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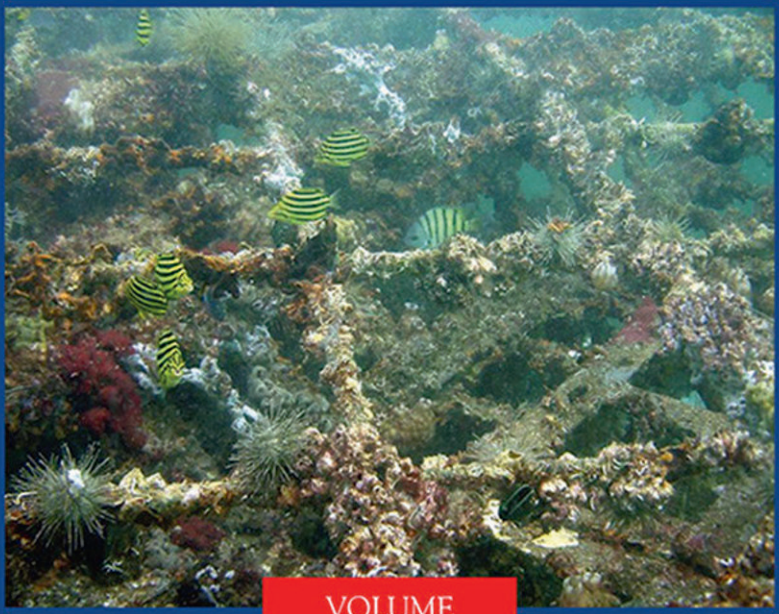

VOLUME 68

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VOLUME SIXTY EIGHT

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525 B Street, Suite 1800, San Diego, CA 92101-4495, USA

First edition 2014

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ISBN: 978-0-12-800169-1
ISSN: 0065-2881

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CHAPTER ONE

Ecology of Artificial Reefs in the Subtropics

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Abstract

The application of artificial reefs (ARs) has a long history, and there is a wealth of information related to the design and performance of ARs in coastal and ocean waters worldwide. However, relatively fewer studies in the literature are focused on the response of benthic communities within the reef areas than those on fish attraction and fish production and on the settlement and colonization of epibiota on the AR structures, especially in the subtropics where seasonal differences and environmental conditions can be large. Recent advances in the understanding of the ecology of ARs in the subtropics are highlighted, with a focus on fish attraction versus fish production, development of epibiota on AR systems and responses of *in situ* benthic communities in the reef areas. Data are also presented on studies of trophic relationships in subtropical AR systems, and further research areas using analyses of biological traits, stable isotope signatures and fatty acid profiles in investigating the ecology of ARs are proposed.

Keywords: Artificial reefs, Subtropical environment, Benthic communities, Colonization, Trophodynamics, Seabed environments

Advances in Marine Biology, Volume 68
ISSN 0065-2881
http://dx.doi.org/10.1016/B978-0-12-800169-1.00001-X
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1. INTRODUCTION

Whether they are sunken boats or purposely built materials, artificial reefs (ARs) are deployed in coastal waters to mimic certain characteristics of natural rocky habitats. These structures can also be categorized as artificial habitats, including any object deliberately placed in the marine environment to protect, enhance and manage natural resources such as fisheries (Baine, 2001; Seaman and Jensen, 2000). Indeed, ARs have been used with a long history to aggregate fish, create new fishing grounds and increase the harvest of primary production. Further applications of ARs have been extended to the promotion of biodiversity, mitigation of degraded environment, development of ecotourism and recreational activities, establishment of marine ranching and protection of benthic habitats from illegal bottom trawling (Seaman, 2007). While most of our understanding of AR projects is derived mainly from observations and studies initiated from Europe and the United States, a substantial progress in AR research has been made in many other countries and regions, particularly in the subtropics, in the recent years.

Subtropical environment lies roughly between 20° and 40° north or south latitude on the world map (Figure 1.1). The general climate in the subtropics varies to a large extent, ranging from constant arid desert conditions to distinct seasonal changes in humid summer and dry winter. In general, the mean temperature in two-thirds of the year is above 10 °C, whereas

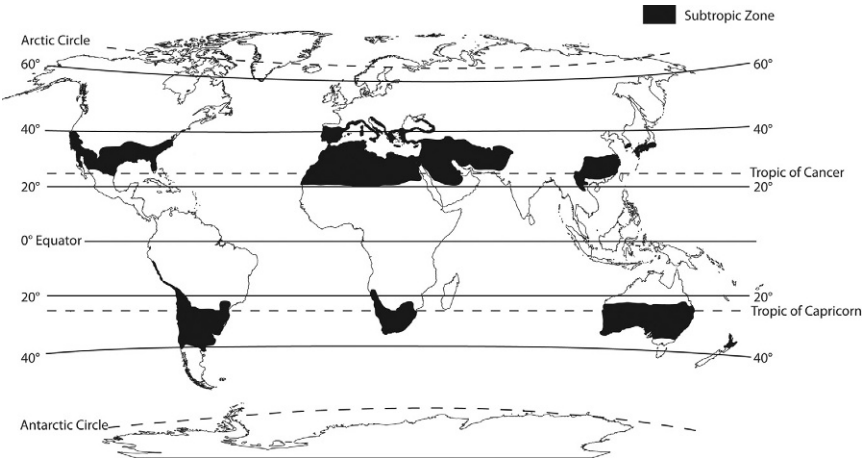

Figure 1.1 Subtropical zones of the world. *Redrawn from http://www.meteoblue.com/en/content/481.*

the lowest average temperature can fall below 5 °C. In humid subtropics, the climate is characterized by hot (up to 30 °C or above), wet summer and warm to cool (10–15 °C), dry winter. Such climatic features also extend to the sea, in which water temperature can reach 30 °C in the summer and 20 °C in the winter. Even within this seasonal range of water temperatures, natural reef communities can still be formed (Vroom and Braun, 2010). However, like other sea areas in the world, the biodiversity and habitat loss in the subtropics is already a major problem (Huettmann, 2013), and the deployment of ARs for restoration of disturbed habitat is not uncommon (Azhdari et al., 2012; Burt et al., 2009; Einbinder et al., 2006).

This chapter attempts to provide an overview of AR systems; review the advances of our understanding of the ecology of ARs in the subtropics in the past 10 years, especially on the studies of colonization and settlement of benthic communities on the ARs and around their deployment areas; present new data on the study of trophic relationships of AR systems; and suggest possible areas of further investigations in the ecology of ARs.

2. AN OVERVIEW OF AR SYSTEMS

Marine resources have been declining all over the world since the 1950s (Ainsworth et al., 2008; Garibaldi and Caddy, 2004; Lotze, 2007; Wilkinson et al., 2006). There have been many reasons cited for this. Apart from intensive fishing, the major causes for the decline are extensive loss and continual degradation of coastal habitats (Lotze et al., 2006; Reise, 2005; Suchanek, 1994; Thrush and Dayton, 2002). One recommended solution is to maintain habitat heterogeneity particularly in coastal areas (Gray, 1997). This may be achieved by the deployment of ARs. These are purpose-built structures or frames that are placed on the seabed in a way so as to simulate natural reefs (Pitcher and Seaman, 2000). The concept of using physical structures to improve marine resources may have arisen by chance discovery in the past in which fish catches taken very near to accidentally sunken vessels were appreciably higher than those taken from adjacent areas.

The earliest evidence of the purposeful use of sunken objects to improve fish catches can be traced back to the seventeenth century in Japan, where stones were sunk into the sea to enhance the yield of the macroalgae *Laminaria* (Simard, 1997). Later, a wide variety of other substrates have been used as ARs (Figure 1.2), ranging from dedicated structures such as concrete blocks to "materials of opportunity" such as tree logs, used tyres, quarry

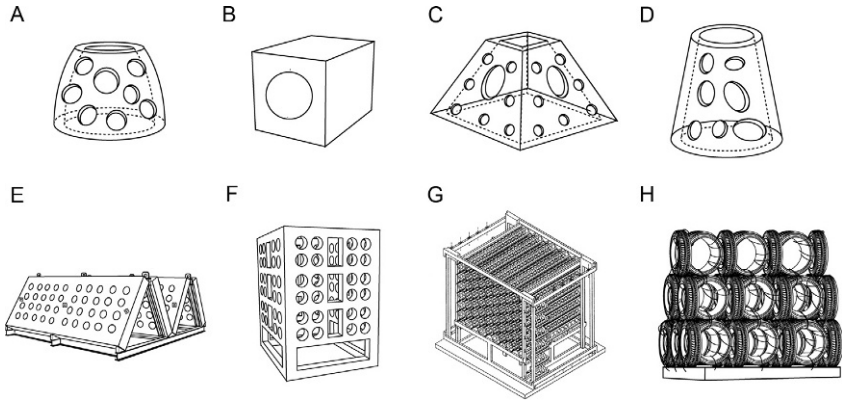

Figure 1.2 Types of artificial reef modules: (A) reef ball, (B) Lindberg block, (C) pyramid, (D) cone, (E) triangular module, (F) cubic block, (G) cubic honeycomb, (H) tyre pyramid. *Redrawn from Gao et al. (2008a) and Hackradt et al. (2011).*

by-products, stabilized ash, automobiles and oil platforms (Baine, 2001; Seaman and Sprague, 1991; Stone et al., 1991). Japan was an early pioneer in large-scale AR deployment as a means of improving commercial fish production. This effort was even supported through government funding (Bortone, 2006; Stone et al., 1991). However, the use of ARs to enhance fisheries worldwide was not used extensively in fishery production enhancement until the late 1970s (Jensen, 2002; Monteiro and Santos, 2000; Polovina, 1991; Spieler et al., 2001; Walker et al., 2002).

According to Pitcher and Seaman (2000), the typical objectives of AR deployment include the enhancement of fisheries production and mitigation of damaged seabed. Basically, new habitat is created to compensate for the loss or damage to natural seabed usually attributed to anthropogenic activities. Research studies showed that AR deployment helps coastal conservation; harbour stabilization, recreation and aquaculture; and habitat protection, complication and rehabilitation (Bombace, 1997; Fabi and Fiorrentini, 1997; Pickering et al., 1998). It has also been recorded that ARs are very successful for attracting and supporting large fish populations, epifauna and other marine organisms (Bohnsack and Sutherland, 1985; Chua and Chou, 1994). These structures serve as important spawning grounds and nursery habitats for fish and colonization areas for epifauna such as barnacles, bivalves and sponges (Chua and Chou, 1994; Leung and Wilson, 1999; Relini et al., 1994). In particular, ARs can provide shadowy crevices for large predatory fish such as barracudas, groupers and snappers to hide. In addition, ARs provide an abundant supply of invertebrates and smaller fishes

around the area and hence increase the diversity of food for the predatory fishes (Hueckel and Stayton, 1982; Prince et al., 1985; Randall, 1963). New food webs may even be created within the ecosystem in the presence of ARs, as ARs can support large populations of fishes and other marine life. ARs can also attract new marine inhabitants to come and accommodate there from other places and thus promote marine biodiversity (Wilson et al., 2002). The reef system can also provide better feeding opportunities for fish by altering the water flow pattern in the marine environment (Hixon and Beets, 1989). This is especially true in areas with strong water currents. As flowing water passes through large AR structures, localized areas of high and low flow are created. Areas of high water flow rate can attract fishes, which feed on plankton, to aggregate. Alternatively, areas of low water flow rates allow fish to congregate.

Many colonized epifauna on the ARs are filter feeders that remove suspended particulate matter from the water column and produce faecal pellets. These pellets are released back into the water body and finally settle on the seabed. Thus, by preferentially rejecting unwanted inorganic matter as pseudofaeces and discharging organic faeces during the feeding and absorption process, filter feeders are able to selectively enrich the organic content of the ingested and absorbed food from the water column. The result of this is that the organic constituents in the water body are reduced, and hence, such a process is referred to "biofiltration" (Hawkins et al., 1998; Navarro and Thompson, 1997). Recently, it was found that through their filter-feeding behaviour, filter feeders play an important role in the process of nutrient cycling in marine ecosystems regarding to their high abundance and high filtration efficiency (Gili and Coma, 1998). Bugrov (1994) and Laihonen et al. (1996) suggested that the deployment of ARs can also serve as "biofiltration units" to remove particulates and dissolved matter from the water column, through the filter-feeding process of the epifauna settled on the AR surface.

Other researchers found that faunal recruitment in natural reefs is generally different from ARs regarding to the alteration of physical environment by the reefs and settlement preference of organisms to different substrata (Glasby and Connell, 1999; Smith and Rule, 2002). These results suggested that epifaunal organisms on the ARs can modify the nutrient flux and create new and complex food webs by changing the density and granularity of particulates, therefore leading to a change in physicochemical characteristics of the nearby benthic environment. Such changes include alteration of particle size distribution and organic content of the deposited sediments together with a change in food availability, quality and quantity.

In fact, it has been found that in productive ecosystems such as in the subtropics, the biogeochemical processes are extremely complex due to the interactions between the sediment and benthic organisms (Fourqurean et al., 1993). In the case of nitrogen, sediments are a source and a major sink in the cycling of this element, regulating its concentration and, thus, the productivity of marine systems (Lohse et al., 1993). Alternatively, phosphorus is an essential nutrient for the growth of marine phytoplankton, and it has been suggested that it is one of the key limiting factors for ocean primary production (Howarth et al., 1995). The removal of most phosphorus from the water column takes place through sedimentation of organic matter (Berner et al., 1993). In order to ensure maximum production, it is of prime importance to know the fate of phosphorous in organic matter when it reaches the sediment (Slomp, 1997). Another prime consideration is the concentration of nitrogen, carbon and phosphorus since an excess of these elements will lead to eutrophication. The instant response of water systems to this condition is to enhance the biomass of phytoplankton and plant matter. This can have important ramifications for environmental factors such as dissolved oxygen, a severe decrease leading to hypoxia/anoxia. On the other hand, harmful bloom species may thrive in such conditions and introduce toxic agents into the upper trophic levels of the food web. The results of either phenomenon may cause a reduction in species diversity and abundance. These conditions may also impact human activity such as cancellation of recreational events and cause health problems from either direct or indirect consumption of toxic organisms in the water or through the food chain.

In the recent years, more research studies have been undertaken in the understanding of artificial habitat ecology, although many questions regarding actual AR performance and environmental impacts remain unanswered (Carr and Hixon, 1997). One of the reasons for the poor understanding of AR ecology is the lack of knowledge of the effects that ARs have on the surrounding natural environment (Sheng, 2000; Svane and Peterson, 2001). There are concerns that these man-made structures may severely impact the surrounding benthic communities especially those living in adjacent soft-bottom sediments. These impacts can be caused by the introduced change to the localized hydrographic regime such as water circulation, wave action and sedimentation rate (Danovaro et al., 2002). The general attitude is that the deployment of ARs tends to alter soft-bottom assemblages by modifying the physical nature of the surrounding substratum. For example, member organisms of the soft-bottom assemblage will be smothered under the reef base. Reduced water currents can also modify the size distribution of

the sediment and alter the sedimentation rate around the immediate adjacent areas. The aggregation of fish at the ARs and the colonization of epifauna on the AR surface may also change the sediment organic matter content through the metabolic activity of both benthic and nektonic reef assemblages. In addition, the aggregation of fish at the ARs enhances the feeding pressure on the part of the infauna close to the AR sites. ARs have been well investigated in relation to their effects on fish populations and near-shore fisheries, even as a tool for protecting areas from trawling, with important consequences on coastal management. However, studies about their effects on sediment physicochemical characteristics, benthic environment and trophodynamics of the benthic communities are limited (Danovaro et al., 2002; Fricke et al., 1986; Guiral et al., 1995; Montagna et al., 2002).

3. ADVANCES IN UNDERSTANDING OF ECOLOGY OF ARs IN THE SUBTROPICS

Most of the recent (within the past 10 years) studies on ARs are primarily focused on the effects of the reef systems on fish populations and production, the development of benthic communities on the AR systems and the ecology of infaunal benthic ecosystems associated with the area where ARs are deployed. The following sections summarize the findings reported in subtropical waters.

3.1. Fish attraction versus fish production

The debate on whether ARs primarily function to attract fish from surrounding habitat as a consequence of fish behaviour or to provide additional habitat for the increase in carrying capacity and fish production has been a focal point in AR research over the years. There is an increasing evidence to show that both hypotheses are not mutually exclusive. Instead, they are either two end points along a continuum (Dance et al., 2011) or two processes complementary to each other (Fowler and Booth, 2012; Simon et al., 2011), resulting in the overall observed enhancement in fish abundance and biomass. Table 1.1 shows examples of recent studies related to fish attraction and/or fish production at ARs. Using a variety of sampling techniques, including underwater visual census, video observations, trap net and acoustic telemetry tracking, these studies generally showed that higher fish abundance, biomass, species richness and recruitment are found close to the ARs as compared to natural reef areas. There are data to report the narrow

Table 1.1 Examples of studies related to fish attraction and/or fish production at artificial reefs from 2005 to 2013

Study	Location	Reef material	Study findings
Jordan et al. (2005)	Fort Lauderdale, Florida, the United States	Concrete reef modules	Total fish abundance and richness increased when isolation distance between ARs increased. Doubling and tripling the number of AR modules also increased total fish abundance and species richness
Reed et al. (2006)	San Clemente, California, the United States	Quarry rocks and recycled concrete rubbles	Fish standing stock, density and species richness and recruitment on all ARs were similar to or greater than that observed in nearby natural reefs
Schroepfer and Szedlmayer (2006)	Gulf of Mexico	Concrete structures	Long-term residence and site fidelity of red snapper on ARs were evident from event analysis of ultrasonic tagging data
Santos and Monteiro (2007)	Algarve, southern Portugal	Concrete units	Fishing yields from the ARs continually exceeded those from the control sites in both the mean number of species and mean catch per unit effort
Dupont (2008)	Tampa Bay, Florida, the United States	Limestone boulders and reef modules	Species richness trends of fish resident among artificial and natural reefs were similar, with certain commercial fish abundances being significantly higher on ARs
Leitão et al. (2008a)	Algarve, southern Portugal	Concrete blocks	Higher mean number of species, diversity, density and biomass in fish assemblage were noted with increase in size of the ARs

Whitmarsh et al. (2008)	Algarve, southern Portugal	Concrete blocks	Fish production and incomes were increased leading to sustainable coastal fisheries
Edelist and Spanier (2009)	Haifa, Israel	Steel reinforced-concrete structures	AR units supported 20 × the fish biomass of control quadrats, creating an enrichment halo within 13 m from the reefs
Redman and Szedlmayer (2009)	Gulf of Mexico	Concrete blocks on polyethylene mat	The presence of epibenthic community growth on ARs was positively related to reef fish abundance probably because of the increase in supply of food resources
Boswell et al. (2010)	Gulf of Mexico	Decommissioned oil and gas platform	Highest acoustic estimates of fish biomass and density were found directly over the ARs
dos Santos et al. (2010)	North coast of Rio de Janeiro, southeastern Brazil	Concrete reef balls	Fish abundance and richness were significantly greater at the nearest distances (0 and 50 m) to the reefs than at 300 m. However, fish responses to reef distance were clearly species-specific
Dance et al. (2011)	Gulf of Mexico	Concrete modules of variable shapes	Total fish density, biomass and species richness increased at ARs with time
Hackradt et al. (2011)	Southern Brazil	Concrete modules of variable shapes	Reef blocks with greater area and complexity possessed the highest fish species richness and abundance
Simon et al. (2011)	Southern Brazil	Sunken ships	Production and attraction of target reef fishes by ARs were evident, with increased abundance of young recruits and presence of other predator fishes.

Continued

Table 1.1 Examples of studies related to fish attraction and/or fish production at artificial reefs from 2005 to 2013—cont'd

Study	Location	Reef material	Study findings
Topping and Szedlmayer (2011)	Mobile Bay, Alabama, the United States	Steel frame pyramid, army tank	Home range data through tracking by manual and passive telemetry showed close proximity of red snapper to the ARs over 24 h periods. Such long-term residency proved that ARs are important habitat for red snapper
Azhdari et al. (2012)	Bandar Lengeh, northern Persian Gulf	Concrete reef balls and pyramids, used concrete materials	A mixed form of ARs showed the best enhancement of catch per unit effort for demersal fishes
Fowler and Booth (2012)	Barrow Island, northwestern Australia	Rectangular prismoidal steel structures	The ARs sustained full population of sea goldie from recent settled juveniles to adults. Depth placement of ARs may not affect the production of fish species, which have naturally wide depth ranges
Syc and Szedlmayer (2012)	Mobile Bay, Alabama, the United States	Metal cages	There was a positive correlation between the mean age of red snapper and age of ARs, supporting the observation that ARs enhanced red snapper production. The presence of fish older than the reef indicated that red snapper were also attracted to ARs
Abecasis et al. (2013)	Southern Portugal	Concrete blocks	Tagged fish used the natural reef areas on a more frequent basis than the ARs. However, excursions to the adjacent ARs and sandy bottoms were also frequently detected, especially during day time

home range (Topping and Szedlmayer, 2011) and strong site fidelity (Schroepfer and Szedlmayer, 2006) of fish associated with ARs. However, fish response to reef distance can be species- or site-specific (dos Santos et al., 2010; Syc and Szedlmayer, 2012). Several factors are also considered important for fish attraction and fish production, including the age (Syc and Szedlmayer, 2012), size/area (Jordan et al., 2005; Leitão et al., 2008a) and complexity (Azhdari et al., 2012; Hackradt et al., 2011) of the ARs, as well as the depth and duration of deployment (Dance et al., 2011; Fowler and Booth, 2012).

Apart from the focus on fish attraction and/or fish production at the ARs, recent studies also examined the effects of scale of spatial isolation of ARs on fish populations. It has been revealed that small-scale isolation can modify the impact of piscivores on fish resident in the AR area, in which the high density of fish on small, isolated reefs is enabled by low predation pressure (Belmaker et al., 2005). Similarly, small-scale variation in predation may play an important function in determining the population dynamics of fish associated with ARs (Forrester and Steele, 2004). Mortality has been found to be density-dependent on reefs that are spatially isolated but highly density-independent on reefs that are aggregated (Overholtzer-McLeod, 2004). Even ARs with the same size and complexity may also have different fish assemblages if they are isolated (even not far from each other) and influenced by different hydrologic regimes and other biological processes such as the proximity of nursery grounds (Santos et al., 2005).

Ecological interactions in the AR areas are also important to dictate the abundance of fish populations. To this end, determining the role of predators in ARs is crucial to advancing the understanding of community interactions (Leitão et al., 2008b). In particular, the effects of interspecific predator–prey interrelationships, especially in the vicinity of artificial bottom habitats, on fish populations are poorly understood and complex and require in-depth investigations. If fish attraction from nearby areas to the ARs is rapid, then it may become difficult to deduce long-term, cumulative and indirect impacts caused by predation (Johnson, 2006; Leitão et al., 2008b).

While there is an increasing evidence to support both hypotheses of fish attraction and fish production at ARs, to ultimately determine which process is more important than the other for increased abundances in the reef area requires careful experimental design including the use of control sites (Brickhill et al., 2005). The analysis of fish otolith microchemistry (Gillanders and Kingsford, 1996; Hale and Swearer, 2008), telemetry tagging and tracking (Abecasis et al., 2013; Boswell et al, 2010) and application

of stable isotope analysis (Davenport and Bax, 2002; Wells et al., 2008) can be employed to help understand the trophodynamics and movement patterns of fish populations on the reefs.

3.2. Development of benthic communities on ARs

In addition to offering refuge places and various niches for fish to aggregate and reside, the surface of ARs provides a variety of space for the settlement and colonization of many benthic organisms, for example, sponges, corals, sea anemones, hydrozoans, corals, barnacles, tube worms, bivalves and tunicates. These organisms serve as an important food source for supporting an abundance of fish species associated with the reef areas. However, the development of benthic communities on ARs depends on a host of factors. Table 1.2 lists examples of recent research findings on the settlement of benthic communities on ARs. One of the key interests in many studies is to compare the development of benthic communities between artificial and natural reefs, which may provide insight into the function of ARs as compared with that of natural reefs (Perkol-Finkel et al., 2005; 2006). Apart from the types of materials used, orientation of reef surface (Boaventura et al., 2006; Knott et al., 2004; Moura et al., 2006; Perkol-Finkel and Benayahu, 2004), complexity and heterogeneity of reef structures (Suzuki et al., 2011; Thanner et al., 2006) and deployment age of ARs (Perkol-Finkel and Benayahu, 2005; Santos et al., 2011) may be of greater importance on the diversities of epibiota on ARs. However, ARs with very narrow interstructural space sizes may have a counter effect to preclude colonization of certain species and reduce species richness (Bartholomew and Shine, 2008). Recent findings have shown that some fauna may also prefer habitats with intermediate space sizes that match their individual body width (Bartholomew and Shine, 2008). Settlement of artificial crevice habitats is less well known, but the exclusion of such cryptofauna on AR surveys can lead to an underestimation of biodiversity in the reef area, if only visual census of the dominance of a few species is conducted (Baronio and Bucher, 2008). Indeed, the success for benthic communities to establish on ARs embraces a synergistic effect of environmental conditions such as current regime (Perkol-Finkel and Benayahu, 2007; 2009), depth (Moura et al., 2007; Walker et al., 2007) and sedimentation (Krohling and Zalmon, 2008; Perkol-Finkel and Benayahu, 2009) as well as the potential source of larval pools (Krohling and Zalmon, 2008) and biological traits of the settled organisms including reproduction strategies, growth rates and competitive abilities of the dominant taxa (Perkol-Finkel et al., 2005).

Table 1.2 Examples of studies related to settlement of benthic communities on artificial reefs from 2004 to 2011

Study	Location	Reef material	Study findings
Knott et al. (2004)	Sydney, Australia	Concrete breakwalls	Orientation of reef surface may be of greater importance on the biological diversities of epibiota on artificial or natural reefs, with invertebrates covering a larger area on vertical than horizontal surfaces
Perkol-Finkel and Benayahu (2004)	Gulf of Eilat, Red Sea	Metal and PVC net	Coral assemblages on artificial and natural reefs were different due to the vertical orientation of ARs, increasing local heterogeneity and space availability
Perkol-Finkel and Benayahu (2005)	Gulf of Eilat, Red Sea	Metal pyramids	The development of diverse benthic communities on ARs could take over 10 years, and species composition can be affected by structure design, spatial orientation, depth of deployment and age of the ARs
Perkol-Finkel et al. (2005)	Northern Red Sea	Sunken vessels	There were distinct differences in the colonization of fouling organisms between artificial and natural reefs and between young and old ARs. Differences in structural features between these reef types may lead to differences in species composition even after 100 years
Boaventura et al. (2006)	Ancão and Algarve, southern Portugal	Concrete cubic units	The bottom surface of ARs had a significant higher colonization of barnacle cover, probably due to lower sedimentation levels

Continued

Table 1.2 Examples of studies related to settlement of benthic communities on artificial reefs from 2004 to 2011—cont'd

Study	Location	Reef material	Study findings
Moura et al. (2006)	Faro, southern Portugal	Concrete reef modules	Surfaces of different orientations had different epibiotic biomasses at different depths of AR deployment, with colonization on horizontal surfaces being higher at shallower depth
Perkol-Finkel et al. (2006)	Sha'ab Ali, Red Sea	Sunken steel vessel	Benthic organisms on ARs would mimic natural reef communities only if structural features were similar to those of the natural habitats. Spatial orientation, complexity and facing of the substratum were important features to be considered in AR systems
Thanner et al. (2006)	Florida, the United States	Concrete and limestone modules and boulders	Benthic assemblages on ARs changed significantly, with increasing density and diversity and increasing similarity to the natural reef areas over a period of 4 years. However, the extent to which the reefs can become similar would depend on the physical characteristics, such as shape, relief and cryptic space, between these reef materials
Moura et al. (2007)	Algarve, southern Portugal	Concrete modules	Distribution of benthic species on ARs was depth-related, especially for barnacle and other colonial forms. Biomass and species number decreased with depth, which was related to light penetration, predation/grazing pressure, larval behaviour and water flow

Perkol-Finkel and Benayahu (2007)	Gulf of Eilat, Red Sea	PVC net, metal pyramids	Benthic filter-feeding organisms were more abundant on the underside of settlement plates deployed at the artificial than natural reefs. Such differential recruitment could result from a synergistic effect of abiotic and biotic factors, including current regime, at these reefs
Walker et al. (2007)	Coast of Mooloolaba, Queensland, Australia	Sunken warship	Depth, surface orientation and exposure were the major environmental drivers controlling the diversity and abundance of epibenthos on ARs
Baronio and Bucher (2008)	Northern New South Wales, Australia	Fibre-cement plates	Recruitment of crevice fauna could be different from that on AR surface. Hence, visual dominance of a few species may not be as sensitive to environmental variables as many of the less obvious taxa of cryptofauna
Bartholomew and Shine (2008)	Dibba, United Arab Emirates	Polyethylene tubes in bundles with bricks	AR habitats with very narrow interstructural space sizes may be too complex to prevent certain fauna to settle, leading to a decrease in species richness. Some fauna may also prefer habitats with intermediate space sizes that match their individual body width
Krohling and Zalmon (2008)	North coast, Rio de Janeiro, Brazil	Concrete reef balls	Sedimentation and high turbidity affected recruitment of epibenthic organisms on ARs. Other biological factors controlling recruitment patterns included low primary production and shortage of larval source

Continued

Table 1.2 Examples of studies related to settlement of benthic communities on artificial reefs from 2004 to 2011—cont'd

Study	Location	Reef material	Study findings
Miller et al. (2009)	Florida, the United States	Quarried limestone surfaces secured with concrete	Benthic assemblages between artificial and natural reefs were different, with a higher abundance of cyanobacterial turfs negatively affecting adult and larval corals
Perkol-Finkel and Benayahu (2009)	Gulf of Eilat, Red Sea	PVC net	Transplanted corals could survive better on artificial reefs than on natural reefs due to their difference in sedimentation load and current velocities
Burt et al. (2011)	Dubai, United Arab Emirates	Concrete breakwalls	Although development of benthic communities on ARs changed with time and became more similar to natural reefs with increasing age, these communities remained distinct
Santos et al. (2011)	Algarve, southern Portugal	Concrete blocks	The variability of benthic communities on ARs was related to the age of the reefs, which was a determining factor in structuring local fish populations
Suzuki et al. (2011)	Urasoko Bay, Japan	Fibreglass-reinforced plastic plates	Initial survival of corals was enhanced on ARs with narrower grid pattern in the design of the ARs

While the development of benthic communities has been well documented in terms of abundance, diversity and rate of settlement, relatively few findings are reported on the actual production of these organisms on ARs. By quantifying the productivity of ARs due to the epibiota, this value is useful in comparing different habitats colonized by various species with different life histories and growth patterns (Burton et al., 2002; Moura et al., 2011) and in determining the contribution of benthic production to local fish stock (Leitão et al., 2007). There are also few studies to estimate the efficacy of filtration by suspension or filter-feeding benthic organisms settled on ARs, which may be useful to reduce organic matter in the water column (Gao et al., 2008a; Haraguchi et al., 2009). A study by Gao (2005) has quantified that epifauna on each square metre of reef surface area can assimilate 590 g carbon, 160 g nitrogen and 26 g phosphorus in 1 year. It was also shown that when ARs were employed at organically enriched bottom sediments of a fish culture site, the levels of nitrogen and phosphorus decreased dramatically and the macrobenthic communities tended to be more stable and diverse when compared with the sediments without the deployment of ARs (Gao et al., 2008a). The biodeposit produced by these suspension feeders may also increase the food sources to the adjacent sediments (Gao, 2005; Leitão et al., 2007).

One emerging issue related to the development of benthic communities on ARs is the potential for invasive species to colonize the deployment area. Artificial structures can facilitate invasion of nonnative fouling species by offering unoccupied habitat for their colonization (Ruiz et al., 2009; Sheehy and Vik, 2010). In fact, ARs may be preferentially favoured by exotic species by increasing local sources of their larvae to colonize all types of substrates (Glasby et al., 2007; Tyrell and Byers, 2007). The extent of invasion can also be more acute if the AR deployment area is close to major shipping lanes. Since the main vectors for marine bioinvasion are ballast waters and ship hulls, submerged habitats may be more susceptible to the colonization of introduced species (Bumbeer and da Rocha, 2012).

3.3. Response of *in situ* benthic communities associated with ARs

The physical presence of ARs on the seabed creates different environments due to possible changes in hydrodynamic and sedimentation regimes (Falcão et al., 2009; Mendonça et al., 2012). AR structures tend to enhance the movement of superficial sediments mostly because of the increase in water

current velocity when passing over the edge of the reef. As shown by Sheng (2000), when an AR obstructs the current flow, a stationary or lee wave is formed, which can trap drifting larvae and other materials. Hence, increased sedimentation and biomass deposition in the lee of the reefs can accelerate remineralization of the sediments and promote recycling of nutrients in pore water (Dedieu et al., 2007; Fabi et al., 2002). Specifically, Falcão et al. (2007) reported that as the results of benthic remineralization processes in the sediments, the organic carbon and nitrogen content in settled particles within the AR area was about 4× higher 2 years after the reef deployment and nutrients and chlorophyll *a* in the water column were higher at the artificial than natural reef areas.

In response to changes in hydrodynamic and sedimentary regimes, the structure of *in situ* benthic communities may differ before and after the deployment of ARs. Table 1.3 contains examples of recent research findings on such responses related to benthic infauna in the sediments in the vicinity where ARs are located. Studies have shown that the macrobenthos surrounding the reef complex generally exhibits a stronger response to variations in sediment granulometry with increase in faunal abundance and diversity (Fukunaga and Bailey-Brock, 2008; Machado et al., 2013; Zalmon et al., 2014). Similarly, an increase in nematodes that possess a *k*-strategy life history and predatory feeding mode was noted in the examination of meiofaunal composition after AR deployment (Liu et al., 2011). Apart from changes in sediment regime, the increase in concentration of nutrients from water column near ARs can also alter the benthic community structure resulting in a more diverse ecosystem (Cheung et al., 2009; Dewsbury and Fourqurean, 2010).

4. FURTHER STUDIES ON TROPHIC RELATIONSHIPS OF ARs IN THE SUBTROPICS

Very little information exists in the literature on functional aspects of nutrient dynamics of ARs. In particular, while the potential of deploying ARs as biofiltration devices to remove excessive nutrients derived from fish culture in the water column is promising (Gao et al., 2008a,b; Haraguchi et al., 2009), further verification of such an application is required. A case in point is to examine the trophic relationships among AR organisms and the release of uneaten feed, faeces and dissolved excretory products from marine fish farming activities, which are becoming popular in subtropical

Table 1.3 Examples of studies related to *in situ* benthic communities in artificial reef areas from 2008 to 2014

Study	Location	Reef material	Study findings
Fukunaga and Bailey-Brock (2008)	Mamala Bay, Hawaii	Sunken fishing vessels	Variation in sediment grain size and depths may play some role in structuring polychaete communities around ARs. Infaunal communities were relatively similar between artificial and natural reefs
Cheung et al. (2009)	Hong Kong	Concrete and steel boats mounted with tyre pyramids, redundant marine structures and concrete modules	More diverse composition of macrobenthos was noted inside the AR area than that outside the reefs. This may be due to lower levels of water content, total organic carbon and total Kjeldahl nitrogen in sediments inside than outside the ARs
Dewsbury and Fourqurean (2010)	Florida Bay, the United States	Concrete blocks in pyramid formation	Microphytoplankton abundance was twice as high in reef plots than in control plots, suggesting that ARs concentrated nutrients and altered benthic community structure
Liu et al. (2011)	Hong Kong	Concrete boats mounted with tyre pyramids	While total meiofaunal and nematode abundance was significantly lower inside than outside the reef area, higher proportions of nematodes with a clavate tail shape, longer adult length, stout body shape and *k*-strategy life history were found within the ARs

Continued

Table 1.3 Examples of studies related to *in situ* benthic communities in artificial reef areas from 2008 to 2014—cont'd

Study	Location	Reef material	Study findings
Machado et al. (2013)	North coast, Rio de Janeiro, Brazil	Concrete reef balls	Macrobenthos richness, abundance and diversity varied spatially, with higher mean values near the ARs, suggesting that the artificial modules created a more heterogeneous grain size of the sediment and higher niche availability for the enrichment of associated macrobenthos
Zalmon et al. (2014)	North coast, Rio de Janeiro, Brazil	Concrete reef balls	The infauna surrounding the reef complex exhibited a stronger response to variations in the sediment grain-size regime associated with the intense hydrodynamics in the study area than to predation pressure

environments (Boyra et al., 2004; Huang et al., 2011; Özgül and Angel, 2013; Silva-Cruz et al., 2011). The following sections highlight two such studies using different approaches.

4.1. Stable isotope analysis

Traditionally, evaluating the gut content of the animals has been used to gather evidence of the particulate matter uptake of suspension and filter-feeding animals (Kamermans, 1994; Wallance et al., 1977). However, gut content analysis can only represent an instant "snapshot" of food ingested by the animals. Sometimes, it is impossible to analyse gut content, due to the small food fragments (Grey et al., 2001). Stable isotopes are transferred along the food chain in predictable ways, and they represent the time-integrated dietary intake of the consumer (Alfaro et al., 2006; Napolitano, 1999; Peterson and Fry, 1987). The feasibility of using stable isotopes to trace the predator–prey relationship is based on the observation that organisms selectively release lighter isotopes during respiration and excretion, so the assimilated food can be differentiated from the initial food (Peterson and Fry, 1987). Moreover, based on the concept that when two sources combine to form a mixture, isotopes can indicate the relative contributions of the sources; thus, the relative contributions of different food sources to a consumer can be calculated (Phillips, 2001).

The following study conducted in subtropical Hong Kong was to identify the potential food sources of the dominant suspension or filter-feeding animals that colonized on the AR surface in the two marine fish culture zones (FCZ), namely, Sham Wan FCZ and Lo Tik Wan FCZ (Figure 1.3), and to quantify the relative contribution of the respective food sources to the assimilation of these animals, using dual carbon and nitrogen stable isotopes as tracers.

4.1.1 Study area and sampling scheme

The effects of ARs on the nutrient dynamics of fish farm environments were carried out in both Sham Wan and Lo Tik Wan FCZs. Sham Wan FCZ is a semiclosed bay located in the northeastern part of Hong Kong (22°26′N and 114°21′E). The site is oceanic in character. It has a water depth ranging from 11 to 14 m, with a rocky coast. It is a relatively clean area, with no river, sewage or industrial discharges to the site. The area of the FCZ is approximately 130,000 m^2, with an estimated fish stock density of 2.5 kg m^{-2}. The cultured species mainly include groupers, snappers and yellowtails, and the fish feed used is mainly trash fish (mainly Sumatran silverside *Hypoatherina*

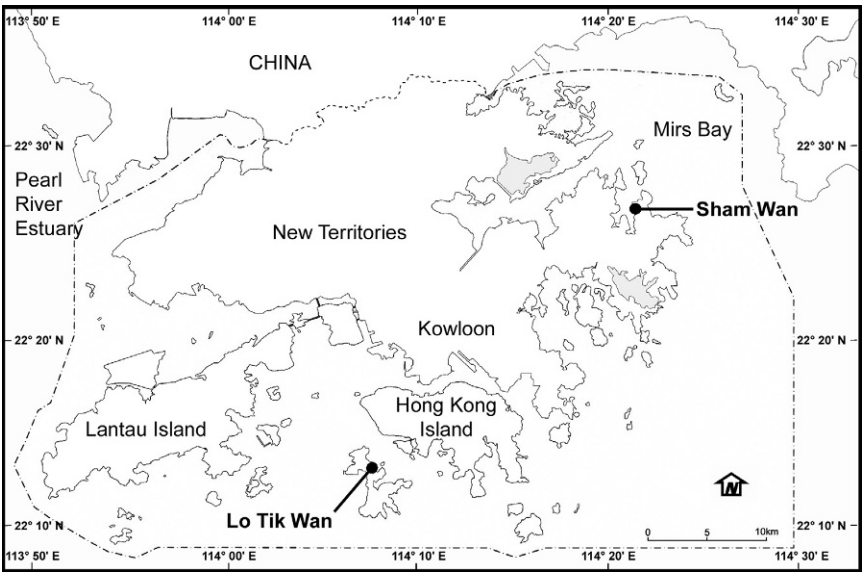

Figure 1.3 Location of study areas in Hong Kong.

valenciennei). Lo Tik Wan FCZ is a semiclosed bay located at an island in the southern part of Hong Kong (22°13′N and 114°07′E). It has a water depth ranging from 8 to 14 m, with partly rocky and partly sandy coast. The water in this FCZ looks more turbid and has a lower salinity in summer due to the effect of Pearl River outflows, which contain a large amount of nutrients and suspended solids (Huang et al., 2003; Ni et al., 2008). This culture zone is also located near a shipping channel, where vessel traffic is intense. The area of the FCZ is approximately 110,000 m^2, with an estimated stock density of 2.6 kg m^{-2}. The cultured species mainly include groupers and snappers. They are fed largely on trash fish (mainly Belanger's croaker, *Johnius belangerii*), but dry feed pellets are also used.

