow growth rate of *Ibacus* spp., along with low survival rates in rearing experiments of larvae, have hindered the development of large-scale aquaculture in this genus (Vijayakumaran & Radhakrishnan, 2011). No *Scyllarides* species is among those cultured. Although specimens of *Scyllarides* spp. readily reproduce and carry eggs in the laboratory (e.g. Martins, 1985a,b; Almog-Shtayer, 1988; Spanier *et al.*, 1988; Bianchini *et al.*,

1998), the long duration of the larval stages (up to 8 months) along with a lack of understanding of dietary requirements, proper thermal, salinity and light–dark regimes, and proper hydrodynamic design of rearing tanks has curtailed aquaculture attempts (Sekiguchi *et al.*, 2007).

Lack of ability to culture most slipper lobsters, along with large gaps in our knowledge of their full life cycle, means that as we exploit these species more and more, we have fewer options to cope with overfishing when it occurs in specific populations. Again, more effort needs to be expended to understand the full life history of slipper lobsters, especially exploited species, to ensure that we do not overexploit local populations.

13.9 Summary

Although the body of knowledge on commercial slipper lobsters has increased considerably in the recent few decades (e.g. Lavalli & Spanier, 2007a), a considerable gap still exists for these species compared with taxa within the clawed and spiny lobster genera. Most information focuses on very

few species but even so that knowledge is incomplete and tends to focus on only one life history stage (e.g. adults or juveniles, but not larvae, or larvae and adults, but not juveniles). Although many of the slipper lobster species are increasing in commercial importance, fisheries statistics are incomplete or altogether absent. Many of the species have been exploited for decades and may even be overexploited. Increasing fishing pressure occasionally accelerates research on species, as is the case of *S. astori* in the Galápagos Islands, but this is not always the case, and as such the existence of populations in many habitats is endangered by our ignorance. There is an urgent need for more research on all aspects of the biology of these genera, particularly that concerning moult and growth, reproduction and incidence of disease. Better knowledge concerning distribution of larval stages, settlement areas of nistos, and ecology of juveniles would be helpful for gaining an understanding of factors influencing recruitment into adult populations. The results of such future studies may enable the development of proper management tools for sustainable utilization of this potential marine resource.

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Chapter 14

Conclusions

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I never fail to be astounded by the number of papers dealing with lobsters in the scientific literature. In Chapter 11 the authors mention 40 articles being published between 2005 and 2011, but this is only part of the story. The inclusion of the new chapters in this edition, Lobsters in Ecosystems (Chapter 1); Genetics of Wild and Captive Populations (Chapter 2); Translocating Lobsters to Improve Yield and Value of the Fisheries (Chapter 3); Climate Change (Chapter 4); Systems to Maximize Economic Benefits in Lobster Fisheries (Chapter 5); Ecolabelling of Lobsters (Chapter 6); Essential Habits and Microhabitats for Tropical Spiny Lobsters (Chapter 7), indicates the vast literature that needs to be reviewed to keep current with the situation.

I expect we may eventually undertake another revision of the book, which will include additional chapters on other topics relevant to lobsters. Melville Smith (2011) identified six main factors as having the potential to influence population resilience to change. These are climate change, the fishery, coastal development, introduced marine pests, infectious diseases and socio-economic influences associated with fishery management. Some of these have been dealt with, although most need to be better understood, and the others could be future chapter headings.

For the current edition, all of the authors of the chapters updating the information on the genera

(*Homarus* Chapter 8, *Jasus* Chapter 9, *Panulirus* Chapter 10, *Palinurus* Chapter 11, *Nephrops* Chapter 12 and Scyllarids Chapter 13, have all produced excellent updates of the literature.

In the 2006 edition the huge increase in the *Homarus americanus* catch since 1992 was mentioned. As the information in the current edition shows, parts of the *H. americanus* fishery are currently contributing huge catches (reaching 93,000 t in 2010) while other sections are declining (see Chapter 8). The reason(s) for both the increases (see Holland, 2011) and declines is uncertain. Parsons (2010) stated that in Canada ‘While the lobster fishery has so far defied doomsayers, it is hard to conceive how it can continue to prosper as currently structured. The question is not if, but when, the lobster bubble will burst.’ We all look forward to the outcomes.

Many spiny lobster fisheries have shown declines in catches, although some such as Indonesia, are recording rapid increases in catches (Chapter 10). In Australia the levels of puerulus settlement in the western rock lobster *Panulirus cygnus* have declined to low levels over the past few years, leading to drastic measures, including reductions of effort/boats and the introduction of total allowable catch (TACs), to maintain sustainability (see Chapter 10). There is also evidence of declining recruitment in the southern rock lobster *Jasus*

edwardsii in south-eastern Australia, as evidenced by the reduced catches, that have occurred (Chapter 9). The factors driving the decline of both species have been the focus of much debate, but point to the need for ecosystem management (see Chapter 1) to understand the processes that are occurring. Ecosystem management of fisheries is in its infancy, but under development. The costs of data collection and analysis appear to be high, but the outputs could be the only possibility for understanding the large-scale changes that are occurring and affecting the fisheries. The signing into law by the US President of the large marine approach to fisheries management under the National Ocean Policy (The White House Council on Environmental Quality, 2010) will give the concept of large marine ecosystem fisheries management, legitimacy and the support that it needs.

Sustainability of the lobster fisheries remains the main objective, but some fisheries are turning from MSY to MEY as the target to achieving not only control of the level of the stocks but economic profitability as well (see Chapters 3 and 10).

Chan (2011) has provided an update of the world's marine lobsters, and Lavalli & Spanier (2010) produced the Infraorder Palinura and Wahle *et al.* (2012) the Infraorder Astacidea. In addition, Yang *et al.* (2012) have made a molecular analysis of phylogenetic relationships in the family Scyllaridae, which contains 20 genera and 89 species. These are all excellent contributions to assist the whole field of research. The inclusion of genetic

studies (Chapter 2) is because of the use of molecular techniques for a range of purposes. The long-recognized problem of the sources of *P. argus* recruitment in the Caribbean countries is being studied again using the most modern genetic methods and the results of a preliminary study are being prepared for publication (Kim Ley-Cooper, pers. comm, Curtin University, Perth, Australia). It is hoped that the results will be used as a stimulus for a more detailed study.

Aquaculture is still the future. The situation for spiny lobsters up to 2012 is summarized in the chapters in this book on the specific genera, and more comprehensively by Phillips & Matsuda (2011). Commercial initiatives on spiny and slipper lobsters have been attempted but continue to fail, often because of a lack of funding. Millions of dollars are being spent pursuing commercial aquaculture of spiny lobsters; however, as stated in the Conclusions of the 2006 edition, little of the research on aquaculture of spiny lobsters is being published as it is considered 'commercial in confidence'. It is so confidential that scientists working on aquaculture will not even admit that this is the area of their research!

Marine protected areas (MPAs) still remain very popular and are often declared without consultation or adequate scientific planning. The importance of habitats for lobsters is stressed in Chapter 7 and lessons identified should be considered by those planning MPAs or the controversial issue of habitat enhancement.

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Plate 1.1 General overview of some of the main activities in the ocean of lobster fisheries which need to be considered in ecosystem management. (Created by Rudy Nugroho, reproduced with permission).