In both study areas, three AR stations near the fish cages, two fish cage stations away from ARs and two control stations outside the culture zone boundary were chosen (Figure 1.4). The structure of the ARs was made of fibreglass with cement concrete coating supported in a steel frame with a dimension of 3 m (L) × 3 m (W) × 5 m (H) (Figure 1.5). The abundance, diversity and succession of epifauna on the AR surface were studied throughout the whole post-AR deployment study period, from November 2007 to February 2009 for Sham Wan and from July 2008 to May 2009 for Lo Tik Wan. Suspension or filter-feeding epifauna, organic wastes derived from fish farming activities (fish feeds and fish faeces of cultured fish),

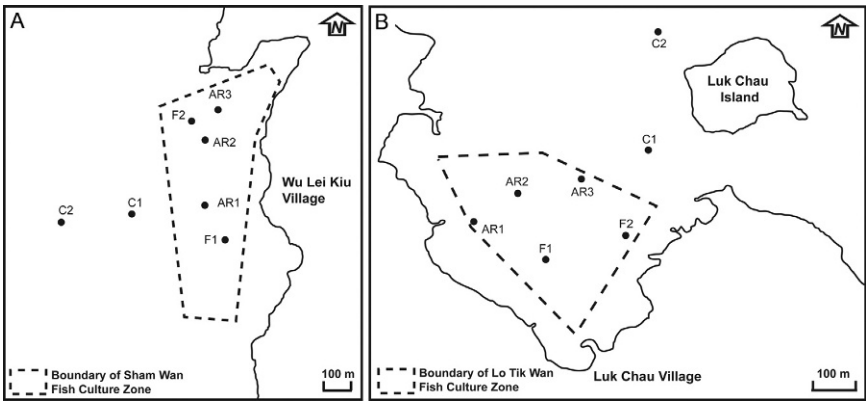

Figure 1.4 Sampling stations in (A) Sham Wan and (B) Lo Tik Wan, Hong Kong. AR, artificial reef station; F, fish cage station; C, control station.

Figure 1.5 Artificial reef structure used in study areas, Hong Kong.

particulate organic matter (POM) and sediment samples were collected from Sham Wan in August 2008 and Lo Tik Wan in May 2009, after deployment of ARs at approximately one and one-half years and one year, respectively.

4.1.2 Collection of samples for stable isotope analysis

Epifaunal samples of the three ARs at the three AR stations, AR1, AR2 and AR3, respectively, were taken for analysis. On each AR, three square-shaped areas, with a surface area of around 500 cm^2, were chosen randomly, and all epifauna on that area were scraped off by the same SCUBA diver using a trowel and placed in labelled plastic bags. In the laboratory, dominant suspension or filter feeder species with sufficient biomass for stable isotope analysis were identified. The barnacle *Balanus* spp. and the tunicate *Styela plicata* from the ARs of Sham Wan in August 2008 were selected for analysis. The barnacle *Balanus* spp., the fanshell *Isognomon perna*, the green-lipped mussel *Perna viridis*, the sponge *Mycale adhaerens* and the tunicate *Styela plicata* from the ARs of Lo Tik Wan in May 2008 were selected for analyses. For Lo Tik Wan samples, each species was analysed separately, and samples taken from the three randomly selected areas on the AR surface were treated as three replicates for each AR. Owing to small biomass obtained, barnacles taken from the same AR were pooled and treated as one replicate. In Sham Wan, since the biomass of epifauna obtained was limited, samples of the same species/taxa taken from the same AR were pooled to form one replicate. For shelled animals, the shells were removed and the tissue was rinsed with distilled water to remove salts on the tissue surface. For unshelled animals, the whole animal was rinsed with distilled water. The tissue was dried at 60 °C over 72 h, to a constant dry weight, homogenized and sieved through a 0.5 mm mesh size sieve. The tissue powder was tightly sealed in glass sample bottles and stored in an ultralow-temperature freezer (−80 °C) for future analysis.

30 L of seawater was collected 1 m beneath surface at the AR stations and at the control stations to obtain POM. The seawater samples were then filtered with precombusted (450 °C for 6 h) 0.45 μm pore size and 90 mm diameter Whatman GF/C glass fibre filters under vacuum suction of less than 1/3 atmospheric pressure. The residue on filter papers was rinsed with distilled water to remove salt adsorbed on the particle surface. Filtered samples were dried and stored following the same method for processing epifaunal tissue.

Trash fish (Sumatran silverside *Hypoatherina valenciennei* for Sham Wan and Belanger's croaker, *Johnius belangerii*, for Lo Tik Wan) used for fish feed were provided by the fishermen. Fillets removed from the trash fish were used for analysis. Three individuals of trash fish were pooled for one replicate

sample, and three replicates were taken. Dry feed pellets were also provided by the fishermen in Lo Tik Wan, and approximately 100 g of dry feed pellets were pooled for one replicate sample, and three replicates were taken. To collect fish faeces, six individuals of green grouper (*Epinephelus coioides*) from Sham Wan and six individuals of areolate grouper (*Epinephelus areolatus*) from Lo Tik Wan, all fed with trash fish, were bought from the fish farms and cultured in the laboratory. The two collections of grouper were separately maintained in fibreglass tanks with circulated seawater for 72 h, and the egested faeces were collected with a pipette. The faeces from green grouper that were fed with dry feed pellets were cultured in fibreglass tanks with circulated seawater *in situ* on fish rafts, with 20–30 individuals cultured separately in one tank. Fish faeces collected from each tank were pooled for one replicate sample, and three replicates were taken. After collection, the fish feed and fish faecal samples were dried and homogenized following the method similar to preparation of epifauna.

Three replicate grabs of sediment were collected using a 0.05 m^2 van Veen grab with 7 L collection volume from each sampling station for stable isotope analysis. The samples were stored in an icebox immediately after being taken from the sea bottom and were stored at −80 °C, once delivered back to the laboratory, prior to analysis. Sediment samples were dried and stored following the same method for processing epifaunal tissue.

4.1.3 Measurement of stable isotopes and elemental concentration

All samples were pretreated by acid fumigation, following the method of Harris et al. (2001). Dried and homogenized samples were weighed in Ag-foil capsules and arranged on a microtitre plate, wetted with water and placed in a desiccator containing a beaker with concentrated (12 M) HCl for 6–8 h, so that all carbonates in the samples were released as CO_2. The samples were then dried at 60 °C and encapsulated in Sn-foil capsules prior to isotope determination. Determination of carbon to nitrogen isotope ratios and carbon and nitrogen concentrations was then analysed at the UC Davis Stable Isotope Facility in California, the United States. Results of isotope ratios were expressed in standard δ-unit notation, which is defined as follows:

$$\delta_X = \left[\left(R_{\text{sample}}/R_{\text{standard}}\right) - 1\right] \times 1000‰$$

where X = ^{13}C or ^{15}N and R is either $^{13}C/^{12}C$ ratio for carbon or $^{15}N/^{14}N$ ratio for nitrogen. The values were reported relative to the Vienna Pee Dee Belemnite (PDB) standard for carbon and to air N_2 for nitrogen.

4.1.4 Statistical analysis and isotope mixing model

The linear mixing model (Phillips, 2001) or the IsoSource mixing model (Phillips and Greggs, 2003) was used to analyse the respective contribution of different food sources to the diet of epifauna. Average fractionation effect of 1‰ for carbon isotope was used to correct stable isotope shift for each trophic level (McClelland and Valiela, 1998; Peterson and Fry, 1987). In order to calculate the respective contribution of a particular food source to the diet of a consumer, the isotopic values of the consumer (after correction for trophic fractionation) must fall into the triangular or convex polygon space enclosed by lines connecting the food sources (Phillips and Greggs, 2003; Phillips and Koch, 2002). Although a low trophic shift value (1‰) has been tried on the $\delta^{15}N$ values of epifauna, in both Sham Wan and Lo Tik Wan (trophic shift of N isotope usually ranges from 1‰ to 5‰ (Davenport and Bax, 2002)), the 1‰ trophic shift-corrected values were too low to fall into the triangular or convex polygon space enclosed by lines connecting the food sources, and no solutions could be obtained using a dual-isotope (C and N) mixing model. Thus, only $\delta^{13}C$ values were used for the food source analysis using the isotopic mixing models.

For the stable isotope data of Sham Wan, as two of the food sources, trash fish and fish faeces, had very close $\delta^{13}C$ values, and since they were logically related (the fish faeces mainly contained the undigested and metabolized portion of trash fish), they were treated as one food source (Phillips et al., 2005). As there were a total of two food sources, including POM and the trash fish–fish faeces group, the two-end-member isotope mixing model was used to estimate the relative contribution of different food sources to the epifauna, as follows:

$$\left(\delta^{13}C'_X - \delta^{13}C_M\right)f_x + \left(\delta^{13}C'_Y - \delta^{13}C_M\right)f_Y = 0$$
$$f_X + f_Y = 1$$

where f_X and f_Y represent the fractions of assimilated C of sources X and Y, respectively, in the mixture M. Isotope signatures for the sources were corrected for trophic shift as designated by the prime (′) symbol. The f represents the proportion of C mass from a food source and not necessarily the proportion of biomass. Also, due to the possible differences in digestibility, f represents the proportion of C assimilated rather than C consumed from a particular food source (Phillips and Koch, 2002).

For the stable isotope data of Lo Tik Wan, there were five food sources (POM, dry feed pellet, faeces of cultured fish fed with pellet, trash fish and

faeces of cultured fish fed with trash fish), which exceeded the number of isotope signatures plus one, and the number of food sources could not be reduced due to distinctive isotopic compositions (Phillips et al., 2005). As such, the IsoSource model (Phillips and Greggs, 2003) was used to estimate the feasible range of the relative contribution of different food sources to the epifauna. All possible combinations of each source contribution (0–100%) were examined in 1% increments. Combinations with a sum total of the observed mixture isotopic signatures, within a small tolerance of ±0.01‰, were considered to be feasible solutions, from which the frequency and range of potential source contributions were determined. The trimmed 1–99th percentile range was reported as the range (minimum to maximum), which was sensitive to small numbers of observations on the tails of the distribution (Phillips and Greggs, 2003).

4.1.5 Isotopic compositions of Sham Wan and Lo Tik Wan samples

Table 1.4 shows the $\delta^{13}C$ and $\delta^{15}N$ values and C and N contents of epifauna, organic wastes derived from fish farming activities, POM and sediment in Sham Wan, and the stable isotope compositions of the samples are also shown in a dual-isotope plot in Figure 1.6. The $\delta^{13}C$ values of epifauna including barnacles and tunicates were -20.4 ± 0.2‰ and -18.6 ± 0.5‰, respectively, while their $\delta^{15}N$ values were 9.7 ± 0.1‰ and 10.6 ± 0.2‰, respectively. Both the $\delta^{13}C$ and $\delta^{15}N$ values of barnacles were significantly higher than those of tunicates (student's *t*-test, for $\delta^{13}C$, $t_4 = -6.1$, $p < 0.01$; for $\delta^{15}N$, $t_4 = -9.6$, $p < 0.01$). The $\delta^{13}C$ values of POM at the control stations and AR stations were -24.8 ± 0.03‰ and -22.7 ± 0.03‰, respectively, while their $\delta^{15}N$ values were 6.9 ± 0.004‰ and 8.0 ± 0.005‰, respectively. Both the $\delta^{13}C$ and $\delta^{15}N$ values of POM at the control stations were significantly lower than those at the AR stations (student's *t*-test, for $\delta^{13}C$, $t_4 = -5.6$, $p < 0.01$; for $\delta^{15}N$, $t_4 = -3.3$, $p < 0.05$). The $\delta^{13}C$ values of trash fish and fish faeces were -19.3 ± 0.4‰ and -19.3 ± 0.04‰, respectively, while their $\delta^{15}N$ values were 12.6 ± 0.1‰ and 12.1 ± 0.01‰, respectively. No significant differences were found in $\delta^{13}C$ and $\delta^{15}N$ values between trash fish and fish faeces (student's *t*-test, for $\delta^{13}C$, $t_4 = -0.1$, $p = 0.92$; for $\delta^{15}N$, $t_4 = 1.4$, $p = 0.23$).

Only $\delta^{13}C$ values were used to analyse the respective contribution of different food sources to the diet of epifauna, as the $\delta^{15}N$ values could not be fit into the isotope mixing model. Also, as the $\delta^{13}C$ values of trash fish and fish faeces were statistically indistinguishable and can be logically related, their $\delta^{13}C$ values were pooled and treated as one food source

Table 1.4 $\delta^{13}C$ and $\delta^{15}N$ values and the C and N contents of POM and organic wastes derived from fish farming activities, epifauna and sediment (mean ± SD; $n = 3$) in Sham Wan

	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C content (%)	N content (%)
POM and organic wastes derived from fish farming activities				
POM_C	-24.77 ± 0.13^{a}	6.87 ± 0.19^{a}	3.02 ± 1.14	0.39 ± 0.13
POM_AR	-22.67 ± 0.23^{b}	8.04 ± 0.19^{b}	3.10 ± 1.49	0.54 ± 0.34
Trash fish	-19.26 ± 0.29^{c}	12.55 ± 0.64^{c}	38.59 ± 10.10	10.87 ± 2.78
Fish faeces	-19.25 ± 0.93^{c}	12.14 ± 0.77^{c}	3.95 ± 0.60	0.85 ± 0.13
Epifauna				
Barnacle	-18.57 ± 0.45^{a}	10.56 ± 0.24^{a}	38.27 ± 11.66	8.45 ± 2.68
Tunicate	-20.42 ± 0.23^{b}	9.69 ± 0.08^{b}	16.91 ± 7.39	2.75 ± 0.92
Sediment				
S_C1	-20.86 ± 0.04^{a}	7.10 ± 0.50^{abc}	1.20 ± 0.17	0.15 ± 0.02
S_C2	-20.95 ± 0.15^{a}	6.54 ± 0.16^{a}	1.61 ± 0.00	0.22 ± 0.01
S_F1	-21.73 ± 0.07^{b}	7.00 ± 0.07^{ab}	1.86 ± 0.04	0.23 ± 0.01
S_F2	-20.92 ± 0.10^{a}	7.24 ± 0.37^{bc}	1.57 ± 0.17	0.21 ± 0.03
S_AR1	-20.83 ± 0.24^{a}	7.70 ± 0.22^{cd}	1.59 ± 0.63	0.23 ± 0.11
S_AR2	-20.60 ± 0.01^{a}	7.78 ± 0.28^{cd}	1.66 ± 0.18	0.25 ± 0.02
S_AR3	-20.84 ± 0.27^{a}	8.20 ± 0.10^{d}	1.67 ± 0.44	0.26 ± 0.07

POM_C, POM at control stations; POM_AR, POM at AR stations; S_C1, sediment at C1 stations, C2, sediment at C2 stations and so on. $\delta^{13}C$ and $\delta^{15}N$ values of POM and organic wastes derived from fish farming activities, epifauna and sediment were compared separately using ANOVA with Tukey test or Games–Howell test for multiple comparisons. Values marked with different letters were significantly different ($p < 0.05$).

(Phillips et al., 2005). The two food sources, POM and the trash fish–fish faeces group, were then placed into a two-end-member carbon isotope mixing model to calculate the respective contribution of those sources to the carbon source of the epifauna; the average fractionation effect of 1‰ was used to correct stable isotope shift of a trophic level (Figure 1.7). The results showed that the contributions of POM and the trash fish–fish faeces group to the carbon source of tunicates were 62.1% and 37.9%, respectively, and their contributions to the carbon source of barnacles were 5.7% and 94.3%, respectively.

The C and N contents of different food sources were also compared (Table 1.4). The C content of trash fish (38.6 ± 10.1%) was about

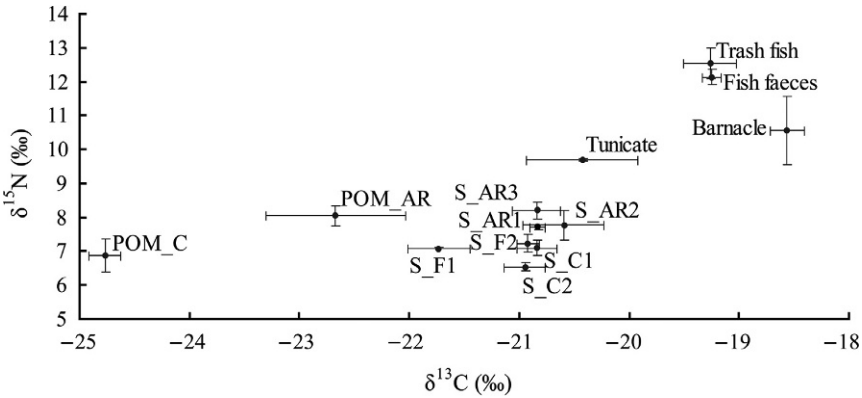

Figure 1.6 Dual-isotope plot showing the isotopic compositions of epifauna, organic wastes derived from fish farming activities, POM and sediment in Sham Wan. Data are presented in mean ± SD, $n = 3$. POM_C, POM at control stations; POM_AR, POM at AR stations; S_C1, sediment at C1 station and S_C2, sediment at C2 station and so on.

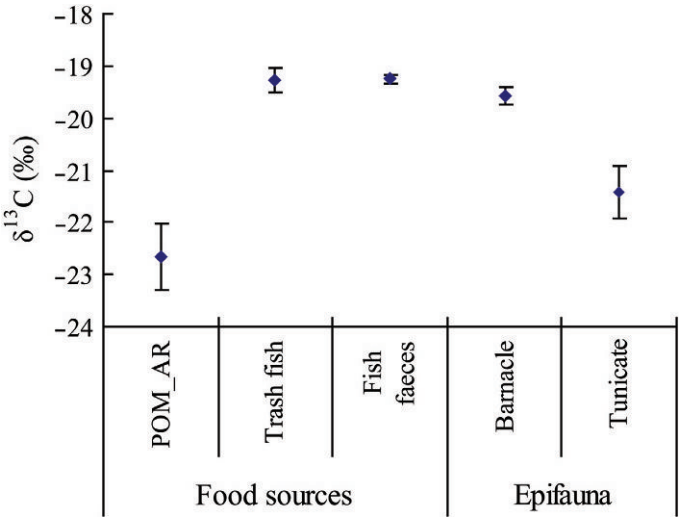

Figure 1.7 $\delta^{13}C$ of epifauna and their potential food sources in Sham Wan. Data are presented in mean ± SD, $n = 3$. Average fractionation effect of 1‰ was used to correct stable isotope shift of a trophic level. POM_AR, POM at AR stations.

10 × higher than those of POM at the AR stations (3.1 ± 1.5%) and fish faeces (4.0 ± 0.6%). It was similar for N content, which the N content of trash fish (10.9 ± 2.8%) was over 10 × higher than those of POM at the AR stations (0.5 ± 0.3%) and fish faeces (0.9 ± 0.1%).

Significant differences were found in both $\delta^{13}C$ and $\delta^{15}N$ values between sediments at different stations (ANOVA, for $\delta^{13}C$, $F_{6,13}=5.9$, $p<0.01$; for $\delta^{15}N$, $F_{6,13}=16.3$, $p<0.01$). Except for the F1 station, which had significantly lower $\delta^{13}C$ (−21.93 to −20.53‰) compared with the other stations, no significant differences were found between $\delta^{13}C$ of the other stations (−21.16 to −20.20‰). For N isotope, the $\delta^{15}N$ values at the C2 station (6.57–6.73‰) were significantly lower than those at the FCZ and AR stations, and the $\delta^{15}N$ values at the AR3 station (6.92–7.30‰) were significantly higher than those of the control and FCZ stations. Overall, $\delta^{15}N$ values tended to be higher in the sediment at the AR station.

In Lo Tik Wan, the $\delta^{13}C$ and $\delta^{15}N$ values and the C and N contents of epifauna, organic wastes derived from fish farming activities, POM and sediment are shown in Table 1.5. The isotopic compositions of the samples are also shown in a dual-isotope plot in Figure 1.8. The $\delta^{13}C$ values of epifauna including barnacles, fanshells, mussels, sponges and tunicates were −18.1 ± 0.2‰, −18.5 ± 0.2‰, −17.5 ± 0.4‰, −20.6 ± 0.3‰ and −18.8 ± 0.4‰, respectively, while their $\delta^{15}N$ values were 8.6 ± 0.2‰, 9.1 ± 0.5‰, 8.3 ± 0.2‰, 7.5 ± 0.6‰ and 7.7 ± 0.8‰, respectively. Significant differences in both $\delta^{13}C$ and $\delta^{15}N$ values were found between epifaunal organisms (ANOVA, for $\delta^{13}C$, $F_{4,45}=114.6$, $p<0.01$; for $\delta^{15}N$, $F_{4,45}=11.2$, $p<0.01$). Within the five potential food sources of epifauna (POM at the AR stations, trash fish, pellet, faeces of cultured fish fed with trash fish and faeces of cultured fish fed with pellet), trash fish had the highest $\delta^{13}C$ and $\delta^{15}N$ values, which were −17.3 ± 0.1‰ and 13.7 ± 0.6‰, respectively. The isotopic values of pellet were much lower than those of trash fish, the $\delta^{13}C$ and $\delta^{15}N$ values of which were −22.0 ± 0.1‰ and 8.9 ± 0.2‰, respectively. The $\delta^{13}C$ and $\delta^{15}N$ values in cultured fish fed with pellet were −24.4‰ and 5.3‰, respectively, with a shift of 2.5‰ for $\delta^{13}C$ and 3.4‰ for $\delta^{15}N$ from pellet to faeces. For POM, no significant differences were found between POM at the control stations and POM at the AR stations (student's *t*-test, for $\delta^{13}C$, $t_4=-0.5$, $p=0.61$; for $\delta^{15}N$, $t_4=0.6$, $p=0.59$). For sediments at different stations, a large range was found in the $\delta^{13}C$ values (−15‰ to −21‰), while a narrow range was found in the $\delta^{15}N$ values (5.4–6.7‰). Significant differences between sediment at different stations were found in both $\delta^{13}C$ (ANOVA, $F_{6,13}=8.3$, $p<0.01$) and $\delta^{15}N$ (ANOVA, $F_{6,13}=6.6$, $p<0.01$) values. Relatively lower $\delta^{13}C$ and $\delta^{15}N$ values were found in the sediment of the control stations, except for the sediment of AR1 station, which had similar $\delta^{13}C$ values with C1 station.

Table 1.5 $\delta^{13}C$ and $\delta^{15}N$ values and C and N contents of POM, organic wastes derived from fish farming activities, epifauna and sediment (mean ± SD; $n = 3$, except for fanshell, mussel, sponge and tunicate where $n = 9$) in Lo Tik Wan

	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C content (%)	N content (%)
POM and organic wastes derived from fish farming activities				
POM_C	-18.84 ± 0.24^{a}	6.74 ± 0.80^{ab}	2.64 ± 1.51	0.52 ± 0.28
POM_AR	-18.77 ± 0.02^{a}	7.16 ± 0.93^{ab}	3.47 ± 0.33	0.66 ± 0.06
Pellet	-21.95 ± 0.13^{b}	8.90 ± 0.18^{bc}	38.12 ± 4.31	7.39 ± 0.99
Trash fish	-17.34 ± 0.11^{c}	13.69 ± 0.62^{d}	32.74 ± 8.46	11.02 ± 2.89
Fish faeces_p	-24.40 ± 0.03^{d}	5.28 ± 0.23^{a}	22.19 ± 1.94	1.88 ± 0.17
Fish faeces_t	-19.19 ± 0.79^{ab}	10.24 ± 2.03^{c}	7.95 ± 7.65	2.07 ± 2.18
Epifauna				
Barnacle	-18.11 ± 0.22^{b}	8.56 ± 0.18^{ab}	19.24 ± 0.94	3.50 ± 0.61
Fanshell	-18.45 ± 0.19^{c}	9.08 ± 0.49^{c}	33.25 ± 2.85	8.12 ± 0.48
Mussel	-17.46 ± 0.37^{a}	8.28 ± 0.16^{bc}	32.10 ± 4.93	8.14 ± 1.69
Sponge	-20.60 ± 0.27^{d}	7.53 ± 0.55^{c}	30.33 ± 4.66	8.37 ± 0.74
Tunicate	-18.76 ± 0.39^{bc}	7.73 ± 0.83^{a}	15.56 ± 3.11	3.42 ± 0.83
Sediment				
S_C1	-21.10 ± 0.88^{ab}	5.37 ± 0.15^{a}	0.93 ± 0.01	0.13 ± 0.01
S_C2	-20.46 ± 0.97^{a}	5.40 ± 0.10^{a}	0.90 ± 0.08	0.12 ± 0.00
S_F1	-17.05 ± 0.92^{ab}	7.06 ± 0.36^{b}	1.74 ± 0.64	0.22 ± 0.06
S_F2	-18.16 ± 3.07^{ab}	6.73 ± 0.75^{ab}	1.38 ± 0.46	0.18 ± 0.05
S_AR1	-21.04 ± 0.17^{a}	6.80 ± 0.60^{ab}	1.20 ± 0.15	0.21 ± 0.03
S_AR2	-15.39 ± 1.66^{ab}	6.60 ± 0.37^{ab}	1.47 ± 0.19	0.17 ± 0.01
S_AR3	-15.13 ± 0.54^{b}	6.72 ± 0.16^{b}	1.49 ± 0.14	0.17 ± 0.01

POM_C, POM at control stations; POM_AR, POM at AR stations; Fish faeces_p, faeces of cultured fish fed with pellet; Fish faeces_t, faeces of cultured fish fed with trash fish; S_C1, sediment at C1 station, S_C2, sediment at C2 station and so on. $\delta^{13}C$ and $\delta^{15}N$ values of POM and organic wastes derived from fish farming activities, epifauna and sediment were compared separately using ANOVA with Tukey test or Games–Howell test for multiple comparisons. Values marked with different letters were significantly different ($p < 0.05$).

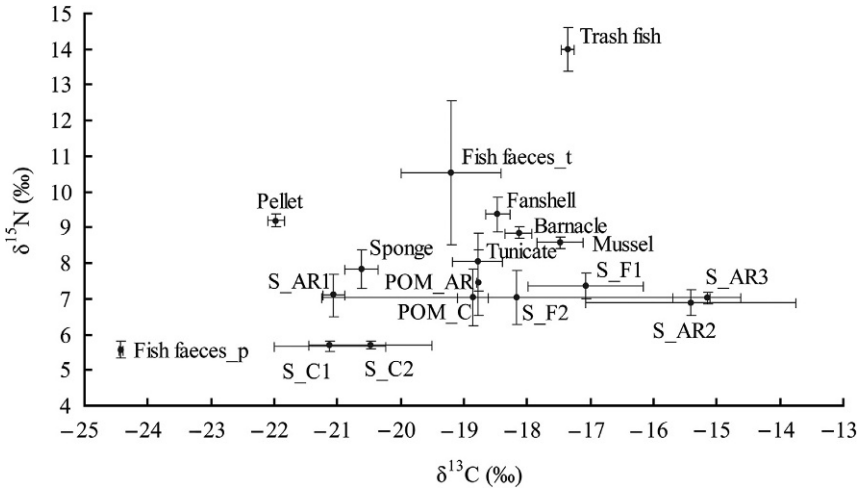

Figure 1.8 Dual-isotope plot showing the isotopic compositions of epifauna, organic wastes derived from fish farming activities, POM and sediment in Lo Tik Wan ($n = 3$, except for fanshells, mussels, sponges and tunicates where $n = 9$). POM_C, POM at control stations; POM_AR, POM at AR stations; Fish faeces_p, faeces of cultured fish fed with feed pellet; Fish faeces_t, faeces of cultured fish fed with trash fish; S_C1, sediment at C1 station; S_C2, sediment at C2 station and so on.

The carbon and nitrogen content of the samples were also compared (Table 1.5). When comparing the C content of different food sources for the epifauna, it was found that the C contents of pellet (38.1 ± 4.3%), trash fish (32.7 ± 8.5%) and faeces of cultured fish fed with pellet (22.2 ± 1.9%) were about 10 × higher than those of POM at the AR stations (3.5 ± 0.3%) and faeces of cultured fish fed with trash fish (8.0 ± 7.6%). While much higher N contents were found in pellet (7.4 ± 1.0%) and trash fish (11.0 ± 2.9%), much lower N contents were found in POM (0.5 ± 0.3% for the control stations and 0.7 ± 0.1% for the AR stations) and fish faeces (~2%).

As the number of food sources in Lo Tik Wan exceeded the number of isotopes plus one and all the food sources had distinct isotopic values that they cannot be combined to reduce the number of food sources (Phillips et al., 2005), the IsoSource model (Phillips and Greggs, 2003) was used instead of the standard linear mixing model (Phillips, 2001), to determine the feasible range of the contribution of each food source to the diet of epifauna. In addition, only $\delta^{13}C$ values were used in the IsoSource model analysis, as the $\delta^{15}N$ values of epifauna were not compatible with the model. The $\delta^{13}C$ values of epifauna and the potential food sources are compared in Figure 1.9.

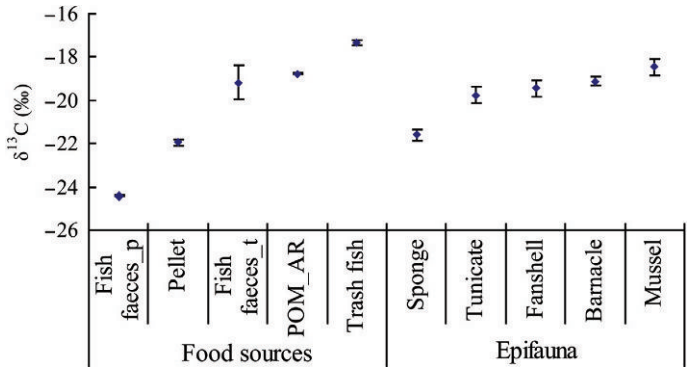

Figure 1.9 $\delta^{13}C$ of epifauna and their potential food sources in Lo Tik Wan. Data area presented in mean ± SD, $n = 3$, except for sponges, tunicates, fanshells and mussels where $n = 9$. Average fractionation effect of 1‰ was used to correct stable isotope shift of a trophic level. POM_AR, POM at the AR stations; Fish faeces_p, faeces of cultured fish fed with pellet; Fish faeces_t, faeces of cultured fish fed with trash fish.

The results of the IsoSource modelling are shown in Figure 1.10. Mussels had the highest mean $\delta^{13}C$ value (−17.5%), which showed the highest dependency on trash fish as food source. The feasible contribution of trash fish to the diet of mussels was 28–78% (1–99th percentile), and the mean was 54.3%. The feasible contributions of POM and faeces of cultured fish fed with trash fish to the carbon source of mussel were 0–65% and 28–78%, respectively, and the means were 20.4% and 54.3%, respectively. The feasible contributions of these two sources were only 0–20% and 0–3% (1–99th percentile), and the means were 6% and 3.7%, respectively.

The IsoSource modelling results were similar for barnacles, fanshells and tunicates, all of which were more dependent on trash fish, POM and faeces of cultured fish fed with trash fish as their carbon sources. The feasible contributions of trash fish to the carbon source of barnacles, fanshells and tunicates were 1–66%, 0–60% and 0–55% (1–99th percentile), respectively, and the means were 30.9%, 25.1% and 21.6%, respectively. The feasible contributions of the faeces of cultured fish fed with trash fish to the carbon sources of barnacle, fanshell and tunicate were 0–78%, 0–80% and 0–75% (1–99th percentile), respectively, and the means were 24.6%, 26.0% and 25.2%, respectively. The feasible contributions of POM to the carbon sources of barnacles, fanshells and tunicates were 0–82%, 0–76% and 0–65% (1–99th percentile), respectively, and the means were 28.1%, 26.5% and 24.6%, respectively.

Sponge has the lowest mean $\delta^{13}C$ value (−20.6‰), and it showed the highest dependency on faeces of cultured fish fed with pellets as food source.

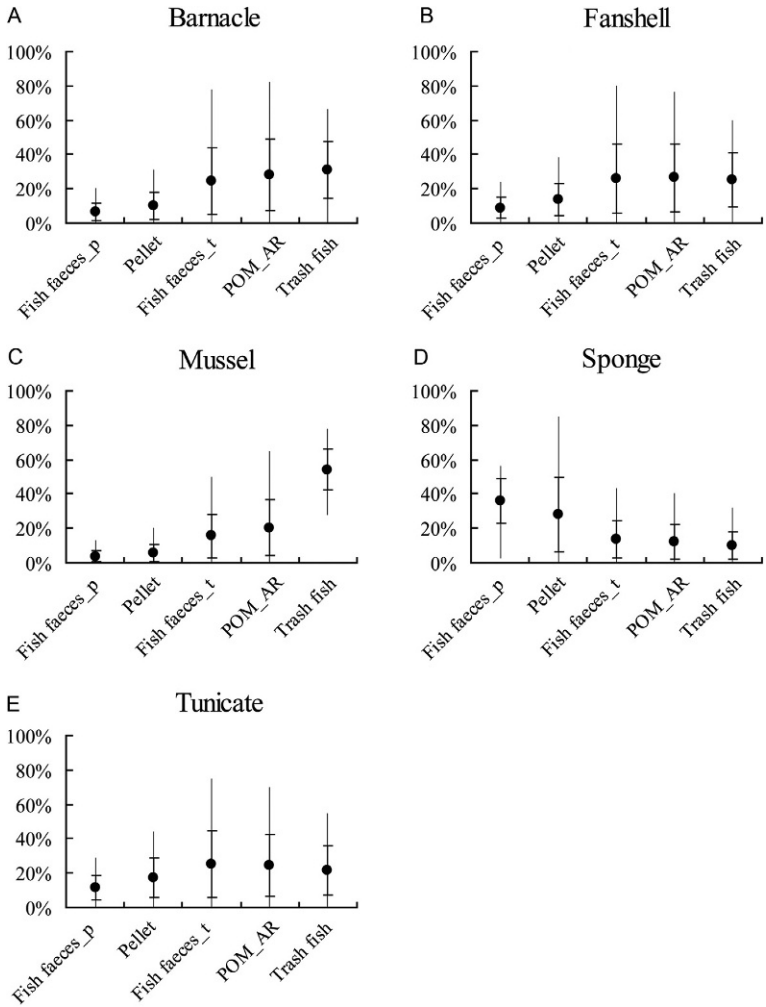

Figure 1.10 Results of IsoSource modelling showing the feasible range of distribution of different potential food sources to the carbon source of epifauna on the AR surface in Lo Tik Wan. (A) Barnacles, (B) fanshells, (C) mussels, (D) sponges, (e) Tunicates. The solid circles represent the mean percentage, the error bars with end caps represent the standard deviations and the error bars without end caps represent the 1–99th percentiles. Fish faeces_p, faeces of cultured fish fed with pellet; Fish faeces_p, faeces of cultured fish fed with trash fish; POM_AR, POM at the AR stations.

The feasible contributions of pellet and faeces of cultured fish fed with pellet on the carbon source of sponge were 0–85% and 3–56% (1–99th percentile), respectively, and the means were 28.2% and 35.8%, respectively. The feasible contributions of POM, trash fish and faeces of cultured fish fed with

trash fish were 0–40%, 0–32% and 0–43% (1–99th percentile), respectively, and the means were 12.5%, 9.9% and 13.5%, respectively.

Although the $\delta^{15}N$ results of Sham Wan samples cannot be fit into the isotope mixing model, it was found that when the average fractionation effect of 3‰ was used to correct stable isotope shift of a trophic level, the fractionation effect-corrected $\delta^{15}N$ values of the epifauna (barnacle: 5.56 ± 0.18‰, fanshell: 6.08 ± 0.49‰, mussel: 5.28 ± 0.16‰, sponge: 4.53 ± 0.55‰, and tunicate: 4.73 ± 0.83‰) were closest to the potential food sources faeces of cultured fish fed with pellet (5.28 ± 0.23‰) and POM (7.16 ± 0.93‰), which may indicate that they depend heavier on faeces of cultured fish fed with pellet and POM for N source, compared with the other potential food sources.

For the use of stable isotopes $\delta^{13}C$ and $\delta^{15}N$ for the determination of trophic relationships, it was commonly accepted that a mean trophic shift for $\delta^{15}C$ is about +1‰ and the mean trophic shift for $\delta^{15}N$ is about +3‰, from diet to consumer (McCutchan et al., 2003; Peterson and Fry, 1987). A study on the uptake of organic wastes by green-lipped mussels *Perna viridis* in a polyculture fish farm in Hong Kong also showed that when assuming that mussels consumed POM exclusively, the $\delta^{13}C_{mussel}$–$\delta^{13}C_{POM}$ and $\delta^{15}N_{mussel}$–$\delta^{15}N_{POM}$ were +1.0‰ and +3.0‰, respectively (Gao et al., 2006), which matched with the commonly agreed mean trophic shift. However, in this study, because the $\delta^{15}N$ values of the epifauna were lower than expected, the dual-isotope results of the epifauna and their potential food sources cannot utilize the isotope mixing model. Two possible reasons can be suggested. First, an important food source may have been missed, especially for Sham Wan in which the $\delta^{15}N$ values of the epifauna were much lower than that of the potential food sources. It has long been recognized that marine organisms also derive nutrition from dissolved organic matters (e.g. free amino acids) (Stephens, 1968; Stewart, 1979). In this study, samples were taken from Sham Wan in August 2008 and from Lo Tik Wan in May 2009, while the dissolved nitrogen in the water of Sham Wan was at its peak, and Lo Tik Wan was eutrophic year round (Tsang, unpublished data). The possibility that the low $\delta^{15}N$ values in the tissue of epifauna was a result of consumption of dissolved nitrogen compounds with relatively low $\delta^{15}N$ values cannot be excluded. Second, although the trophic shift for $\delta^{15}N$ is commonly assumed to be about +3‰ from food to consumer, the range of trophic shift for $\delta^{15}N$ recorded was as large as −0.8‰ to +5.9‰ (excluding fluid-feeding consumers) (McCutchan et al., 2003). The unexpectedly low $\delta^{15}N$ values of epifauna may be due to the variations in trophic shift of $\delta^{15}N$.

For Lo Tik Wan, the results of the IsoSource modelling showed that the feasible range of dietary importance for each food source to the carbon sources of the epifaunal organisms was large. The diet composition of barnacles, fanshells and tunicates were similar, which mainly depended on trash fish, faeces of cultured fish fed with trash fish and POM, while mussels depended more heavily on trash fish and sponges preferentially dieted on pellet food and faeces of cultured fish that were fed with pellet food.

It was expected that in the water column of Lo Tik Wan, the concentration of pellet food was lower compared with those of trash fish and POM, because pellet food was only a minor food source, and lower feed wastage was expected when pellet food was used instead of trash fish, due to the lower production of small particles and higher digestibility (Wu et al., 1994). In this study, most epifaunal organisms depend more on trash fish and POM and less on pellet food for carbon source, which may indicate that they were able to consume nutrients in proportion to their availability. The present findings also indicated that these epifaunal organisms were able to consume a mixture of phytoplanktonic matter and animal tissues. However, as the feasible ranges of dietary importance for each food source to the carbon source of the epifaunal organisms could be large, the present results should only be treated as a rough index. It should also be noted that the "potential food sources of epifauna" in this study were not independent, especially for POM. POM is generally a mixture of different matters, which mainly consists of phytoplankton, bacteria and sedimentary matter resuspended from the seabed, and it is technically difficult to separate specific POM components for analysis (Dalsgaard et al., 2003). Although in this study, POM was obtained by taking water samples near the sea surface to avoid fish farm waste contamination in the POM taken, it is impossible to completely avoid particles of fish feed remains and fish faeces in the POM. Especially, the stable isotope analysis for Sham Wan showed that the stable isotopic compositions in the POM at the AR stations were closer to that of fish feed and fish faeces, compared to POM at the control stations, which implied that POM may contain particles of fish feed remains and fish faeces.

Previous studies suggested that most sessile filter feeders can efficiently consume seston fractions in proportion to their availability (Coma et al., 2001; Hughes, 1980). Gili and Coma (1998) also concluded that benthic sessile suspension feeders are able to feed in the typically stochastic environments they live in and have adapted to a wide spectrum of prey type and size. The results of the food source analysis of the suspension or filter-feeding

epifaunal organisms in Lo Tik Wan agreed with these previous findings. In addition, there were evidences showing that bivalves, ascidians and sponges have different efficiencies in retaining particles of different sizes, in which bivalves prefer larger particles, followed by tunicates and sponges. Stuart and Klumpp (1984) summarized that most bivalve species can retain, completely, all particles greater than 4 μm, while smaller particles are retained with a reduced efficiency; tunicates can retain particles greater than 1–4 μm in diameter completely, while sponges were found to retain very small particles (i.e. bacteria) with the greatest efficiency. The results in this study agreed with these findings on food resource partitioning by suspension or filter feeders, as the bivalves (mussels and fanshells) tended to assimilate a higher proportion of carbon from trash fish, as compared to tunicates and sponges, in which trash fish remains were expected to appear as relatively larger particles in the water compared with other food sources. It is unclear whether the relatively lower $\delta^{13}C$ value in sponges was a result of the consumption of a greater amount of bacteria, because the bacteria were too small to be analysed separately for stable isotope composition.

For sediment, it was observed that higher $\delta^{15}N$ values were found in the sediment at the AR stations, compared to the fish cage and the control stations. The increase in $\delta^{15}N$ values in the sediment at the AR stations was probably due to the die-off of epifauna on the AR surface, which were isotopically heavier and eventually accumulated on the seabed.

4.2. Fatty acid analysis

Lipids are major sources of metabolic energy and essential materials for the formation of cell and tissue membranes. They are extremely important in the physiology and reproductive processes of marine benthic organisms. Lipids are important to the marine environment because of their significant constitution to the total carbon flux through the trophic levels (Lee et al., 1971; Reuss and Poulsen, 2002; Sargent et al., 1977). They are a compact and concentrated form of energy storage for plants and animals and constitute a source of essential nutrients, vitamins and chemical messengers (Napolitano et al., 1997). Fatty acids (FAs), comprising a long hydrocarbon chain bonded with a carboxyl group, constitute the main part of the lipids in marine organisms. They remain unchanged or in recognized form when transferred to high trophic levels (Napolitano et al., 1997; Reuss and Poulsen, 2002). Particular fatty acids, groups of fatty acids and fatty acid ratios can be used as biomarkers of various sources, especially of autotrophic

organisms like phytoplankton, which biosynthesize a great diversity of fatty acids (Budge et al., 2001; Dalsgaard et al., 2003). By examining the fatty acid profiles of various organisms, such analysis can complement stable isotope analysis to determine the food sources of the consumer and elucidate the trophic interactions within complex food webs (Alfaro et al., 2006; Gao et al., 2006). The following data demonstrated the analysis of FA profiles from samples obtained from Section 4.1.2.

4.2.1 Fatty acid extraction and gas chromatography analysis

Lipids of preweighed samples were extracted by a 2:1 dichloromethane–methanol solvent mixture (v/v), overnight, following a slightly modified method of Bligh and Dyer (1959). The crude extract was then washed with 0.04% $CaCl_2$ solution (0.2 of the crude extract's volume). The organic and aqueous layers were separated by centrifugation. The lower layer was dried with a stream of nitrogen, and the extracts were further dried, overnight, in a vacuum desiccator. Fatty acid methyl esters (FAMEs) of the lipids were prepared and determined as follows: 6% H_2SO_4 in methanol was added to the lipid extract and the solution was incubated in an oven at 60 °C for 2 h for esterification. After cooling, 1 ml distilled water and 2 ml petroleum ether were added into the tube and mixed in vortex. The upper organic layer was transferred to a vial and dried by a nitrogen stream. FAMEs were analysed by gas chromatography on a fused silica capillary column (DB-225MS, 30 m × 0.25 mm ID × 0.25 μm film, in a Hewlett Packard model 6890 Series Injector), equipped with flame ionization detector (GC-FID). Fatty acid standards were purchased from Supelco (Supelco 37 component FAME mix, Supelco, Bellefonte, PA). Methyl nonadecanoate (19:0) was used as the internal standard, and the carrier gas was helium with speed of 26 cm s^{-1}. The operating conditions for the GC-FID were as follows: initial column temperature was 50 °C for 2 min and then increased to 210 °C at rate 4 °C min^{-1}. The detector was held at 250 °C, with splitless injector at 240 °C and flame ionization detector. The fatty acids were identified by their respective retention time with reference to those of the standards. Shorthand notation was used for the fatty acid structure X:YnZ, where X represents the carbon chain length, Y is the number of ethylenic bonds and nZ is the position of the double bond closest to the terminal methyl group.

4.2.2 Fatty acid profiles of Sham Wan and Lo Tik Wan samples

The fatty acid profiles of epifauna, organic wastes derived from fish farming activities, POM and sediment are shown in Table 1.6. A total of 23 fatty

Table 1.6 Fatty acid profiles of epifauna, organic wastes derived from fish farming activities, POM and sediment in Sham Wan (mean ± SD; $n = 3$)
(A) Dry weight of fatty acid (mg g^{-1})

	POM_C	POM_AR	Trash fish	Fish faeces	Barnacle	Tunicate	S_C1	S_C2	S_F1	S_F2	S_AR1	S_AR2	S_AR3
Saturated fatty acids													
4:0	ND	ND	5.17 ± 4.60	8.03 ± 1.21	ND	ND	ND	ND	ND	ND	ND	ND	ND
10:0	ND	ND	0.47 ± 0.68	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
11:0	4.33 ± 0.43	3.91 ± 0.48	ND	ND	ND	ND	3.54 ± 0.16	3.47 ± 0.12	3.43 ± 0.11	3.42 ± 0.11	3.45 ± 0.03	3.50 ± 0.15	2.46 ± 2.13
12:0	ND	ND	ND	ND	8.11 ± 0.33	ND	7.15 ± 0.10	7.58 ± 0.41	ND	ND	7.15 ± 0.14	7.19 ± 0.17	7.69 ± 0.54
13:0	4.96 ± 0.88	4.72 ± 1.42	ND	ND	ND	ND	ND	3.69 ± 0.15	3.78 ± 0.18	ND	3.52 ± 0.01	3.57 ± 0.08	3.74 ± 0.18
14:0	58.20 ± 19.61	42.72 ± 21.12	43.36 ± 12.	2.05 ± 0.98	67.17 ± 7.65	19.75 ± 4.92	10.12 ± 0.99	11.65 ± 1.94	11.76 ± 3.04	10.75 ± 2.09	9.59 ± 0.85	9.54 ± 1.29	12.48 ± 1.87
15:0	10.35 ± 2.98	7.80 ± 2.39	3.34 ± 0.15	0.75 ± 0.15	6.36 ± 0.32	5.65 ± 0.65	4.04 ± 0.27	4.34 ± 0.36	4.12 ± 0.39	3.99 ± 0.23	3.93 ± 0.08	4.04 ± 0.19	4.26 ± 0.25
16:0	170.32 ± 67.39	76.24 ± 41.98	106.61 ± 27.61	16.96 ± 3.89	104.02 ± 12.53	44.69 ± 14.58	6.62 ± 2.76	10.69 ± 3.78	6.53 ± 0.62	8.84 ± 4.67	6.39 ± 2.15	6.09 ± 2.69	13.01 ± 3.58
17:0	3.33 ± 1.36	2.40 ± 2.28	4.81 ± 1.89	1.44 ± 0.25	4.83 ± 0.65	4.28 ± 1.15	0.29 ± 0.50	1.11 ± 0.28	0.52 ± 0.47	0.97 ± 0.22	0.79 ± 0.10	0.76 ± 0.17	1.17 ± 0.13
18:0	52.91 ± 26.21	40.87 ± 21.52	27.48 ± 7.35	14.87 ± 6.38	34.50 ± 3.41	22.06 ± 7.56	7.42 ± 2.94	9.26 ± 3.82	4.73 ± 2.45	6.77 ± 3.88	5.22 ± 1.34	4.97 ± 1.80	14.14 ± 9.35
20:0	5.87 ± 1.82	5.99 ± 2.93	0.70 ± 0.86	0.45 ± 0.13	6.14 ± 0.64	3.27 ± 0.31	ND	ND	ND	ND	ND	ND	ND
21:0	3.33 ± 0.82	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Subtotal	313.60 ± 114.33	184.66 ± 93.09	191.95 ± 54.12	44.56 ± 10.15	231.12 ± 25.19	99.70 ± 29.01	39.18 ± 7.14	51.79 ± 10.63	34.87 ± 6.63	34.74 ± 10.80	40.02 ± 4.24	39.66 ± 6.47	58.94 ± 17.02
Monounsaturated fatty acids													
14:1	5.10 ± 0.60	ND	ND	ND	3.94 ± 0.03	ND	ND	ND	ND	ND	ND	3.73 ± 0.04	ND
15:1	0.91 ± 0.81	ND	ND	0.18 ± 0.31	ND	ND	ND	ND	ND	ND	ND	0.31 ± 0.27	0.57 ± 0.01
16:1	76.50 ± 30.87	29.96 ± 14.39	30.99 ± 8.68	1.33 ± 0.42	75.73 ± 10.98	19.63 ± 5.08	1.07 ± 0.39	2.71 ± 0.63	1.21 ± 0.09	1.63 ± 0.87	1.45 ± 0.97	1.38 ± 0.76	2.30 ± 0.48
17:1	3.82 ± 1.42	ND	ND	ND	5.40 ± 0.49	0.96 ± 0.05	ND	ND	ND	ND	ND	ND	ND
18:1n9	47.32 ± 19.90	20.63 ± 15.70	22.27 ± 6.56	3.35 ± 0.96	28.92 ± 3.57	11.61 ± 2.39	0.86 ± 0.10	1.31 ± 0.24	1.05 ± 0.25	1.29 ± 0.51	1.09 ± 0.18	0.91 ± 0.23	1.55 ± 0.18
20:1	ND	ND	ND	ND	2.73 ± 0.26	ND	ND	ND	ND	ND	ND	ND	ND
Subtotal	133.6 4 ± 51.99	50.59 ± 30.05	53.26 ± 15.20	4.86 ± 1.63	116.73 ± 14.84	32.21 ± 7.48	1.92 ± 0.48	4.02 ± 0.87	2.27 ± 0.31	2.92 ± 1.37	2.55 ± 1.09	6.33 ± 0.96	4.41 ± 0.59

Continued

Table 1.6 Fatty acid profiles of epifauna, organic wastes derived from fish farming activities, POM and sediment in Sham Wan (mean ± SD; $n = 3$)—cont'd

(A) Dry weight of fatty acid (mg g^{-1})

	POM_C	POM_AR	Trash fish	Fish faeces	Barnacle	Tunicate	S_C1	S_C2	S_F1	S_F2	S_AR1	S_AR2	S_AR3
Polyunsaturated fatty acids													
18:2n6	18.27 ± 10.75	9.15 ± 7.23	ND	3.18 ± 2.15	5.35 ± 0.62	4.78 ± 1.01	0.65 ± 0.58	1.50 ± 0.47	1.79 ± 0.70	1.15 ± 0.54	0.97 ± 0.06	0.80 ± 0.14	1.75 ± 0.64
18:3n6	2.14 ± 0.74	1.04 ± 0.96	ND	ND	3.32 ± 0.30	1.62 ± 0.31	ND	ND	ND	ND	ND	ND	ND
20:3n3	2.32 ± 0.37	2.30 ± 0.65	0.35 ± 0.13	ND	8.86 ± 0.69	ND	ND	ND	ND	ND	ND	ND	ND
20:5n3	7.77 ± 3.65	6.30 ± 1.11	ND	ND	77.88 ± 8.25	19.56 ± 5.63	ND	ND	ND	ND	ND	ND	ND
22:6n3	ND	ND	ND	ND	35.54 ± 3.04	16.86 ± 5.91	ND	ND	ND	ND	ND	ND	ND
Subtotal	30.50 ± 11.27	18.78 ± 8.69	0.35 ± 0.13	3.18 ± 2.15	130.95 ± 12.59	42.82 ± 12.79	0.65 ± 0.58	1.50 ± 0.47	1.79 ± 0.70	1.15 ± 0.54	0.97 ± 0.06	0.80 ± 0.14	1.75 ± 0.64
Total	447.74 ± 177.22	254.02 ± 131.74	245.56 ± 69.42	52.60 ± 13.08	478.80 ± 43.49	174.73 ± 47.24	41.75 ± 7.44	57.31 ± 11.91	38.93 ± 6.80	38.81 ± 12.68	43.54 ± 5.28	46.78 ± 7.55	65.11 ± 17.54

(B) Percent in total fatty acid

	POM_C	POM_AR	Trash fish	Fish faeces	Barnacle	Tunicate	S_C1	S_C2	S_F1	S_F2	S_AR1	S_AR2	S_AR3
Saturated fatty acids													
4:0	ND	ND	1.90 ± 1.36	16.47 ± 7.26	ND	ND	ND	ND	ND	ND	ND	ND	ND
10:0	ND	ND	0.15 ± 0.20	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
11:0	1.00 ± 0.37	1.75 ± 0.62	ND	ND	ND	ND	8.61 ± 1.16	6.20 ± 1.04	8.97 ± 1.38	9.56 ± 3.48	8.00 ± 0.94	7.59 ± 0.95	3.51 ± 3.13
12:0	ND	ND	ND	ND	1.70 ± 0.11	ND	17.47 ± 2.92	13.51 ± 2.07	ND	ND	16.55 ± 1.78	15.62 ± 2.31	12.21 ± 2.24
13:0	1.11 ± 0.30	2.00 ± 0.48	ND	ND	ND	ND	ND	6.60 ± 1.10	9.88 ± 1.59	ND	8.16 ± 1.02	7.75 ± 1.14	5.96 ± 1.22
14:0	12.41 ± 1.56	17.01 ± 1.04	17.63 ± 0.24	3.79 ± 1.10	14.01 ± 0.43	11.38 ± 0.79	24.49 ± 2.20	20.44 ± 0.81	30.49 ± 7.90	28.77 ± 4.90	22.09 ± 1.31	20.45 ± 0.59	19.56 ± 2.29
15:0	2.27 ± 0.49	3.30 ± 0.69	1.43 ± 0.39	1.48 ± 0.39	1.33 ± 0.06	3.34 ± 0.61	9.82 ± 1.19	7.69 ± 0.91	10.69 ± 0.90	11.07 ± 3.67	9.11 ± 0.95	8.77 ± 1.16	6.87 ± 1.89
16:0	35.34 ± 1.71	29.72 ± 0.89	43.60 ± 0.94	32.38 ± 0.97	21.69 ± 1.01	25.31 ± 1.80	15.43 ± 3.75	18.32 ± 2.63	16.26 ± 6.42	21.50 ± 6.53	14.39 ± 3.21	12.60 ± 3.88	20.01 ± 1.32
17:0	0.69 ± 0.09	0.87 ± 0.52	1.92 ± 0.19	2.79 ± 0.29	1.01 ± 0.06	2.45 ± 0.07	0.59 ± 1.02	1.92 ± 0.10	1.32 ± 1.14	2.62 ± 0.70	1.82 ± 0.13	1.61 ± 0.12	1.84 ± 0.27
18:0	10.97 ± 2.55	15.96 ± 2.91	11.22 ± 0.36	27.25 ± 6.39	7.21 ± 0.44	12.49 ± 1.27	17.38 ± 5.30	15.73 ± 3.16	11.83 ± 4.36	16.41 ± 5.31	11.90 ± 2.29	10.37 ± 2.34	20.28 ± 8.22

20:0	1.27 ± 0.24	2.39 ± 0.21	0.33 ± 0.45	0.91 ± 0.41	1.28 ± 0.05	1.96 ± 0.49	ND	ND	ND	ND	ND	ND	ND
21:0	0.73 ± 0.13	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Subtotal	65.79 ± 0.60	73.01 ± 1.06	78.18 ± 0.20	85.07 ± 2.27	48.23 ± 1.82	56.94 ± 2.90	93.78 ± 1.76	90.40 ± 0.54	89.45 ± 1.81	89.93 ± 1.89	92.03 ± 1.51	84.76 ± 0.36	90.23 ± 2.22
Monounsaturated fatty acids													
14:1	1.17 ± 0.42	ND	ND	ND	0.83 ± 0.07	ND	ND	ND	ND	ND	ND	8.11 ± 1.32	ND
15:1	0.16 ± 0.14	ND	ND	0.31 ± 0.53	ND	ND	ND	ND	ND	ND	ND	0.69 ± 0.63	0.91 ± 0.20
16:1	15.86 ± 1.38	11.96 ± 0.54	12.63 ± 0.38	2.51 ± 0.33	15.76 ± 0.94	11.27 ± 0.19	2.50 ± 0.48	4.71 ± 0.13	3.15 ± 0.32	3.95 ± 1.20	3.21 ± 1.81	2.81 ± 1.27	3.76 ± 1.53
17:1	0.80 ± 0.08	ND	ND	ND	1.13 ± 0.06	0.58 ± 0.17	ND	ND	ND	ND	ND	ND	ND
18:1n9c	9.80 ± 0.97	7.52 ± 1.81	9.05 ± 0.19	6.35 ± 0.80	6.04 ± 0.43	6.74 ± 0.57	ND	2.29 ± 0.08	2.71 ± 0.41	3.26 ± 0.29	2.51 ± 0.21	1.93 ± 0.18	2.46 ± 0.59
20:1	ND	ND	ND	ND	0.57 ± 0.04	ND	ND	ND	ND	ND	ND	ND	ND
Subtotal	27.79 ± 0.88	19.48 ± 1.47	21.68 ± 0.22	9.17 ± 1.63	24.33 ± 1.14	18.59 ± 0.92	4.57 ± 0.38	7.01 ± 0.06	5.86 ± 0.49	7.21 ± 1.48	5.72 ± 1.80	13.54 ± 0.35	7.13 ± 2.29
Polyunsaturated fatty acids													
18:2n6c	3.68 ± 1.15	3.28 ± 0.91	ND	5.76 ± 2.90	1.12 ± 0.05	2.77 ± 0.21	1.65 ± 1.62	2.60 ± 0.51	4.69 ± 1.96	2.87 ± 0.54	2.26 ± 0.29	1.70 ± 0.04	2.65 ± 0.27
18:3n6	0.46 ± 0.05	0.35 ± 0.31	ND	ND	0.69 ± 0.03	0.94 ± 0.09	ND	ND	ND	ND	ND	ND	ND
20:3n3	0.52 ± 0.15	1.02 ± 0.45	0.14 ± 0.02	ND	1.86 ± 0.17	ND	ND	ND	ND	ND	ND	ND	ND
20:5n3	1.76 ± 0.79	2.86 ± 1.15	ND	ND	16.32 ± 1.80	11.23 ± 1.55	ND	ND	ND	ND	ND	ND	ND
22:6n3	ND	ND	ND	ND	7.46 ± 0.88	9.53 ± 1.57	ND	ND	ND	ND	ND	ND	ND
Subtotal	6.42 ± 0.48	7.52 ± 0.41	0.14 ± 0.02	5.76 ± 2.90	27.44 ± 2.89	24.47 ± 3.08	1.65 ± 1.62	2.60 ± 0.51	4.69 ± 1.96	2.87 ± 0.54	2.87 ± 0.54	1.70 ± 0.04	2.65 ± 0.27
Total	100	100	100	100	100	100	100	100	100	100	100	100	100

POM_C, POM at control stations; POM_AR, POM at AR stations; S_C1, sediment at C1 station, S_C2, sediment at C2 station and so on. ND, not detected.

acids were identified, including 12 saturated fatty acids, six monounsaturated fatty acids and five polyunsaturated fatty acids. The saturated fatty acids 14:0, 16:0 and 18:0 were found to be the most dominant fatty acids and were ubiquitous among all samples, which corresponded to 2.2–39.4%, 8.4–44.3% and 6.8–31.9% of total fatty acids, respectively.

The fatty acid profiles of POM at the control stations and POM at the AR stations were similar, and both of them contained a number of common phytoplankton biomarkers, including the brown algae biomarker 18:1n9 (6.4–10.9%), the green algae biomarker 18:2n6 (2.6–5.0%) and the diatom biomarkers 20:5n3 (0.8–3.6%) and 16:1 (11.5–17.5%). A higher proportion of these fatty acids were found in the tissue of epifauna (11.1–16.3% of 18:2n6, 5.8–6.5% of 18:1n9, and 1.1–3.0% of 18:2n6) compared to POM. It was also noted that, among these phytoplankton biomarkers, the diatom biomarker 20:5n3 was accumulated in the highest concentration (9.8–18.0%) in the epifauna. Although trash fish and POM shared most of the saturated fatty acids and monounsaturated fatty acids, only one polyunsaturated fatty acid (20:3n3) was found in trash fish, compared to four polyunsaturated fatty acids (18:2n6, 18:3n6, 20:3n3 and 20:5n3) found in POM. Fish faeces shared most of the fatty acids with trash fish. 20:3n3 was only found in trash fish ($0.14 \pm 0.02\%$), and 15:1 and 18:2n6 were only found in fish faeces ($0.3 \pm 0.5\%$ and $5.8 \pm 2.9\%$, respectively). Although the fatty acid 22:6n3 (DHA) was not detected in any of the potential food sources of epifauna, it was found to be abundant in both barnacles ($7.5 \pm 0.9\%$) and tunicates ($9.5 \pm 1.6‰$).

Fatty acid profiles were compared among epifauna, POM, fish farm wastes and sediment using principal component analysis (PCA), and the PCA ordination plots are shown in Figure 1.11. The number of fatty acids was reduced by excluding 21:0, 14:1, 15:1 and 20:1, which had the lowest effects on principal component (PC) loadings in the PCA. The results showed that 79.6% of the variability among samples was explained by the first three PCs. PC1, PC2 and PC3 explained 47.0%, 19.9% and 12.7% of the variability, respectively. PC1 (47.0%) explained the differences in fatty acid profiles between sediment (positive PC1 scores) and the other samples including epifauna, POM and fish farm wastes (negative PC1 scores), as sediment contained a comparatively higher proportion of saturated fatty acids (84.4–95.7%) compared with the other samples ($\leq$85%). Many of these saturated fatty acids in sediment were odd carbon-number fatty acids (11:0, 13:0 and 15:0). PC2 (19.9%) mainly explained the differences in fatty acid profiles between "epifauna and POM" (positive PC2 scores) and "fish farm

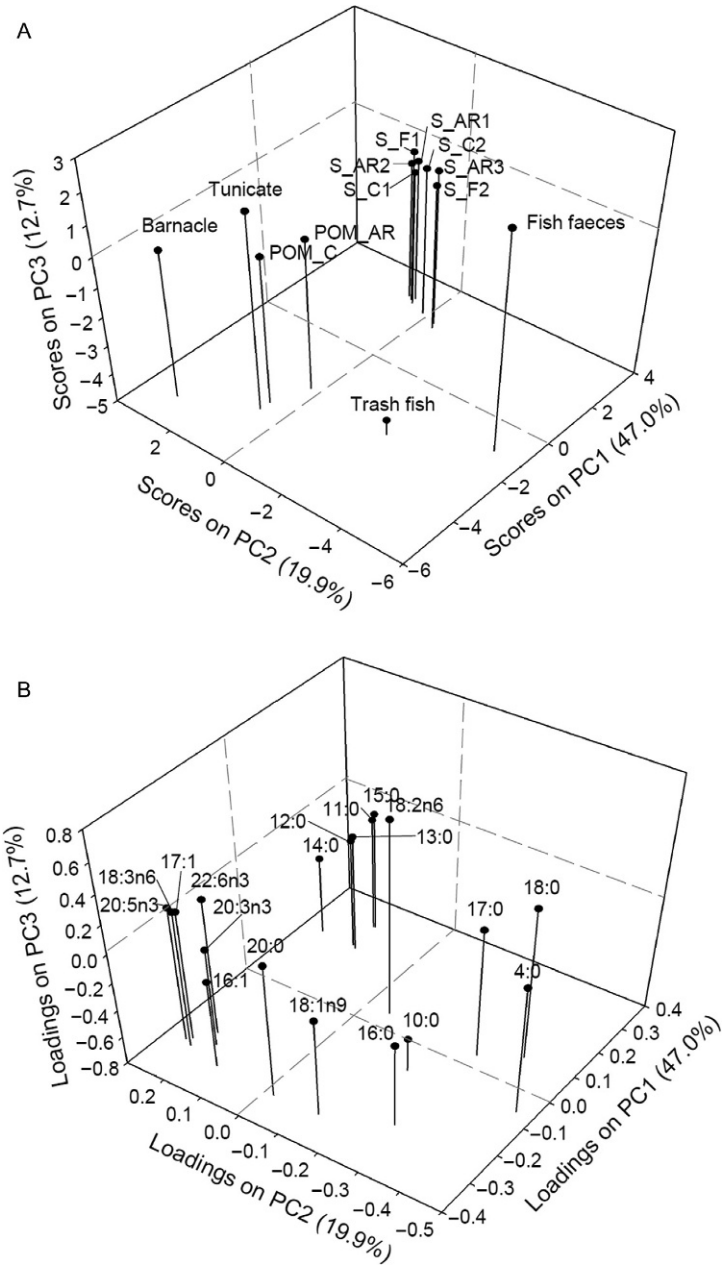

Figure 1.11 PCA ordination plots showing the relationships of fatty acid profiles of epifauna, organic wastes derived from fish farming activities, POM and sediment in Sham Wan. (A) Scores on the first three principal components (PC1 to PC3). (B) Loadings on the first three principal components (PC1 to PC3). The bracketed numbers represent the percentages of variance in fatty acid profiles that were explained by the principal component. POM_C, POM at control stations; POM_AR, POM at AR stations; S_C1, sediment at C1 station, S_C2, sediment at C2 station and so on.

wastes" (negative PC2 scores), as both POM and epifauna contained comparatively higher proportions of unsaturated fatty acids ($\geq 30\%$). In addition, on the score plot, epifauna was positioned further away from the origin shared by the axes of PC1 and PC2. Epifauna had higher scores on PC1 and PC2, compared to POM, as higher concentrations of the unsaturated fatty acids 18:2n6, 18:3n6, 20:3n3 and 20:5n3 were found in the tissue of epifauna. PC3 (12.7%) mainly explained the differences in fatty acid profiles between trash fish and fish faeces, as fish faeces contained an especially high proportion of 4:0 ($16.5 \pm 7.3\%$).

The fatty acid profiles of Lo Tik Wan are shown in Table 1.7. A total of 27 fatty acids were identified in the epifauna (barnacle *Balanus* spp., fanshell *Isognomon perna*, mussel *Perna viridis*, sponge *Mycale adhaerens* and tunicate *Styela plicata*), organic wastes derived from fish farming activities (trash fish, faeces of cultured fish fed with trash fish, pellet and faeces of cultured fish fed with pellet), POM and sediment samples of Lo Tik Wan, including 12 saturated fatty acids, six monounsaturated fatty acids and nine polyunsaturated fatty acids. As seen in Sham Wan, the ubiquitous phytoplankton biomarkers 14:0, 16:0 and 18:0 (Hu et al., 2006) were the most dominant fatty acids in Lo Tik Wan, and they were found in all samples, which corresponded to 2.85–14.4%, 19.3–41.8% and 5.4–38.3% of total fatty acids, respectively.

Fatty acid profiles were compared among different samples using PCA, and the PCA ordination plots are shown in Figure 1.12. The number of fatty acids was reduced by excluding 4:0, 17:0, 24:0, 14:1, 15:1, 16:1, 17:1 and 22:2, which had the lowest effects on PC loadings in the PCA analysis. The results showed that 70.2% of variability among samples was explained by the first three PCs. PC1, PC2 and PC3 explained 40.0%, 17.1% and 13.0% of the variability, respectively.

PC1 (40.0%) mainly accounted the differences in fatty acid profiles between pellet, faeces of cultured fish fed with pellet and trash fish and the other samples including epifauna, faeces of cultured fish fed with trash fish and sediment. It is because they contained relatively higher proportion of unsaturated fatty acids, as compared with other samples (5–45%), and they also contained unique fatty acids, including 20:2 and 22:6n3. PC2 (17.1%) mainly explained the differences in the fatty acid profiles between the "trash fish" and "pellet and faeces of cultured fish fed with pellet". The trash fish contained several unique fatty acids or fatty acids that were in much higher proportion compared with the other samples, including 20:0 ($7.6 \pm 1.3\%$), 21:0 ($3.5 \pm 1.4\%$), 18:3n3 ($2.9 \pm 1.3\%$) and 20:3n3 ($9.9 \pm 4.8\%$), while the pellets and faeces of cultured fish fed with pellets contained a much higher

Table 1.7 Fatty acid profiles of epifauna, organic wastes derived from fish farming activities, POM and sediment in Lo Tik Wan (mean ± SD; $n = 3$, except for fanshells, mussels, sponges and tunicates where $n = 9$)

(A) Dry weight of fatty acid (mg g^{-1})

	POM_C	POM_AR	Pellet	Trash fish	Fish faeces_p	Fish faeces_t	Barnacle	Fanshell	Mussel	Sponge	Tunicate	S_C1	S_C2	S_F1	S_F2	S_AR1	S_AR2	S_AR3
Saturated fatty acids																		
4:0	ND	ND	ND	ND	ND	9.15 ± 1.81	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
12:0	0.71 ± 1.24	0.18 ± 0.32	ND	0.31 ± 0.54	ND	1.05 ± 0.58	0.81 ± 0.28	0.06 ± 0.18	ND	0.04 ± 0.13	0.09 ± 0.27	0.98 ± 0.34	1.05 ± 0.06	1.38 ± 0.92	1.22 ± 0.84	0.23 ± 0.40	0.80 ± 0.07	ND
13:0	ND	0.55 ± 0.60	ND	ND	ND	0.23 ± 0.40	ND	1.47 ± 4.13	ND	ND	ND	1.08 ± 1.34	0.43 ± 0.38	ND	0.88 ± 1.11	ND	0.27 ± 0.47	0.67 ± 0.64
14:0	10.89 ± 3.45	3.22 ± 0.54	16.20 ± 3.00	13.58 ± 5.41	16.69 ± 4.58	9.45 ± 12.64	21.80 ± 12.15	20.29 ± 13.05	22.71 ± 8.27	4.38 ± 1.87	19.08 ± 5.15	3.65 ± 1.44	3.10 ± 0.82	3.98 ± 2.06	3.52 ± 2.92	2.80 ± 0.85	2.41 ± 0.33	2.24 ± 1.17
15:0	ND	1.28 ± 0.05	ND	4.57 ± 0.18	4.87 ± 0.73	1.83 ± 2.75	3.22 ± 1.77	3.24 ± 1.65	2.18 ± 0.96	0.65 ± 0.52	1.69 ± 1.09	2.06 ± 0.71	1.72 ± 0.32	0.94 ± 0.11	2.40 ± 1.16	1.01 ± 0.09	0.64 ± 0.55	1.02 ± 1.10
16:0	30.59 ± 9.54	10.87 ± 1.72	51.94 ± 16.58	136.37 ± 16.58	63.65 ± 32.77	62.85 ± 80.87	64.85 ± 40.01	77.74 ± 27.63	37.04 ± 30.53	14.17 ± 7.37	44.69 ± 12.74	12.03 ± 5.05	10.34 ± 2.36	10.43 ± 5.51	14.7 ± 4.81	8.19 ± 2.40	9.91 ± 1.85	6.53 ± 4.20
17:0	ND	1.25 ± 0.16	1.85 ± 0.49	6.99 ± 0.31	2.28 ± 1.09	2.79 ± 3.18	5.18 ± 3.00	6.39 ± 1.77	4.50 ± 1.31	1.62 ± 0.34	3.77 ± 1.04	1.29 ± 0.22	1.17 ± 0.13		1.51 ± 0.39	0.64 ± 0.56	0.75 ± 0.65	0.34 ± 0.60
18:0	28.84 ± 8.08	14.59 ± 2.39	14.48 ± 4.29	65.28 ± 10.89	18.52 ± 9.20	34.12 ± 30.09	30.37 ± 16.32	34.16 ± 8.62	27.68 ± 7.05	15.39 ± 4.65	25.12 ± 6.12	6.30 ± 2.96	6.66 ± 1.05	7.18 ± 3.10	6.66 ± 3.73	5.20 ± 2.90	4.64 ± 0.32	3.29 ± 1.33
20:0	ND	ND	ND	36.27 ± 6.31	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
21:0	ND	ND	ND	16.71 ± 6.45	ND	ND	ND	0.17 ± 0.52	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
22:0	ND	ND	25.65 ± 8.25	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
24:0	ND	ND	ND	ND	ND	ND	ND	ND	ND	11.65 ± 7.09	ND	ND	ND	ND	ND	ND	ND	ND

Continued

Table 1.7 Fatty acid profiles of epifauna, organic wastes derived from fish farming activities, POM and sediment in Lo Tik Wan (mean ± SD; $n = 3$, except for fanshells, mussels, sponges and tunicates where $n = 9$)—cont'd

(A) Dry weight of fatty acid (mg g^{-1})

	POM_C	POM_AR	Pellet	Trash fish	Fish faeces_p	Fish faeces_t	Barnacle	Fanshell	Mussel	Sponge	Tunicate	S_C1	S_C2	S_F1	S_F2	S_AR1	S_AR2	S_AR3
Subtotal	72.06 ± 22.70	31.94 ± 4.44	110.12 ± 32.61	280.08 ± 21.79	106.01 ± 48.31	121.46 ± 132.17	126.23 ± 73.52	143.52 ± 49.12	94.12 ± 36.17	47.90 ± 19.01	94.43 ± 24.34	27.38 ± 11.95	24.48 ± 5.08	23.91 ± 9.69	30.90 ± 14.38	18.08 ± 6.66	19.42 ± 1.50	14.10 ± 7.44
Monounsaturated fatty acids																		
14:1	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
15:1	ND	ND	ND	ND	ND	0.99 ± 0.27	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
16:1	2.84 ± 0.60	2.99 ± 0.51	15.29 ± 5.03	38.93 ± 10.59	16.38 ± 8.51	ND	13.74 ± 7.57	15.28 ± 6.94	31.70 ± 11.52	5.43 ± 2.10	25.70 ± 7.09	3.49 ± 1.41	2.38 ± 0.81	1.08 ± 0.95	4.09 ± 0.89	1.40 ± 0.31	2.08 ± 0.53	1.50 ± 1.47
17:1	ND	ND	0.75 ± 1.29	ND	ND	ND	0.46 ± 0.80	0.72 ± 0.55	1.08 ± 0.66	0.31 ± 0.62	ND	ND	ND	ND	ND	ND	ND	ND
18:1n9	0.93 ± 0.85	2.68 ± 0.30	60.62 ± 21.52	42.91 ± 6.30	110.03 ± 62.42	3.82 ± 2.94	7.62 ± 4.58	13.67 ± 8.44	3.47 ± 1.12	2.46 ± 1.56	14.43 ± 15.84	3.50 ± 2.00	3.46 ± 0.70	1.96 ± 0.61	3.52 ± 1.39	1.55 ± 0.39	2.21 ± 0.07	1.59 ± 0.58
20:1	ND	ND	8.21 ± 3.08	3.12 ± 0.68	9.27 ± 5.47	ND	1.02 ± 1.76	1.94 ± 2.00	9.34 ± 3.50	ND	ND	ND	ND	ND	ND	ND	ND	ND
Subtotal	3.77 ± 1.42	5.67 ± 0.59	84.86 ± 30.05	84.96 ± 11.84	135.69 ± 76.33	4.82 ± 2.81	22.83 ± 14.71	31.94 ± 15.91	45.59 ± 16.72	8.21 ± 2.87	40.13 ± 15.22	6.99 ± 3.40	5.84 ± 1.51	3.04 ± 0.67	7.61 ± 2.23	2.95 ± 0.70	4.29 ± 0.60	3.09 ± 2.02
Polyunsaturated fatty acids																		
18:2n6	ND	4.26 ± 0.56	35.91 ± 11.48	7.32 ± 2.20	56.47 ± 28.36	ND	4.03 ± 3.32	6.96 ± 4.61	4.77 ± 2.05	2.13 ± 1.33	2.36 ± 1.10	4.16 ± 3.25	4.07 ± 1.96	1.96 ± 0.17	5.71 ± 4.32	0.66 ± 0.01	1.73 ± 0.55	0.98 ± 0.94
18:3n6	ND	ND	3.22 ± 0.72	0.50 ± 0.18	1.74 ± 0.62	ND	0.81 ± 0.85	ND	0.28 ± 0.51	ND	ND	ND	ND	ND	ND	ND	ND	ND
18:3n3	ND	ND	ND	13.80 ± 5.89	3.11 ± 2.70	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
20:2	ND	ND	1.54 ± 0.36	1.51 ± 1.31	3.25 ± 1.59	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND

20:3n6	ND	ND	ND	0.97 ± 1.68	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
20::3n3	ND	ND	4.09 ± 0.48	46.94 ± 23.74	2.65 ± 0.94	ND	14.18 ± 8.84	6.79 ± 10.51	25.35 ± 8.54	4.91 ± 1.78	6.24 ± 2.88	ND	ND	ND	ND	ND	ND	ND
20:5n3	ND	ND	ND	ND	10.63 ± 4.61	ND	ND	ND	ND	2.33 ± 1.75	ND	ND	ND	ND	ND	ND	ND	ND
22:2	ND	ND	ND	19.93 ± 7.37	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
22:6n3	ND	ND	28.38 ± 8.31	19.62 ± 7.87	17.29 ± 7.69	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Subtotal	ND	4.26 ± 0.56	73.13 ± 21.00	110.60 ± 7.54	95.14 ± 44.71	ND	19.02 ± 12.99	13.75 ± 12.79	30.39 ± 9.79	9.38 ± 4.37	8.60 ± 3.67	4.16 ± 3.25	4.07 ± 1.96	1.96 ± 0.17	5.71 ± 4.32	0.66 ± 0.01	17.3 ± 0.55	0.98 ± 0.94
Total	75.83 ± 23.98	41.88 ± 5.41	268.11 ± 83.63	475.63 ± 30.50	336.84 ± 164.20	126.28 ± 134.97	168.08 ± 101.184	189.21 ± 75.56	170.10 ± 50.51	65.48 ± 24.51	143.16 ± 31.57	38.54 ± 18.58	34.40 ± 8.36	28.91 ± 9.76	44.21 ± 20.86	21.68 ± 5.99	25.43 ± 2.63	18.17 ± 10.17

(B) Percent in total fatty acid

	POM_C	POM_AR	Pellet	Trash fish	Fish faeces_p	Fish faeces_t	Barnacle	Fanshell	Mussel	Sponge	Tunicate	S_C1	S_C2	S_F1	S_F2	S_AR1	S_AR2	S_AR3
Saturated fatty acids																		
4:0	ND	ND	ND	ND	ND	13.26 ± 9.34	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
12:0	0.69 ± 1.20	0.41 ± 0.71	ND	0.07 ± 0.12	ND	1.26 ± 0.74	0.53 ± 0.13	0.03 ± 0.10	ND	0.10 ± 0.30	0.05 ± 0.17	2.68 ± 0.46	3.17 ± 0.67	5.34 ± 4.24	2.60 ± 0.53	0.79 ± 1.36	3.20 ± 0.58	ND
13:0	ND	1.32 ± 1.33	ND	ND	ND	0.08 ± 0.14	ND	1.24 ± 3.50	ND	ND	ND	2.08 ± 2.25	1.11 ± 0.96	ND	1.62 ± 1.57	ND	1.17 ± 2.02	5.39 ± 7.31
14:0	14.36 ± 0.06	7.68 ± 0.77	6.25 ± 1.00	2.85 ± 1.05	5.38 ± 1.31	5.65 ± 2.68	13.18 ± 0.53	9.87 ± 4.05	13.32 ± 3.46	6.95 ± 2.22	13.32 ± 1.94	9.79 ± 0.97	9.00 ± 0.27	13.44 ± 5.00	7.47 ± 4.39	12.79 ± 1.19	9.44 ± 0.48	12.84 ± 2.76
15:0	1.32 ± 1.28	3.09 ± 0.30	ND	0.96 ± 0.04	1.65 ± 0.65	1.06 ± 0.93	1.96 ± 0.09	1.68 ± 0.68	1.27 ± 0.41	1.12 ± 0.92	1.22 ± 0.72	5.61 ± 0.85	5.05 ± 0.34	3.53 ± 1.26	5.41 ± 0.16	4.88 ± 1.47	2.66 ± 2.30	4.31 ± 3.86
16:0	40.38 ± 1.08	25.89 ± 0.82	19.33 ± 0.19	28.62 ± 2.08	18.52 ± 3.55	38.83 ± 18.99	38.35 ± 0.69	41.78 ± 2.99	21.28 ± 14.21	20.59 ± 7.03	31.06 ± 4.14	31.99 ± 2.52	30.12 ± 1.01	34.71 ± 6.19	34.60 ± 4.58	37.42 ± 0.16	38.75 ± 3.18	34.57 ± 4.52

Continued

Table 1.7 Fatty acid profiles of epifauna, organic wastes derived from fish farming activities, POM and sediment in Lo Tik Wan (mean ± SD; $n = 3$, except for fanshells, mussels, sponges and tunicates where $n = 9$)—cont'd

(B) Percent in total fatty acid

	POM_C	POM_AR	Pellet	Trash fish	Fish faeces_p	Fish faeces_t	Barnacle	Fanshell	Mussel	Sponge	Tunicate	S_C1	S_C2	S_F1	S_F2	S_AR1	S_AR2	S_AR3
17:0	ND	3.00 ± 0.45	0.70 ± 0.04	1.47 ± 0.07	0.68 ± 0.01	2.17 ± 0.57	3.11 ± 0.08	3.57 ± 0.66	2.66 ± 0.26	2.63 ± 0.57	2.64 ± 0.42	3.76 ± 1.33	3.50 ± 0.57	ND	3.63 ± 0.66	2.80 ± 2.62	2.83 ± 2.45	2.17 ± 3.77
18:0	38.31 ± 1.75	34.81 ± 2.96	5.42 ± 0.11	13.71 ± 1.97	5.43 ± 1.00	32.04 ± 8.44	18.49 ± 1.08	19.22 ± 3.69	16.65 ± 0.59	24.08 ± 2.89	17.71 ± 2.93	16.58 ± 1.50	19.67 ± 1.91	24.55 ± 4.80	14.70 ± 3.09	22.77 ± 6.47	18.46 ± 3.11	19.15 ± 3.18
20:0	ND	ND	ND	7.63 ± 1.26	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
21:0	ND	ND	ND	3.54 ± 1.43	ND	ND	ND	0.14 ± 0.43	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
22:0	ND	ND	9.54 ± 0.12	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
24:0	ND	ND	ND	ND	ND	ND	ND	ND	ND	17.00 ± 5.72	ND	ND	ND	ND	ND	ND	ND	ND
Subtotal	95.06 ± 1.01	76.2 ± 0.99	41.25 ± 0.84	58.85 ± 0.83	31.66 ± 4.33	94.36 ± 2.98	75.62 ± 1.46	77.54 ± 5.75	55.17 ± 0.94	72.47 ± 6.81	66.00 ± 7.97	72.48 ± 4.94	71.63 ± 2.87	81.56 ± 5.81	70.04 ± 0.92	81.45 ± 0.97	76.49 ± 2.01	78.43 ± 2.68
Monounsaturated fatty acids																		
14:1	ND	ND	ND	ND	ND	ND	ND	0.28 ± 0.85	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
15:1	ND	ND	ND	ND	ND	1.58 ± 1.11	ND	ND	ND	ND	ND	ND	ND	ND	ND	0.69 ± 1.19	ND	ND
16:1	3.82 ± 0.40	7.12 ± 0.37	5.68 ± 0.16	8.18 ± 2.05	4.86 ± 0.40	ND	8.33 ± 0.43	7.98 ± 0.68	18.56 ± 4.85	8.53 ± 1.87	17.91 ± 2.42	9.33 ± 0.82	6.86 ± 0.95	3.66 ± 3.36	9.95 ± 2.48	6.93 ± 2.87	8.10 ± 1.20	6.61 ± 5.73
17:1	ND	ND	0.25 ± 0.43	ND	ND	ND	0.16 ± 0.28	0.32 ± 0.24	0.60 ± 0.40	0.55 ± 1.21	ND	ND	ND	ND	ND	ND	ND	ND
18:1n9	1.12 ± 0.97	6.49 ± 1.26	22.36 ± 1.27	9.00 ± 0.90	32.42 ± 4.75	4.06 ± 2.12	4.53 ± 0.06	6.88 ± 1.40	2.03 ± 0.38	4.51 ± 4.83	10.01 ± 10.90	8.72 ± 1.38	10.19 ± 1.33	7.66 ± 3.92	8.13 ± 0.61	7.75 ± 3.47	8.72 ± 0.62	9.57 ± 2.54

20:1	ND	ND	3.01 ± 0.25	0.65 ± 0.12	2.74 ± 0.54	ND	0.36 ± 0.62	0.95 ± 1.01	5.42 ± 1.38	ND	ND	ND	ND	ND	ND	ND	ND	ND
Subtotal	4.94 ± 1.01	13.61 ± 1.19	31.30 ± 1.71	17.83 ± 1.68	40.02 ± 5.70	5.64 ± 2.98	13.38 ± 0.54	16.41 ± 1.82	26.61 ± 6.92	13.58 ± 6.23	27.92 ± 8.75	18.04 ± 0.87	17.05 ± 1.92	11.32 ± 4.66	18.08 ± 3.08	15.37 ± 5.14	16.81 ± 0.63	16.18 ± 3.24
Polyunsaturated fatty acids																		
18:2n6	ND	10.18 ± 0.31	13.36 ± 0.14	1.53 ± 0.43	16.75 ± 0.66	ND	2.20 ± 0.49	3.35 ± 1.47	2.69 ± 0.79	2.99 ± 1.28	1.61 ± 0.50	9.47 ± 4.33	11.32 ± 3.44	7.12 ± 1.57	11.88 ± 3.30	3.18 ± 0.84	6.70 ± 1.42	5.39 ± 3.87
18:3n6	ND	ND	1.25 ± 0.31	0.10 ± 0.03	0.54 ± 0.09	ND	0.40 ± 0.27	ND	0.16 ± 0.30	ND	ND	ND	ND	ND	ND	ND	ND	ND
18:3n3	ND	ND		2.92 ± 1.28	0.77 ± 0.68	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
20:2	ND	ND	0.59 ± 0.07	0.33 ± 0.28	0.99 ± 0.19	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
20:3n6	ND	ND		0.20 ± 0.35	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
20:3n3	ND	ND	1.61 ± 0.39	9.87 ± 4.82	0.83 ± 0.12	ND	8.40 ± 0.69	2.69 ± 4.04	15.37 ± 5.22	7.65 ± 1.38	4.47 ± 1.77	ND	ND	ND	ND	ND	ND	ND
20:5n3	ND	ND	ND	ND	3.23 ± 0.69	ND	ND	ND	ND	3.30 ± 1.69	ND	ND	ND	ND	ND	ND	ND	ND
22:2	ND	ND	ND	4.22 ± 1.63	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
22:6n3	ND	ND	10.64 ± 0.56	4.15 ± 1.70	5.21 ± 1.06	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Subtotal	0.00 ± 0.00	10.18 ± 0.31	27.46 ± 0.89	23.32 ± 2.22	28.32 ± 1.37	0.00 ± 0.00	11.00 ± 0.92	6.05 ± 4.35	18.22 ± 5.27	13.94 ± 3.08	6.08 ± 2.06	9.47 ± 4.33	11.32 ± 3.44	7.12 ± 1.57	11.88 ± 3.30	3.18 ± 0.84	6.70 ± 1.42	5.39 ± 3.87
Total	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100

POM_C, POM at control stations; POM_AR, POM at AR stations; Fish faeces_p, faeces of cultured fish fed with feed pellet; Fish faeces_t, faeces of cultured fish fed with trash fish; S_C1, sediment at C1 station and S_C2, sediment at C2 station and so on. ND, not detected.