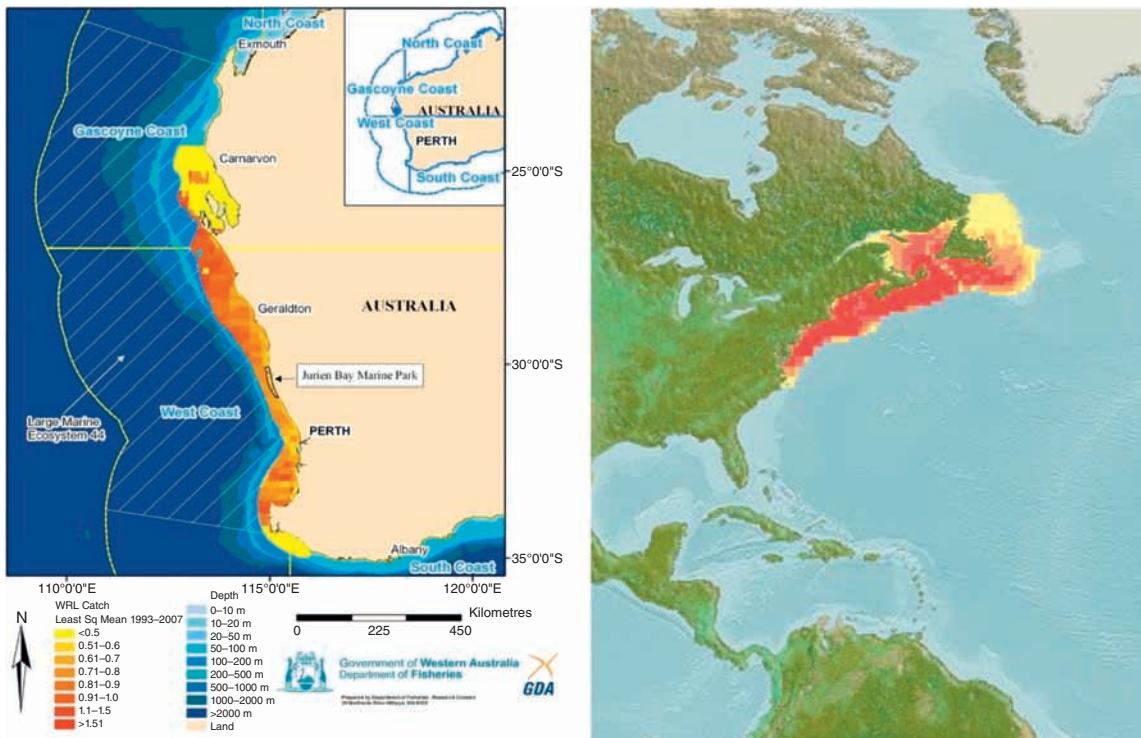


Plate 1.2 Map of Western Australia showing the location of Large Marine Ecosystem 44. Large Marine Ecosystems of the world from <http://www.lme.noaa.gov/> 17/November 2010; and B Map of the north east coasts of Canada and the east coast of the USA showing the location of the fisheries for *Homarus americanus* in Large Marine Ecosystems 7, 8 and 9. (Computer Generated native Distribution Map of *Homarus americanus* (reviewed) www.aquamaps.org, version Aug. 2010. Web Accessed 19 March 2012.)

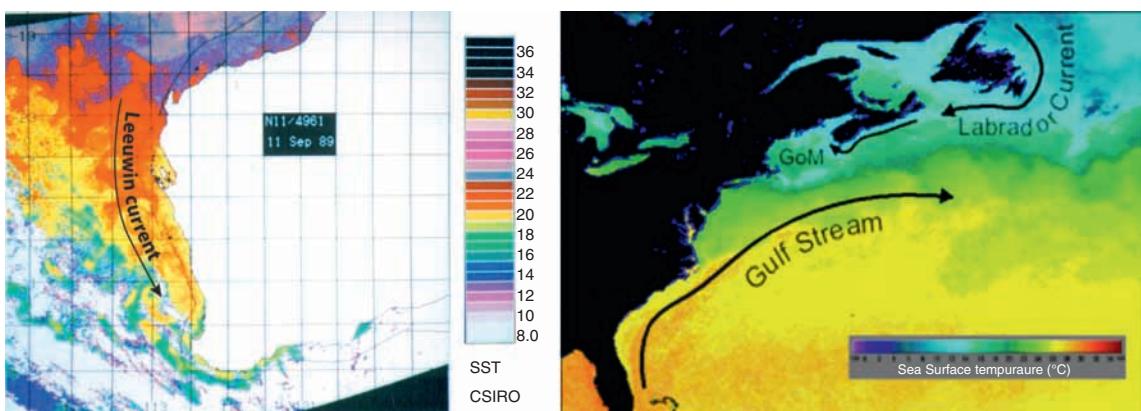


Plate 1.3 Satellite Imagery showing in (A) the oceanography off the coast of Western Australia; and (B) the east coasts of the USA and Canada. (A) Data from CSIRO, LAS server <http://www.marine.csiro.au/las/servlets/dataset>, Sea Surface Temperature 11 September 1989. (B) Data for the USA and Canada from SeaWiFS Project, NASA/Goddard Space Flight Center and ORBIMAGE – <http://oceancolor.gsfc.nasa.gov>.

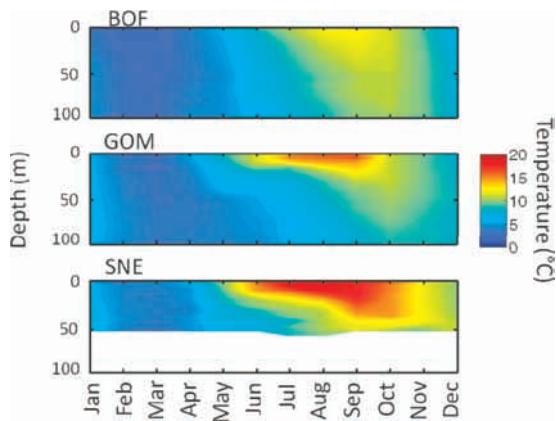


Plate 1.4 Thermal contrasts at three oceanographically contrasting locations within the range of *H. americanus*. Seasonal changes in thermal stratification for Bay of Fundy (BOF) (44.5°N to 45.5°N and 64.75°W to 67.2°W), Gulf of Maine (GOM) (43.33°N to 44.07°N and 69.22°W to 70.62°W), and southern New England (SNE) (40.87°N to 41.6°N and 70.43°W to 73.55°W). Data represent 10 year mean from 1995–2004. No temperature data were available below 60 m in SNE because of the shallower shelf area. (Source: Canada Department of Fisheries and Oceans (DFO), Hydrographic Climate Database <http://www2.mar.dfo-mpo.gc.ca/science/ocean/sci/sci-e.html> taken at 1m ($\pm 0.5\text{m}$) intervals) (From Bergeron 2011).

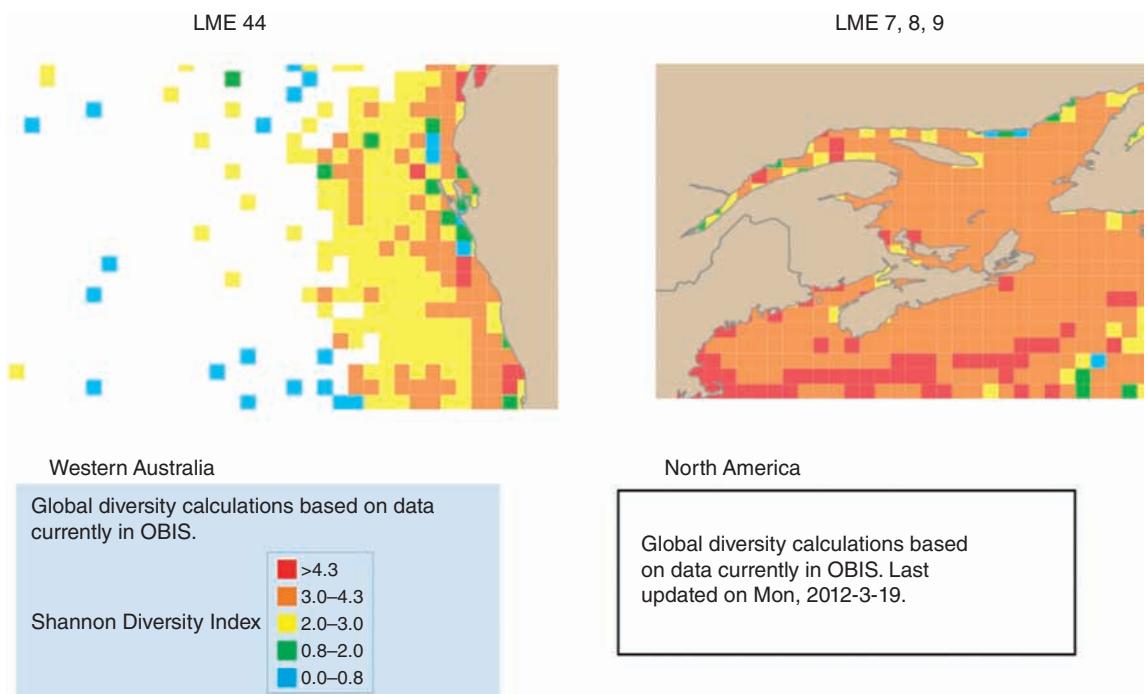


Plate 1.5 Diagrams showing (A) Biodiversity in Large Marine Ecosystem 44; and (B) Biodiversity in Large Marine Ecosystems 7, 8 and 9. Data from Global diversity calculations based on data currently in OBIS. Last updated 19 March 2012.