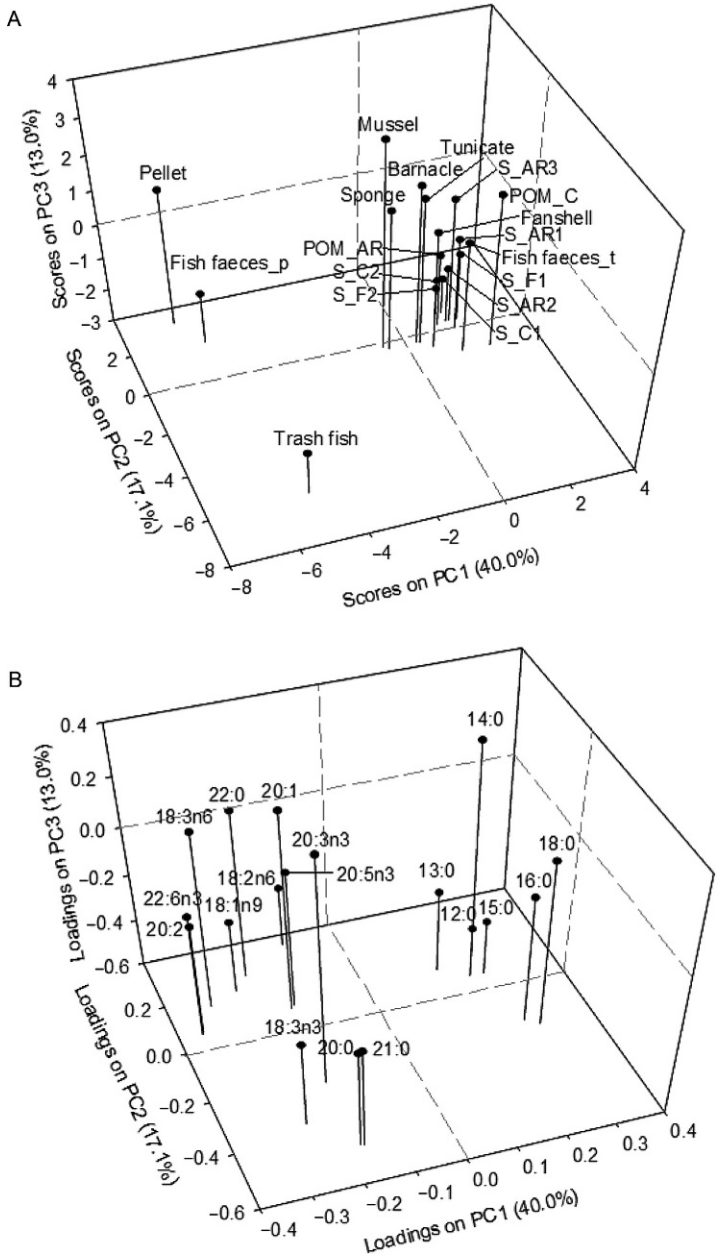

Figure 1.12 PCA ordination plots showing the relationship of fatty acid profiles of epifauna, organic wastes derived from fish farming activities, POM and sediment in Lo Tik Wan. (A) Scores on the first three principal components (PC1 to PC3). (B) Loadings on the first three principal components (PC1 to PC3). The bracketed numbers represent the percentages of variance in fatty acid profiles that were explained by the principal component. POM_C, POM at control stations; POM_AR, POM at AR stations; Fish faeces_p, faeces of cultured fish fed with pellet; Fish faeces_t, faeces of cultured fish fed with trash fish; S_C1, sediment at C1 station; S_C2, sediment at C2 station and so on.

proportion of 18:1n9 (22.4 ± 1.3% and 32.4 ± 4.8%) and 18:2n6 (13.4 ± 0.1% and 16.8 ± 0.7%), compared to trash fish (9.0 ± 0.9% of 18:1n9 and 1.5 ± 0.4% of 18:2n6). PC3 (13.0%) mainly explained the differences in fatty acid profiles between "POM at the control stations and POM at the AR stations" and "pellet and faeces of cultured fish fed with pellet". Although POM at the control stations and POM at the AR stations shared a number of common phytoplankton biomarkers, including the diatom biomarker 16:1 (3.8 ± 0.4% at the control stations and 7.1 ± 0.4% at the AR stations) and the brown algae biomarker 18:1n9 (1.1 ± 1.0% at the control stations and 6.5 ± 1.3% at the AR stations), the POM at the AR stations contained additional fatty acids that were not found in POM at the control stations, including 17:0 (3.0 ± 0.5%) and 18:2n6 (10.2 ± 0.3%).

Although the fatty acid profiles of different epifaunal organisms cannot be clearly differentiated by the PCA scores plot, some clear differences can still be found in their fatty acid compositions. Sponges contained a high proportion of 24:0 (17:0 ± 5.7%), which was not detected in any of the other samples. It also contained 20:5n3, which was unique among the epifaunal organisms. Mussels were characterized by containing a much higher proportion of 20:3n3 (15.4 ± 5.2%), as compared with other epifaunal organisms (<9%).

The fatty acid analysis results showed that a number of common phytoplankton biomarkers, including the brown algae biomarker 18:1n9, the green algae biomarker 18:2n6 and the diatom biomarkers 20:5n3 and 16:1, were abundant in the tissue of epifauna in Sham Wan, which may be due to the consumption of POM by epifauna and the eventual accumulation of these fatty acids. As the fatty acid profile in trash fish largely overlapped with that of POM, the relative dependency of barnacles and tunicates on these two food sources could not be distinguished by fatty acid analysis. Nevertheless, unique isotopic compositions were found on these two epifaunal organisms, and the results of isotopic analysis indicated that barnacles consumed a higher proportion of carbon from trash fish and a lower proportion of carbon from POM, compared to tunicates in Sham Wan.

Data of fatty acid analysis supported the IsoSource modelling results in Section 4.1.5 that mussels consumed a higher proportion of trash fish in their diet compared with other epifaunal organisms, as especially higher concentrations of 20:3n3 (15.4 ± 5.2%) were found in mussels; this fatty acid was present in especially high concentration of trash fish (9.9 ± 4.8%), compared with the other food sources. The results of fatty acid analysis also supported the results of IsoSource modelling that sponges consumed a higher

proportion of faeces of cultured fish that were fed with pellet food, as sponges were the only epifaunal organism that contained 20:5n3, while the faeces of cultured fish fed with pellet food uniquely contained this fatty acid among all the food sources.

Previous studies on Demospongiae (the class of sponge that *Mycale adhaerens* belongs to) demonstrated that their natural diet was highly heterogeneous (Reiswig, 1971; Ribes et al., 1999), and some other studies showed that there are symbiotic bacteria associated with *Mycale adhaerens*, and a high concentration of 24 carbon-numbered fatty acids in this sponge was associated with the bacterial community on the sponge surface (Lee et al., 2007). In this study, the high concentration of the fatty acid 24:0 was found in the sponge *Mycale adhaerens* in Lo Tik Wan, which was very probably due to the symbiotic bacteria on its surface. It is possible that these bacteria had effects on the isotopic compositions of the sponge. For the mussel *Perna viridis*, previous studies showed that they can undergo preingestive food selection, and pseudofaeces were rejected when filtered matter had a lower organic content (Wong and Cheung, 1999). It may be speculated that in this study, mussels selectively consumed trash fish particles, which had higher nutrient concentration.

Sediment contained a high proportion of saturated fatty acids, many of which were odd carbon-numbered including 11:0, 13:0 and 15:0, commonly produced by bacteria (Budge and Parrish, 1998). It implied that the fatty acids in the sediment mainly came from bacteria. Also, low levels of polyunsaturated fatty acids were found in the sediment of both Sham Wan and Lo Tik Wan, suggesting that fatty acids derived from algae were recycled effectively during the whole settling and deposition process (Hu et al., 2006).

5. FURTHER RESEARCH AREAS

The application of ARs has a long history and there is a wealth of information related to the design and performance of ARs in coastal and ocean waters worldwide (Jensen et al., 2000; Seaman, 2000). However, relatively fewer studies in the literature are focused on the response of benthic communities within the reef areas than those on fish attraction and fish production and on the settlement and colonization of epibiota on the AR structures, especially in the subtropics. Recent findings suggested that changes in sediment regime in the reef area can alter the structure of benthic communities in different scales depending on the distance from the location of the ARs (Wai, 2009). Further work can be conducted to elaborate the response

of benthic communities to the shift of dominant taxa with different life histories, morphology, behaviour and feeding modes through biological traits analysis (Boström et al., 2010; Bremner et al., 2006; Paganelli et al., 2012). Such analysis examines ecological functioning of marine benthic communities and provides a link between species, environments and ecosystem processes. The approach is potentially useful for the study of impact of the AR structures on ecological functioning of the entire reef systems.

In the literature, research on the trophodynamics of AR systems is also very limited. This is an important area for future studies in order to elucidate the mechanisms contributing to increased fisheries production: whether shelter offered by ARs or food derived from AR organisms is limiting fish production (Miller and Falace, 2000). The AR food web can also be very complicated in view of the interactions of the current and sediment regimes and the biodeposits generated from the epibiota colonized on the AR systems. One such area of investigations to enhance our understanding of reef trophodynamics is the application of stable isotopes such as the use of $\delta^{13}C$ to decipher trophic levels (Sweeting et al., 2007), $\delta^{15}N$ to determine trophic relationships (Rooker et al., 2006), and $\delta^{14}S$ to clarify feeding habits (Peterson and Fry, 1987). With the incorporation of stable isotope mixing models (Hopkins and Ferguson, 2012; Phillips, 2001; Phillips et al., 2005), the contribution of various trophic compartments to the AR systems can be identified (Wai et al., 2011; Wells et al., 2008). To complement stable isotope analysis is the examination of fatty acid profiles of the organisms associated with ARs in different trophic levels in order to deduce their trophic relationships (Cheung et al., 2010). This approach of using fatty acid profiles as natural dietary tracers can provide additional discriminatory power of food sources and finer resolution of prey types than bulk isotopic analysis and has been used with stable isotope signatures to examine food web structure in various marine ecosystems (Couturier et al., 2013; Jo et al., 2013; Kharlamenko et al., 2001; Petursdottir et al., 2012; Rooker et al., 2006). A recent development in this research area is to assess the reliability of compound-specific isotope analysis of fatty acids, particularly in ecosystems where accurate and precise knowledge of isotopic composition at natural abundance level is important and to provide further insights into the pathways conveying these particular fatty acids to consumers in the field (Bec et al., 2011).

The filtration capability of many epibiota colonized on the AR surface can be an efficient means of removing a large amount of nutrients in the vicinity of the reef areas. Data have been presented in this chapter to trace

the food sources of these epibiota using stable isotope and fatty acid analyses. The application of such biofiltration units of ARs is particularly useful in areas where fish cage farming is intense in semiconfined waters such as inshore bays (Angel et al., 2002; Israel, 2012; Shin et al., 2011). Further research can be conducted on the efficacy of these biofiltration units with different designs and orientations and the possible coculture of bivalves with these ARs to enhance biofiltration efficiency and biomass production (Gao et al., 2006).

ACKNOWLEDGMENTS

Part of the material in this chapter is based on the research work of T. Y. T. and H. Y. W. supported by the postgraduate studentships from the City University of Hong Kong. We would like to thank Jonathan Leung and Billy Kwan for the compilation of the literature related to AR ecology and Michael Chiang for the preparation of the graphics and figures.

REFERENCES

Abecasis, D., Bentes, L., Lino, P.G., Santos, M.N., Erzini, K., 2013. Residency, movements and habitat use of adult white seabream (*Diplodus sargus*) between natural and artificial reefs. Estuar. Coast. Shelf Sci. 118, 80–85.

Ainsworth, C.H., Pitcher, T.J., Rotinsulu, C., 2008. Evidence of fishery depletions and shifting cognitive baselines in Eastern Indonesia. Biol. Conserv. 141, 848–859.

Alfaro, A.C., Thomas, F., Sergent, L., Duxbury, M., 2006. Identification of trophic interactions within an estuarine food web (northern New Zealand) using fatty acid biomarkers and stable isotopes. Estuar. Coast. Shelf Sci. 70, 271–286.

Angel, D.L., Eden, N., Breitstein, S., Yurman, A., Katz, T., Spanier, E., 2002. *In situ* biofiltration: a means to limit the dispersal of effluents from marine finfish cage aquaculture. Hydrobiologia 469, 1–10.

Azhdari, H., Mohd, I., Aziz, A., Shamarina, S., Ajdari, Z., Zelina, Z.I., 2012. The effect of artificial reefs on fish assemblage versus natural sites in the Bandar Lengeh-Iran. Iran. J. Fish. Sci. 11, 1–12.

Baine, M., 2001. Artificial reefs: a review of their design, application management and performance. Ocean Coast. Manage. 44, 241–259.

Baronio, M.D.A., Bucher, D.J., 2008. Artificial crevice habitats to assess the biodiversity of vagile macro-cryptofauna of subtidal rocky reefs. Mar. Freshw. Res. 59, 661–670.

Bartholomew, A., Shine, R.L., 2008. Space size relative to prey width (Sp/Py) influences macrofaunal colonization of artificial structures. Mar. Ecol. Prog. Ser. 358, 95–102.

Bec, A., Perga, M.-E., Koussoroplis, A., Bardoux, G., Desvilettes, C., Bourdier, G., Mariotti, A., 2011. Assessing the reliability of fatty acid-specific stable isotope analysis for trophic studies. Methods Ecol. Evol. 2, 651–659.

Belmaker, J., Shashar, N., Ziv, Y., 2005. Effects of small-scale isolation and predation on fish diversity on experimental reefs. Mar. Ecol. Prog. Ser. 289, 273–283.

Berner, R.A., Ruttenberg, K.C., Ingall, E.D., Rao, J.L., 1993. The nature of phosphorus burial in modern marine sediments. In: Wollast, R., Mackenzie, F.T., Chou, L. (Eds.), Interactions of C, N, P and S Biogeochemical Cycles and Global Change. Springer-Verlag, New York, NY, pp. 365–378.

Bligh, E.G., Dyer, W.J., 1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37, 911–917.

Boaventura, D., Moura, A., Leitao, F., Carvalho, S., Curdia, J., Pereira, P., da Fonseca, L.C., dos Santos, M.N., Monteiro, C.C., 2006. Macrobenthic colonisation of artificial reefs on the southern coast of Portugal (Ancão, Algarve). Hydrobiologia 555, 335–343.

Bohnsack, J.A., Sutherland, D.L., 1985. Artificial reef research—a review with recommendations for future priorities. Bull. Mar. Sci. 44, 631–645.

Bombace, G., 1997. Protection of biological habitats by artificial reefs. In: Jensen, A.C. (Ed.), European Artificial Reef Research. Proceedings of the 1st Conference of the European Artificial Reef Research Network, Ancona, Italy, 26–30 March 1996. Southampton Oceanography Centre, pp. 1–15.

Bortone, S.A., 2006. A perspective on artificial reef research. Bull. Mar. Sci. 78, 1–8.

Boström, C., Törnroos, A., Bonsdorff, E., 2010. Invertebrate dispersal and habitat heterogeneity: expression of biological traits in a seagrass landscape. J. Exp. Mar. Biol. Ecol. 390, 106–117.

Boswell, K.M., Wells, R.J., Cowan Jr., J.H., Wilson, C.A., 2010. Biomass, density, and size distributions of fishes associated with a large-scale artificial reef complex in the Gulf of Mexico. Bull. Mar. Sci. 86, 879–889.

Boyra, A., Sanchez-Jerez, P., Tuya, F., Espino, F., Haroun, R., 2004. Attraction of wild coastal fishes to an Atlantic subtropical cage fish farms, Gran Canaria, Canary Islands. Environ. Biol. Fishes 70, 393–401.

Bremner, J., Rogers, S.I., Frid, C.L.J., 2006. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). Ecol. Indic. 6, 609–622.

Brickhill, M.J., Lee, S.Y., Connolly, R.M., 2005. Fishes associated with artificial reefs: attributing changes to attraction or production using novel approaches. J. Fish Biol. 67 (Suppl. B), 53–71.

Budge, S.M., Parrish, C.C., 1998. Lipid biogeochemistry of plankton, settling matter and sediments in Trinity Bay. Newfoundland. II. Fatty acids. Org. Geochem. 29, 1547–1559.

Budge, S.M., Parrish, C.C., Mckenzie, C.H., 2001. Fatty acid composition of phytoplankton, settling particulate matter and sediments at a sheltered bivalve aquaculture site. Mar. Chem. 76, 285–303.

Bugrov, L.Y., 1994. Fish-farming and artificial reefs: complex for waster technology. Bull. Mar. Sci. 55, 1332, abstract.

Bumbeer, J.D.A., da Rocha, R.M., 2012. Detection of introduced sessile species on the near shore continental shelf in southern Brazil. Zoologica 29, 126–134.

Burt, J., Bartholomew, A., Bauman, A., Saif, A., Sale, P.F., 2009. Coral recruitment and early benthic community development on several materials used in the construction of artificial reefs and breakwaters. J. Exp. Mar. Biol. Ecol. 373, 72–78.

Burt, J., Bartholomew, A., Sale, P.F., 2011. Benthic development on large-scale engineeredreefs: a comparison of communities among breakwaters of different age and natural reefs. Ecol. Eng. 37, 191–198.

Burton, W.H., Farrar, J.S., Steimle, F., Conlin, B., 2002. Assessment of out-of-kind mitigation success of an artificial reef deployed in Delaware Bay, USA. ICES J. Mar. Sci. 59, S106–S110.

Carr, M.H., Hixon, M.A., 1997. Artificial reefs: the importance of comparisons with natural reefs. Fisheries 22, 28–33.

Cheung, S.G., Wai, H.Y., Zhou, H., Shin, P.K., 2009. Structure of infaunal macrobenthos in the presence of artificial reefs in subtropical Hong Kong. Mar. Pollut. Bull. 58, 934–939.

Cheung, S.G., Wai, H.Y., Shin, P.K.S., 2010. Fatty acid profiles of benthic environment associated with artificial reefs in subtropical Hong Kong. Mar. Pollut. Bull. 60, 303–308.

Chua, C.Y.Y., Chou, L.M., 1994. The use of artificial reefs in enhancing fish communities in Singapore. In: Sasekumar, A., Marshall, N., Macintosh, D.J. (Eds.), Ecology and Conservation of Southeast Asian Marine and Freshwater Environments Including Wetlands, Hydrobiologia, vol. 285, pp. 177–187.

Coma, R., Ribes, M., Gili, J.M., Hughes, R.N., 2001. The ultimate opportunists: consumers of seston. Mar. Ecol. Prog. Ser. 219, 305–308.

Couturier, L.I.E., Rohner, C.A., Richardson, A.J., Marshall, A.D., Jaine, F.R.A., Bennett, M.B., Townsend, K.A., Weeks, S.J., Nichols, P.D., 2013. Stable isotope and signature fatty acid analyses suggest reef manta rays feed on demersal zooplankton. PLoS ONE 8, e77152. http://dx.doi.org/10.1371/journal.pone.0077152.

Dalsgaard, J., St John, M., Kattner, G., Muller-Navarra, D., Hagen, W., 2003. Fatty acid trophic markers in the pelagic marine environment. Adv. Mar. Biol. 46, 225–340.

Dance, M.A., Patterson III, W.F., Addis, D.T., 2011. Fish community and trophic structure at artificial reef sites in the northeastern Gulf of Mexico. Bull. Mar. Sci. 87, 301–324.

Danovaro, R., Gambi, C., Mazzola, A., Mirto, S., 2002. Influence of artificial reefs on the surrounding infauna: analysis of meiofauna. ICES J. Mar. Sci. 59, 356–362.

Davenport, S.R., Bax, N.J., 2002. A trophic study of a marine ecosystem off southeastern Australia using stable isotopes of carbon and nitrogen. Can. J. Fish. Aquat. Sci. 59, 514–530.

Dedieu, K., Rabouille, C., Gilbert, F., Soetaert, K., Metzger, E., Simonucci, C., Jézéquel, D., Prévot, F., Anschutz, P., Hulth, P., Ogler, S., Mesnage, V., 2007. Coupling of carbon, nitrogen and oxygen cycles in sediments from a Mediterranean lagoon: a seasonal perspective. Mar. Ecol. Prog. Ser. 346, 45–59.

Dewsbury, B.M., Fourqurean, J.W., 2010. Artificial reefs concentrate nutrients and alter benthic community structure in an oligotrophic, subtropical estuary. Bull. Mar. Sci. 86, 813–829.

dos Santos, L.N., Brotto, D.S., Zalmon, I.R., 2010. Fish responses to increasing distance from artificial reefs on the Southeastern Brazilian Coast. J. Exp. Mar. Biol. Ecol. 386, 54–60.

Dupont, J.M., 2008. Artificial reefs as restoration tools: a case study on the West Florida shelf. Coast. Manage. 36, 495–507.

Edelist, D., Spanier, E., 2009. Influence of Levantine Artificial Reefs on the fish assemblage of the surrounding seabed. Mediterr. Mar. Sci. 10, 35–54.

Einbinder, S.E., Perelberg, A., Ben-Shaprut, O., Foucart, M.H., Shashar, N., 2006. Effect on artificial reefs on fish grazing in their vicinity: Evidence from algae presentation experiments. Mar. Environ. Res. 61, 110–119.

Fabi, G., Fiorrentini, L., 1997. Molluscan aquaculture on reefs. In: Jensen, A.C. (Ed.), European Artificial Reef Research. Proceedings of the 1st Conference of the European Artificial Reef Research Network, Ancona, Italy, 26–30 March 1996. Southampton Oceanography Centre, pp. 123–140.

Fabi, G., Luccarini, F., Panfili, M., Solustri, C., Spagnolo, A., 2002. Effects of an artificial reef on the surrounding soft-bottom community (central Adriatic Sea). ICES J. Mar. Sci. 59, S343–S349.

Falcão, M., Santos, M.N., Vicente, M., Monteiro, C.C., 2007. Biogeochemical processes and nutrient cycling within an artificial reef off Southern Portugal. Mar. Environ. Res. 63, 429–444.

Falcão, M., Santos, M.N., Drago, T., Serpa, D., Monteiro, C., 2009. Effect of artificial reefs (southern Portugal) on sediment-water transport of nutrients: importance of the hydrodynamic regime. Estuar. Coast. Shelf Sci. 83, 451–459.

Forrester, G.E., Steele, M.A., 2004. Predator, prey refuges and the spatial scaling of density-dependence prey mortality. Ecology 85, 1332–1342.

Fourqurean, J.W., Jones, R.D., Zieman, J.C., 1993. Processes influencing water column nutrient characteristics and phosphorus limitation of phytoplankton biomass in Florida Bay, FL, USA: inferences from spatial distributions. Estuar. Coast. Shelf Sci. 36, 295–314.

Fowler, A.M., Booth, D.J., 2012. Evidence of sustained populations of a small reef fish on artificial structures. Does depth affect production on artificial reefs? J. Fish Biol. 80, 613–629.

Fricke, A.H., Koop, K., Cliff, G., 1986. Modification of sediment texture and enhancement of interstitial meiofauna by an artificial reef. Trans. R. Soc. S. Afr. 46, 27–34.

Fukunaga, A., Bailey-Brock, J.H., 2008. Benthic infaunal communities around two artificial reefs in Mamala Bay, Oahu, Hawaii. Mar. Environ. Res. 65, 250–263.

Gao, Q.F., 2005. Use of artificial reefs and green mussels (*Perna viridis*) for removal of nutrients from marine fish farming. Ph.D. thesis, City University of Hong Kong, Hong Kong, 192 pp.

Gao, Q.F., Shin, P.K.S., Lin, G.H., Chen, S.P., Cheung, S.G., 2006. Stable isotopic and fatty acid evidence for uptake of organic wastes from fish farming through green mussels (*Perna viridis*) in a polyculture system. Mar. Ecol. Prog. Ser. 317, 273–283.

Gao, Q.F., Shin, P.K.S., Xu, W.Z., Cheung, S.G., 2008a. Amelioration of marine farming impact on the benthic environment using artificial reefs as biofilters. Mar. Pollut. Bull. 57, 652–661.

Gao, Q.F., Xu, W.Z., Liu, X.S., Cheung, S.G., Shin, P.K.S., 2008b. Seasonal changes in C, N and P budgets of green-lipped mussels *Perna viridis* and removal of nutrients from fish farming in Hong Kong. Mar. Ecol. Prog. Ser. 353, 137–146.

Garibaldi, L., Caddy, J.F., 2004. Depleted marine resources: an approach to quantification based on the FAO capture database. FAO Fish. Circ. 1011, 32.

Gili, J., Coma, R., 1998. Benthic suspension feeders: their paramount role in littoral marine food webs. Trends Ecol. Evol. 13, 316–321.

Gillanders, B.M., Kingsford, M.J., 1996. Elements in otoliths may elucidate the contribution of estuarine recruitment to sustaining coastal reef populations of a temperate reef fish. Mar. Ecol. Prog. Ser. 141, 13–20.

Glasby, T.M., Connell, S.D., 1999. Urban structures as marine habitats. Ambio 28, 595–598.

Glasby, T.M., Connell, S.D., Hollway, M.G., Hewitt, C.L., 2007. Nonindigenous biota on artificial structures: could habitat creation facilitate biological invasions? Mar. Biol. 151, 887–893.

Gray, J.S., 1997. Marine biodiversity pattern, threats and conservation needs. Biodiv. Conserv. 6, 153–175.

Grey, J., Jones, R.I., Sleep, D., 2001. Seasonal changes in the importance of the source of organic matter to the diet of zooplankton in Loch Ness, as indicated by stable isotope analysis. Limnol. Oceanogr. 46, 505–513.

Guiral, D., Gourbault, N., Helleouet, M.N., 1995. Sediment nature and meiobenthos of an artificial reef (Acadja) used for extensive aquaculture. Oceanol. Acta 18, 543–555.

Hackradt, C.W., Félix-Hackradt, F.C., García-Charton, J.A., 2011. Influence of habitat structure on fish assemblage of an artificial reef in southern Brazil. Mar. Environ. Res. 72, 235–247.

Hale, R., Swearer, S.E., 2008. Otolith microstructural and microchemical changes associated with settlement in the diadromous fish *Galaxias maculatus*. Mar. Ecol. Prog. Ser. 354, 229–234.

Haraguchi, K., Yamamoto, T., Katayama, T., Matsuda, O., 2009. Carbon flow through the food web established on an artificial fish reef. Nippon Suisan Gakkaishi 75, 810–818, Japanese with English abstract.

Harris, D., Horwáth, W.R., van Kessel, C., 2001. Acid fumigation of soils to remove carbonates prior to total organic carbon or carbon-13 isotope analysis. Soil Sci. Soc. Am. J. 65, 1853–1856.

Hawkins, A.J.S., Simth, R.F.M., Tan, S.H., Yasin, Z.B., 1998. Suspension-feeding behaviour in tropical bivalve molluscs: *Perna viridis*, *Crassostrea belcheri, Crassostrea iradelei, Saccostrea cucullata* and *Pinctada margarifera*. Mar. Ecol. Prog. Ser. 166, 173–185.

Hixon, M.A., Beets, J.P., 1989. Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. Bull. Mar. Sci. 44, 666–680.
Hopkins III, J.B., Ferguson, J.M., 2012. Estimating the diets of animals using stable isotopes and a comprehensive Bayesian mixing model. PLoS ONE 7, e28478. http://dx.doi.org/10.1371/journal.pone.0028478.
Howarth, R.W., Jensen, H.S., Marino, R., Postma, H., 1995. Transport to and processing of P in near-shore and oceanic waters. In: Tiessen, H. (Ed.), Phosphorus in the Global Environment: Transfers, Cycles and Management (SCOPE 54). John Wiley & Sons, Chichester, UK, pp. 323–345.
Hu, J., Zhang, H., Peng, P., 2006. Fatty acid composition of surface sediments in the subtropical Pearl River estuary and adjacent shelf, Southern China. Estuar. Coast. Shelf Sci. 66, 346–356.
Huang, X.P., Huang, L.M., Yue, W.Z., 2003. The characteristics of nutrients and eutrophication in the Pearl River estuary, South China. Mar. Pollut. Bull. 47, 1–6.
Huang, Y.-C.A., Hsieh, H.J., Huang, S.-C., Meng, P.-J., Chen, Y.-S., Keshavmurthy, S., Nozawa, Y., Chen, C.A., 2011. Nutrient enrichment caused by marine cage culture and its influence on subtropical coral communities in turbid waters. Mar. Ecol. Prog. Ser. 423, 83–93.
Hueckel, G.J., Stayton, R.L., 1982. Fish foraging on an artificial reef in Puget Sound, Washington. Mar. Fish. Rev. 44, 38–44.
Huettmann, F., 2013. Tropical and subtropical oceanic regions. In: Howarth, R.W., Mohan, J.E. (Eds.), Biomes and Ecosystems, vol. 1. Grey House Publishing Inc, New York, NY, pp. 54–55.
Hughes, R.N., 1980. Optimal foraging in the marine context. Oceanogr. Mar. Biol. Annu. Rev. 18, 428–449.
Israel, D., 2012. Do artificial reefs reduce the accumulation of feeding remains around mariculture cages in Skutulsfjörður? Master thesis, University of Akureyri, Iceland, 91 pp.
Jensen, A.C., 2002. Artificial reefs of Europe: perspective and future. ICES J. Mar. Sci. 59, 3–13.
Jensen, A.C., Collins, K.J., Lockwood, A.P.M. (Eds.), 2000. Artificial Reefs in European Seas. Kluwer Academic Publishers, Dordrecht, The Netherlands, 508 pp.
Jo, H.-S., Lim, Y.C., Hanchet, S.M., Lee, D.-W., Kang, C.-K., 2013. Fatty acid and stable isotope analysis to infer diet of Antarctic toothfish caught in the southern Ross Sea. CCAMLR Sci. 20, 21–36.
Johnson, D.W., 2006. Predation, habitat complexity, and variation in density-dependent mortality of temperate reef fishes. Ecology 87, 1179–1188.
Jordan, L.K., Gilliam, D.S., Spieler, R.E., 2005. Reef fish assemblage structure affected by small-scale spacing and size variations of artificial patch reefs. J. Exp. Mar. Biol. Ecol. 326, 170–186.
Kamermans, P., 1994. Similarity in food source and timing of feeding in deposit- and suspension feeding bivalves. Mar. Ecol. Prog. Ser. 104, 63–75.
Kharlamenko, V.I., Kiyashko, S.I., Imbus, A.B., Vyshkvartzev, D.I., 2001. Identification of food sources of invertebrates from seagrass *Zostera marina* community using carbon and sulphur isotope ratios and fatty acid analyses. Mar. Ecol. Prog. Ser. 220, 103–117.
Knott, N.A., Underwood, A.J., Chapman, M.G., Glasby, T.M., 2004. Epibiota on vertical and on horizontal surfaces on natural reefs and on artificial structures. J. Mar. Biol. Ass. U.K. 84, 1117–1130.
Krohling, W., Zalmon, I.R., 2008. Epibenthic colonization on an artificial reef in a stressed environment off the north coast of the Rio de Janeiro State, Brazil. Braz. Arch. Biol. Technol. 51, 213–221.
Laihonen, P., Hännunen, J., Chojnacki, J., Vuorinen, I., 1996. Some prospects of nutrient removal with artificial reefs. In: Jensen, A.C. (Ed.), European Artificial Reef Research. Proceedings of the 1st Conference of the European Artificial Reef Research

Network, Ancona, Italy, 26–30 March 1996. Southampton Oceanography Centre, pp. 85–96.
Lee, R.F., Nevenze, J.C., Paffenhöfer, G.A., 1971. Importance of wax esters and other lipids in the marine food chain: phytoplankton and copepods. Mar. Chem. 51, 315–324.
Lee, O.O., Yang, L.H., Li, X., Pawlik, J.R., Qian, P.Y., 2007. Surface bacterial community, fatty acid profile, and antifouling activity of two congeneric sponges from Hong Kong and the Bahamas. Mar. Ecol. Prog. Ser. 339, 25–40.
Leitão, F., Santos, M.N., Monteiro, C.C., 2007. Contribution of artificial reefs to the diet of the white sea bream (*Diplodus sargus*). ICES J. Mar. Sci. 64, 473–478.
Leitão, F., Santos, M.N., Erzini, K., Monteiro, C.C., 2008a. Fish assemblages and rapid colonization after enlargement of an artificial reef off the Algarve coast (Southern Portugal). Mar. Ecol. 29, 435–448.
Leitão, F., Santos, M.N., Erzini, K., Monteiro, C.C., 2008b. The effect of predation on artificial reef juvenile demersal fish species. Mar. Biol. 153, 1233–1244.
Leung, A.W.Y., Wilson, K.D.P., 1999. Preliminary assessment of artificial reef deployment in marine protected areas in Hong Kong. In: Proceedings of the 7th International Conference on Artificial Reefs (7th CARAH), pp. 181–189.
Liu, X.S., Xu, W.Z., Cheung, S.G., Shin, P.K., 2011. Response of meiofaunal community with special reference to nematodes upon deployment of artificial reefs and cessation of bottom trawling in subtropical waters, Hong Kong. Mar. Pollut. Bull. 63, 376–384.
Lohse, L., Malschaert, J.F.P., Slomp, C.P., Helder, W., VanRaaphorst, W., 1993. Nitrogen cycling in North Sea sediments: interaction of denitrification and nitrification in offshore and coastal areas. Mar. Ecol. Prog. Ser. 101, 283–296.
Lotze, H.K., 2007. Rise and fall of fishing and marine resource use in the Wadden Sea, southern North Sea. Fish. Res. 87, 208–218.
Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H., Jackson, J.B.C., 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312, 1806–1809.
Machado, P.M., de Sá, F.S., de Rezende, C.E., Zalmon, I.R., 2013. Artificial reef impact on macrobenthic community on south-eastern Brazil coast. Mar. Biodiver. Rec. 6, e40. http://dx.doi.org/10.1017/S1755267213000183.
McClelland, J.W., Valiela, I., 1998. Changes in food web structure under the influence of increased anthropogenic nitrogen inputs to estuaries. Mar. Ecol. Prog. Ser. 168, 259–271.
McCutchan, J.H., Lewis, W.M., Kendall, C., McGrath, C.C., 2003. Variations in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102, 378–390.
Mendonça, A., Fortes, C.J., Capitão, R., Neves, M.G., Moura, T., Simão, J., do Carmo, A., 2012. Wave hydrodynamics around a multi-functional artificial reef at Leirosa. J. Coast. Conserv. 16, 543–553.
Miller, M.W., Falace, A., 2000. Evaluation methods for trophic resource factors—nutrients, primary production, and associated assemblages. In: Seaman, W. (Ed.), Artificial Reef Evaluation with Application to Natural Marine Habitats. CRC Press, Boca Raton, FL, pp. 96–126.
Miller, M.W., Valdivia, A., Kramer, K.L., Mason, B., Williams, D.E., Johnston, L., 2009. Alternate benthic assemblages on reef restoration structures and cascading effects on coral settlement. Mar. Ecol. Prog. Ser. 387, 147–156.
Montagna, P.A., Jarvis, S.C., Kennicutt, M.C., 2002. Distinguishing between contaminant and reef effects on meiofauna near offshore hydrocarbon platforms in the Gulf of Mexico. Can. J. Fish. Aquat. Sci. 59, 1584–1592.
Monteiro, C.C., Santos, M., 2000. Portuguese artificial reefs. In: Jensen, A.C., Collins, K.J., Lockwood, A.P.M. (Eds.), Artificial Reefs in European Seas. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 249–261.

Moura, A., Boaventura, D., Cúrdia, J., Santos, M.N., Monteiro, C.C., 2006. Biomass production of early macrobenthic communities at the Faro/Ancão artificial reef (Portugal): effect of depth and reef layer. Bull. Mar. Sci. 78, 83–92.

Moura, A., Boaventura, D., Cúrdia, J., Carvalho, S., da Fonseca, L.C., Leitão, F.M., Santos, M.N., Monteiro, C.C., 2007. Effect of depth and reef structure on early macrobenthic communities of the Algarve artificial reefs (southern Portugal). Hydrobiologia 580, 173–180.

Moura, A., da Fonseca, L.C., Boaventura, D., Santos, M.N., Monteiro, C.C., 2011. Estimation of secondary production of the Faro/Ancão artificial reefs. Braz. J. Oceanogr. 59, 91–94.

Napolitano, G.E., 1999. Fatty acids as trophic and chemical markers in freshwater ecosystems. In: Arts, M.T., Wainman, B.C. (Eds.), Lipids in Freshwater Ecosystems. Springer, New York, NY, pp. 21–37.

Napolitano, G.E., Pollero, R.J., Gayoso, A.M., Macdonald, B.A., Thompson, R.J., 1997. Fatty acids as trophic markers of phytoplankton blooms in the Bahia Blanca Estuary (Buenos Aires, Argentina) and in Trinity Bay (Newfoundland, Canada). Biochem. Syst. Ecol. 25, 739–755.

Navarro, J.M., Thompson, R.J., 1997. Biodeposition by the horse mussel *Modiolus modiolus* (Dillwyn) during the spring diatom bloom. J. Exp. Mar. Biol. Ecol. 209, 1–13.

Ni, H., Lu, F., Luo, X., Tian, H., Zeng, E.Y., 2008. Riverine inputs of total organic carbon and suspended particulate matter from the Pearl River Delta to the coastal ocean off South China. Mar. Pollut. Bull. 56, 1150–1157.

Overholtzer-McLeod, K.L., 2004. Variance in reef spatial structure masks density dependence in coral-reef populations on natural versus artificial reefs. Mar. Ecol. Prog. Ser. 276, 269–280.

Őzgül, A., Angel, D., 2013. Wild fish aggregations around fish farms in the Gulf of Aqaba, Red Sea: implications for fisheries management and conservation. Aquacult. Environ. Interact. 4, 135–145.

Paganelli, D., Marchini, A., Occhipinti-Ambrogi, A., 2012. Functional structure of marine benthic assemblages using Biological Traits Analysis (BTA): a study along the Emilia-Romagna coastline (Italy, North-West Adriatic Sea). Estuar. Coast. Shelf Sci. 96, 245–256.

Perkol-Finkel, S., Benayahu, Y., 2004. Community structure of stony and soft corals on vertical unplanned artificial reefs in Eilat (Red Sea): comparison to natural reefs. Coral Reefs 23, 195–205.

Perkol-Finkel, S., Benayahu, Y., 2005. Recruitment of benthic organisms onto a planned artificial reef: shifts in community structure one decade post-deployment. Mar. Environ. Res. 59, 79–99.

Perkol-Finkel, S., Benayahu, Y., 2007. Differential recruitment of benthic communities on neighboring artificial and natural reefs. J. Exp. Mar. Biol. Ecol. 340, 25–39.

Perkol-Finkel, S., Benayahu, Y., 2009. The role of differential survival patterns in shaping coral communities on neighboring artificial and natural reefs. J. Exp. Mar. Biol. Ecol. 369, 1–7.

Perkol-Finkel, S., Shashar, N., Barneah, O., Ben-David-Zaslow, R., Oren, U., Reichart, T., Yacobovich, T., Yahel, G., Yahel, R., Benayahu, Y., 2005. Fouling reefal communities on artificial reefs: does age matter? Biofouling 21, 127–140.

Perkol-Finkel, S., Shashar, N., Benayahu, Y., 2006. Can artificial reefs mimic natural reef communities? The roles of structural features and age. Mar. Environ. Res. 61, 121–135.

Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. 18, 293–320.

Petursdottir, H., Falk-Petersen, S., Gislason, A., 2012. Trophic interactions of meso- and macrozooplankton and fish in the Iceland Sea as evaluated by fatty acid and stable isotope analysis. ICES J. Mar. Sci. 69, 1277–1288.

Phillips, D.L., 2001. Mixing models in analyses of diet using multiple stable isotope: a critique. Oecologia 127, 166–170.

Phillips, D.L., Greggs, J.W., 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136, 261–269.
Phillips, D.L., Koch, P.L., 2002. Incorporating concentration dependence in stable isotope mixing models. Oecologia 130, 114–125.
Phillips, D.L., Newsome, S.D., Gregg, J.W., 2005. Combining sources in stable isotope mixing models: alternative methods. Oecologia 144, 520–527.
Pickering, H., Whitmarsh, D., Jensen, A., 1998. Artificial reefs as a tool to aid rehabilitation of coastal ecosystems: investigating the potential. Mar. Pollut. Bull. 37, 505–514.
Pitcher, T.J., Seaman, W., 2000. Petrarch's principles: how protected human-made reefs can help the reconstruction of fisheries and marine ecosystems. Fish Fish. 1, 73–81.
Polovina, J.J., 1991. Fisheries applications and biological impacts of artificial reefs. In: Seaman Jr., W., Sprague, L.M. (Eds.), Artificial Habitats for Marine and Freshwater Fisheries. Academic Press, San Diego, CA, pp. 153–176.
Prince, E.D., Maughan, O.E., Brouha, P., 1985. Summary and update of the Smith Mountain Lake Artificial Reef Project. In: D'Itri, F.M. (Ed.), Artificial Reefs: Marine and Freshwater Applications. Lewis Publishers, Chelsea, MI, pp. 401–430.
Randall, J.E., 1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. Caribb. J. Sci. 3, 31–46.
Redman, R.A., Szedlmayer, S.T., 2009. The effects of epibenthic communities on reef fishes in the northern Gulf of Mexico. Fish. Manage. Ecol. 16, 360–367.
Reed, D.C., Schroeter, S.C., Huang, D., Anderson, T.W., Ambrose, R.F., 2006. Quantitative assessment of different artificial reef designs in mitigating losses to kelp forest fishes. Bull. Mar. Sci. 78, 133–150.
Reise, K., 2005. Coast of change: habitat loss and transformations in the Wadden Sea. Helgol. Mar. Res. 59, 9–21.
Reiswig, H.M., 1971. Particle feeding in natural populations of three marine demosponges. Biol. Bull. 141, 568–591.
Relini, G., Zamboni, N., Tixi, F., Torchia, G., 1994. Patterns of sessile macrobenthos community on an artificial reef in the Gulf of Genoa (northwestern Mediterranean). Bull. Mar. Sci. 55, 745–771.
Reuss, N., Poulsen, L.K., 2002. Evaluation of fatty acids as biomarkers for a natural plankton community. A field study of a spring bloom and a post-bloom period off West Greenland. Mar. Biol. 141, 423–434.
Ribes, M., Coma, R., Gili, J.M., 1999. Natural diet and grazing rate of the temperate sponge *Dysidea avara* (Demospongiae, Dendroceratida) throughout an annual cycle. Mar. Ecol. Prog. Ser. 176, 179–190.
Rooker, J.R., Turner, J.P., Holt, S.A., 2006. Trophic ecology of *Sargassum*-associated fishes in the Gulf of Mexico determined from stable isotopes and fatty acids. Mar. Ecol. Prog. Ser. 313, 249–259.
Ruiz, G.M., Freestone, A.L., Fofonoff, P.W., Simkann, C., 2009. Habitat distribution and heterogeneity in marine invasion dynamics: the importance of hard substrate and artificial structure. In: Wahl, M. (Ed.), Marine Hard Bottom Communities: Patterns, Dynamics, Diversity and Change. Springer, Heidelberg, Germany, pp. 321–332.
Santos, M.N., Monteiro, C.C., 2007. A fourteen-year overview of the fish assemblages and yield of the two oldest Algarve artificial reefs (southern Portugal). Hydrobiologia 580, 225–231.
Santos, M.N., Monteiro, C.C., Lasserre, G., 2005. Observations and trends on the intra-annual variation of the fish assemblages on two artificial reefs in Algarve coastal waters (southern Portugal). Sci. Mar. 69, 415–426.
Santos, M.N., Leitão, F., Moura, A., Cerqueira, M., Monteiro, C.C., 2011. *Diplodus* spp. on artificial reefs of different ages: influence of the associated macrobenthic community. ICES J. Mar. Sci. 68, 87–97.

Sargent, J.R., Gatten, R.R., McIntosh, R., 1977. Wax esters in the marine environment—their occurrences, formation, transformation and ultimate fates. Mar. Chem. 5, 573–584.
Schroepfer, R.L., Szedlmayer, S.T., 2006. Estimates of residence and site fidelity for red snapper *Lutjanus campechanus* on artificial reefs in the northeastern Gulf of Mexico. Bull. Mar. Sci. 78, 93–101.
Seaman, W. (Ed.), 2000. Artificial Reef Evaluation with Application to Natural Marine Habitats. CRC Press, Boca Raton, FL, 245 pp.
Seaman, W., 2007. Artificial habitats and the restoration of degraded marine ecosystems and fisheries. Hydrobiologia 580, 143–155.
Seaman, W., Jensen, A.C., 2000. Purposes and practices of artificial reef evaluation. In: Seaman, W. (Ed.), Artificial Reef Evaluation with Application to Natural Marine Habitats. CRC Press, Boca Raton, FL, pp. 2–19.
Seaman, W., Sprague, L.M., 1991. Artificial habitat practices in aquatic systems. In: Seaman, W., Sprague, L.M. (Eds.), Artificial Habitats for Marine and Freshwater Fisheries. Academic Press, San Diego, CA, pp. 1–29.
Sheehy, D.J., Vik, S.F., 2010. The role of constructed reefs in non-indigenous species introduction and range expansions. Ecol. Eng. 36, 1–11.
Sheng, Y.P., 2000. Physical characteristics and engineering at reef sites. In: Seaman, W. (Ed.), Artificial Reef Evaluation with Application to Natural Marine Habitats. CRC Press, Boca Raton, FL, pp. 51–94.
Shin, P.K.S., Gai, Q., Cheung, S.G., 2011. Nutrient assimilation by organisms on artificial reefs in a fish culture (Example of Hong Kong). In: Aral, F., Doğu, Z. (Eds.), Recent Advances in Fish Farms. InTech, Rijeka, Croatia, pp. 41–60. Available from:http://www.intechopen.com/articles/show/title/nutrient-assimilation-by-organisms-on-artificial-reefs-in-a-fish-culture-example-of-hong-kong-.
Silva-Cruz, Y., Castañeda-Chávez, M.del R., Lango-Reynoso, F., Landeros-Sánehez, C., 2011. Environmental impact of fish farming in floating cages in Isla Arena, Campeche. Trop. Subtrop. Agroecosyst. 13, 291–298.
Simard, F., 1997. Socio-economic aspects of artificial reefs in Japan. In: Jensen, A.C. (Ed.), European Artificial Reef Research. Proceedings of the 1st Conference of the European Artificial Reef Research Network, Ancona, Italy, 26–30 March 1996. Southampton Oceanography Centre, pp. 223–240.
Simon, T., Pinheiro, H.T., Joyeux, J.C., 2011. Target fishes on artificial reefs: evidences of impacts over nearby natural environments. Sci. Total Environ. 409, 4579–4584.
Slomp, C.P., 1997. Early diagenesis of phosphorus in continental margin sediment. Ph.D. thesis, Wageningen Agricultural University, The Netherlands, 176 pp.
Smith, S.D.A., Rule, M.J., 2002. Artificial substrata in a shallow sublittoral habitat: do they adequately represent natural habitats or the local species pool? J. Exp. Mar. Biol. Ecol. 277, 25–41.
Spieler, R.E., Gilliam, D., Sherman, R., 2001. Artificial substrate and coral reef restoration: what do we need to know to know what we need? Bull. Mar. Sci. 69, 1013–1030.
Stephens, G.C., 1968. Dissolved organic matter as a potential source of nutrition for marine organisms. Am. Zool. 8, 95–106.
Stewart, M.G., 1979. Absorption of dissolved organic nutrients by marine invertebrates. Oceanogr. Mar. Biol. Annu. Rev. 17, 163–192.
Stone, R.B., McGurrin, J.M., Sprague, L.M., Seaman, W., 1991. Artificial habitats of the world: synopsis and major trends. In: Seaman, W., Sprague, L.M. (Eds.), Artificial Habitats for Marine and Freshwater Fisheries. Academic Press, San Diego, CA, pp. 31–60.
Stuart, V., Klumpp, D.W., 1984. Evidence for food-resource partitioning by kelp-bed filter feeders. Mar. Ecol. Prog. Ser. 16, 27–37.
Suchanek, T.H., 1994. Temperate coastal marine communities—biodiversity and threats. Am. Zool. 34, 100–114.
Suzuki, G., Kai, S., Yamashita, H., Suzuki, K., Iehisa, Y., Hayashibara, T., 2011. Narrower grid structure of artificial reef enhances initial survival of *in situ* settled coral. Mar. Pollut. Bull. 62, 2803–2812.

Svane, I.B., Peterson, J.K., 2001. On the problems of epibiosis, fouling and artificial reefs, a review. Mar. Ecol. 33, 169–188.
Sweeting, C.J., Barry, J.T., Polunin, N.V.C., Jennings, S., 2007. Effects of body size and environment on diet-tissue $\delta^{13}C$ fractionation in fishes. J. Exp. Mar. Biol. Ecol. 352, 165–176.
Syc, T.S., Szedlmayer, S.T., 2012. A comparison of size and age of red snapper (*Lutjanus campechanus*) with the age of artificial reefs in the northern Gulf of Mexico. Fish. Bull. 110, 458–469.
Thanner, S.E., McIntosh, T.L., Blair, S.M., 2006. Development of benthic and fish assemblages on artificial reef materials compared to adjacent natural reef assemblages in Miami-Dade County, Florida. Bull. Mar. Sci. 78, 57–70.
Thrush, S.F., Dayton, P.K., 2002. Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. Annu. Rev. Ecol. Syst. 33, 449–473.
Topping, D.T., Szedlmayer, S.T., 2011. Home range and movement patterns of red snapper (*Lutjanus campechanus*) on artificial reefs. Fish. Res. 112, 77–84.
Tyrell, M.C., Byers, J.E., 2007. Do artificial substrates favour non-indigenous fouling species over native species? J. Exp. Mar. Biol. Ecol. 342, 54–60.
Vroom, P.S., Braun, C.L., 2010. Benthic composition of a healthy subtropical reef: baseline species-level cover, with an emphasis on algae, in the Northwestern Hawaiian Islands. PLoS ONE 5, e9733. http://dx.doi.org/10.1371/journal.pone.0009733.
Wai, H.Y., 2009. Effects of deployment of artificial reefs on the marine benthic environment, with special reference to sediment physic-chemical characteristics. M.Phil. thesis, University of Hog Kong, Hong Kong, 194 pp.
Wai, T.-C., Leung, K.M.Y., Wu, R.S.S., Shin, P.K.S., Cheung, S.G., Lee, J.H.W., 2011. Stable isotopes as a useful tool for revealing the environmental fate and trophic effect of open-sea-cage fish farm wastes on marine benthic organisms with different feeding guilds. Mar. Pollut. Bull. 63, 77–85.
Walker, B.K., Henderson, B., Spieler, R.E., 2002. Fish assemblages associated with artificial reefs of concrete aggregates or quarry stone offshore Miami Beach, Florida. USA. Aquat. Living Resour. 15, 95–105.
Walker, S.J., Schlacher, T.A., Schlacher-Hoenlinger, M.A., 2007. Spatial heterogeneity of epibenthos on artificial reefs: fouling communities in the early stages of colonization on an Eastern Australian shipwreck. Mar. Ecol. 28, 435–445.
Wallance, J.B., Webster, J.R., Woodall, W.R., 1977. The role of filter feeders in flowing water. Arch. Hydrobiol. 79, 506–532.
Wells, R.J.D., Cowan Jr., J.H., Fry, B., 2008. Feeding ecology of red snapper *Lutjanus campechanus* in the northern Gulf of Mexico. Mar. Ecol. Prog. Ser. 361, 213–225.
Whitmarsh, D., Santos, M.N., Ramos, J., Monteiro, C.C., 2008. Marine habitat modification through artificial reefs off the Algarve (southern Portugal): an economic analysis of the fisheries and the prospects for management. Ocean Coast. Manage. 51, 463–468.
Wilkinson, C., Caillaud, A., DeVantier, L., South, R., 2006. Strategies to reverse the decline in valuable and diverse coral reefs, mangroves and fisheries: the bottom of the J-Curve in Southeast Asia? Ocean Coast. Manage. 49, 764–778.
Wilson, K.D.P., Leung, A.W.Y., Kennish, R., 2002. Restoration of Hong Kong fisheries through deployment of artificial reefs in marine protected areas. ICEC J. Mar. Sci. 59, 157–163.
Wong, W.H., Cheung, S.G., 1999. Feeding behaviour of the green mussel, *Perna viridis* (L.): responses to variation in seston quantity and quality. J. Exp. Mar. Biol. Ecol. 236, 191–207.
Wu, R.S.S., Lam, K.S., MacKay, D.W., Lau, T.C., Yam, V., 1994. Impact of marine fish farming on water quality and bottom sediment: a case study in the sub-tropical environment. Mar. Environ. Res. 38, 115–145.
Zalmon, I.R., Saleme de Sá, F., Neto, E.J.D., de Rezende, C.E., Mota, P.M., de Almeida, T.C.M., 2014. Impacts of artificial reef spatial configuration on infaunal community structure—Southeastern Brazil. J. Exp. Mar. Biol. Ecol. 454, 9–17.

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CHAPTER TWO

Reproductive Biology of Female Norway Lobster, *Nephrops norvegicus* (Linnaeus, 1758) Leach, in Icelandic Waters During the Period 1960–2010: Comparative Overview of Distribution Areas in the Northeast Atlantic and the Mediterranean

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Advances in Marine Biology, Volume 68
ISSN 0065-2881
http://dx.doi.org/10.1016/B978-0-12-800169-1.00002-1

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Abstract

Maturity size, reproductive cycle, sex ratio and fecundity of female *Nephrops* were investigated at SW, S and SE Iceland for the period 1960–2010. Time series of biological parameters and fisheries data displayed significant relationships. In addition, female biological data from 20 areas in the Atlantic and Mediterranean were compared. Fifty percentage maturity estimates had an overall range of 23.9–34.4 mm CL with some anomalies in the 2000s. The reproductive cycle in Iceland has been biennial during the whole study period from mid-1960s to 2010 with minor change in phase in the 2000s. Biennial moulting retards female growth more than annual spawning, and the length of incubation and hatch time of year show significant relationships with latitude and sea temperature. Variations in sex ratio were observed and relationships found between female sex ratio and CL, CPUE and stock biomass during 1961–2010, displaying apparent fishery-induced effects on sex ratio. Potential and realized fecundity estimates in Iceland are 35–50% of those reported from more southerly waters. Biennial spawning and low fecundity limit the number of progeny in Icelandic *Nephrops* and necessitate lower fishing mortality. Ambient temperature in Icelandic waters has risen by 1 °C since the late 1990s, generating around 30 days shorter incubation time in the 2000s, but around 3 °C rise is necessary for possible annual spawning.

Keywords: *Nephrops norvegicus*, Size of maturity, Biennial spawning, Sex ratio, Fecundity, Sea temperature, Geographical variations

1. INTRODUCTION

The Norway lobster, *Nephrops norvegicus* (Linnaeus, 1758) Leach, is widely distributed on the continental shelf of the Northeast Atlantic and the Mediterranean, supporting important trawl fisheries and lesser creel fisheries in various countries bordering these waters. In Iceland, *Nephrops* is only found off the southern part of the country, in the relatively warm waters of the North Atlantic current, at depths of about 100–300 m (Figure 2.1).

The history of the *Nephrops* fishery in Icelandic waters dates back to the early 1950s when Belgian trawlers began targeting the species at the end of their fishing trips to southeast Iceland (Leloup and Gilis, 1965). A few years later, in 1958, an Icelandic fishery was initiated off the southwest coast. The fishery expanded rapidly, reaching an all-time record of 6000 tonnes in 1963, of which 5550 tonnes were taken by Icelandic boats. During the five decades since then, landings have fluctuated from around 1500–4500 tonnes, thereof amounting to 2000–2500 tonnes annually in 2005–2010 (Figure 2.2). Typically, the southern continental shelf of Iceland contains banks of 100–150 m depth crossed by a series of intervening troughs 200–300 m below sea level. As a rule, the average monthly sea water temperatures on these grounds have ranged from 5 to 9 °C in the recent decades. The distribution of *Nephrops* is

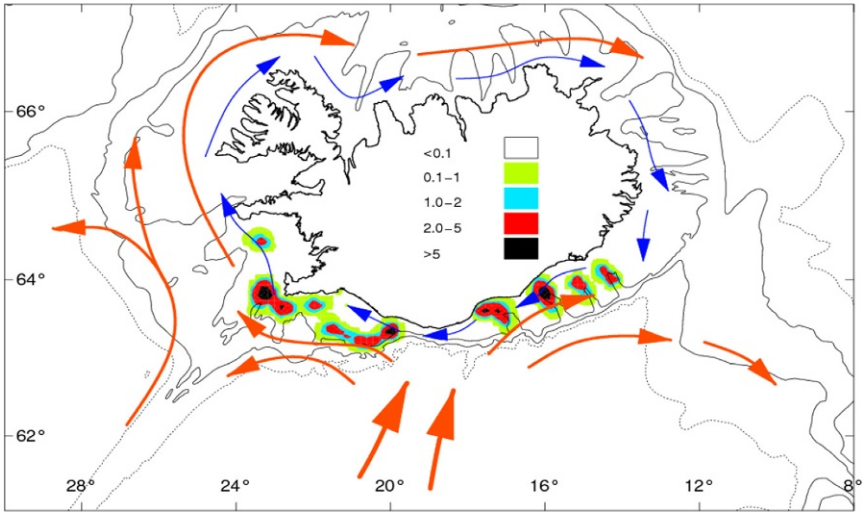


Figure 2.1 *Nephrops* fishing areas off southern Iceland. The scale indicates the density of catches from 2005 to 2009 (t nautical mile^{-2}). Arrows denote the main currents affecting south Icelandic waters: grey, branch of the warm North Atlantic Current; black, coastal current. *Modified from Pampoulie et al. (2011)*.

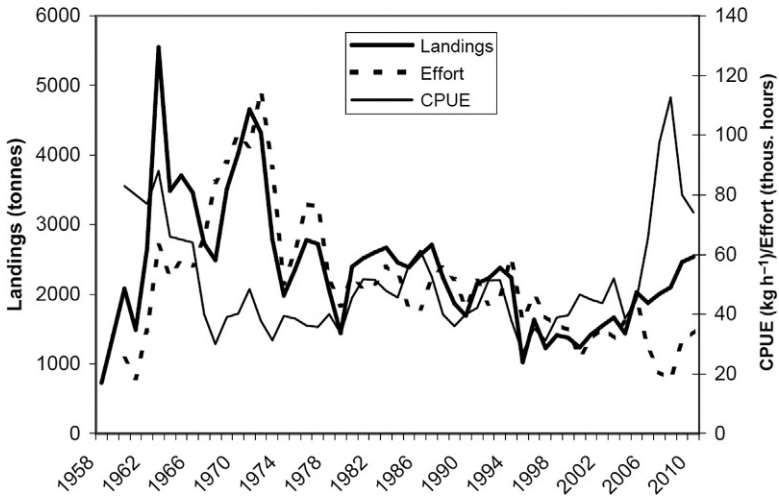


Figure 2.2 Fisheries data for the Icelandic *Nephrops* fishery during the years 1958–2010. Bold line, landings (tonnes); dotted line, effort ('000 h); line, catch per unit effort (kg h^{-1}).

mainly limited to substrates of high concentration (generally >50%) of clay and silt within these areas (Boulton et al., 1988).

Sæmundsson (1937) mentioned personal findings of specimens of *Nephrops*, in both bottom trawls and cod stomachs in relatively cold waters

off the southern part of east Iceland (e.g. Litladjúp and Hvalbaksbanki) as well as off northwest Iceland (Vestfirðir), and Stephensen (1939) also referred to occurrences off northwest Iceland (Látrabjarg) and even in north Iceland (Eyjafjörður). Although North Atlantic waters enjoyed a period of warm water regimes in the period 1930 to the mid-1960s, followed by a colder period until the mid-1990s, a consistent warming period has reoccurred over the last 15 years. No records are listed, however, in the Icelandic fisheries research database in 1985–2010 (Marine Research Institute, Reykjavík), of *Nephrops* being either caught or found in cod stomachs off the east, north and northwest of Iceland in the recent warm era. Yet, in late 2012, northern shrimp fishers in Ísafjarðardjúp (northwest Iceland) caught three to four male *Nephrops* of approximately 50–55 mm carapace length (CL) that apparently had recently moulted (Hjalti Karlsson, personal communication). Therefore, the survival and growth of *Nephrops* appear to have been successful in somewhat colder waters than previously certified although successful reproduction still remains unresolved.

On the other hand, the anomalous records of *Nephrops* in the relatively much colder waters off Greenland, Spitsbergen and Bear Island must be doubted, although indicated by Sæmundsson (1937), Thomas (1961) and Farmer (1975) and quoted by later authors. The presence of *Nephrops* in those relatively cold waters must be not only incidental but also equivocal, being obviously too cold for both reproduction and growth, although not necessarily survival, of this species.

Nephrops, typical of lobsters, mates shortly after the female moults or while the female is in a soft-shelled condition. In addition, the female carries the eggs externally and therefore cannot moult for the duration of the ovigerous period without the loss of the eggs. Thus, one observes an intertwining cycle of moulting, mating, ovarian maturation, spawning, incubation period and hatching among mature female *Nephrops*.

The Norway lobster can be a very elusive "kettle of fish", particularly due to its burrowing behaviour that can vary temporally for mature females depending upon the phase of the breeding cycle (see overviews by Anonymous, 1982; Farmer, 1975; Figueiredo and Thomas, 1967a,b) and according to the size of males (Andersen, 1962). Moreover, numerous environmental variables have been known to affect the availability of *Nephrops* at any given time, such as sea temperature (Eiríksson, 1970a, 2009; Poulsen, 1946), hypoxia (Bagge, 1988; Bagge and Munch-Petersen, 1979; Froglia and Gramitto, 1982; Hallbäck and Ulmestrand, 1990), light intensity and depth (Chapman, 1980; Chapman and Howard, 1979; Chapman et al.,

1972; Eiríksson, 1980; Hillis, 1972; Höglund and Dyber, 1965; Redant and De Clerck, 1984; Simpson, 1965), light attenuation related to phytoplankton density (Eiríksson, 2009) and predators (personal observation).

A study that is limited both temporally and spatially may for a number of reasons lead to results somewhat atypical of a particular stock of *Nephrops*. Therefore, the author has chosen to aggregate data to some extent, since a general picture is being considered rather than a transient one, normally associated with such major biological parameters as recruitment, growth and mortality. Moreover, a good knowledge of long-term averages can often be useful in describing instantaneous, monthly, seasonal or annual observations.

This study includes almost the whole period of *Nephrops* exploitation in Iceland from 1960 to 2010. Moreover, for studying geographical variations, some comparisons in biology are made between *Nephrops* females in some of the most important fishing areas at southwest, south and southeast Iceland, as well as a comparative overview of other *Nephrops* distribution areas in the Northeast Atlantic and the Mediterranean (Figure 2.3).

For evaluating transient changes in the stock of *Nephrops* and the development of the fishery, the author has also included some results of short-term data during the course of approximately 60 years from the early 1960s to 2010.

2. PREVIOUS INVESTIGATIONS

Numerous investigations have contributed to our knowledge of the biology of female *Nephrops,* including observations on maturity, reproduction, fecundity and seasonal variations in availability. These date at least back to McIntosh (1908), Gauss-Garady (1912) and Storrow (1912, 1913), working on *Nephrops* in the Firth of Clyde, west Scotland; in the Adriatic Sea; and off North Shields, Northeast England, respectively, but comprehensive reports over a wider geographical range are relatively recent (Bell et al., 2006; Chapman, 1980; Farmer, 1975; Figueiredo and Thomas, 1967a,b; ICES Working Group reports (e.g. Anonymous, 1982, 1984); Sardà, 1995; and most recently Powell and Eriksson, 2013).

Previous work in Iceland has been described by Eiríksson (1968a,b) concerning the monthly and annual changes in female sex ratio during 1962–1967 and the breeding cycle and fecundity of Norway lobster at southwest Iceland in 1965–1970 (Eiríksson, 1969, 1970b). Furthermore, Eiríksson (1993) discussed the biennial breeding cycle of *Nephrops* at Iceland and how it relates to the fishery.

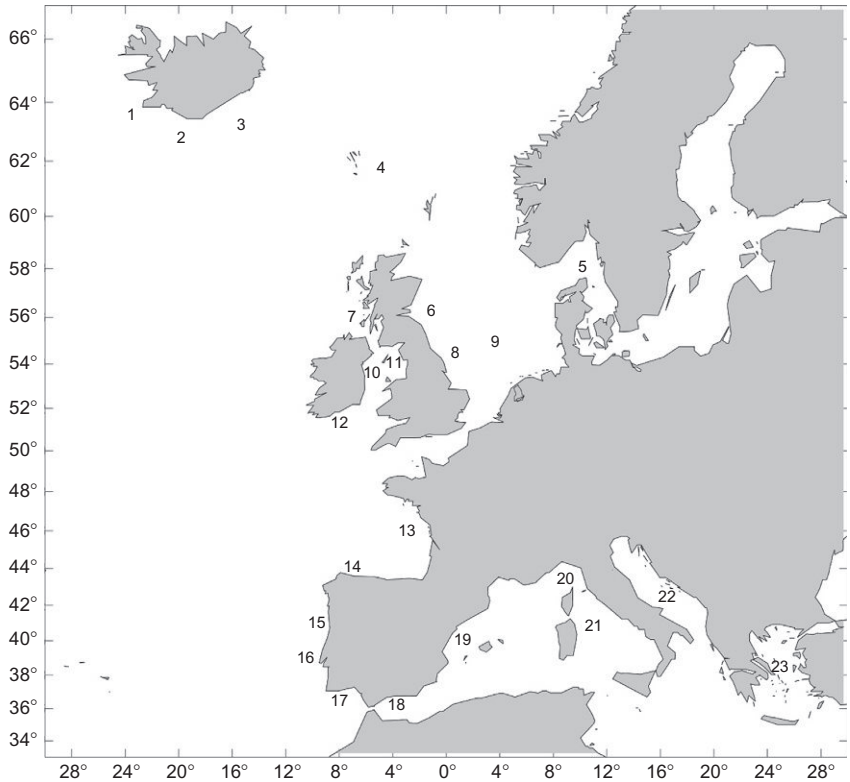


Figure 2.3 Overview of *Nephrops* fishing areas in the Northeast Atlantic and Mediterranean waters. The following study and review areas are indicated in figure: (1) SW Iceland; (2) S Iceland; (3) SE Iceland; (4) Faeroes; (5) Skagerrak–Kattegat; (6) E Scotland; (7) W Scotland; (8) Farne Deeps, NE England; (9) Botney Gut–Silver Pit, North Sea; (10) W Irish Sea; (11) E Irish Sea; (12) Celtic Sea; (13) Bay of Biscay; (14) Galicia, NW Spain; (15–16) W Portugal; (17) S Portugal; (18) Alboran Sea; (19) Catalan Sea; (20) Ligurian Sea; (21) Tyrrhenian Sea; (22) Adriatic Sea; (23) Aegean Sea.

Figueiredo and Barraca (1963) classified six stages (1–6) of ovary maturation, according to the size and colour of ovaries and diameter of oocytes, and Thomas (1964) described six stages (0–5) depending on the size and colour of ovaries and weight of individual eggs. Other classifications have been used by later investigators, for example, Farmer (1974b), describing five stages (1–5) according to the colour and size of oocytes, stage 5 being mottled-green/cream resorbing stage; Symonds (1972) and Figueiredo (1982) adding a new resorption stage (R); and Bailey (1984) including a separate stage (S) for spent ovaries.

Figueiredo and Barraca (1963) classified the external eggs according to the colour and size and width of the embryo eye. They described five stages (A–E), during which the eggs pass gradually from very dark green, just after spawning, to green and pinkish-green to a pale-pinkish brown colour just before hatching. This egg development scale was also modified somewhat by Dunthorn (1967). Fontaine and Warluzel (1969) also used embryonic stages 0–6, diminished to five stages by Farina et al. (1999). Figueiredo (see Anonymous, 1982) had also shown further subdivisions of her egg stages B, C and D.

Female *Nephrops* attain maturity when still relatively small. Moreover, size at first maturity of females (primiparity) appears to vary between different stocks (Figueiredo and Thomas, 1967b), at least in some cases depending on the density and growth (Bailey, 1986; Bailey and Chapman, 1983; Chapman, 1980). Annual variations in size at maturity have also been recorded (Bailey, 1984; Morizur, 1980, 1983). Furthermore, since the availability of mature females changes in phase with the breeding cycle, estimates of average size at maturity (L_{50} = size at which 50% of animals are mature) can vary according to the criteria used, the year and the time of year studied or the different rates of resorption of the ovaries (Bailey, 1984; Figueiredo, 1982). Therefore, one calendar year results may differ from those of adjacent years.

Smallest size at maturity, based on females carrying external eggs, has been recorded for many areas: off Northeast England (Storrow, 1912); Skagerrak–Kattegat (Havinga, 1929; Höglund, 1942; Poulsen, 1946); Firth of Clyde, west Scotland (Bagenal, 1953; Barnes and Bagenal, 1952); the Adriatic Sea (Karlovac, 1953); the Faeroes (Andersen, 1962); and the Irish Sea (O´Riordan, 1964). In later years, investigators have increasingly dealt with the estimation of the size at which 50% of females are mature (L_{50}), using different methods in various waters (Anonymous, 1982; Arrobas, 1982; Ayza et al., 2011; Bailey, 1984; Bailey and Chapman, 1983; Bianchini et al., 1998; Briggs, 1988; Figueiredo, 1982; Figueiredo and Thomas, 1967a,b; McQuaid et al., 2006; Mente et al., 2009; Morizur, 1980, 1983; Orsi Relini and Relini, 1989; Orsi Relini et al., 1998; Sardà, 1991; Thomas, 1964; Thomas and Figueiredo, 1965; Tuck et al., 2000).

Although the ideal approach to maturity and sex ratio studies is generally to compare animals of the same age (Anonymous, 1984), this presents problems with respect to *Nephrops* because of the inherent difficulties in determining the age of crustaceans. Nevertheless, Morizur (1983) described annual changes in size and age at maturity between 2 years in the Bay of Biscay. Bailey and Chapman (1983) and Bailey (1984) showed a significant

difference in size at maturity between two Scottish areas, although the age at maturity was the same, due to the different growth rates of the two populations. More recently, Tuck et al. (2000) showed a considerable difference in age of smallest ovigerous females and in L_{50} within seven locations in the Firth of Clyde, west Scotland.

In addition, other indicators of maturation in female *Nephrops* have been used by a few authors, such as comparing allometric growth data of various body parts, for example, CL and abdominal width (Farmer, 1974c; McQuaid et al., 2006; Tuck et al., 2000).

As previously mentioned, estimations of size at maturity in female *Nephrops* have been shown to vary a great deal, depending on the method used and time of year or years sampled (e.g. Anonymous, 1982). In view of this, a few different methods have been tested in this study, for estimating size at maturity within the female populations at southwest, south and southeast Iceland, respectively.

Associated with their wide distribution (Figure 2.3), Norway lobsters show great variations in their breeding cycle. Several authors have described the percentage composition of ovary stages in samples over a period of 1 year or more, using such data along with information on the presence of egg-bearing females to determine the frequency and periods of spawning and hatching (Bailey, 1984; Briggs, 1988; Eiríksson, 1969, 1970b, 1993; Farmer, 1974b; Figueiredo and Barraca, 1963; Morizur, 1980, 1981b; Nicolajsen, 1989; Nicolajsen and Eiríksson, 1990; Orsi Relini and Relini, 1989; Orsi Relini et al., 1998; Sterk and Redant, 1989; Symonds, 1972; Thomas, 1964). Changes in the weight of ovaries over time have been described by Vives and Suau (1963) and Bailey (1984). In addition, a number of investigators have based their evaluations concerning the frequency or period of spawning on catch composition or egg-bearing females only (e.g. Andersen, 1962; Conan, 1978; Farina, 1989; Hillis, 1972; Höglund, 1942; Karlovac, 1953; O´Riordan, 1964; Poulsen, 1946; Sardà and Caballín, 1977; Storrow, 1912; Thomas, 1954). The occurrence of *Nephrops* larvae has also, in a number of cases, been investigated, indicating the season of hatching (Andersen, 1962; Conan, 1978; Eiríksson, 1969; Fraser, 1965; Hillis, 1968, 1974; Jorgensen, 1925; Karlovac, 1953; Milligan and Nichols, 1988; O´Riordan, 1964; Thomas, 1954).

The sex ratio in the catch of Norway lobster is highly variable, due to changes in the availability of females depending upon the phase of the breeding cycle and different growth rates of the sexes. Some early descriptions of the sex ratio of *Nephrops* include those of McIntosh (1908), Gauss-Garady (1912), Storrow (1912, 1913) and somewhat later Poulsen (1946), Barnes

and Bagenal (1952), Karlovac (1953) and Thomas (1954). Andersen (1962), studying *Nephrops* at the Faeroes, also gave a good overview of earlier investigations from other areas. Monthly variations in sex ratio by geographical areas have been described by a number of later authorities, including reviews by Figueiredo and Thomas (1967a,b) and the ICES Working Group on *Nephrops* (e.g. Anonymous, 1982, 1984).

The ideal approach to sex ratio studies is by comparing animals of the same age rather than by using similar size groups, which has been the general rule due to the difficulties of crustacean age determination (Anonymous, 1984). However, age-based sex ratio studies have been attempted by Briggs (1988) on data from the Irish Sea.

Some early investigators estimated the number of eggs carried by berried females of different sizes, but no reference was made to the female size/egg number relationships or the stage of development of the eggs although early green eggs must be considered most likely (Bagenal, 1953; Gauss-Garady, 1912; Höglund, 1942; Storrow, 1912). A number of authors have studied fecundity and female size relationships at one or more stages of external egg development (Abelló and Sardà, 1982; Allonso-Allende, 1979; Briggs et al., 2002; Chapman and Ballantyne, 1980; Farina et al., 1999; Farmer, 1974b; Orsi Relini and Relini, 1989; Orsi Relini et al., 1998), while others have estimated the fecundity from the number of oocytes of mature ovaries (Fontaine and Warluzel, 1969; Morizur and Rivoalen, 1982; Thomas, 1964). Finally, some authors have used both oocyte and abdominal egg counts (Eiríksson, 1970b; Figueiredo and Nunes, 1965; Figueiredo et al., 1982; Froglia and Gramitto, 1979; Gramitto and Froglia, 1980; McQuaid et al., 2009; Mori et al., 1998; Morizur, 1980; Morizur et al., 1981; Tuck et al., 2000).

Preliminary results on the fecundity of *Nephrops* in Iceland were described by Eiríksson (1969, 1970b) and showed that the number of both ovary and external eggs in Icelandic *Nephrops* is curvilinearly related to CL. Furthermore, although apparently undamaged recent spawners had been sampled, these studies revealed that the loss of eggs from ovary stage 6 to external egg stage A amounted to approximately 33% in average-sized females of 35 mm CL. The fecundity at southwest Iceland was also shown to be much lower than previously documented for Scottish and Portuguese waters (Figueiredo and Nunes, 1965; Thomas, 1964).

3. MATERIALS AND METHODS

Nephrops (one basket or ~20 kg) from both research and commercial vessel catches from various fishery rectangles have been sampled annually

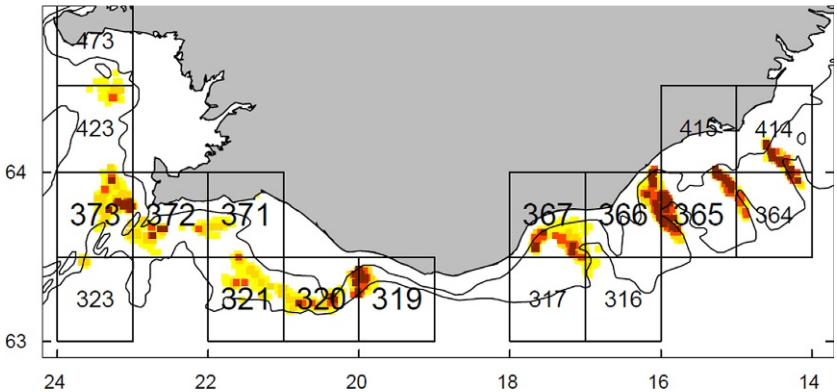


Figure 2.4 Fishery statistical rectangles of *Nephrops* fishing grounds at Iceland, subdivided into the southwest (rectangles 323, **373**, **372**, **371**, 423, and 473), south (321, **320**, and **319**) and southeast areas (317, 316, **367**, **366**, **365**, 364, 415, and 414). Bold figures indicate those areas utilized since the early years of the fishery around 1960, normally preferred in certain fishery-related time-series data such as carapace length and sex ratio.

since around 1960. The CL, from the posterior edge of the eye socket to the posterior edge of the carapace midline, of male and female *Nephrops*, has been measured to the nearest millimetre by a sliding steel calliper.

These measurements constitute the Marine Research Institute's *Nephrops* database of some 1,090,887 males and 184,713 females (14.5% of total) registered from *Nephrops* trawl catches in 1960–2010. Such a massive amount of data, collected relatively unsystematically in the earlier years from a total of around 15 statistical rectangles, is apt to be in many respects somewhat incongruous. Therefore, when describing trends such as in sex ratio or mean size of animals, the author has chosen to concentrate the work on the most important fishing areas, located within a total of eight rectangles and, for unbroken time series, often pooling the data into groups of three areas of adjacent rectangles each, that is, denoted southwest, south and southeast Iceland, respectively (Figure 2.4).

3.1. Classification of female maturity stages

During the years 1964–1970, 450 female *Nephrops* were sampled for oocyte diameter and 199 collected for external egg diameter measurements off southwest Iceland (Table 2.1). The latter include 71 females sampled for studying the relationship between external egg diameter and female CL. The samples were preserved either in 4% formalin, buffered with sea water,

Table 2.1 Classification of ovaries and external eggs into categories 1–6 and A–E, respectively, depending on the colour and oocyte diameter

	Ovaries						**Eggs**			**Stage 1 larvae**
Maturity stage	**1**	**2**	**3**	**4**	**5**	**6**	**A**	**D**	**E**	
Colour	Translucent-white–opaque	Creamy-white	Yellow-pink–greenish	Light green–green	Green–dark green	Dark green–blacky green	Dark green–blacky green	Pinkish-green	Pinkish-brown	
Diameter of oocytes: range (mm)	0–0.25	0.20–0.40	0.40–0.60	0.55–0.80	0.70–1.10	1.00–1.60	1.15–1.64	1.35–1.85	2.05–2.35	
Mean (mm)	~0.20	0.32	0.49	0.64	0.84	1.33	1.41	1.50	2.20	1.78 mm CL
No. of animals	8	45	100	121	80	99	71	32	37	20

The mean carapace length (CL) of stage I larvae shown for comparison.

or in Gilson's fluid. For both ovary oocyte and external egg diameter, some 30–45 individual measurements were made from each female in the sample. The individual eggs from the frontal lobe of each ovary, or from the spawn, were measured by a micrometre, thus giving a mean ovarian or external egg size for each female.