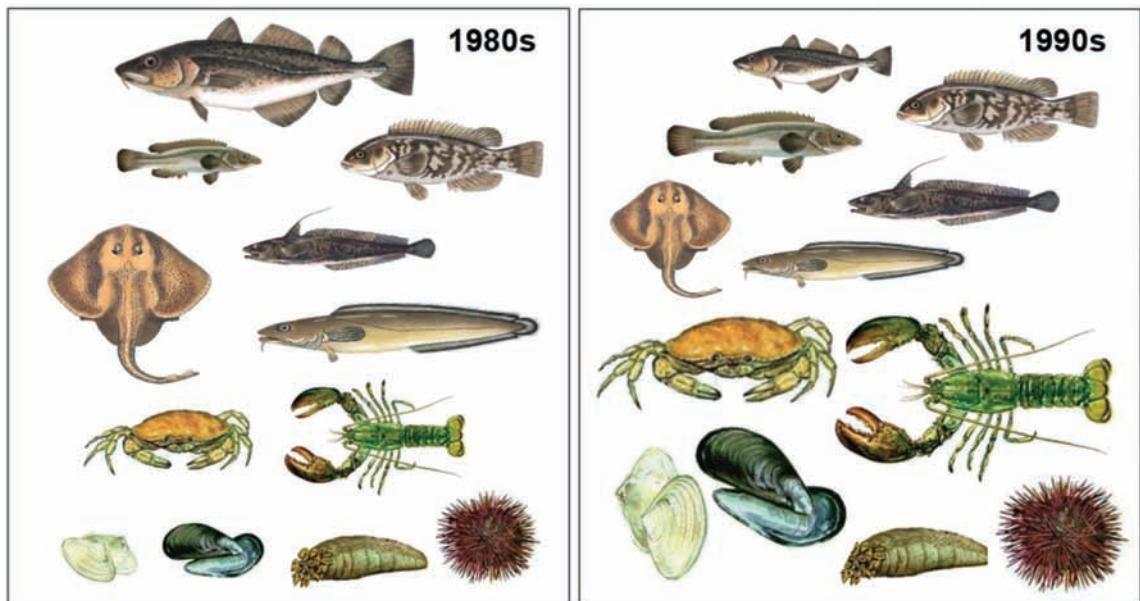


Plate 1.6 Changes in species composition and volume in the Gulf of Maine between the 1980s and 1990s. Constructed from data in Zhang & Chen (2007).



Plate 3.1 Southern rock lobster, *Jasus edwardsii* that was ongrown from puerulus and about to be released as part of a research scale enhancement operation. The acoustic tag attached to the carapace enabled movement and foraging to be monitored after release. Photo Credit – Caleb Gardner, has not been published before.

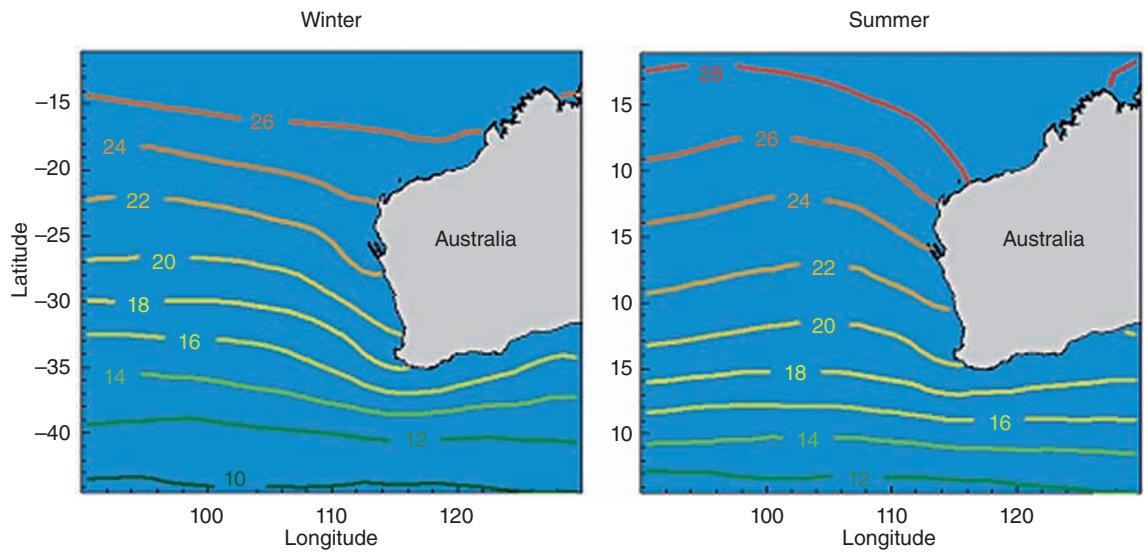


Plate 4.1 Mean Reynolds sea surface temperature (Reynolds & Smith, 1994) contours along the lower west coast of Australia in winter (June–August) and summer (December–February).

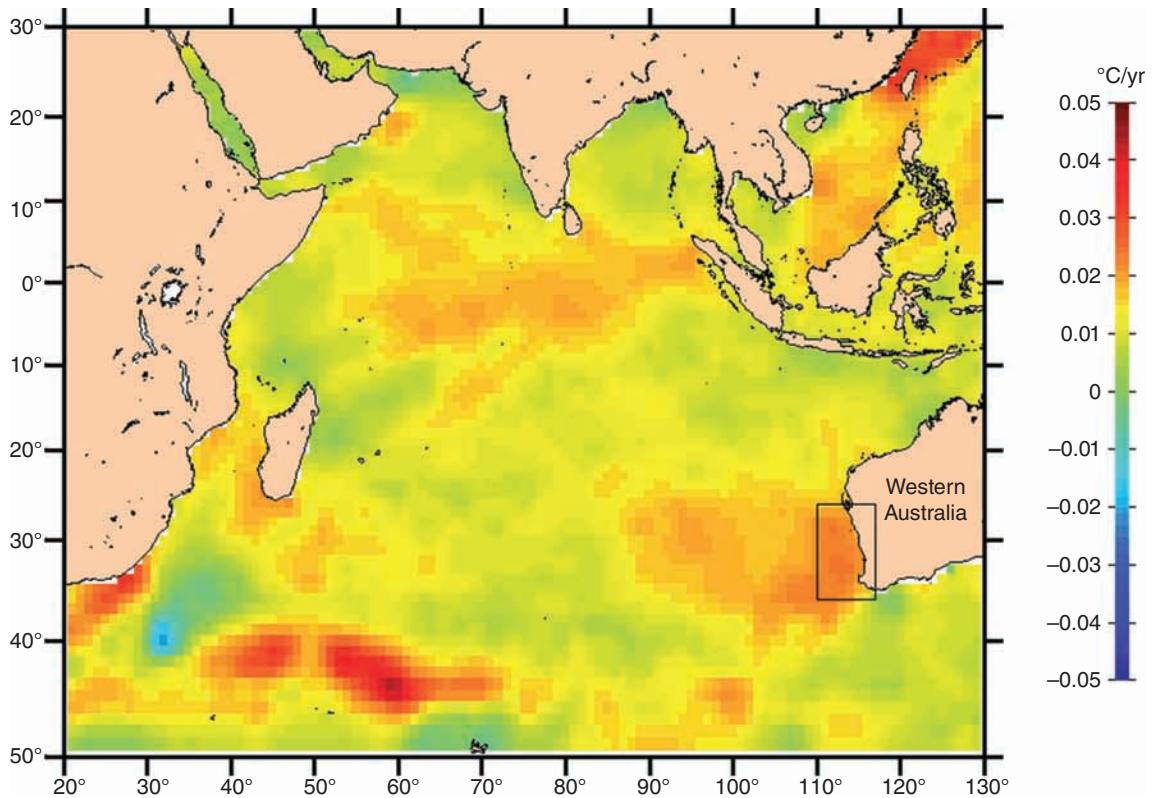


Plate 4.2 Rate of change in sea surface temperature over the Indian Ocean. Pearce, A. & Feng, M. (2007). Reproduced with permission of CSIRO.

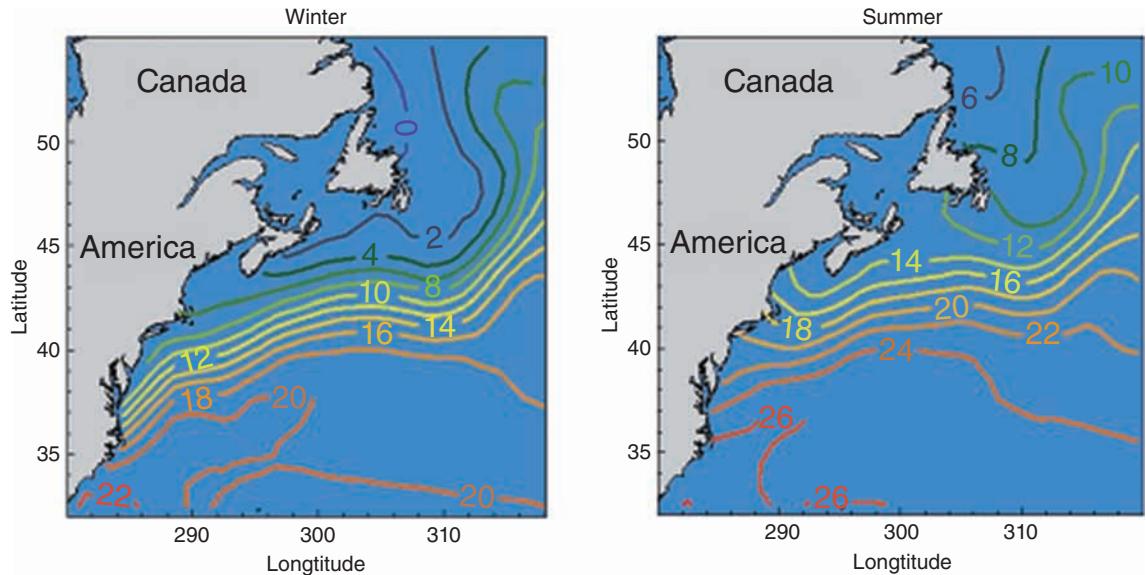


Plate 4.3 Mean Reynolds sea surface temperature (Reynolds & Smith, 1994) contours along the east coast of North America in winter (December–February) and summer (June–August).



Plate 5.1 A commercial trap configured according to regulations including being affixed with a tag required in the Florida spiny lobster fishery. The plastic tags are numbered and are issued each year in a different colour to enable regulations to be enforced (Source: Kari MacLauchlin).

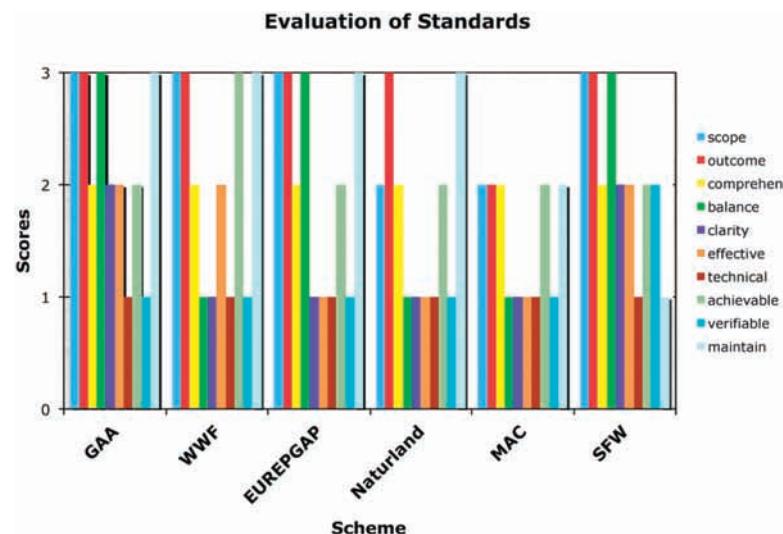


Plate 6.1 Evaluation of the standards of each of six well-known certification schemes against 10 criteria that represent the key attributes of ‘stringency’ of a well-formed aquaculture product certification scheme (from Ward *et al.*, 2011, with permission). The criteria scored are described in Table A2 in the Appendix to Chapter 6. Schemes assessed: GAA Global Aquaculture Alliance, WWF World Wildlife Fund Aquaculture Dialogues, EUREPGAP, Naturland Association for Organic Agriculture, MAC Marine Aquarium Council, SFW Seafood Watch Monterey Bay Aquarium. Ward, T.J., Phillips, B.F. & Porter, R. (2011). Reproduced with permission of World Aquaculture Magazine.

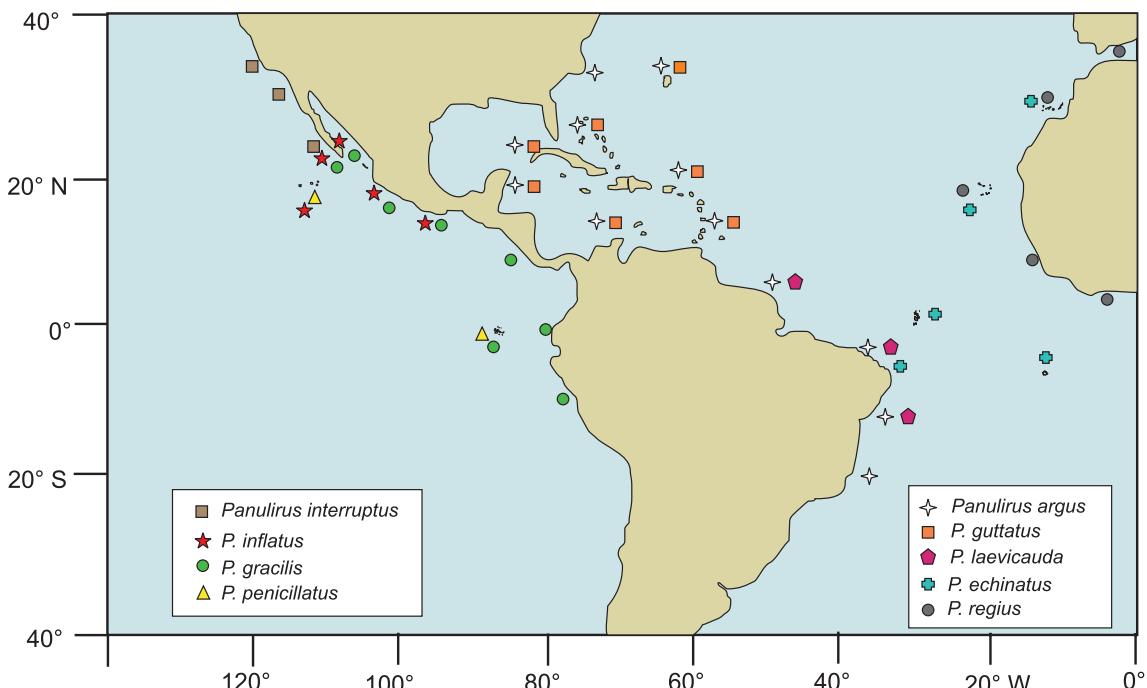


Plate 7.1 Eastern Pacific and Atlantic locations where two or more *Panulirus* species co-occur (composite data from Williams, 1986; Holthuis, 1991; Phillips & Melville-Smith, 2006).