Moreover, when sampled, the ovaries were classified visually into six stages (1–6), according to the colour from the storage of ovoverdins and ovary size, and the external eggs were denoted into stages A–D–E by colour and the appearance of embryo eyes (see Figueiredo and Barraca, 1963). Stages ascribing to B and C were only sampled very rarely, presumably due to greater burrowing behaviour of females carrying eggs at these stages and more limited sampling during autumn–winter, that is, outside the major fishing season (mainly April–May to August–September) during the course of the decades. However, a small-scale sampling of ovigerous females in typical off-season *Nephrops* landings in October–November 2009–2010 has revealed a certain proportion of stage B eggs in these months.

3.2. Maturity size

The data on size at maturity consist of 58,919 females overall (Table 2.2), including 48,302 sampled in May, 4244 in June and 2781 in July during the period 1971–2007 off southwest, south and southeast Iceland. Also, 1625 females were obtained during May–August in the years 1965–1970 off southwest Iceland and 1967 females in April 2001–2007 in the southeast. As indicated by the reproductive cycle (see Sections 3.3 and 4.3), the major sampling that has taken place in May coincides well with the peak abundance of females with fully mature (stage 6) ovaries or recently extruded (stage A) eggs, being one of the underlying factors in the sampling strategy for that month.

The 50% maturity size (L_{50}), sometimes defined as size at onset of maturity (SOM), was calculated from the proportion of females with ovary stages 3–6 and ovigerous out of all females sampled in each length class in May during the almost four decades 1971–2007 off southwest, south and southeast Iceland and similarly for comparison in April, June and July in certain decades and areas described above. Moreover, the L_{50} was studied in the same manner for the months of May–August and July alone during the period 1965–1970 at southwest Iceland.

L_{50} was also studied from the proportion of prespawning ovary stage 6 and ovigerous animals in each length class out of all females, thus

Table 2.2 Number of female *Nephrops* sampled for size of maturity, by areas and periods during 1965–2007

Year/month	SW Iceland	S Iceland	SE Iceland	Overall
1965–1970 (May–August)	1625			1625
1971–1980 (May)	2103	1605	3080	6788
1971–1980 (June)	1598			1598
1971–1980 (July)	1069			1069
1981–1990 (May)	2737	1845	4235	8817
1981–1990 (June)		861	1785	2646
1981–1990 (July)			1712	1712
1991–2000 (May)	4978	4023	12,195	21,196
2001–2007 (April)			1967	1967
2001–2007 (May)	1230	2108	8163	11,501
Total 1965–2007	15,340	10,442	33,137	58,919

investigating what the author refers to as the 50% breeding length (referred to as BL_{50} hereafter). This was done for the month of May 1971–2007 in all sampling areas and for April 2001–2007 off southeast Iceland.

Lastly, a further breeding ratio criterion was investigated, based on 50% ovigerous females (referred to as OV_{50} hereafter) in each length class out of all females in May 1971–2007 at all sampling locations and similarly for June and July 1971–1980 and May–August 1965–1970 off southwest Iceland.

All 50% maturity estimations were calculated by a sigmoid logistic curve (Pearl and Reed, 1920), fitted by a least-squares model and iterations to each decadal sample, according to the formula:

$$P_i = \frac{1}{1 + e^{-(a + bx_i)}}$$

where P_i designates proportion maturing for the first time and mature females (L_{50}), proportion spawning with ovary stage 6 and berried (BL_{50}) or only berried animals (OV_{50}), x_i denoting length group in decadal area sample i and a and b being constants. An example of L_{50} estimation is shown in Figure 2.5.

In view of the biennial nature of reproduction in Icelandic female *Nephrops*, the maxima of 100% mature animals are only realized in the case

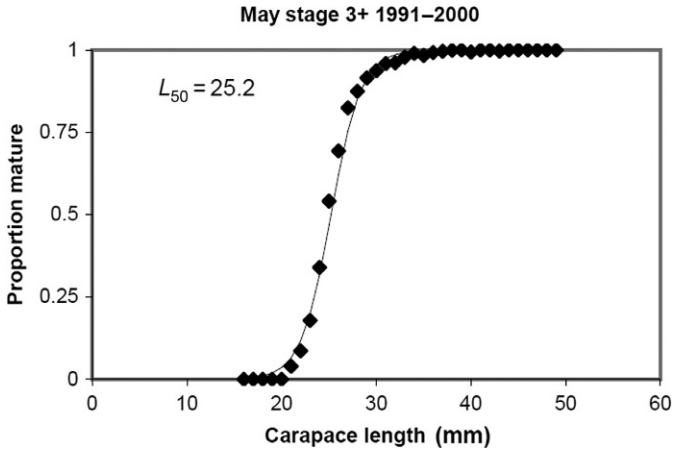


Figure 2.5 Example of maturity estimate of females in the Icelandic *Nephrops* stock. L_{50} = 50% maturity length (also included in the chapter, BL_{50} = 50% breeding length, i.e. final fully mature ovary stage (6) and ovigerous animals; OV_{50} = 50% ovigerous length).

of the L_{50} calculations but cannot, however, peak at more than approximately 50% or less when studying the spawning population in a particular spawning season. Therefore, the author had to raise the sigmoid maturity curves in an appropriate manner when considering BL_{50} and OV_{50}.

A relatively simple method for estimating minimum size of maturity is by studying the smallest recorded ovigerous animals. Thus, the 14,879 ovigerous females investigated during the period 1965–2010 (see Table 2.3) gave some information of variations in the minimum size of maturity during the course of the last five decades.

In addition, for investigating possible changes in relative growth rate and SOM, the maximum width of the second abdominal segment of 1183 females at varying CL was measured at southwest and southeast Iceland in 1969–1970. Moreover, female relative growth was compared to that of 1742 male individuals measured simultaneously in the same areas.

3.3. Reproductive cycle

In the years 1965–2010, 94,322 females were investigated for reproduction studies as a part of regular sampling of unsorted *Nephrops* trawl catches from major fishing grounds off Iceland (Table 2.3). All females were measured to the nearest millimetre CL. Ovaries were allocated macroscopically by eye to stages 1–6 and berried females categorized with external eggs A and D or E,

Table 2.3 Number of females sampled by maturity stages for stated months at southwest, south and southeast Iceland, respectively, during the years 1965–2010

Southwest Iceland 1965–2010

Month	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.–Dec.
Ovary													
1	0	0	0	9	174	82	84	148	9	0	0	0	506
2	0	0	0	13	550	188	85	23	31	0	0	1	891
3	0	0	0	56	1766	737	1102	211	25	2	13	0	3912
4	13	1	3	21	2482	1019	2628	599	467	143	231	4	7611
5	28	2	7	40	658	192	175	201	234	53	273	20	1883
6	77	3	19	331	4008	63	11	7	1	0	0	9	4529
Ovigerous													
A2	0	0	0	3	2166	453	328	48	37	10	11	0	3056
D3	0	0	0	0	95	8	2	0	0	0	0	0	105
D4	0	0	0	0	178	3	1	0	0	0	0	0	182
E3	0	0	0	0	124	19	8	0	0	0	0	0	151
E4	0	0	0	0	163	9	20	1	0	0	0	0	193
Total	118	6	29	473	12,364	2773	4444	1238	804	208	528	34	23,019

Continued

Table 2.3 Number of females sampled by maturity stages for stated months at southwest, south and southeast Iceland, respectively, during the years 1965–2010—cont'd

Southwest Iceland 1965–2010

Month	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.–Dec.
Ovary													
1			0	5	317	57	150	0	18	0	0		547
2			0	1	800	104	78	0	28	0	0		1011
3			0	12	2174	998	795	29	69	1	0		4078
4			0	19	2227	1207	1663	243	884	67	89		6399
5			10	22	291	67	96	13	213	34	103		849
6			11	83	2333	37	9	0	0	0	2		2475
Ovigerous													
A2			0	5	1831	164	178	5	77	2	14		2276
D3			0	1	38	1	0	0	0	0	0		40
D4			0	0	26	0	1	0	1	0	0		28
E3			0	0	153	6	3	0	0	0	0		162
E4			0	0	144	3	2	0	0	0	0		149
Total			21	148	10,334	2644	2975	290	1290	104	208		18,014

Southeast Iceland 1965–2010													
Month	**Jan.**	**Feb.**	**Mar.**	**Apr.**	**May**	**Jun.**	**Jul.**	**Aug.**	**Sep.**	**Oct.**	**Nov.**	**Dec.**	**Jan.–Dec.**
Ovary													
1	0	1	0	26	644	232	391	83	58	1	0	0	1436
2	0	3	3	30	1611	100	194	4	33	0	0	2	1980
3	7	14	6	235	6610	1414	2381	201	166	2	2	2	11,040
4	18	1	2	340	6846	1975	6098	219	681	123	102	18	16,423
5	101	99	58	426	1064	218	605	179	700	71	72	387	4043
6	92	559	286	2058	6731	46	76	0	0	0	0	45	9830
Ovigerous													
A2	0	2	1	188	5812	657	573	37	73	3	4	3	7353
D3	2	0	1	2	103	3	1	0	0	0	0	0	112
D4	1	0	0	1	88	1	1	0	0	0	0	0	92
E3	0	0	0	2	413	41	4	0	0	0	0	0	460
E4	0	0	0	0	445	64	11	0	0	0	0	0	520
Total	221	679	357	3308	30,367	4751	10,335	723	1711	200	180	457	53,289
Overall	339	685	407	3929	53,065	10,168	17,754	2251	3805	512	916	491	94,322

respectively, for the recent spawners and prehatchers (Figueiredo and Barraca, 1963). This classification was based on Icelandic microscopic data from 1964 to 1970 (see Table 2.1). In addition, a soft condition of the shell was recorded—ecdysis being a typical posthatching and a mating characteristic. All data were registered by area rectangles and compiled for the continental shelf and channels southwest, south and southeast of Iceland, respectively (see Figure 2.4).

Resorption does not appear to be a very prominent feature in ovaries of Icelandic *Nephrops* (incidence 0–4% when investigated in samples during the spawning seasons of May 1990–1992 and 2006–2010). However, green to dark green ovaries with a small proportion of yellow or creamy specks were normally assigned to stages 5–6. If the major part of the ovary was a mosaic of lighter colorations of green and yellow, it was grouped as stage 4. Females with apparently fully resorbed ovaries, having mostly creamy but relatively filled out follicles, were allocated to stage 3. In those cases, parts or even the whole animal was often tinted green, probably because of the dark green carotenoprotein pigments from the resorbing ovaries turning the haemolymph green and thus darkening the articular membranes and abdomen, sometimes called "black lobster" in *Homarus americanus* (Phillips et al., 1980; Waddy and Aiken, 1991). Ovaries of newly berried females (abdominal egg stage A), sometimes with a few remaining ripe dark green oocytes in the ovary, were grouped at stage 2. These females had light coloured oocytes that correspond in mean size to those of stage 2 ovary in first-time maturing (primiparous) females (see Table 2.1). In addition, females with external eggs in stages D and E carried invariably ovaries in stages 3–4.

3.4. Sex composition

Seasonal and annual variations in female sex ratio in catches have been obtained from all *Nephrops* samples with a minimum monthly number of 100 individuals, collected within the study area at southwest, south and southeast Iceland during the 50-year period 1960–2010. These include 1,122,928 animals investigated.

Monthly samples were all weighted by numbers within fishery rectangles in the southwest, south and southeast. Also, in order to minimize the effect of other sampling variance when dealing with seasonal or monthly variations in female sex ratio, it was chosen to describe those in terms of decadal averages. Also, annual or decadal variations in sex ratio are largely detailed in terms of weighted averages for each month and unweighted seasonal

May–August means by years, since these months include the largest part of the annual fishing season and therefore the bulk of the available data.

The relationships between female sex ratio and mean size of animals in the catch are described in terms of unweighted seasonal May–August data. However, relationships with various fishery data such as catch per unit of effort (CPUE) and fishable stock biomass estimates are shown with weighted female percentage data for the month of May, being as a rule the most important month as regards landings and CPUE.

3.5. Fecundity

Information on the fecundity of *Nephrops* was obtained by sampling with trawl prespawning (dark green ovaries at stage 6) and recently berried (dark green eggs at stage A) females, apparently undamaged, in May–June 1968–1970 at southwest Iceland (statistical fishery rectangle 373).

Ovaries (stage 6) from 91 individuals were sampled and preserved in either 4% formalin or Gilson's fluid. After weighing the whole ovary, a portion (25–35%) was weighed and a direct count made of the number of ripe oocytes to obtain a total fecundity measure. Furthermore, 130 recent spawners (stage A) were sampled and preserved in 4% formalin. A direct egg count was then made of the whole spawn for a fecundity estimate.

Fecundity (F) was represented as a function of CL, correlating by least-squares linear regression the power equation $F = a \times \mathrm{CL}^b$ with a and b as constants.

4. RESULTS AND DISCUSSION

4.1. Female maturity stages

Table 2.1 and Figure 2.6 depict the distribution and individual means of the microscopic diameter observations for ovary stages 1–6 and external egg stages A, D and E at southwest Iceland. These measurements show an average diameter of stage 6 ova (1.33 mm), stage A eggs (1.41 mm) and stage E eggs (2.20 mm), indicating those close to spawning (6), recently berried (A) and the about to hatch (E).

As shown in Figure 2.7, there is a significant positive correlation between stage A egg diameter and the size of females ($r^2 = 0.226$; $p < 0.001$), with an overall individual range of 1.15–1.64 mm in females of 27–46 mm CL.

Overall, the Icelandic measurements for ovary oocyte measurements are in good conformity with the results from Portuguese waters (Anonymous,

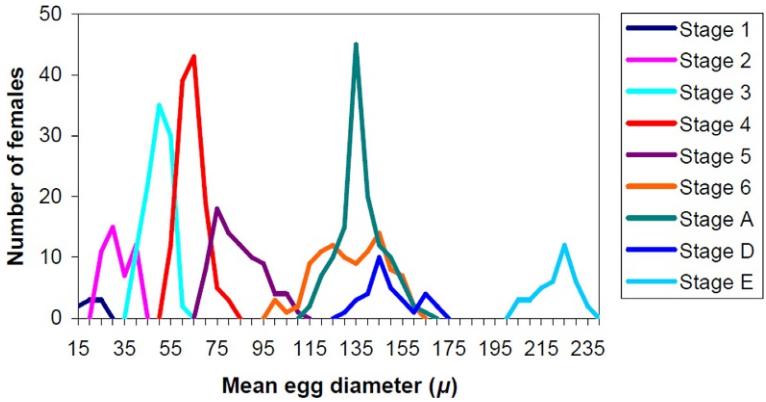


Figure 2.6 Diameter (μ) range of ovary stage 1–6 oocytes and external egg stages A, D, and E (35–45 measurements per individual sampled).

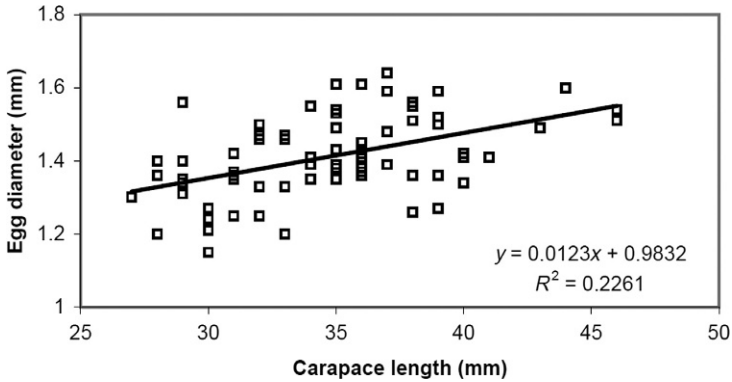


Figure 2.7 Correlation between female carapace length (CL) and external egg stage A diameter (mm) ($p < 0.001$; diam. SD = 0.112).

1982; Figueiredo and Barraca, 1963), the Irish Sea (Farmer, 1974b) and the northern Tyrrhenian Sea, west of Italy (Mori et al., 1998). The Icelandic data, however, give an indication of larger oocytes at ovary stage 6 than in Irish waters (Farmer's stage 4). Possibly, the small size of females in the Irish Sea could account for lesser mean size of oocytes at advanced stages of development shown by Farmer. Moreover, Tuck et al. (2000) found that in areas of low values of asymptotic male CL (L_∞) in the Firth of Clyde, females appeared to have smaller oocytes but a larger size-specific fecundity, possibly conforming well with areas in the Irish Sea.

The size-related diameter of stage A eggs in Iceland is in agreement with results from Morizur and Rivoalen (1982), which showed that the average diameter of external eggs in the Celtic Sea, south of Ireland, varies according

to the size of females. Adversely, however, regression analyses in studies from Scotland and the Irish Sea found no relationship between female size and egg diameter (McQuaid et al., 2009; Smith, 1987), and results from the northern Tyrrhenian Sea in the Mediterranean concluded that egg volume did not vary with female size although it did decrease with depth indicating the causative factor as lesser food availability (Mori et al., 2001).

However, the mean size of stage A eggs appears somewhat smaller at same size groups in the Celtic Sea (Morizur and Rivoalen, 1982) than in Icelandic waters. Similarly, the external stage A eggs described for Portuguese waters (Figueiredo and Barraca, 1963), although of approximately the same diameter as in Iceland, 1.05–1.55 versus 1.15–1.64 mm, were sampled from females with an average CL of 41.8 mm compared with that of only 34.8 mm in the present Icelandic data. According to the relationship for Iceland in Figure 2.7, the average CL given for the Portuguese data would therefore indicate a relatively larger egg diameter in Icelandic waters.

The average egg diameter shown for the prehatching stage E in Iceland appears to be equivalent to those previously shown for identical stages described by Fontaine and Warluzel (1969) for the Bay of Biscay. Mori et al. (1998), although describing similar sizes for stages A and D, reported considerably smaller eggs for the ready-to-hatch stage E than in the present Icelandic data. However, in the absence of comparable female size data, a geographical difference between areas cannot be ruled out. Thus, there are strong indications that a geographical comparison of ovary oocyte and external egg diameter has to be based on similar sizes of females.

Egg size is known to vary with female size in some lobster species, but not in others. It has been presented here for *Nephrops* at southwest Iceland and has also been described for *Nephrops* in the Celtic Sea (Morizur and Rivoalen, 1982). Also, in the European lobster *Homarus gammarus*, egg size has been shown to be positively, but only weakly, related to female CL (Lizàrraga-Cubedo et al., 2003; Tully et al., 2001) and similarly in the American lobster *H. americanus* (Attard and Hudon, 1987; Ouellet and Plante, 2004).

Considering all the available data, however, it is not unreasonable to assume somewhat larger egg sizes in areas of longer incubation periods and less fecundity, as has been described for the waters off southwest Iceland (Eiríksson, 1969, 1970b) and detailed later in results and discussion on *Nephrops* reproduction cycle and fecundity observations (see Sections 4.3 and 4.5). A comprehensive study of larval sizes could possibly give further indications of such differences in the early life history of *Nephrops* between geographical areas.

4.2. Maturity and breeding size variations

As will be detailed in Section 4.3, the month of May is a predominant period of spawning and hatching in female *Nephrops* at Iceland. Therefore, in view of the high proportion of animals with fully ripe ovaries or in the process of spawning in May, the study of size at maturity was largely concentrated on data from that month. The SOM is best described by including relatively small primiparous females, that is, maturing for the first time and recruiting into the fishery. Thus, all stages of maturity are included in the assessment of size at 50% maturity or L_{50}.

Primiparous females in spring will not, however, spawn for the first time until springtime the year after. Therefore, the annual reproductive capacity or female spawning stock biomass as a fisheries management tool is probably best described by defining the annual breeding population. Thus, the inclusion of those primiparous females in the annual mature population of *Nephrops* at spawning and hatching time is more of an academic nature than of importance as a tool for determining such parameters as annual spawning stock biomass and potential production of larval progeny. With that in mind, the author chose in this chapter to describe the 50% breeding length parameter, designating it as BL_{50} when fully mature prespawning ovaries and ovigerous stages are included or OV_{50} when considering only ovigerous or berried females. The breeding maturity ogives (BL_{50} and OV_{50}) are inevitably shifted to the right in size compared to L_{50}, due to the exclusion of primiparous females and growth for a whole year until spawning in springtime a year later. Nevertheless, the very prominent burrowing habit of ovigerous females can pose some uncertainty to the evaluation of BL_{50} and OV_{50}, especially if the timing of spawning or retreating into the burrows is in any way dependent on the size or environmental factors.

Finally, due to certain incongruity of the data, such as varying number of animals sampled annually, pooling of data was considered necessary, and thus, spatial and temporal variations are largely compared as decadal averages by areas or overall.

4.2.1 Spatial and temporal variations in maturity ogives

The length of 50% maturity (L_{50}), during May at southwest, south and southeast Iceland, respectively, in the years 1971–2007, gave similar ogives for all three areas in question, the L_{50} ranging from an overall average of 25.6 mm CL in the southeastern area to 26.1 and 26.6 mm CL, respectively, at southwest and south Iceland (Figure 2.8 and Table 2.4).

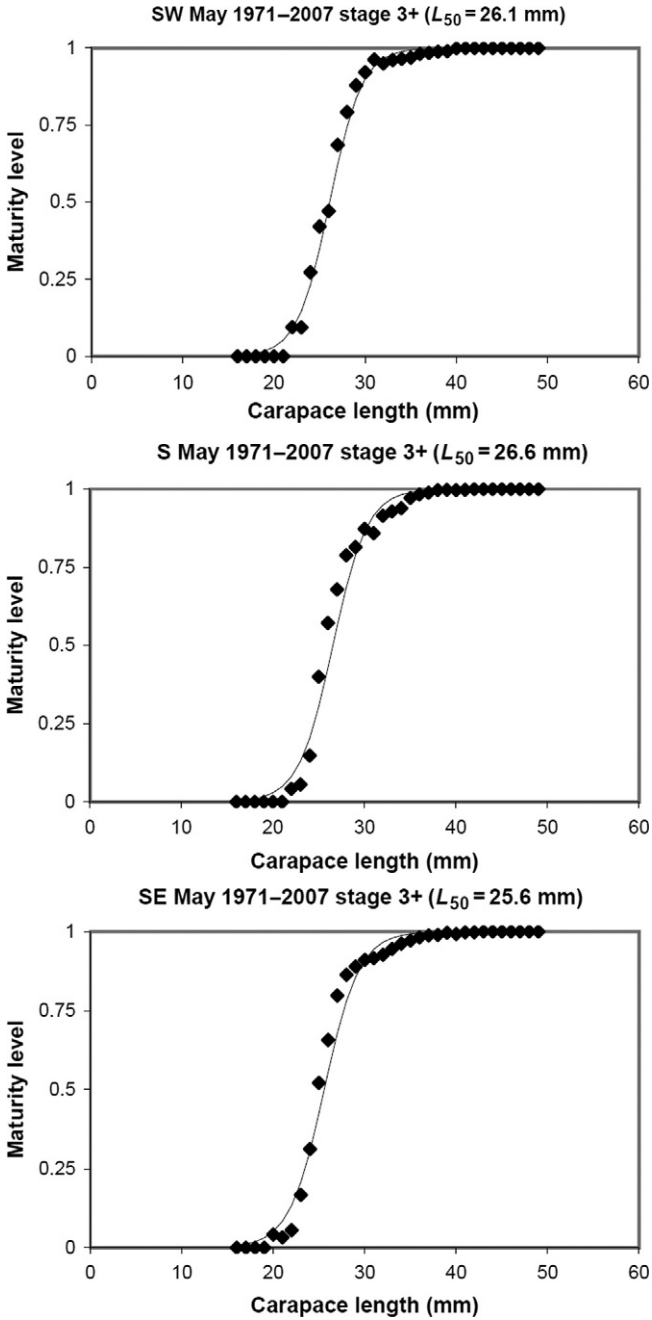


Figure 2.8 Maturity ogives indicating average mean size (CL) at onset of maturity (L_{50}) off SW, S and SE Iceland during May 1971–2007.

Table 2.4 Size of 50% maturity (L_{50}) and 50% breeding (BL_{50}; OV_{50}) in *Nephrops* at Iceland by areas and decades during 1965–2007

Area	Month	Year	L_{50} mm	BL_{50} mm	OV_{50} mm	*a*	*b*	Method (see footnotes)	No. sampled
SW Iceland	May–Aug.	1965–1970	26.67			−12.2281	0.45449	Ovary 3+	1625
SW Iceland	May–Aug.	1965–1970			28.45	−22.7937	0.80119	Ovigerous	
SW Iceland	Jul.	1965–1970	27.33			−12.691	0.46434	Ovary 3+	797
SW Iceland	May	1971–1980	25.55			−15.6758	0.61365	Ovary 3+*	2103
SW Iceland	May	1971–1980		30.00		−14.7858	0.4928	Ovary 6+**	
SW Iceland	May	1971–1980			30.74	−21.2998	0.69293	Ovigerous***	
SW Iceland	Jun.	1971–1980	25.42			−11.7804	0.63438	Ovary 3+	1598
SW Iceland	Jun.	1971–1980			29.49	−11.4404	0.38791	Ovigerous	
SW Iceland	Jul.	1971–1980	25.49			−28.2772	1.10921	Ovary 3+	1069
SW Iceland	July	1971–1980			28.69	−16.06	0.5598	Ovigerous	
S Iceland	May	1971–1980	25.90			−15.6914	0.60592	Ovary 3+	1605
S Iceland	May	1971–1980		27.25		−14.7297	0.54045	Ovary 6+	
S Iceland	May	1971–1980			28.02	−13.3125	0.47513	Ovigerous	
SE Iceland	May	1971–1980	25.99			−16.6894	0.64222	Ovary 3+	3080
SE Iceland	May	1971–1980		30.52		−13.2981	0.43567	Ovary 6+	
SE Iceland	May	1971–1980			31.47	−14.311	0.45476	Ovigerous	

SW Iceland	May	1981–1990	25.19			−14.4922	0.57521	Ovary 3+	2737
SW Iceland	May	1981–1990		30.85		−15.5327	0.50346	Ovary 6+	
SW Iceland	May	1981–1990			30.64	−20.8462	0.68031	Ovigerous	
S Iceland	May	1981–1990	25.67			−17.3639	0.67631	Ovary 3+	1845
S Iceland	May	1981–1990		30.84		−13.9303	0.45176	Ovary 6+	
S Iceland	May	1981–1990			31.71	−19.128	0.60314	Ovigerous	
S Iceland	Jun.	1981–1990	26.13			−13.1332	0.50296	Ovary 3+	861
SE Iceland	May	1981–1990	24.92			−16.9032	0.67822	Ovary 3+	4235
SE Iceland	May	1981–1990		32.43		−11.2812	0.3479	Ovary 6+	
SE Iceland	May	1981–1990			30.71	−19.6641	0.64026	Ovigerous	
SE Iceland	Jun.	1981–1990	24.83			−14.6143	0.58857	Ovary 3+	1785
SE Iceland	Jul.	1981–1990	26.33			−17.8283	0.67701	Ovary 3+	1712
SW Iceland	May	1991–2000	25.90			−13.8515	0.53479	Ovary 3+	4978
SW Iceland	May	1991–2000		31.60		−12.5531	0.39725	Ovary 6+	
SW Iceland	May	1991–2000		30.42		−10.1498	0.33366	Ovary 6+ A	
SW Iceland	May	1991–2000			29.66	−21.4545	0.72345	Ovigerous	
S Iceland	May	1991–2000	26.33			−12.0516	0.45768	Ovary 3+	4023

Continued

Table 2.4 Size of 50% maturity (L_{50}) and 50% breeding (BL_{50}; OV_{50}) in *Nephrops* at Iceland by areas and decades during 1965–2007—cont'd

Area	Month	Year	L_{50} mm	BL_{50} mm	OV_{50} mm	*a*	*b*	Method (see footnotes)	No. sampled
S Iceland	May	1991–2000		30.20		−13.3448	0.44191	Ovary 6+	
S Iceland	May	1991–2000			30.61	−19.5045	0.63715	Ovigerous	
SE Iceland	May	1991–2000	25.22			−15.8932	0.63027	Ovary 3+	12195
SE Iceland	May	1991–2000		29.99		−12.2728	0.4092	Ovary 6+	
SE Iceland	May	1991–2000		29.24		−13.4431	0.45971	Ovary 6+ A	
SE Iceland	May	1991–2000			29.54	−19.6437	0.66497	Ovigerous	
SW Iceland	May	2001–2007	28.11			−21.1793	0.75345	Ovary 3+	1230
SW Iceland	May	2001–2007		29.77		−21.4628	0.72086	Ovary 6+	
SW Iceland	May	2001–2007			32.18	−25.1271	0.78095	Ovigerous	
S Iceland	May	2001–2007	27.23			−14.0899	0.51735	Ovary 3+	2108
S Iceland	May	2001–2007		27.92		−14.2923	0.51185	Ovary 6+	
S Iceland	May	2001–2007		28.95		−8.76322	0.30269	Ovary 6+ A	
S Iceland	May	2001–2007			34.37	−11.8504	0.34484	Ovigerous	
SE Iceland	Apr.	2001–2007	25.58			−17.4348	0.68162	Ovary 3+	1967
SE Iceland	Apr.	2001–2007		27.21		−31.8246	1.16976	Ovary 6+	
SE Iceland	May	2001–2007	25.63			−11.2848	0.44024	Ovary 3+	8163

SE Iceland	May	2001–2007		27.07		−23.8851	0.88241	Ovary 6+	
SE Iceland	May	2001–2007			33.13	−13.3431	0.40274	Ovigerous	
		Overall mean							
SW Iceland	May	1971–2007	26.11			−14.7721	0.56571	Ovary 3+	11,048
SW Iceland	May	1971–2007		30.82		−14.3217	0.46462	Ovary 6+	
SW Iceland	May	1971–2007			30.80	−20.799	0.67523	Ovigerous	
S Iceland	May	1971–2007	26.55			−14.2219	0.53571	Ovary 3+	9581
S Iceland	May	1971–2007		29.89		−13.07	0.4373	Ovary 6+	
S Iceland	May	1971–2007			31.24	−12.4949	0.39991	Ovigerous	
SE Iceland	May	1971–2007	25.58			−13.3505	0.52199	Ovary 3+	27,673
SE Iceland	May	1971–2007		30.99		−11.8203	0.38147	Ovary 6+	
SE Iceland	May	1971–2007			31.21	−14.8175	0.47472	Ovigerous	

*Ovary stages 3–6 and ovigerous out of total number of females.
**Ovary stage 6 and ovigerous out of total number of females.
***Ovigerous out of total number of females.
Values of constants *a* and *b* given in the logistic least-squares model used.

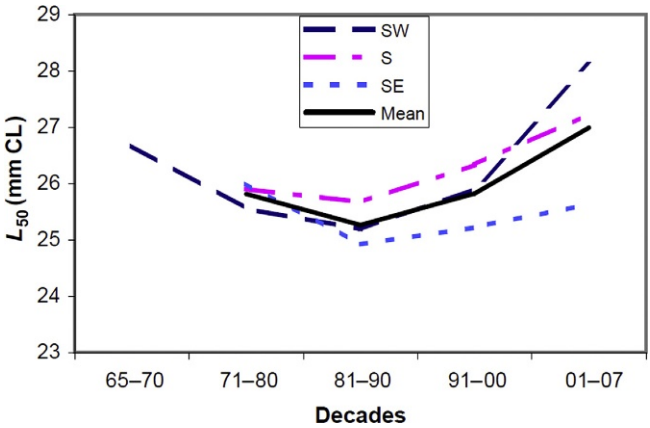


Figure 2.9 Decadal trends in L_{50} at SW, S and SE Iceland during May 1971–2007 (also 1965–1970 for SW Iceland).

The L_{50} has an overall decadal range of 24.9–28.1 mm CL (standard deviation (SD) = 0.89). By areas, however, it ranged from 24.9–26.0 mm (SD = 0.47) in the southeast to 25.7–27.2 mm (SD = 0.69) and 25.2–28.1 mm (SD = 1.31) in the south and southwest, respectively. Moreover, as depicted in Figure 2.9 and Table 2.5, the L_{50} was lowest in all areas in the 1980s, from 24.9 mm CL at southeast Iceland to 25.7 mm CL in the southern area. The highest L_{50}'s have been observed, however, in the years after 2000, being 28.1 mm CL at southwest Iceland and 27.2 mm in the southern area. At southeast Iceland, on the other hand, the L_{50} in the 2000s (25.6 mm) is surpassed by a value of 26.0 mm CL in the 1970s. The oldest available data, from 1965 to 1970 in the southwest, also show a relatively high L_{50} estimate of 26.7 mm CL for the overall May–August period. Fully comparable May figure, however, is unavailable due to limited sampling. Thus, apparently, there is an overall decreasing decadal trend in L_{50} from the 1960s to 1980s but increasing again in the 1990s and 2000s. The record high L_{50} in the southwestern and southern areas in the 2000s is probably the result of an increased growth rate affecting the size of onset of age-related maturity and, therefore, possibly linked with the highest ambient sea temperatures since the early 1960s (Anonymous, 2009; Eiríksson, 2009).

Density-dependent factors may also be important in this respect since recruitment rates have been relatively lower in the 2000s except in the southeast. Therefore, a strong recruiting year class with large numbers of small immature females may affect the estimated size of L_{50}. As displayed in Figure 2.10, the mean size (mm CL) of female *Nephrops* shows a

Table 2.5 Decadal L_{50}, BL_{50} and OV_{50} in May with standard deviations (SD), by areas and overall

	Decade	L_{50}	BL_{50}	OV_{50}
Southwest	1965–1970	26.67		28.45
	1971–1980	25.55	30	30.74
	1981–1990	25.19	30.85	30.64
	1991–2000	25.9	31.6	29.66
	2001–2007	28.11	29.77	32.18
SD	1971–2007	1.314	0.837	1.038
South	1971–1980	25.9	27.25	28.02
	1981–1990	25.67	30.84	31.71
	1991–2000	26.33	30.2	30.61
	2001–2007	27.23	27.92	34.37
SD	1971–2007	0.688	1.736	2.631
Southeast	1971–1980	25.99	30.52	31.47
	1981–1990	24.92	32.43	30.71
	1991–2000	25.22	29.99	29.54
	2001–2007	25.63	27.07	33.13
SD	1971–2007	0.468	2.218	1.505
Overall SD	1971–2007	0.886	1.666	1.768

somewhat similar trend by decades and areas as L_{50}, decreasing from the 1960s to 1970s and increasing again to an overall high in the 2000s ($p = 0.10$) and similarly for males ($p < 0.02$). In this context, the relatively lower L_{50} at southeast Iceland than elsewhere in the 1980s–2000s can probably be attributed to relatively higher average recruitment rates in that area compared to the south and the southwest in particular (Anonymous, 1996b, 2008). Adversely, the record high L_{50} at southwest Iceland in the 2000s corresponds well with low recruitment and very large mean size of both males and females experienced there in the recent years.

Monthly variations in L_{50} were also studied at southwest Iceland in the 1970s, showing a slight decrease from 25.55 mm CL in May to 25.42–25.49 mm CL in June–July. In the southern area in the 1980s, however, a slight increase was seen from 25.67 mm CL in May to 26.13 mm in

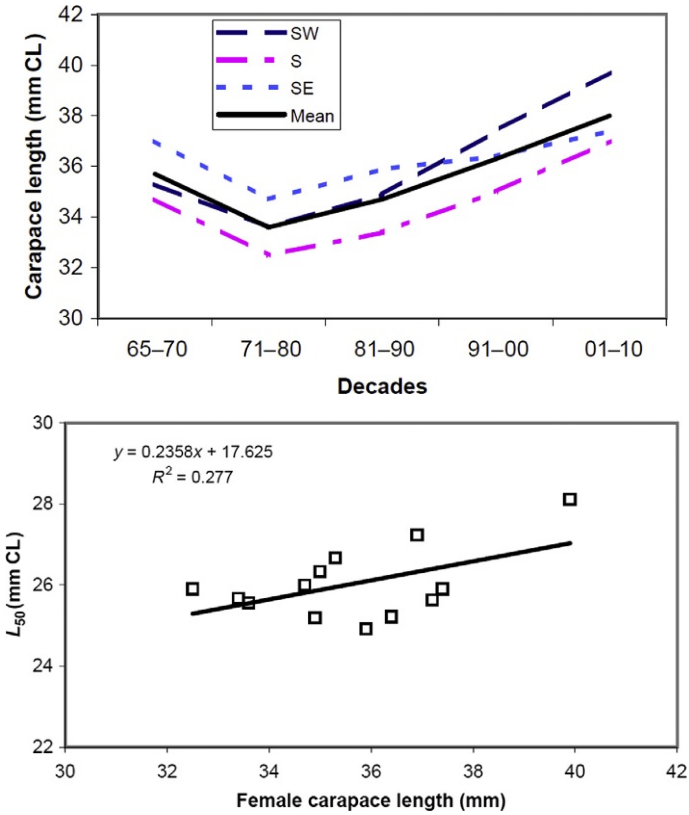


Figure 2.10 Decadal trends in mean carapace length (mm CL) of females during the period 1965–2009 (above). Correlation between mean decadal female L_{50} and carapace length (mm CL) of females ($p < 0.02$) at SW, S and SE Iceland during 1965–2010 (below).

June, and similarly, the July average for southeast Iceland is notably highest at 26.33 mm CL compared to those of 24.92 and 24.83 mm for May and June (Table 2.4). The relatively higher L_{50} observed in June and July at south and southeast Iceland in the 1980s compared to those of May could be artefacts due to less sampling although some growth effects cannot be ruled out. Similarly, the L_{50} average for April 2001–2007 at southeast Iceland, 25.58 mm CL, compares well with that of May (25.63 mm) (Table 2.4).

The 50% breeding size (BL_{50}) was estimated firstly from the ratio of prespawning females at ovary stage 6 and berried out of the total catch of females in May at southwest, south and southeast Iceland in the years 1971–2007 (Figure 2.11). The overall average BL_{50} differed from 29.9 mm CL at south Iceland to a maximum of 31.0 mm CL in the southeastern area (Table 2.4).

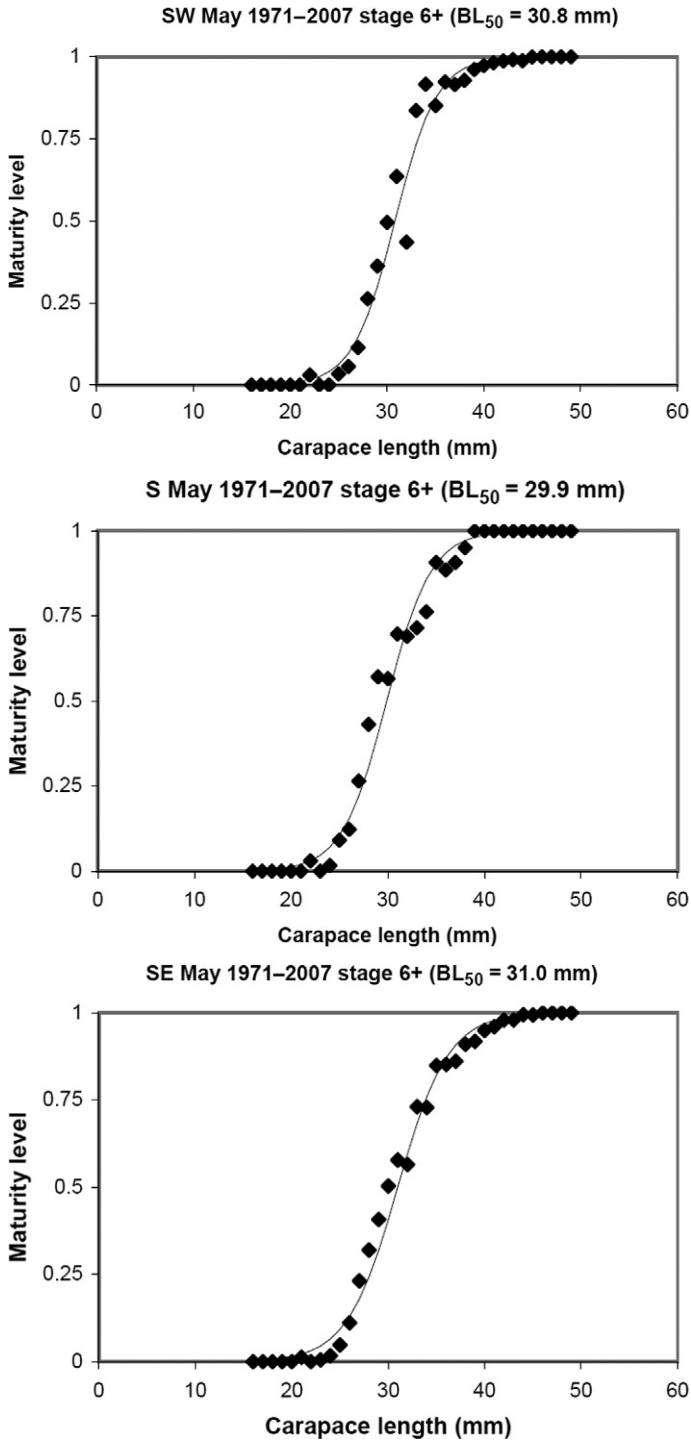


Figure 2.11 Maturity ogives indicating average 50% breeding length (BL_{50}) at SW, S and SE Iceland during May 1971–2007.

The overall decadal BL_{50} for the three areas are shifted by 3.9 mm to the right compared to the L_{50} ogives, mainly as a result of the omission of first-time maturing primiparous females that are due to spawn the following year and 1 year's growth since primiparity.

By decades, the overall range of BL_{50} turns out at 27.1–32.4 mm CL (SD = 1.67). By areas, on the other hand, it ranged from 29.8–31.6 mm CL (SD = 0.84) in the southwest to 27.3–30.8 mm (SD = 1.74) and 27.1–32.4 mm (SD = 2.22), respectively, in the south and southeast (Table 2.5). Moreover, the decadal trend over the whole 1971–2007 period shows a relatively highest BL_{50} on average in the 1980s or from 30.8 and 30.9 mm in the south and southwest to 32.4 mm in the southeastern area but decreases to 27.1, 27.9 and 29.8 mm at southeast, south and southwest Iceland, respectively, in the 2000s (Figure 2.12). Also, the BL_{50} average for April 2001–2007 at southeast Iceland, 27.2 mm CL, compares well with that of May (27.1 mm) (Table 2.4). The apparent trend over the four decades is shown to be somewhat opposite to that of L_{50} (see Figure 2.9). The smaller difference in size between L_{50} and BL_{50}, seen especially in all areas in the 2000s, is by no means clear although one could assume slower growth rate during the time elapsing between the onset of maturity and first spawning in spring the following year compared to previous decades. This is somewhat indicated by the high proportion of small prespawning stage 6 females observed in the 2000s, signifying later spawning by a relatively large number of small first-time spawners (Figure 2.13).

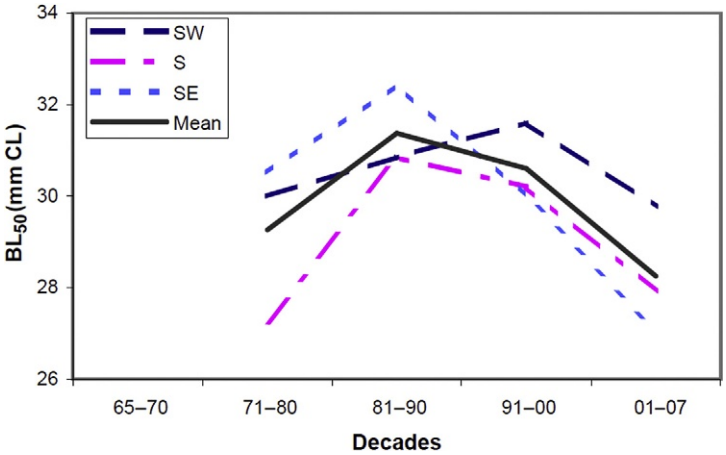


Figure 2.12 Decadal trends in BL_{50} at SW, S and SE Iceland during May 1971–2007.

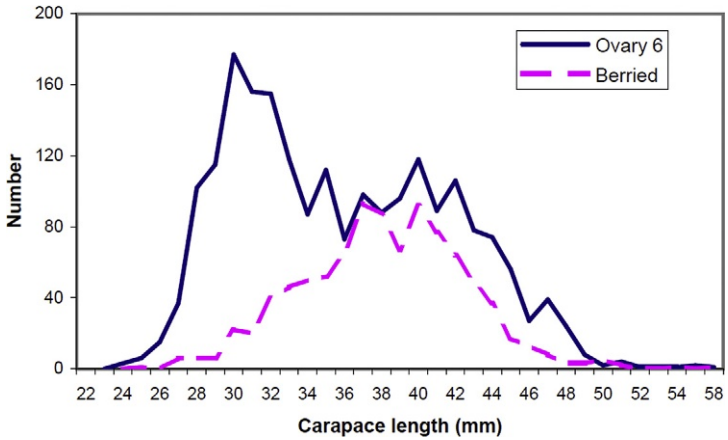


Figure 2.13 Length distribution of prespawning (stage 6) and berried females at SE Iceland in 2001–2010, indicating later spawning by smaller animals (largely first-time spawners).

The 50% ovigerous length (OV_{50}), estimated out of the total catch of females in May, was studied as another criterion for investigating 50% breeding length of females at all locations investigated in 1971–2007. The overall average OV_{50} ranged from 30.8 mm CL at southwest Iceland to 31.2 mm CL in the southeastern and southern areas (Table 2.4) and the ogives are shifted to the right by 5.1 mm in comparison with the L_{50} ogives, mainly as a result of the omission of first-time maturing females not due to spawn until a year later and growth for a whole year since primiparity (Figure 2.14).

On decadal basis, the OV_{50} ranged from 28.0 to 34.4 mm (SD = 1.77). By areas, the OV_{50} measured from 28.5 to 32.2 mm (SD = 1.04) in the southwest, 29.5 to 33.1 mm (SD = 1.51) in the southeast and 28.0 to 34.4 mm (SD = 2.63) in the south (Table 2.5). Moreover, decadal variations in OV_{50} follow a relatively consistent pattern between areas except for the very low value for the southern area in the 1970s (Figure 2.15). The same could be said, although not altogether comparable, about the low OV_{50} in May–August 1965–1970 at southwest Iceland. The OV_{50} trend, not unexpectedly, resembles that of BL_{50} apart from the 2000s when the two are seen to be totally out of phase (Figures 2.12 and 2.15). This appears to be related to the high proportion of small prespawning stage 6 females seen in the 2000s, particularly at southeast Iceland, signifying later spawning by a relatively large number of small first-time spawners resulting in an unusually low BL_{50} and a high OV_{50} (Figure 2.13).

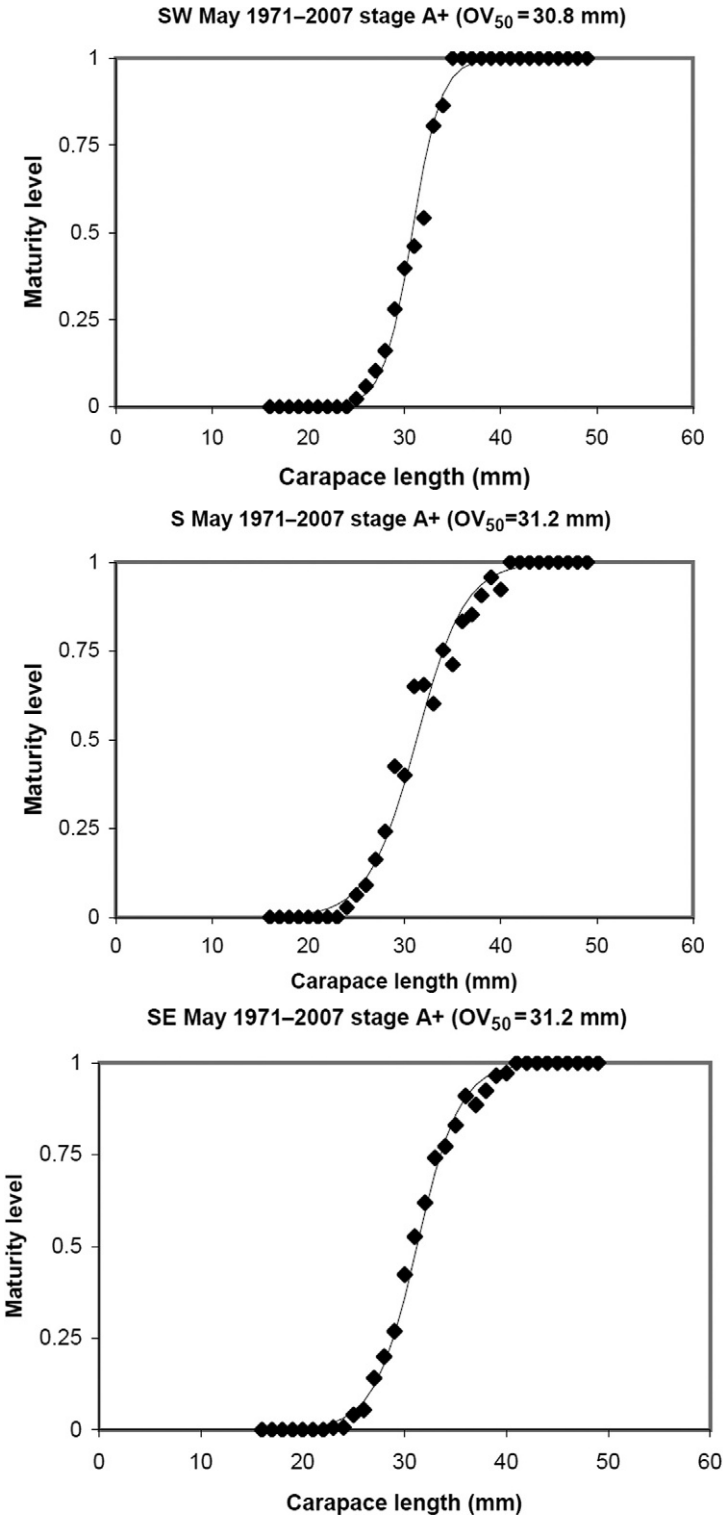


Figure 2.14 Maturity ogives indicating average 50% ovigerous size (OV_{50}) at SW, S and SE Iceland during May 1971–2007.

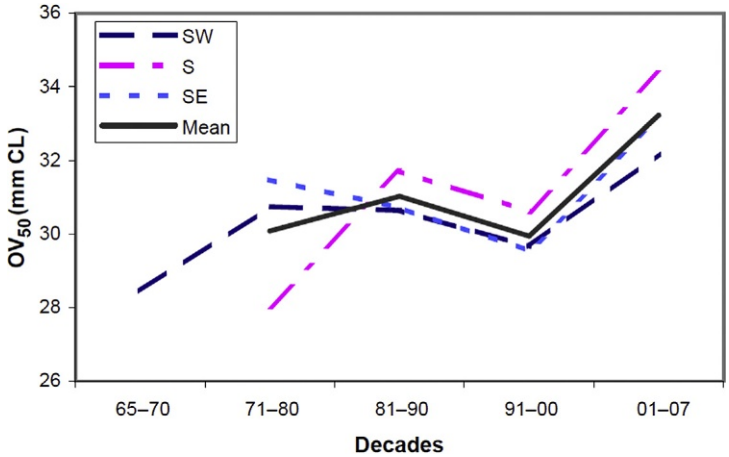


Figure 2.15 Decadal trends in 50% ovigerous size (OV_{50}) at SW, S and SE Iceland during May 1971–2007 (also 1965–1970 for SW Iceland).

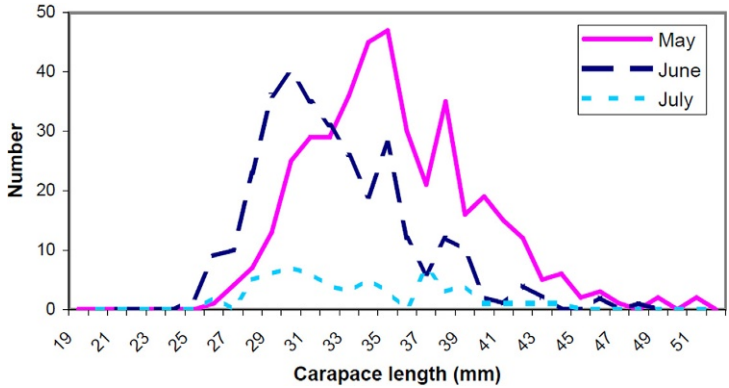


Figure 2.16 Length distributions of ovigerous females during May, June and July at SW Iceland in the 1970s, indicating a difference in time of spawning according to female size.

Monthly variations in OV_{50} were also compared for May, June and July at southwest Iceland in the 1970s, showing a decrease from 30.7 mm CL in May to 29.5 and 28.7 mm, respectively, in June and July (Table 2.4). As shown in Figure 2.16, this is apparently related to later spawning of greater number of smaller females and more dissipation of those earlier larger spawners into their burrows. In addition, the low OV_{50} mentioned above for the southern area in the 1970s, as well as the comparably low BL_{50}, would be explained by large numbers of small mature animals indicating

good recruitment and/or slow growth compared to the other areas. This demonstrates well the temporal effect that spawning and burrowing regimes can have on calculations of size at maturity in female *Nephrops*. Therefore, results may vary considerably according to the methods used and time of year or individual years sampled, making comparisons between areas, not to mention the whole geographical distribution of *Nephrops*, very difficult.

The annual or indeed decadal average timing of size-related spawning appears to explain the main variations shown in the size of BL_{50} versus OV_{50} during the sampling in May over the whole study period. Although the annual *Nephrops* survey has normally been undertaken within only 2–3 weeks in May, that may suffice to explain some of the variability shown in length of BL_{50} versus OV_{50} over the decades.

As listed in Table 2.5, decadal variations in all size of maturity scenarios are considerable, although primarily so for the 2000s. The most apparent variability shown in the 2000s scenarios are undoubtedly the small size differences seen between L_{50} and BL_{50} on one hand and the large size difference of BL_{50} and OV_{50} on the other. Looking at the ratio of prespawning ovary stage 6 female numbers and sizes, however, compared to the recent ovigerous stage A animals in Figure 2.13, it appears evident that for some reason or another, spawning is not as well advanced among smaller individuals, in particular, in the 2000s. This strongly suggests overall later spawning in the last decade, preeminently of the smaller individuals and mostly so at southeast Iceland. This would explain the small BL_{50}, notably in the southeast, where a low BL_{50} value is intensified by relatively good recruitment in the 2000s. At the same time, very high values are seen for the estimate of OV_{50} due to relatively earlier spawning by medium or larger individuals in the 2000s. Overall, small size differences of L_{50} and BL_{50} in the 2000s may be the result of ovary maturation, taking precedence over growth leading to delayed spawning of smaller and largely first-time spawners. Whether the underlying factor is environmental change, for example, related to the fact that bottom sea temperatures have risen by as much as 1 °C in the last decade (Anonymous, 2009; Eiríksson, 2009), however, needs a further study.

Lastly, the breeding parameter OV_{50} is seen to correlate significantly with the average monthly May–July female percentage in *Nephrops* catch samples, by areas and decades, from the 1960s to 2000s ($r^2 = 0.52$; $p < 0.01$) (Figure 2.17) and showing positive, although not significant, correlations with mean decadal CL of females ($r^2 = 0.28$; $p > 0.05$) and males ($r^2 = 0.26$; $p > 0.05$). Such relationships relate directly to phases in recruitment and fishing intensity over the decades and areas.

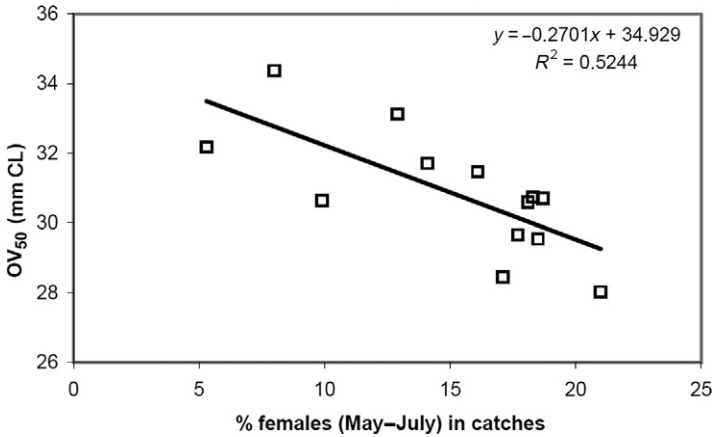


Figure 2.17 Overall correlation between decadal OV_{50} and average May–July % of females in catches ($p < 0.01$).

4.2.2 Spatial and temporal variations in minimum ovigerous size

A relatively easy method for approximating minimum size of maturity is by studying smallest berried females measured by areas and years. Based on measurements of 14,879 ovigerous females from all locations investigated in 1962–2010, a relatively wide range of minimum size of females in berry is observed in all areas (Figure 2.18). The minimum recorded ovigerous size of 23 mm CL was measured in the southeastern area in 1997. At southwest Iceland, a minimum of 24 mm CL was recorded in 1963 and 1970 and in the southern area in 1973 and 1975. However, the annual mean minimum size of berried *Nephrops* in the Icelandic database since the early 1960s ranges from 26.8 mm CL (SD = 2.07) in the southeast to some 27.8 mm (SD = 1.80) and 27.9 mm (SD = 2.29), respectively, in the south and southwest.

Temporal trends differ considerably between the areas studied as displayed in Figure 2.18. At southwest Iceland, the annual minimum ovigerous females measured on average (3-year mean) between 26 and 28 mm CL from the early 1960s to the mid-1990s, however, increasing to over 30 mm by the 2000s. At south Iceland, on the other hand, the average minimum ovigerous size showed a decreasing trend from over 30 mm CL in the mid-1960s to some 25–26 mm CL on average in the early to mid-1970s, remaining relatively stable at around 28 mm CL from about 1980 to the mid-2000s. In the southeastern area, the average minimum berried size fell from over 30 mm CL in the first years of the fishery to around 26 mm in the

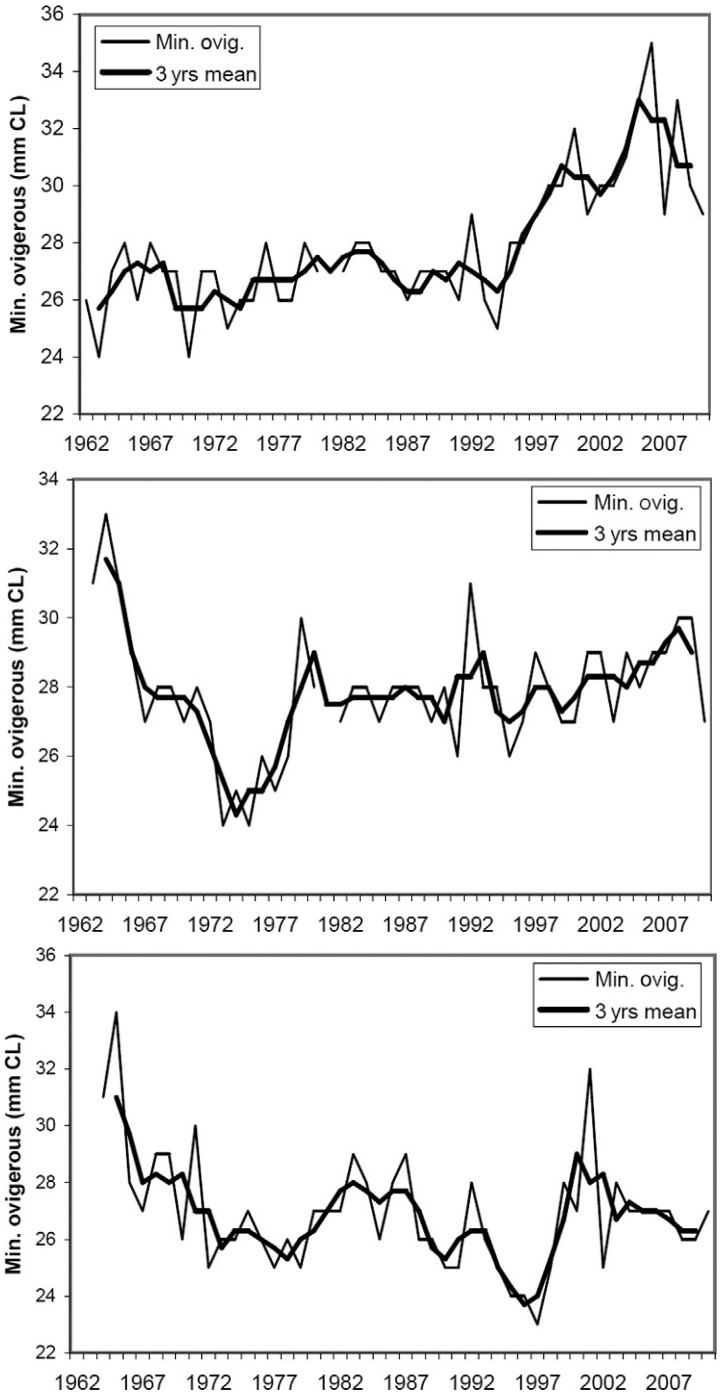


Figure 2.18 Annual trends in minimum ovigerous size at SW (A), S (B) and SE (C) Iceland from the early 1960s to 2010.

early 1970s and quite contrary to the other areas showed a decreasing trend from 27–28 mm CL in the 1980s to only some 24 mm in the mid-1990s. Following a temporary peak of 28–29 mm in the early 2000s, the minimum ovigerous size tapered again down to around 26–27 mm in the latter half of the 2000s.

In regard to various temporal and spatial trends shown in Icelandic *Nephrops*, certain correlations can be distinguished that relate to a varying significance to annual minimum berried size. For example, minimum ovigerous size at southwest Iceland during 1964–2010 shows a positive and highly significant relationship to average annual CL of both males ($r^2 = 0.64$; $p < 0.001$) and females ($r^2 = 0.57$; $p < 0.001$) (Figure 2.19) and similarly in the south ($r^2 = 0.35$; $p < 0.001$ and $r^2 = 0.36$; $p < 0.001$) and southeastern areas ($r^2 = 0.46$; $p < 0.001$ and $r^2 = 0.25$; $p = 0.001$).

Apparently, the historical time series trends of minimum ovigerous measurements detailed in Figure 2.18 may at least be partly ascribed to fishing intensity and its effect on stock abundance and sex and size compositions. Therefore, the relatively small ovigerous females found in the early 1960s at southwest Iceland can be related to the very high exploitation rate imposed on the stock in that area already by 1962–1963. Equally, the increasing minimum ovigerous size and mean CL in 1995–2005 associate well with the low fishing intensity in the southwest during that period (Anonymous, 2008). In the south and southeast, however, exploitation rates intensified relatively later or in the mid- to late 1960s, leading to decreasing mean carapace and ovigerous sizes from around 1965 to the early 1970s. Moreover, the very low ovigerous size and decreasing mean size of both sexes at southeast Iceland in the mid-1990s can be attributed to very high fishing intensity and notable decrease in stock abundance at that time (Anonymous, 2008). The intrinsic relationships between *Nephrops* stock abundance and the concurrent fishery and female biological time series will be dealt with further in Section 4.4.

Finally, observed changes in size at maturity, using comparable criteria, and the possible linkage to growth rate or environmental conditions, as well as the coinciding influence of such important stock aspects as overall abundance, year-class strength and recruitment, are worth further consideration.

4.2.3 Relative growth and SOM

An additional criterion for estimating the SOM in female *Nephrops* includes studying possible changes in relative growth rate of separate body parts. For that purpose, the maximum width of the second abdominal somite was

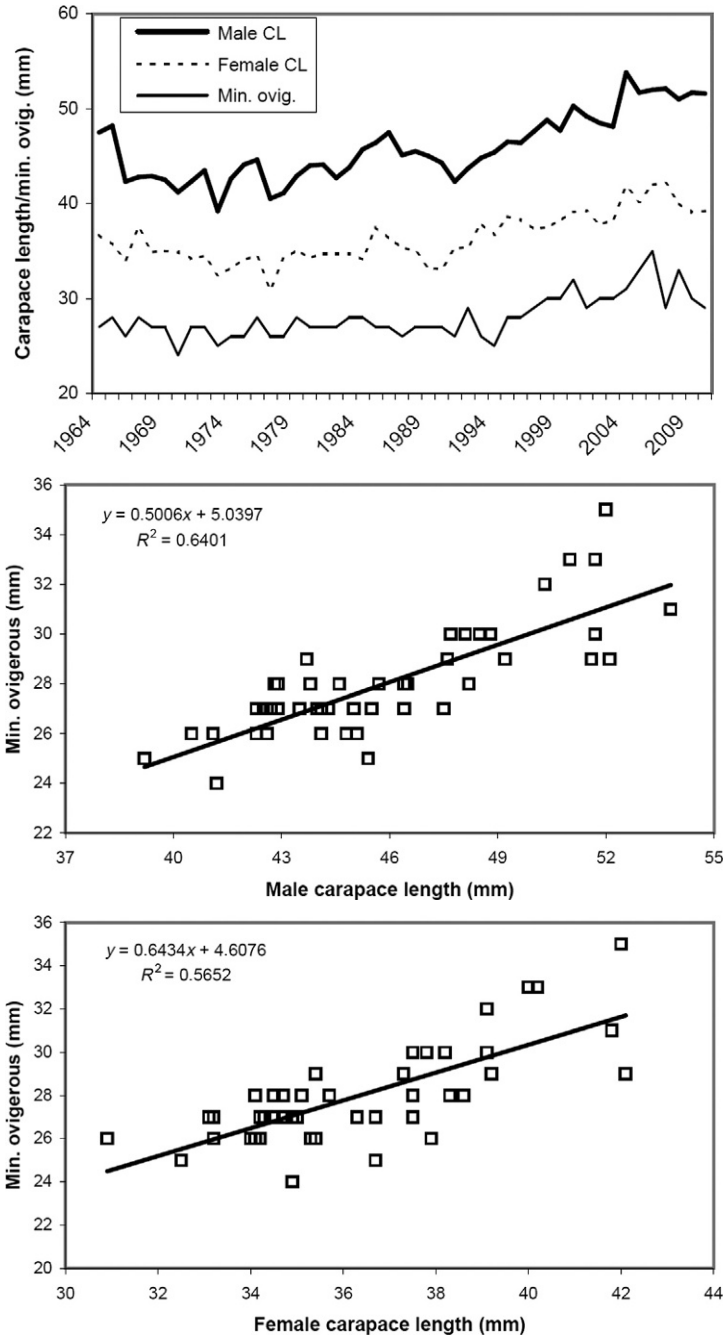


Figure 2.19 Trends in minimum annual ovigerous size and average annual carapace length (mm) of males and females at SW Iceland during 1964–2010 along with correlations between annual minimum ovigerous size (mm CL) and annual average carapace length of males ($p < 0.001$) and females ($p < 0.001$) in 1964–2010 (also studied S ($p < 0.001$, males and females) and SE ($p < 0.001$, males and $p = 0.001$, females)).

measured respective to CL. Thus, 1183 females at varying CL were measured at southwest and southeast Iceland in 1969–1970 and a comparison made to male relative growth by measuring the same body parts of 1784 males from the same locations and time period.

In cases of allometric growth, some body part (e.g. abdominal width in crustaceans) grows at a different rate relative to a reference dimension (e.g. CL), generating a change in body proportions. Sometimes, such changes are abrupt, marking crucial developmental stages, such as maturity of an animal (Hartnoll, 1978, 1982). In the present study, the allometric equation $y = ax^b$ is mainly used in the logarithmic transformation, that is,

$$\log Y = \log a + b \log X$$

where Y is the abdominal width (AW), X carapace length and a and b constants, a being the Y intercept and b the slope of the regression line representing the allometric growth constant (Hartnoll, 1978).

The allometric growth regressions for Icelandic male and female *Nephrops* show positive allometry in males and juvenile and adult females or are as follows:

Juvenile females: $\log \mathrm{AW} = -0.8913 + 1.4334 \log \mathrm{CL}$

Mature females: $\log \mathrm{AW} = -0.4269 + 1.0965 \log \mathrm{CL}$

Males: $\log \mathrm{AW} = -0.3521 + 1.0207 \log \mathrm{CL}$

As demonstrated in Figure 2.20, the relationship between AW and CL shows a high level of allometry in juvenile *Nephrops* females with a reduction of the allometry level at 23.90 mm CL. The relationships were also investigated for log-transformed AW and untransformed CL with similar results or an inflection point of 25.35 mm CL (Figure 2.20), both corresponding reasonably well with the prevalent decadal L_{50} of 25–26 mm CL described previously (Table 2.4 and Section 4.2.1). Therefore, juvenile females seem to prepare a voluminous egg-carrying capacity by a high growth rate of abdominal width at least as early as from the size of 17 to 18 mm CL, that is, well before the size of first-time maturing ovaries in primiparous individuals (21–22 + mm CL) or first spawning (23–24 + mm CL). Posterior to individual maturity, however, retarding abdominal growth seems in most respects a pragmatic solution, the abdominal width otherwise becoming with size an impediment to the animals' mobility and burrowing behaviour.

Since males do not need a voluminous egg-carrying capacity, their relatively low level of positive allometry appears unchanged at all sizes or near

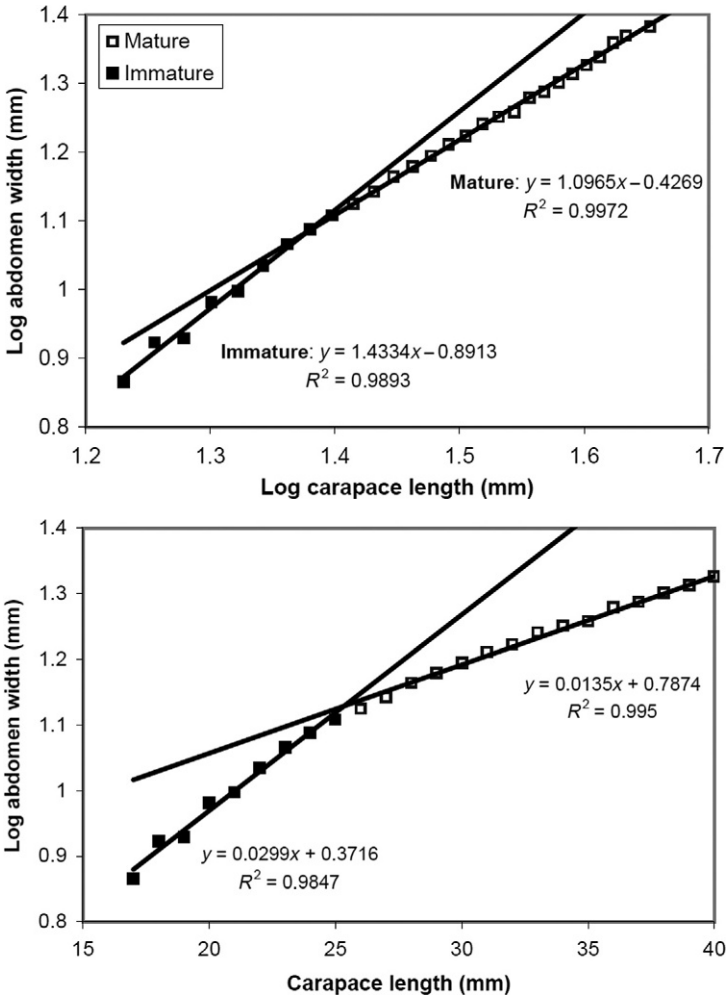


Figure 2.20 Relationship between log-transformed carapace length (CL) and log-transformed abdominal width (AW) in female *Nephrops* at SW Iceland, indicating a reduction in allometry level at an inflection point of 23.90 mm CL (above) and relationship between untransformed carapace length and log-transformed abdominal width in female *Nephrops*, indicating a reduction in allometry level at an inflection point of 25.35 mm CL (male *Nephrops* show an unchanged level of allometry over the whole size range studied).

the level of isometric growth ($b = 1$) as shown above. This sex variation is demonstrated in Figure 2.21, showing the morphological differences on the ventral side of the thorax and abdomen of mature female and male *Nephrops*.

Figure 2.21 Ventral view of mature female and male *Nephrops*, demonstrating morphological differences of the thorax and abdomen in the two sexes.

4.2.4 Discussion

4.2.4.1 Estimations of size at maturity and breeding

It has been pointed out that maturity and, in particular, sex ratio studies of *Nephrops* should ideally be age-based rather than length-based due to the slower growth rate of females (Anonymous, 1984). However, owing to the inherent difficulties of age determination of crustaceans, age at maturity has been described only very rarely (Bailey, 1984; Bailey and Chapman, 1983; Morizur, 1980, 1983; Tuck et al., 2000).

Area variations in the size of 50% maturity (L_{50}) in Icelandic waters appear to be negligible at all sites investigated (Figures 2.8, 2.11 and 2.14 and Table 2.4). However, as indicated from other geographical regions (Bailey, 1984; Figueiredo, 1982), different values were obtained for all three Icelandic areas according to the criteria or methods used. Based on CL ogives of females with ovaries at stages 3–6 and ovigerous out of total females

in each length group, using a logistic least-squares model, the overall average L_{50} varied from 25.6 to 26.6 mm CL by areas for the month of May in the period 1971–2007. Moreover, the decadal average was lowest in all areas in the 1980s, from 24.9 mm CL in the southeast to 25.7 mm in the south, but highest in the 2000s, from 25.6 mm in the southeast to 28.1 in the southwest (overall SD = 0.89) (Figure 2.9 and Table 2.5). Comparable estimates of L_{50} for the months of April, June and July gave inconclusive variations from the May results for different areas in the 1970s, 1980s and 2000s.

The record high L_{50} in the southwestern area in the 2000s can best be described by late onset of maturity relative to size, possibly linked with increased growth rate concurring with the highest sea temperatures since the early 1960s (Anonymous, 2009; Eiríksson, 2009). However, density-dependent growth may also have played a part since recruitment rates seem to have been low in the southwest in the 2000s, especially compared to the southeast where the L_{50} value stayed similar to those of earlier decades. Also, mean decadal CL from catch samples since the 1960s depict a positive correlation with L_{50} (females $r^2 = 0.277$; $p = 0.10$) (Figure 2.10) (males $r^2 = 0.43$; $p < 0.02$), indicating a possible effect of recruitment and fishery fluctuations on estimated values of L_{50}.

Due to the biennial spawning cycle at Iceland, the smallest females experiencing ovary developmental stages 3–4 for the first time in their life, that is, primiparity, in May each year, will not spawn until at the earliest springtime next year or after at least a whole year of potential growth. In more southerly areas of annual spawning, however, they would probably spawn already by late summer or autumn, only some months later. For that reason, the L_{50} criterion is considered unsatisfactory for defining the annual spawning stock at spawning time in May at Iceland, although it may well apply to areas of annual spawning.

The size at which 50% of females are breeding (denoted as BL_{50}), that is, prespawners with ovary stage 6 and ovigerous, has been considered the most conducive method for defining maturity size in Icelandic *Nephrops*, for both research and fisheries counselling purposes. In view of the biennial nature of reproduction in Icelandic female *Nephrops*, however, the maxima cannot peak at more than approximately 50% when studying the spawning population in a particular spawning season. Therefore, the sigmoid maturity curves had to be raised when considering BL_{50} and OV_{50} (berried animals only).

Using the percentage of breeders out of total catch of females in May during 1971–2007, the overall average BL_{50} ranged from 29.9 to 31.0 mm CL by areas for the month of May in the period 1971–2007 (Figure 2.11 and Table 2.4). The decadal area averages, however, exhibit

a much greater range or from 27.1–29.8 mm CL in the 2000s to 30.8–32.4 mm CL in the 1980s (overall SD = 1.67) or quite the opposite trend to that of L_{50} (Figure 2.12 and Table 2.5). The increase in size by some 3.9 mm on average between the L_{50} and BL_{50} ogives can best be explained by the omission of primiparous females in the latter ogives. In some cases, the considerable difference between the two estimates is even indicative of more than 1 years' growth in at least some part of the primiparous population.

The low BL_{50} estimates seen in the 2000s are concurrent with record high L_{50} values that have been explained previously by increased growth rate and delayed onset of age-related maturity. The resulting low BL_{50}, however, indicating slow growth rate and relatively late spawning of first-time spawners in particular, compared to earlier decades remains uncertain (Figure 2.13). Nevertheless, Icelandic grounds in the 2000s have been experiencing the highest sea temperatures and catch rates since the early 1960s (Anonymous, 2009; Eiríksson, 2009), suggesting possibly some changing phases of metabolic activity in the recent years.

Estimations based on ovigerous females alone out of the total catch of females in May gave a little higher overall average 50% maturity level (denoted OV_{50}) than BL_{50} for the month of May in 1971–2007 or 30.8–31.2 mm CL by areas (Figure 2.14 and Table 2.4). The decadal area averages, however, show a greater range or from as low as 28.0 mm CL in the 1970s to 34.4 mm in the 2000s in the south (overall SD = 1.77) (Table 2.5). Also, decadal variations in OV_{50} follow a relatively consistent pattern between areas except for the very low value for the southern area in the 1970s (Figure 2.15).

Monthly variations in OV_{50} for May, June and July at southwest Iceland in the 1970s showed a decrease from 30.7 mm CL in May to 29.5 and 28.7 mm, respectively, in June and July (Table 2.4). As depicted in Figure 2.16, this apparently relates to the fact that a greater number of medium to large females were spawning earlier than the smaller animals and dissipation of those early spawners into their burrows by June–July. Moreover, the timing of such size-related spawning appears to explain the main variations observed in size of BL_{50} versus OV_{50} at any one time, demonstrating well the temporal effects that spawning and burrowing regimes can have on calculations of size at maturity in female *Nephrops*.

Therefore, as shown in Table 2.5, decadal variations in all size of maturity scenarios are considerable, although mostly so for the last decade 2001–2007. The most apparent variations shown in the 2000s scenarios are the small size differences seen between L_{50} and BL_{50}, described earlier by growth variations, and, in particular, the large size differences observed

between BL_{50} and OV_{50}. Looking at the ratio of prespawning ovary stage 6 female numbers and sizes, however, compared to newly berried stage A animals, it appears evident that for some reason or another, spawning is not as well advanced, particularly among smaller individuals in the 2001–2007 data as in earlier decades. This applies to all areas and strongly suggests later spawning in the last decade, notably among the smaller individuals and mostly so at southeast Iceland (Figure 2.13). This would explain the relatively small BL_{50} in the south and especially southeast where the low BL_{50} value is intensified by good recruitment in the 2000s. At the same time, very high values are seen for OV_{50} due to earlier spawning seen by larger individuals in the 2000s (see also Section 4.3).

The breeding parameter OV_{50} depicts a significant regression with the average monthly May–July female % in *Nephrops* catch samples, by areas and decades, from the 1960s to 2000s ($r^2 = 0.52$; $p < 0.01$) (Figure 2.17), and correlating with female and male CL, somewhat emphasizing relationships to phases in recruitment and fishing intensity over the years and decades.

Whether the underlying factor of variations in maturity estimates in the period 2001–2007 is environmental changes, for example, related to the fact that bottom sea temperatures have risen by as much as 1 °C in the last decade (Anonymous, 2009; Eiríksson, 2009), however, needs some further studies. Yet the recent available data from 2008 to 2010 do support the 2001–2007 results, suggesting possibly some changing phases of reproductive activity in the recent years. Therefore, maturity estimates may vary considerably according to the criteria used and time of year or individual years sampled, making geographical comparisons within the whole distribution area of *Nephrops* very difficult.

4.2.4.2 Minimum ovigerous size

Records of the smallest berried size *Nephrops* have been published by many authors dating back to the early twentieth century. This proposes a relatively easy method for approximating minimum size of maturity in crustaceans. A relatively wide range of minimum size of females in berry was observed in all areas off Iceland or from 23 to 35 mm CL (Figure 2.18). The minimum ovigerous size of 23 mm CL has been measured in the southeastern area, whereas a minimum of 24 mm CL has been recorded at southwest and south Iceland.

Various temporal and spatial trends displayed in Icelandic *Nephrops* were found to relate to a varying degree to minimum ovigerous size. Firstly, the average annual CL of both males and females relates positively and highly

significantly to minimum annual ovigerous size, mostly so in the southwest (males and females $p < 0.001$; Figure 2.19), but relatively less so in the south and southeast. Secondly, minimum berried size in all areas shows a distinctly similar decadal pattern as described above for 50% ovigerous size (OV_{50}), the overall correlation being at the $p = 0.01$ level of significance, and thirdly, minimum ovigerous size correlates negatively and highly significantly to that of average monthly May–July female % in *Nephrops* catch samples, by areas and decades, from the 1960s to 2000s ($p > 0.001$), accentuating still further the effect of the fishery.

Thus, historical time series trends of minimum ovigerous size appear to be mainly related to trends in fishing intensity and its effect on stock abundance and sex and size compositions. As depicted in Figure 2.18A, the relatively small ovigerous females found in the early 1960s to early 1970s at the southwest can be related to the very high exploitation rates imposed on the stock in that area already by 1962–1963 and good recruitment around 1970 (Eiríksson, 1976, 1979). Adversely, the increasing minimum ovigerous size as well as mean CL in 1995–2005 (Figure 2.19) relates well to the low fishing intensity of that period in the southwest accompanied by low recruitment (Anonymous, 2008). At south and southeast Iceland, however, exploitation rates intensified relatively later or in the mid- to late 1960s, leading to decreasing mean ovigerous and body size from around 1965 to the early 1970s (Figure 2.18). In addition, the historically low minimum ovigerous sizes at southeast Iceland in the mid-1990s can be partly attributed to notably good recruitment rates at the time and historically low fishable stock estimates (Anonymous, 2008). The inherent relationships between stock abundance and the fishery with female biological time series will be dealt with further in Section 4.4.

4.2.4.3 Relative growth and maturity

Changes in proportion of various body parts or relative growth has been described in various studies on crustaceans (e.g. Hartnoll, 1978; Teissier, 1960).