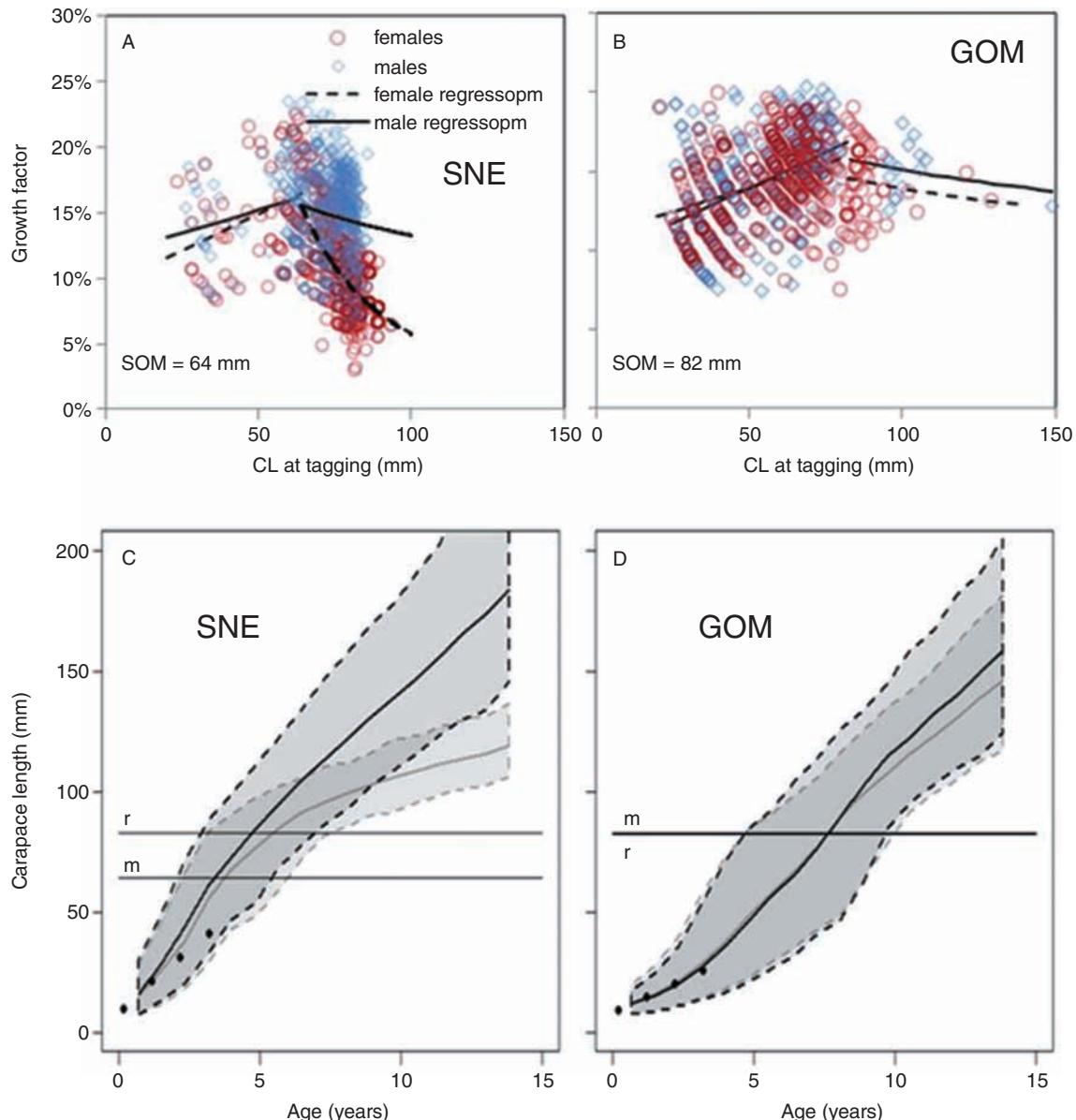


Plate 8.1 Growth of *Homarus americanus* in two thermally contrasting regions of the species range, the Gulf of Maine (GOM) and southern New England (SNE). (A,B) Relationship between growth factor (growth increment/initial size) and carapace length measured at time of tagging; males: blue points; females red. (B,C) Results of stepwise growth model simulations. Mean (solid line) and 95% confidence intervals (shaded area between dashed lines) derived from 1000 simulations shown for males (dark grey) and females (light grey). Black points on each graph represent mean-size-at-age estimates for ages 0+ to 3+ years from independent modal analysis of lobsters collected in nurseries by suction sampling. Horizontal lines labeled “m” and “r” denote female size at 10% maturity and harvestable size (82.5 mm), respectively. Bergeron, C.E. (2011) Reproduced with permission of University of Maine.

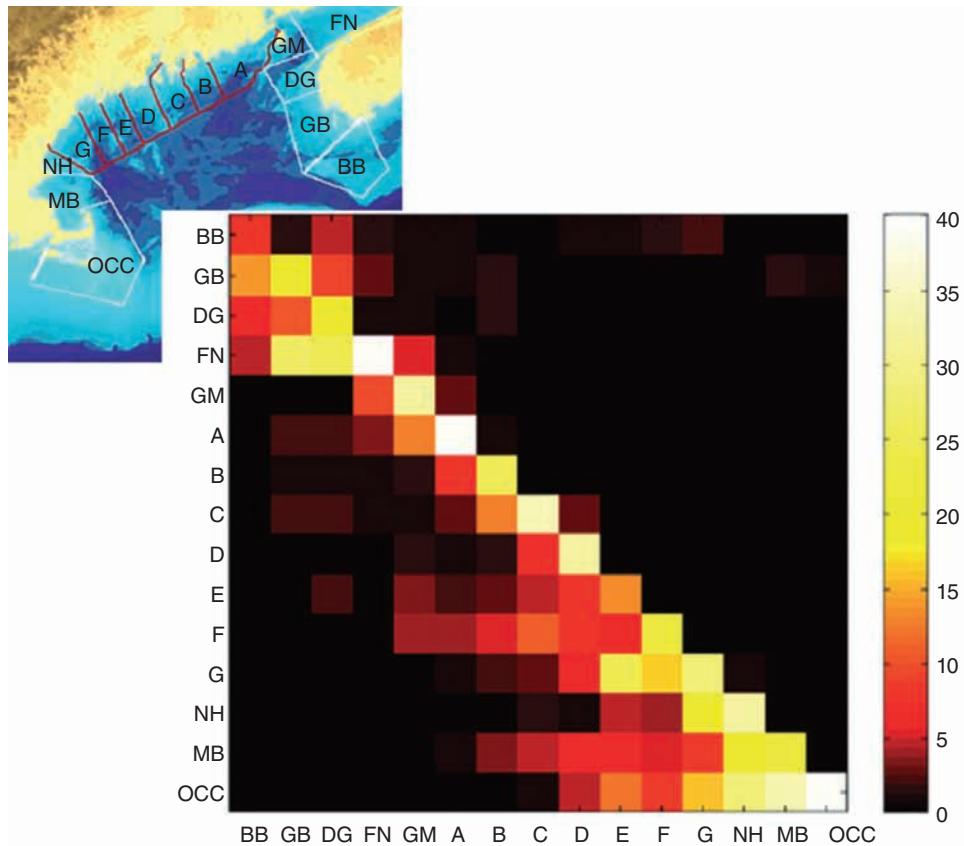


Plate 8.2 Connectivity matrix, percent of particles in each analysis cell on y-axis (sink) originating from each cell on the x axis (source), for particles released in August, 2003. Inset shows location of analysis cells. In this scenario particles contacting the landward boundary remained there, but the outcome varie slightly under different assumptions. Xue, H., et al. (2008) Reproduced with permission of Elsevier.

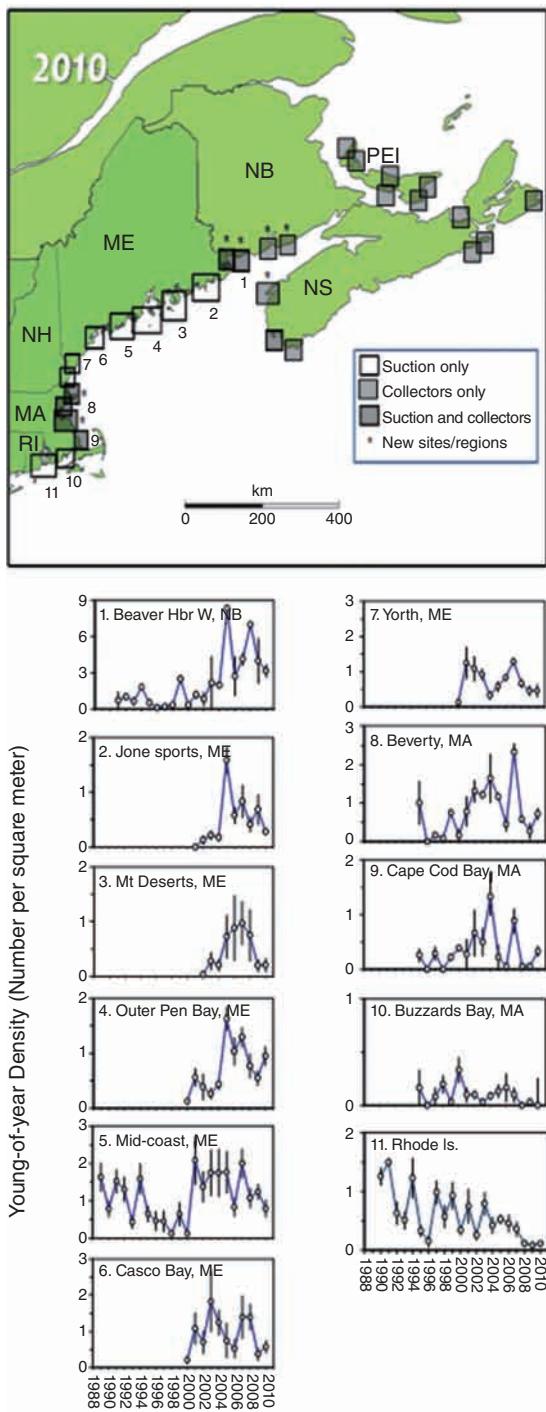


Plate 8.3 (A) Study areas (boxes) where settlement data are collected by suction sampling, passive collectors, or both. (B) Annual mean density of settlers is shown for the 11 study areas with the longest time series of suction sampling data through 2010.

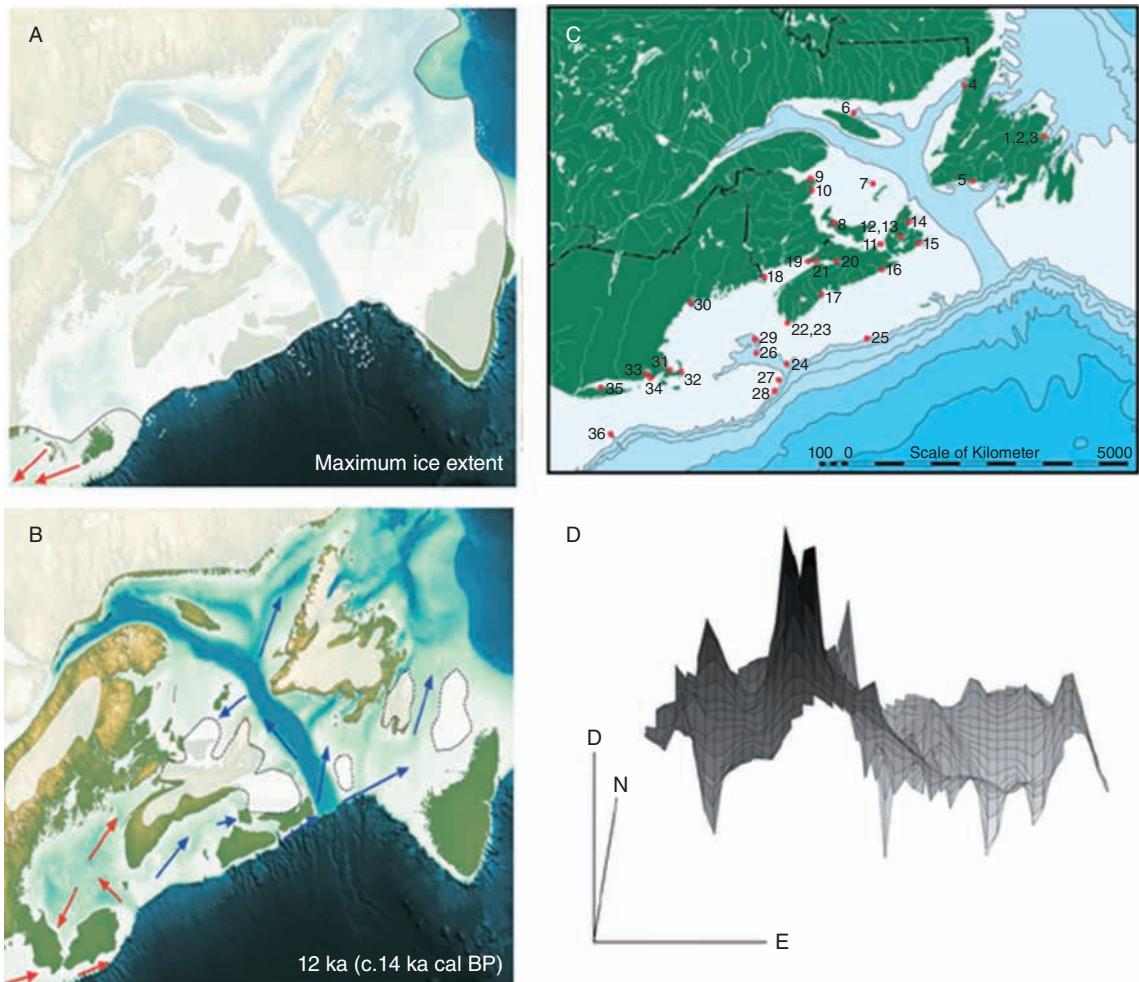


Plate 8.4 *Homarus americanus* population structure in the context of glacial history of eastern North America. Figures and captions excerpted from Kenchington *et al.* (2009). (A) Maximum ice extent, 20,000 years Before Present (BP); (B) Ice retreat and coastal plain at 12,000 years BP during the Pleistocene, with general movement of lobster indicated by arrows. Red arrows indicate original population while blue areas indicate area colonized by a subset of the original population according to the authors' hypothesis. (C) Sampling locations (red dots) where lobsters were collected for this study. (D) Landscape genetic surface interpolation plot of D , Nei's genetic distance; N, northerly; E, easterly directions. Latitude and longitude axes on a 50×50 grid. Shaw, J., Piper, D.J.W., Fader, G.B.J. *et al.* (2006) Reproduced with permission of John Wiley & Sons.

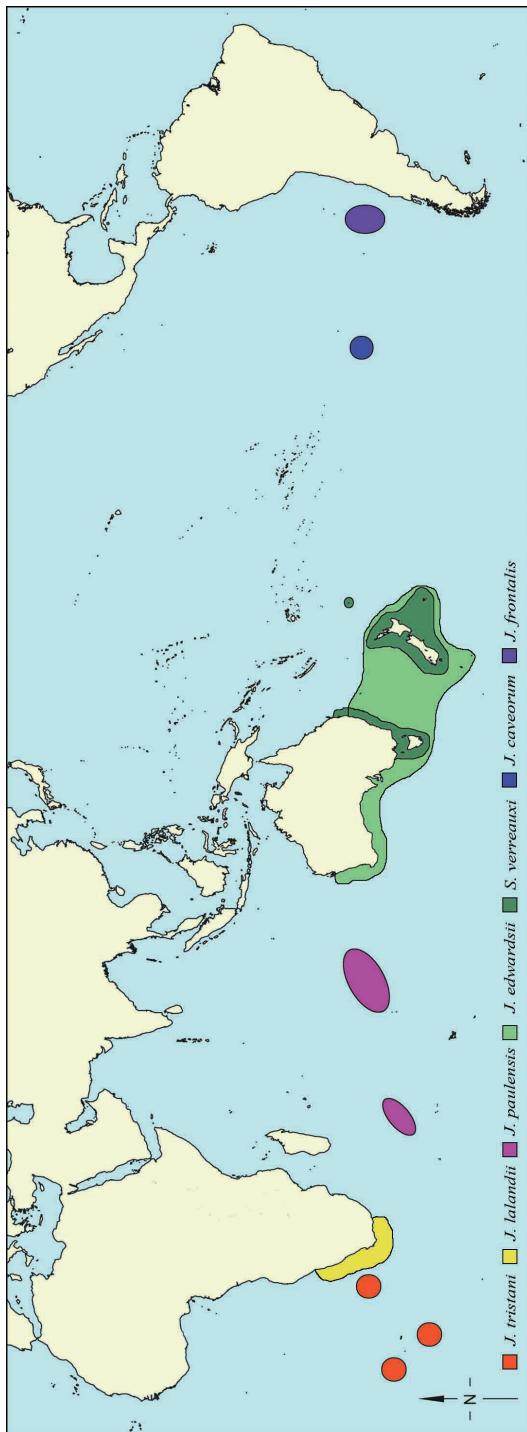


Plate 9.1 Global distribution of *Jasus* and *Sagmariasus* species. *Jasus paulensis* is known to occur south and southwest of Madagascar, but *J. lalandii* may also be present at this location. The distribution of *J. paulensis* is extended to the northeast of St. Paul and Amsterdam Islands, and this species may also be occasionally taken at Kerguelen Island (e.g. de la Rue, 1954 in Holthius, 1991). Also, the results of a recent DNA study shows that *J. tristani* and *J. paulensis* should be synonymized as *J. paulensis* (J. Groeneveld, pers. comm.).

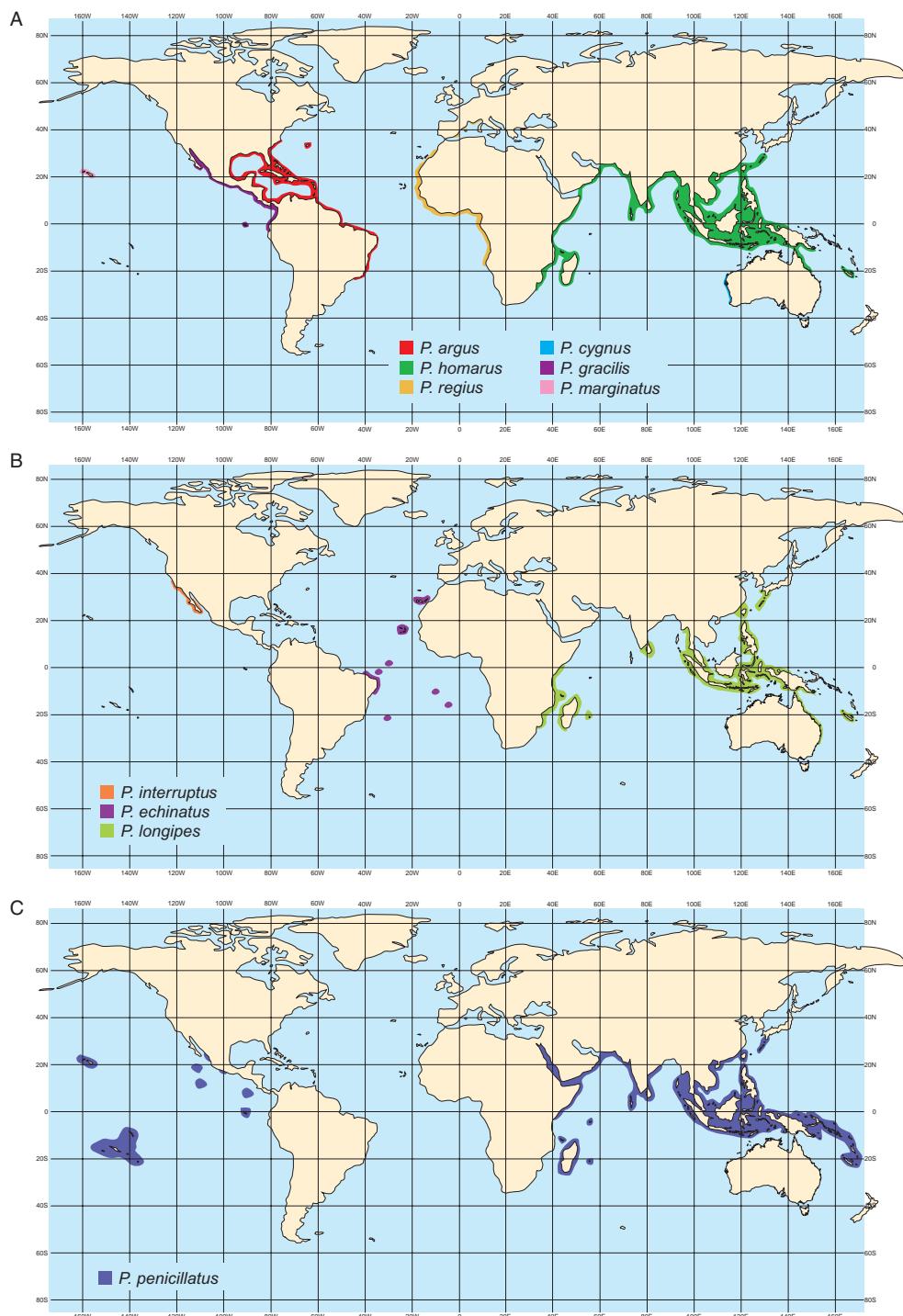


Plate 10.1 (A–F) Indicative distributions of *Panulirus* species (adapted from Holthuis, 1991).

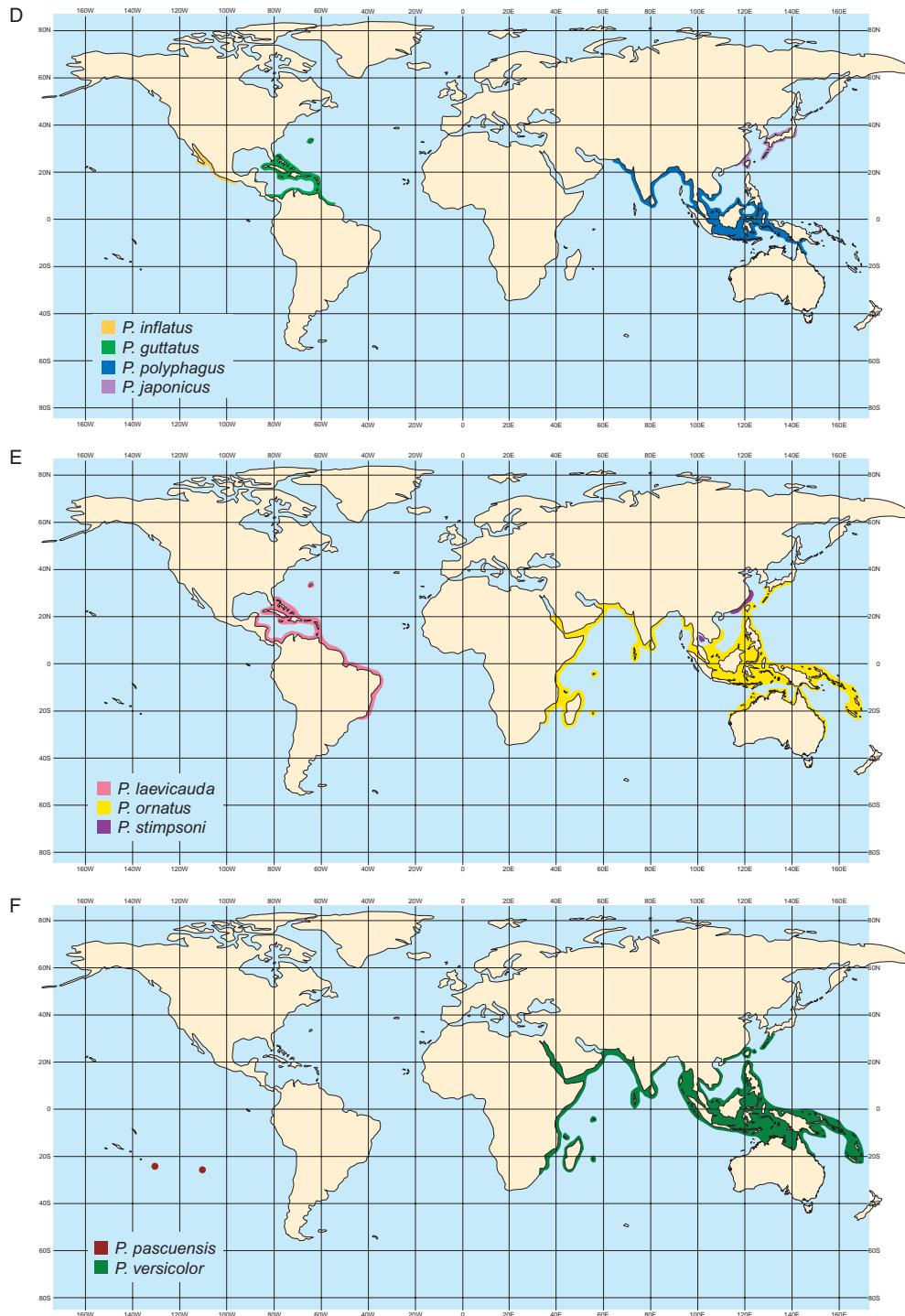


Plate 10.1 *continued*

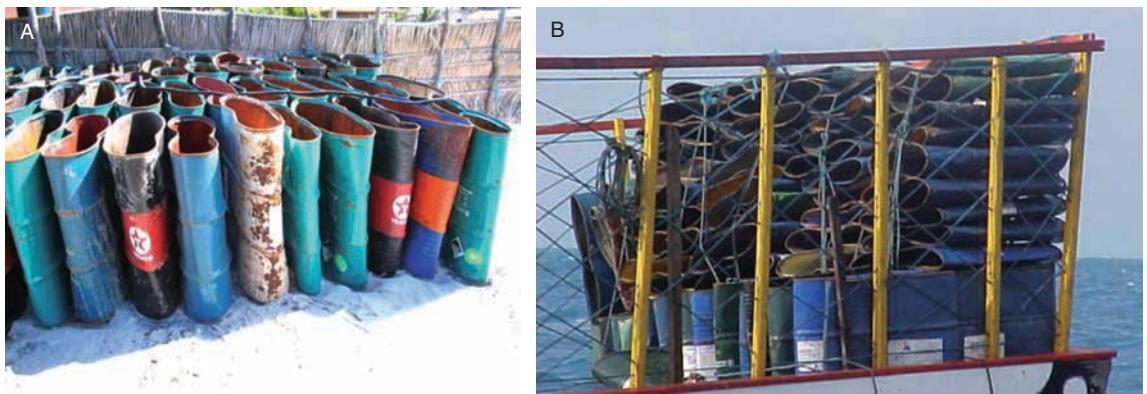


Plate 10.2 (A, B) Types of recycled steel drums used as lobster aggregating devices in Brazil. Data from René Schärer, Brazil (pers. comm.).

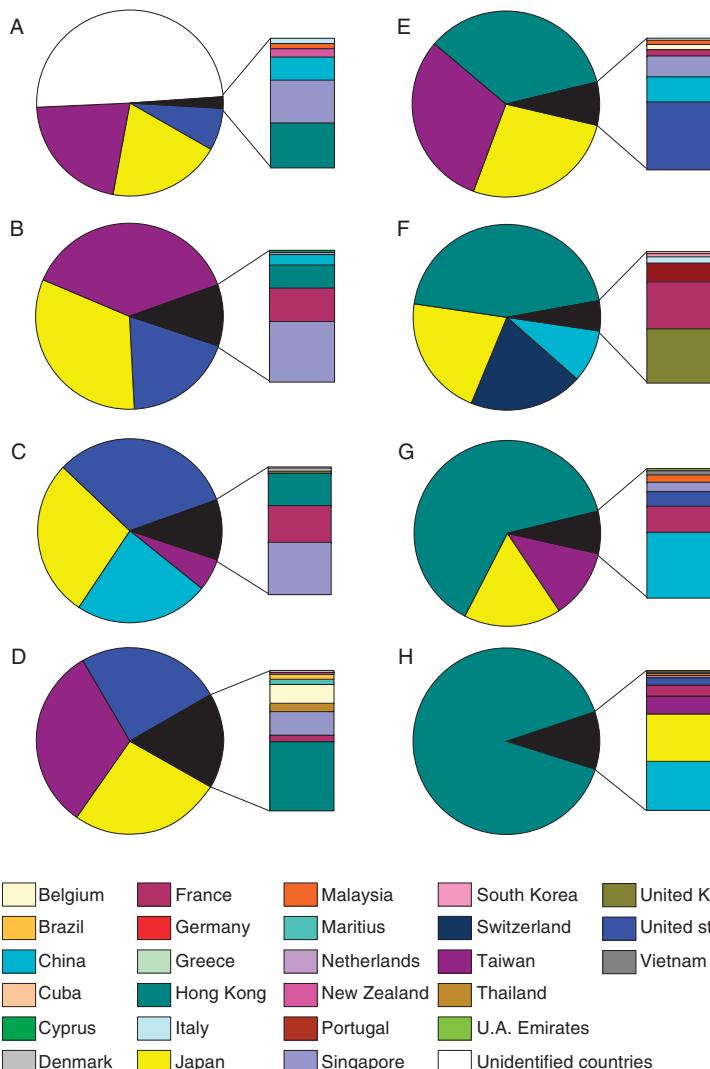


Plate 10.3 Exports of frozen lobster from Australia for (A) 1995 (B) 1999 (C) 2004 and (D) 2010, and exports of live lobster for (E) 1995 (F) 1999 (G) 2010 and (H) 2010, by percentage of volume exported to each country. 2010 data provided courtesy of Greg Hart, Western Australia.

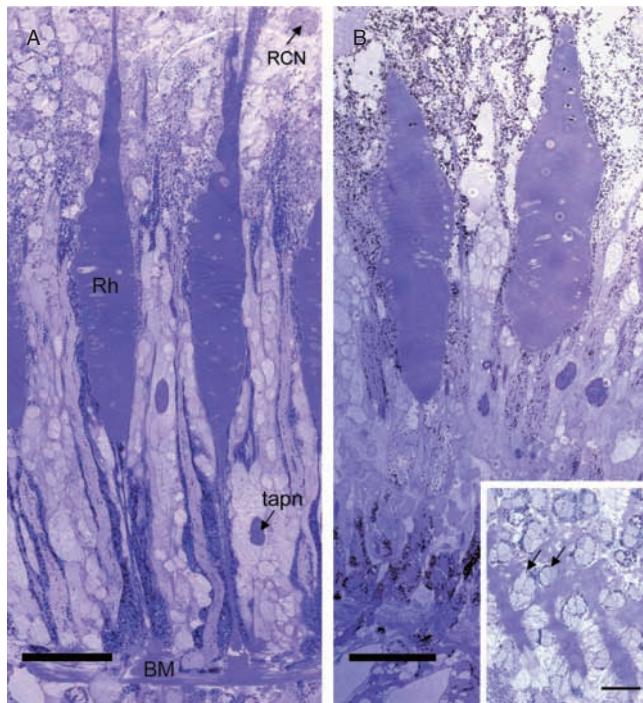


Plate 13.1 Light micrographs of longitudinally sectioned ommatidia of the eye of the Mediterranean slipper lobster, *Scyllarides latus*. (A) Dark-adapted night time retina with black screening pigments predominantly in a proximal position (thick black arrow) below the spindle-shaped rhabdoms (RH) just above the basement membrane (BM). Retinula cell nuclei (RCN) occupy distal and tapetal cell nuclei (TapCN) proximal positions. The scale is 50 µm. (B) In the light-adapted state (irrespective of time of day) the retinal screening pigment migrated away from the basement membrane into a more distal location near the tips of the rhabdoms (thick black arrow). Scale is 50 µm. Inset shows axon bundles (arrows) just below the basement membrane. Scale is 50 µm. Anatomy and ultrastructural organisation of the eye of the Mediterranean slipper lobster, *Scyllarides latus*: preliminary results. Lau, S.T.F, Spanier E. & Meyer-Rochow, V.B. (2009) © The Royal Society of New Zealand reprinted by permission of Taylor & Francis Ltd. on behalf of The Royal Society of New Zealand.