In this study, the allometric equation $y = ax^b$ was used in both the logarithmic transformation log AW/log CL (abdominal width and CL) and log-transformed AW and untransformed CL. Allometric growth analyses were shown to indicate notable changes in allometry with inflection points at 23.90 and 25.35 mm CL in regressions of the two body parts, comparing relatively well with the obtained least-squares values for L_{50} of some 25–26 mm CL (Figure 2.20). Moreover, juvenile females seem to prepare

a voluminous abdominal egg-carrying capacity by a high growth rate of abdominal width as early as from the size of 17 to 18 mm CL, that is, well before the size of first-time maturing ovaries in primiparous individuals (21–22 + mm CL) or spawning individuals (23–24 + mm CL). Mature females at Iceland, like males in general, therefore approximate their abdominal growth to that of relative to CL. Finally, however, it has to be pointed out that such an investigation of a population en bloc may lead to results that differ from those of studies of individual animals (Hartnoll, 1974).

Changes in size at maturity using comparable criteria and the apparent linkage to growth rates, as well as the influence of such important stock aspects as year-class strength and recruitment, deserve further consideration.

4.2.4.4 Geographical variations in female maturity

The smallest maturity size based on berried females (23 mm CL) was found at southeast Iceland in 1997, and a minimum of 24 mm CL was recorded in 1963 and 1970 and 1973 and 1975 in the southwestern and southern area, respectively. However, annual area records have ranged from 23 to 35 mm CL since the early 1960s.

Many authors have given maturity estimates based on the presence of abdominal eggs. The values have ranged from 16–18 mm CL in the Adriatic (Froglia and Gramitto, 1979, 1981; Gramitto and Froglia, 1980; Karlovac, 1953) to 32 mm in Scotland (Tuck et al., 2000) and 30 mm CL in the Skagerrak–Kattegat off Sweden and Denmark (Höglund, 1942; Poulsen, 1946), as well as in the Alboran, Catalan and Tyrrhenian Seas off the Spanish and Italian coasts of the Mediterranean (Matta, 1959; Orsi Relini et al., 1998; Vives and Suau, 1963). Low estimates of 19 mm CL have also been reported from the Moray Firth, east Scotland (Thomas and Figueiredo, 1965) and 20 mm CL in the Firth of Clyde and Sound of Jura on the Scottish west coast (Bagenal, 1953; Bailey, 1984; Thomas, 1954), as well as 19–20 mm CL from the western Irish Sea and the Irish south coast (Briggs, 1988; Farmer, 1974a,b; Gibson, 1967; McQuaid et al., 2006; O´Riordan, 1964), 19–22 mm CL in the Bay of Biscay (Fontaine and Warluzel, 1969; Morizur, 1979a, 1980), 21 mm CL off south Portugal (Arrobas, 1982) and 22 mm CL in the Strait of Sicily (Bianchini et al., 1998). Intermediate estimates of 23–28 mm CL have also been reported from the whole geographical range from Iceland (this study), the Faeroes (Andersen, 1962), to the northeast coast of England (Storrow, 1912; Symonds, 1972) down to the Gulfs of Euboikos and Pagasitikos, Aegean coast of Greece (Mente et al., 2009; Orsi Relini et al., 1998) (Tables 2.6 and 2.7).

Table 2.6 Female maturity size estimates by countries/areas, including methods, periods and references

Country/area	Smallest berried/ smallest onset of maturity (mm CL) (total length in parentheses)	Mean size of maturity (L_{50} mm CL)	Methods/month of year	References
Iceland				
SW 1965–1970		26.67	Ovaries (stages 3–6) and ovigerous (May–Aug.)	Eiríksson (this study)
SW 1965–1970		27.33	Ovaries (stages 3–6) and ovigerous (Jul.)	
SW 1962–1970	24	28.45	Ovigerous (May–Jul.)	
SW 1969–1970		23.90–25.35	Relative growth (allometry)	
SW 1971–1980		25.55	Ovaries (stages 3–6) and ovigerous (May)	
SW 1971–1980		25.42	Ovaries (stages 3–6) and ovigerous (Jun.)	
SW 1971–1980		25.49	Ovaries (stages 3–6) and ovigerous (Jul.)	
SW 1971–1980		30.00	Ripe ovaries (stage 6) and ovigerous (May)	
SW 1971–1980		30.74	Ovigerous (May)	
SW 1971–1980		29.49	Ovigerous (Jun.)	
SW 1971–1980		28.69	Ovigerous (Jul.)	
SW 1971–1980	25		Ovigerous (all year)	

Continued

Table 2.6 Female maturity size estimates by countries/areas, including methods, periods and references—cont'd

Country/area	Smallest berried/ smallest onset of maturity (mm CL) (total length in parentheses)	Mean size of maturity (L_{50} mm CL)	Methods/month of year	References
SW 1981–1990		25.19	Ovaries (stages 3–6) and ovigerous (May)	
SW 1981–1990		30.85	Ripe ovaries (stage 6) and ovigerous (May)	
SW 1981–1990		30.64	Ovigerous (May)	
SW 1981–1990	26		Ovigerous (all year)	
SW 1991–2000		25.90	Ovaries (stages 3–6) and ovigerous (May)	
SW 1991–2000		31.60	Ripe ovaries (stage 6) and ovigerous (May)	
SW 1991–2000		29.66	Ovigerous (May)	
SW 1991–2000	25		Ovigerous (all year)	
SW 2001–2007		28.11	Ovaries (stages 3–6) and ovigerous (May)	
SW 2001–2007		29.77	Ripe ovaries (stage 6) and ovigerous (May)	
SW 2001–2007		32.18	Ovigerous (May)	
SW 2001–2010	29		Ovigerous (all year)	
S 1963–1970	27		Ovigerous (all year)	

Table 2.6 Female maturity size estimates by countries/areas, including methods, periods and references—cont'd

Country/area	Smallest berried/ smallest onset of maturity (mm CL) (total length in parentheses)	Mean size of maturity (L_{50} mm CL)	Methods/month of year	References
S 1971–1980		25.90	Ovaries (stages 3–6) and ovigerous (May)	
S 1971–1980		27.25	Ripe ovaries (stage 6) and ovigerous (May)	
S 1971–1980		28.02	Ovigerous (May)	
S 1971–1980	24		Ovigerous (all year)	
S 1981–1990		25.67	Ovaries (stages 3–6) and ovigerous (May)	
S 1981–90		26.13	Ovaries (stages 3–6) and ovigerous (Jun.)	
S 1981–1990		30.84	Ripe ovaries (stage 6) and ovigerous (May)	
S 1981–1990		31.71	Ovigerous (May)	
S 1981–1990	27		Ovigerous (all year)	
S 1991–2000		26.33	Ovaries (stages 3–6) and ovigerous (May)	
S 1991–2000		30.20	Ripe ovaries (stage 6) and ovigerous (May)	
S 1991–2000		30.61	Ovigerous (May)	
S 1991–2000	26		Ovigerous (all year)	

Continued

Table 2.6 Female maturity size estimates by countries/areas, including methods, periods and references—cont'd

Country/area	Smallest berried/ smallest onset of maturity (mm CL) (total length in parentheses)	Mean size of maturity (L_{50} mm CL)	Methods/month of year	References
S 2001–2007		27.23	Ovaries (stages 3–6) and ovigerous (May)	
S 2001–2007		27.92	Ripe ovaries (stage 6) and ovigerous (May)	
S 2001–2007		34.37	Ovigerous (May)	
S 2001–2010	27		Ovigerous (all year)	
SE 1964–1970	26		Ovigerous (all year)	
SE 1971–1980		25.99	Ovaries (stages 3–6) and ovigerous (May)	
SE 1971–1980		30.52	Ripe ovaries (stage 6) and ovigerous (May)	
SE 1971–1980		31.47	Ovigerous (May)	
SE 1971–1980	25		Ovigerous (all year)	
SE 1981–1990		24.92	Ovaries (stages 3–6) and ovigerous (May)	
SE 1981–1990		24.83	Ovaries (stages 3–6) and ovigerous (Jun.)	
SE 1981–1990		26.33	Ovaries (stages 3–6) and ovigerous (Jul.)	
SE 1981–1990		32.43	Ripe ovaries (stage 6) and ovigerous (May)	

Table 2.6 Female maturity size estimates by countries/areas, including methods, periods and references—cont'd

Country/area	Smallest berried/ smallest onset of maturity (mm CL) (total length in parentheses)	Mean size of maturity (L_{50} mm CL)	Methods/month of year	References
SE 1981–1990		30.71	Ovigerous (May)	
SE 1981–1990	25		Ovigerous (all year)	
SE 1991–2000		25.22	Ovaries (stages 3–6) and ovigerous (May)	
SE 1991–2000		29.99	Ripe ovaries (stage 6) and ovigerous (May)	
SE 1991–2000		29.54	Ovigerous (May)	
SE 1991–2000	23		Ovigerous (all year)	
SE 2001–2007		25.58	Ovaries (stages 3–6) and ovigerous (Apr.)	
SE 2001–2007		25.63	Ovaries (stages 3–6) and ovigerous (May)	
SE 2001–2007		27.21	Ripe ovaries (stage 6) and ovigerous (Apr.)	
SE 2001–07		27.07	Ripe ovaries (stage 6) and ovigerous (May)	
SE 2001–2007		33.13	Ovigerous (May)	
SE 2001–2010	25		Ovigerous (all year)	
Faeroes	27 (90)		Ovigerous	Andersen (1962)

Continued

Table 2.6 Female maturity size estimates by countries/areas, including methods, periods and references—cont'd

Country/area	Smallest berried/ smallest onset of maturity (mm CL) (total length in parentheses)	Mean size of maturity (L_{50} mm CL)	Methods/month of year	References
Denmark/Sweden				
Skagerrak	28–30		Ovigerous	Poulsen (1946)
Kattegat	30		Ovigerous	Höglund (1942)
Scotland				
Firth of Clyde	20 (70)		Ovigerous	Bagenal (1953)
Firth of Clyde	20 (70)		Ovigerous	Thomas (1954)
Scottish waters		23 (22–29)	Ovaries/ spermatophores	Thomas (1964)
Moray Firth	19	21–22	Ovigerous	Thomas and Figueiredo (1965)
Clyde	24	25.5–28 (different months, years)	Ovigerous, ovaries,	Bailey (1984)
Clyde	22–32 (different locations)	21.4–34.6 (different locations)	Ovigerous, ovaries; allometry	Tuck et al. (2000)
Sound of Jura	20	22.7–23.2 (different months)	Ovigerous, ovaries	Bailey (1984)
England				
NE England	23		Ovigerous	Storrow (1912)
Farne Deeps	27		Ovigerous	Symonds (1972)
Ireland/N Ireland				
W Irish Sea	20		Ovigerous	O´Riordan (1964)

Table 2.6 Female maturity size estimates by countries/areas, including methods, periods and references—cont'd

Country/area	Smallest berried/ smallest onset of maturity (mm CL) (total length in parentheses)	Mean size of maturity (L_{50} mm CL)	Methods/month of year	References
Irish south coast	20		Ovigerous	Gibson (1967)
W Irish Sea	19–22		Ovaries, spermatophores	Farmer (1974a)
NW Irish Sea	20	23–24	Ovigerous, ovaries	Briggs (1988)
Irish Sea	19–20	21–23	Ovaries/ spermatophores	McQuaid et al. (2006)
Irish Sea		23.2–27.6	Relative growth (allometry)	McQuaid et al. (2006)
Celtic Sea	26		Ovigerous	Morizur and Rivoalen (1982)
France				
Bay of Biscay	22	24–25	Ovaries, spermatophores	Fontaine and Warluzel (1969)
Bay of Biscay	19	23–24 (different years)	Ovaries, spermatophores, second characters	Morizur (1979a, 1980, 1981b, 1983)
Portugal				
W Portugal	26		Ovigerous	Figueiredo and Barraca (1963)
Portuguese waters	25		Ovigerous	Figueiredo and Nunes (1965)
Portuguese waters		32	Ovigerous	Figueiredo and Thomas (1967b)
Algarve	21	30	Ovigerous	Arrobas (1982)
Algarve		23–29 (different months)	Ovaries	Figueiredo (1982)

Continued

Table 2.6 Female maturity size estimates by countries/areas, including methods, periods and references—cont'd

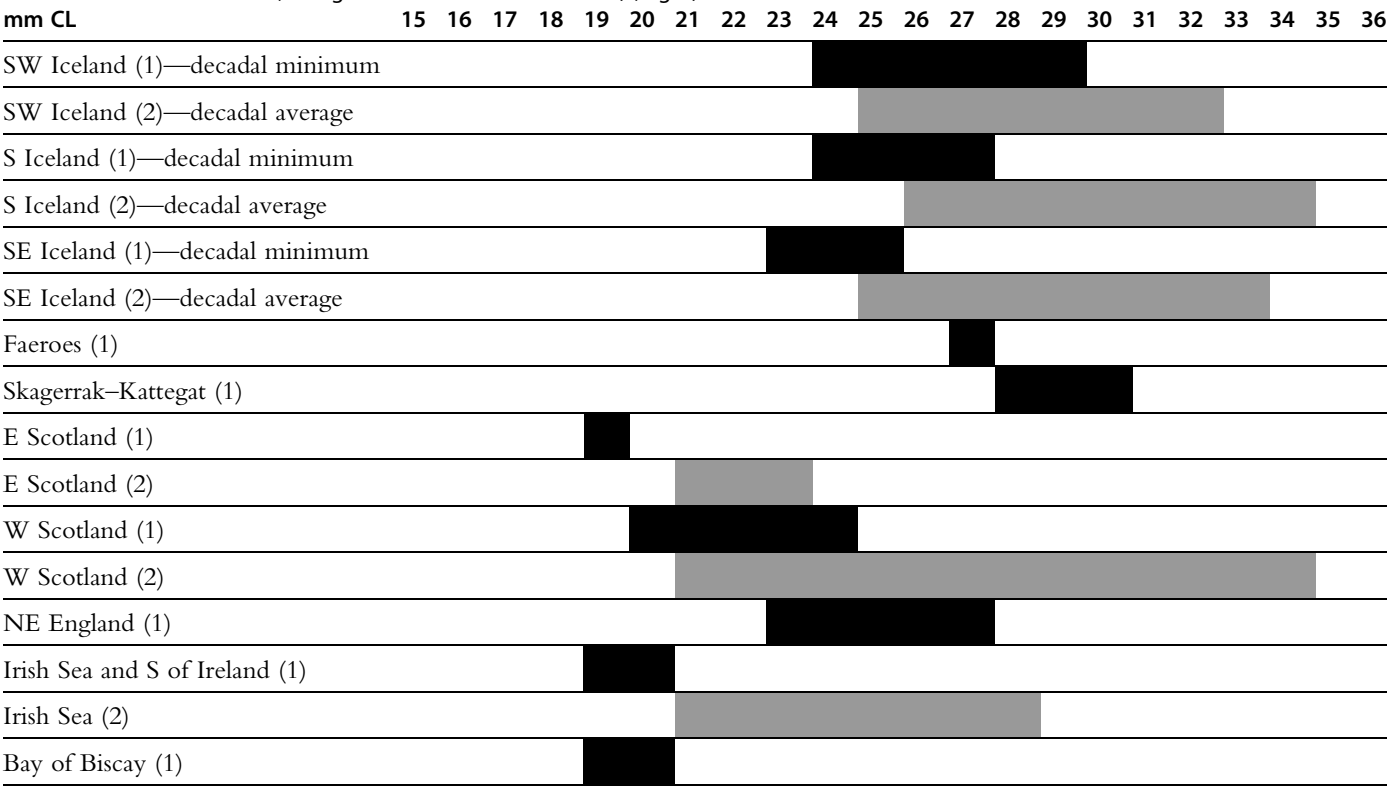
Country/area	Smallest berried/ smallest onset of maturity (mm CL) (total length in parentheses)	Mean size of maturity (L_{50} mm CL)	Methods/month of year	References
Algarve	24	30	Ovaries	Orsi Relini et al. (1998)
Alentejo		31	Ovaries	Figueiredo (1982)
N Portugal	36	50.7	Ovigerous	Ayza et al. (2011)
SW Portugal	36	46.9	Ovigerous	Ayza et al. (2011)
Mediterranean				
E Spain	27–30		Ovaries	Vives and Suau (1963)
Alboran Sea	30	36	Ovaries	Orsi Relini et al. (1998)
Catalan Sea	25–27	30–33	Ovaries	Sardà (1991)
Catalan Sea	27	30	Ovaries	Orsi Relini et al. (1998)
Ligurian Sea	28	31–32	Ovaries	Orsi Relini and Relini (1989)
Ligurian Sea	27	32	Ovaries	Orsi Relini et al. (1998)
Tyrrhenian Sea	30			Matta (1959)
Tyrrhenian Sea	27	32	Ovaries	Orsi Relini et al. (1998)
Strait of Sicily	22	29.9–32.1	Ovigerous, ovaries	Bianchini et al. (1998)
Adriatic Sea				
High Adriatic	18	27 (90)	Ovigerous	Karlovac (1953)

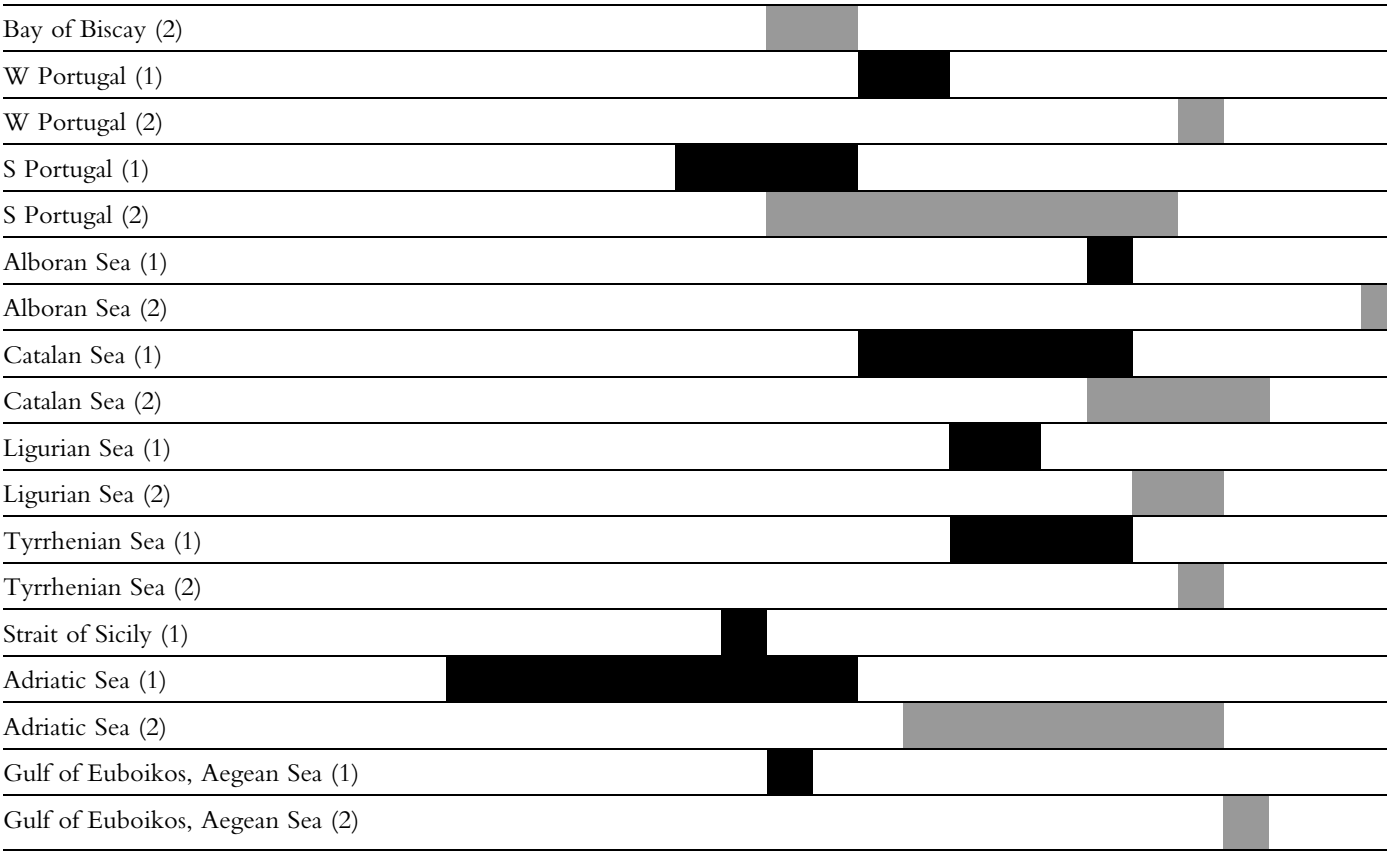
Table 2.6 Female maturity size estimates by countries/areas, including methods, periods and references—cont'd

Country/area	Smallest berried/ smallest onset of maturity (mm CL) (total length in parentheses)	Mean size of maturity (L_{50} mm CL)	Methods/month of year	References
North Adriatic	17–17.5	29–30 (95–100)	Ovigerous	Karlovac (1953)
Adriatic, Ancona	17	32.5	Ovigerous	Froglia and Gramitto (1979)
Adriatic, Ancona	16–17	32	Ovigerous	Gramitto and Froglia (1980)
Adriatic, Ancona	16–17	32 (105)	Ovigerous	Froglia and Gramitto (1981)
Adriatic, Ancona	24	30	Ovaries	Orsi Relini et al. (1998)
Adriatic, Pomo Pit		25.0	Ovigerous	Froglia and Gramitto (1979)
Adriatic, Pomo Pit	21	26	Ovigerous	Gramitto and Froglia (1980)
Adriatic, Pomo Pit		26 (85)	Ovigerous	Froglia and Gramitto (1981)
Aegean Sea				
Gulf of Euboikos	23	33	Ovigerous, ovaries	Orsi Relini et al. (1998)
Pagasitikos Gulf		28.0	Ovaries	Mente et al. (2009)

As detailed previously, Icelandic estimates of 50% maturity (L_{50}) and 50% breeding (BL_{50} and OV_{50}) do not indicate notable variability since the late 1960s with the exception of the 2000s when female samples showed a distinctly higher L_{50} and OV_{50} but lower BL_{50}, being indicative of a higher rate of growth prior to the first maturity followed by a relatively later spawning of those primiparous females compared to larger individuals.

Table 2.7 Smallest ovigerous records (1, dark) and estimations of 50% maturity length (L_{50}) by distribution areas of *Nephrops* in the North Atlantic and Mediterranean, using different methods/criteria (2, light)




Bay of Biscay (2)
W Portugal (1)
W Portugal (2)
S Portugal (1)
S Portugal (2)
Alboran Sea (1)
Alboran Sea (2)
Catalan Sea (1)
Catalan Sea (2)
Ligurian Sea (1)
Ligurian Sea (2)
Tyrrhenian Sea (1)
Tyrrhenian Sea (2)
Strait of Sicily (1)
Adriatic Sea (1)
Adriatic Sea (2)
Gulf of Euboikos, Aegean Sea (1)
Gulf of Euboikos, Aegean Sea (2)

A number of authorities have studied the size at 50% maturity (L_{50}) in females, ranging from 21 mm CL in the Moray Firth and Firth of Clyde, east and west Scotland, respectively (Thomas and Figueiredo, 1965; Tuck et al., 2000), and the Irish Sea (McQuaid et al., 2006) to 36 mm CL in the Alboran Sea on the Mediterranean south coast of Spain (Orsi Relini et al., 1998). Relatively great variations in L_{50} estimates are seen in certain areas, such as 24–34 mm CL on Icelandic grounds (this study), 21–35 mm CL in the Firth of Clyde (Tuck et al., 2000), 21–28 mm CL in the Irish Sea (McQuaid et al., 2006) and 23–31 mm CL off south Portugal (Figueiredo, 1982) (Tables 2.6 and 2.7).

Variable estimates can be largely accounted for by the physiological or morphological criteria defined for maturity, such as berried females, state of ovary maturation, observations on presence of thelycal spermatophores or allometric growth measurements of different body parts. Also, area variations in L_{50} can be substantial, even very localized, be it for reasons of density-dependent growth and/or type of bottom substrate (Tuck et al., 2000). Finally, same or similar criteria can lead to differing L_{50} estimates on a temporary scale, for example, by months or years even in the same area (e.g. Bailey, 1984; Figueiredo, 1982; Morizur, 1979a, 1980, 1981b). Therefore, relatively greatest variations in L_{50} estimates are observed in areas where most variable methods or criteria have been used.

In this respect, Figueiredo (1982) using ovary maturity as a criterion had shown that in Portuguese *Nephrops* stocks, L_{50} estimates increased during the spawning season from July to September–October due to resorption of ovaries by the smaller animals just before spawning. Bailey (1984), using a similar method of ovary development as a criterion, also noted an increase in the size of maturity from June to August in two Scottish stocks, that is, just prior to spawning, possibly due to the smallest *Nephrops* spawning first and disappearing from the catch. On the other hand, L_{50} based on berried females (OV_{50}) is seen to decrease from May to July at SW Iceland according to the data from the 1970s, since a higher proportion of medium to large females was spawning first and dissipating into their burrows by June–July (Figure 2.16). Also, in the 2000s, relatively later spawning of smaller animals in May accentuated the large difference in the values of BL_{50} and OV_{50}, with the former being much lower (Figure 2.13). Estimates of size at maturity can therefore be biased if females disappear from the catchable stock during the spawning season as previously indicated by French data (Anonymous, 1982), although such a bias should be minimal unless the spawning time and disappearance from the catch vary according to female size.

SOM was seen to vary over 10 mm CL within only few tens of km in the Firth of Clyde, with estimates being similar using both ovary maturity and ovigerous as well as allometric growth characteristics (Tuck et al., 2000). Also, SOM estimates were positively related to mean CL in the catches of both males and females (Tuck et al., 2000). Likewise, the size of maturity estimates in Iceland (L_{50}, OV_{50} and minimum annual ovigerous size) all relates positively to both female and male CLs during the approximately last four decades, ranging in significance from $p=0.10$ to $p<0.001$. Furthermore, there was a strong negative correlation between OV_{50} and minimum berried size and average monthly May–July female % in *Nephrops* catch samples, by areas and decades from the 1960s to 2000s. Thus, a strong relationship is indicated between the effects of fishing intensity and estimates of size at maturity.

In the Irish Sea, the value of L_{50} from mature ovaries gave a 2 mm higher estimate than the one including all females found to have spermatophores in the thelycum. However, the females within the range of those two values of L_{50}, although with spermatophores, had undeveloped ovaries (McQuaid et al., 2006). Since these females would be of little importance for the transient spawning season, this Irish study emphasizes that the best estimate of size of maturity and thus the effectual spawning stock should be based on maturity ogives of well enough developed ovaries prior to a spawning season. This corroborates well the authors' distinction of 50% breeding length (BL_{50}), which only includes fully mature pre- and postspawners in the spawning season but excludes those primiparous maturing females not due to spawn until next year.

The larger size at maturity found in the Firth of Clyde than in the Sound of Jura, west Scotland, which is accompanied by overall larger animals in the Clyde area, has been ascribed to variations in density and growth, although the L_{50} seemingly occurs at a similar age (Bailey, 1984; Bailey and Chapman, 1983). Moreover, Morizur (1980, 1983) has described year to year variations in mean size of maturity with the estimated age remaining the same, however, in the Bay of Biscay. The high L_{50} observed in Portuguese and some Mediterranean waters could therefore be best explained by rapid growth of *Nephrops* in these warm southerly waters, possibly also linked with low density of animals as indicated by relatively low CPUE in these areas (see Anonymous, 1984, 1992). In contrast, one observes low maturity sizes in areas of very high density and relatively slow growth such as in some Scottish waters and the Irish Sea (Anonymous, 1982, 1992; Bailey and Chapman, 1983; Hillis, 1979) (Tables 2.6 and 2.7).

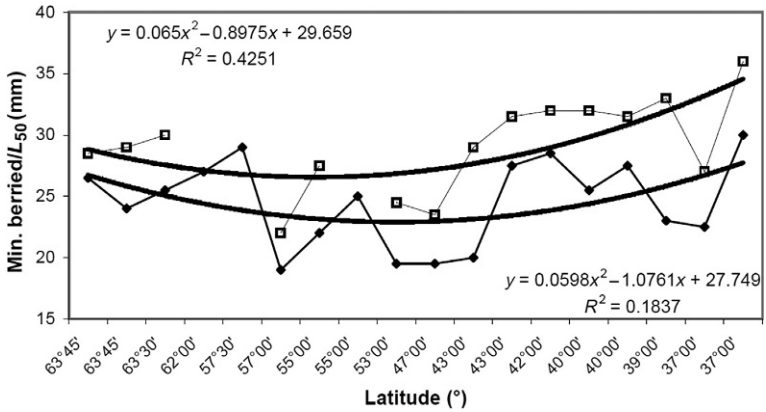


Figure 2.22 Latitudinal variations in L_{50} and minimum berried size of female *Nephrops* in NE Atlantic and Mediterranean waters, indicating relatively highest values in the more southerly areas, lowest values in the intermediate latitudes and more transitional values at the most northerly latitudes.

Although no obvious relationship can be observed between size at maturity of females and latitude, at least over the whole geographical range, some general indications thereof are shown in Table 2.7 and Figure 2.22. Thus, the highest latitudes tend to demonstrate relatively higher values for the parameters L_{50} and records of minimum berried size compared to the lowest recorded values between latitudes 57°N and 47°N. The highest values, however, are normally indicated at the lowest latitudes.

Also, L_{50} is apparently largest where Norway lobsters grow to their maximal size, as noted for Portuguese waters by Figueiredo and Thomas (1967b). Therefore, a positive correlation at a significance level of $p < 0.001$ and $p < 0.01$ can be seen between maximum CL of males and females, respectively, and L_{50} within the Atlantic geographical range (Figure 2.23). As indicated, the L_{50} is on average somewhat higher in the Mediterranean than in the Atlantic or in agreement with Orsi Relini et al. (1998), who considered the variations observed in reproductive sizes relating to different somatic growth rates. Furthermore, there are relatively higher L_{50}'s in Icelandic grounds compared to the observed maximum sizes of females, as a result of the biennial reproductive cycle and, therefore, slower postmaturity growth than in, for example, Scottish, Irish, French and Portuguese waters of mostly annual spawning (see further in Section 4.3).

Templeman (1936, 1940) related variations in size at maturity and time of spawning and hatching of *H. americanus* to differing temperature regimes. Thus, areas with the highest summer temperatures appear to produce the

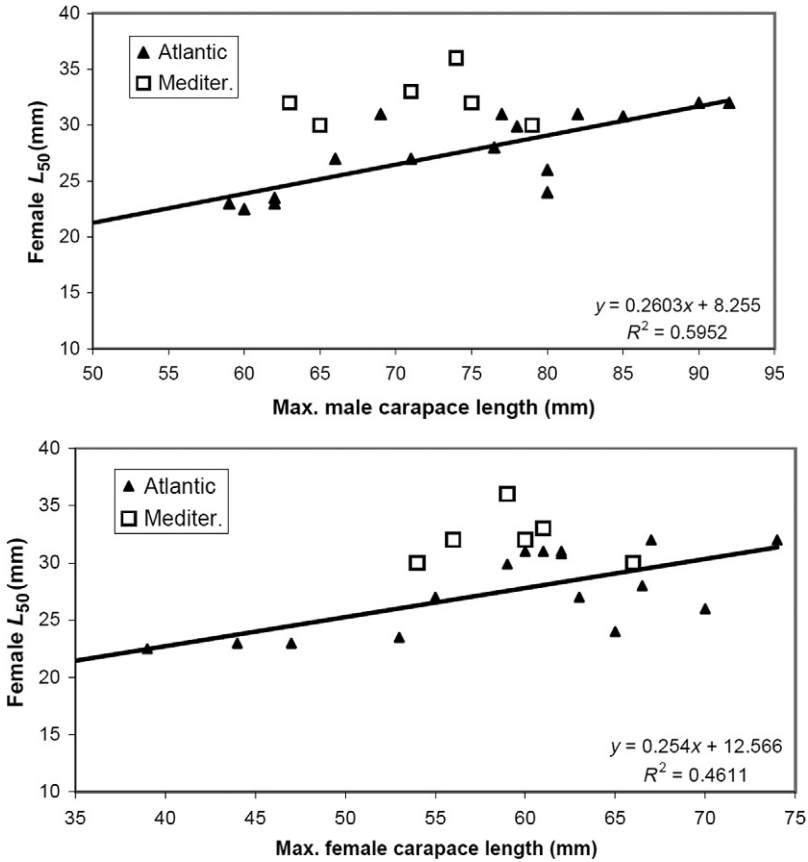


Figure 2.23 Correlations between female L_{50} and maximum carapace length of males ($p < 0.001$) and females ($p < 0.01$) in the N Atlantic, showing also values for different areas of the Mediterranean (open squares).

smallest sizes of eggs/larvae at first spawning. However, high summer sea temperatures, while favourable for early maturation, also favour growth rate. Conversely, low sea temperature delays the onset of maturation, allowing the animal to grow, although more slowly, to a larger size before becoming sexually mature (Waddy and Aiken, 1991). In some areas, however, it has also been suggested that high population density and warm waters may influence size at maturity in *H. americanus* (Waddy and Aiken, 1991). Since neither maximum size of the sexes nor the size at maturity of females appears to be markedly related to latitude in *Nephrops*, other variables besides temperature, such as density of animals and available food, are apparently influencing growth rate and thus size at maturity.

Changes in the proportion of various body parts or relative growth have been described in various studies on crustaceans, particularly brachyuran crabs (e.g. Hartnoll, 1978; Teissier, 1960). In cases of allometric growth, some body part (e.g. abdominal width in crustaceans) grows at a different rate relative to a reference dimension (e.g. CL), generating a change in body proportions. Sometimes, such changes are abrupt, marking crucial developmental stages, such as at maturity of an animal (Hartnoll, 1978, 1982). Relatively few investigations of this kind have been carried out on *Nephrops* body measurements in order to evaluate SOM. Farmer (1974c), studying the relationships between the width of the second abdominal segment and CL in Irish Sea *Nephrops*, found an inflection point in the relationship at a CL of 16 mm for both sexes, although a sharper break was seen for females. Since the increased growth rate in females occurred well before sexual maturity, as estimated by other methods, he concluded that the female abdomen had already enlarged by the time of first egg-laying by primiparous animals (Farmer, 1974a,b), which is in good conformity with the present Icelandic results. Tuck et al. (2000) obtained variable estimates from seven stations in the Firth of Clyde, west Scotland. However, the SOM values obtained, using allometric growth techniques (width of second abdominal somite and CL) and primary sexual characteristics (ovary maturity), were both found in a similar range of 21–34 mm CL between stations. Also, McQuaid et al. (2006) estimated SOM in females by examining abdominal width at the widest point across the pleura of the second segment in several areas of the Irish Sea. They demonstrated that there is a distinct decrease in the growth rate of abdominal width relative to CL in females, differing in inflection points by areas.

4.3. Reproductive cycle

4.3.1 Biennial cycle of spawning and hatching

During the winter period September to March, individuals preparing for spawning the following spring dominate in the female catch, with ovaries increasingly maturing from stages 4–5 to 6. Other parts of the female population, that is, immature and in particular ovigerous animals, are virtually nonapparent, presumably staying in the burrows (Figure 2.24 and Table 2.3).

By April, spawning initiates and females increasingly pass from ovary stage 6 to external egg stage A, reaching a peak in May. The spent ovary, with an average oocyte diameter of 0.28 mm, classifies nearest to stage 2 (mean size of 0.32 mm), as shown previously in Table 2.1. Simultaneously, the hatching population starts appearing in the catch after leaving the burrows, as indicated

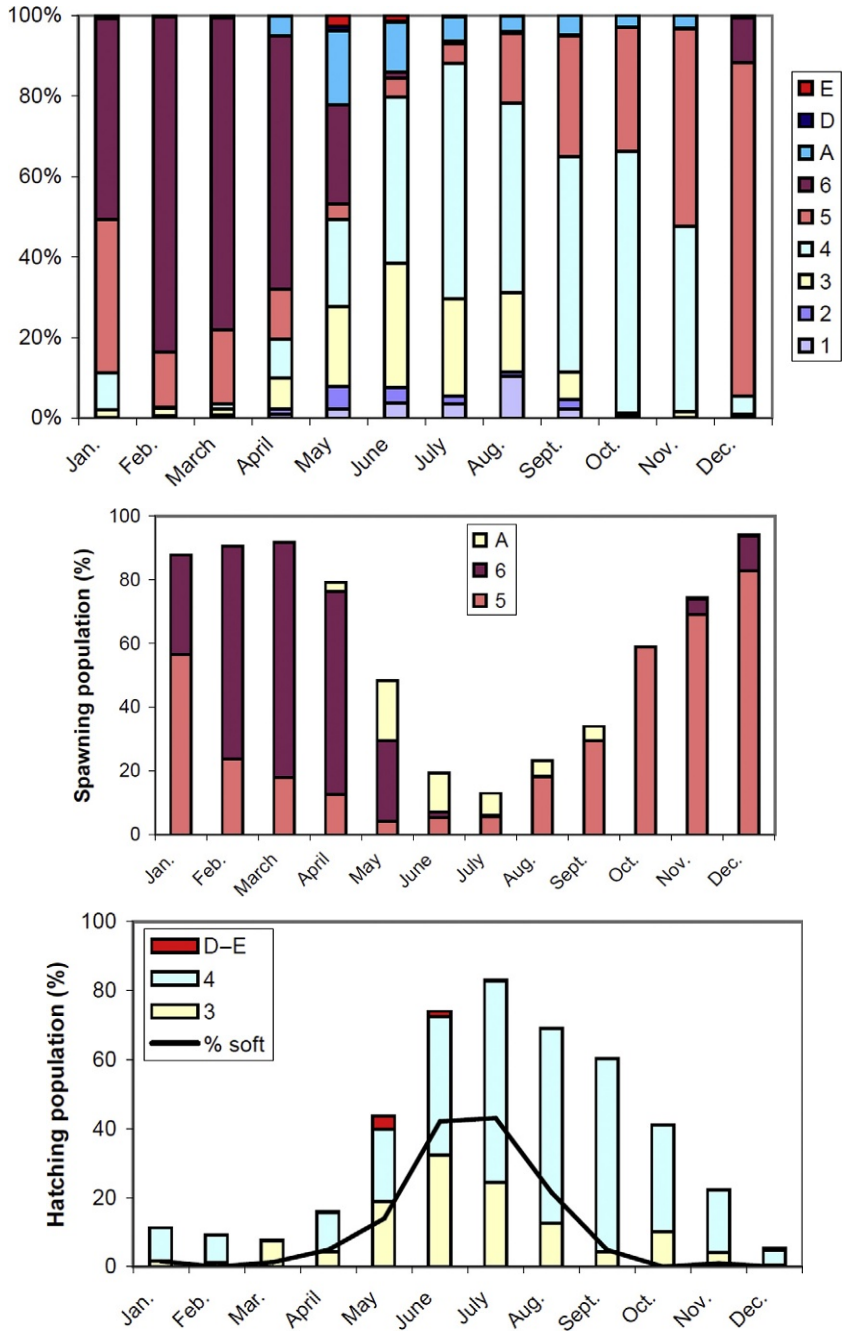


Figure 2.24 Monthly reproductive stages of female *Nephrops* in Icelandic waters, based on overall data during 1965–2010 (above). Monthly progress of the spawning and hatching populations (below). Ovary and egg stages indicated as well as % of females in a soft-shelled condition (ecdysis).

by the gradually increasing incidence, although relatively low, of prehatchers with external egg stages D and E and posthatchers bearing ovaries in stages 3 and 4 and already to some extent in a soft-shelled condition.

Early June, ovary stage 6 has virtually elapsed indicating the end of spawning, although newly berried females remain in the catch in decreasing numbers until mostly burrowing by August–September. Prehatchers with late spawn (abdominal egg stages D and E) still constitute a small proportion of the catch in June, although lesser so than in May. The occurrence of moulting posthatchers, with ovaries predominantly at stage 3 or 4, is, however, greatly enhanced in June, continuing until the end of July. Thus, the culmination of hatching in May–June nearly coincides with that of the peak of spawning in May.

From August onwards, ovaries of the non-ovigerous population advance increasingly from stages 4 to 5, the latter dominating among females in the catch during November–December. Thereafter, the spawning population increasingly matures to stage 6 in January–March in preparation for spawning in the spring. At the same time, the ovigerous population from the previous spawning in May remains largely in the burrows during the winter, not reappearing in the catches until May–June of the following year, when hatching occurs.

Although the whole population of female *Nephrops* is not easily sampled, due to the burrowing nature of berried individuals, an annual spawning cycle can be ruled out in Icelandic waters, and spawning appears to be predominantly biennial, that is, occurring every other year with an incubation period of 12–13 months. This is clearly demonstrated by the first appearance in April and highest incidence in May of ovigerous stage A females and the almost total disappearance of ovary stage 6 by June (spawning) (Figure 2.24), coinciding with a peak occurrence, although relatively low, of ovigerous stage D–E females in May and successive moulting maximum in June–July (hatching) (Figure 2.24). Since ovigerous stages D–E and the following soft-shelled condition are almost invariably accompanied by ovary stages 3–4, a steep rise in the incidence of those ovary stages can be observed in May to July, coinciding with hatching and the succeeding moulting and mating. Subsequent to the termination of hatching by July, the incidence of moulting posthatchers diminishes rapidly after peaking in June–July (Figure 2.24).

4.3.2 Spatial variations

Seemingly, there are relatively minor overall monthly variations in maturity development at southwest, south and southeast Iceland as depicted in Figure 2.25, although some annual variations can be seen (see Section 4.3.3).

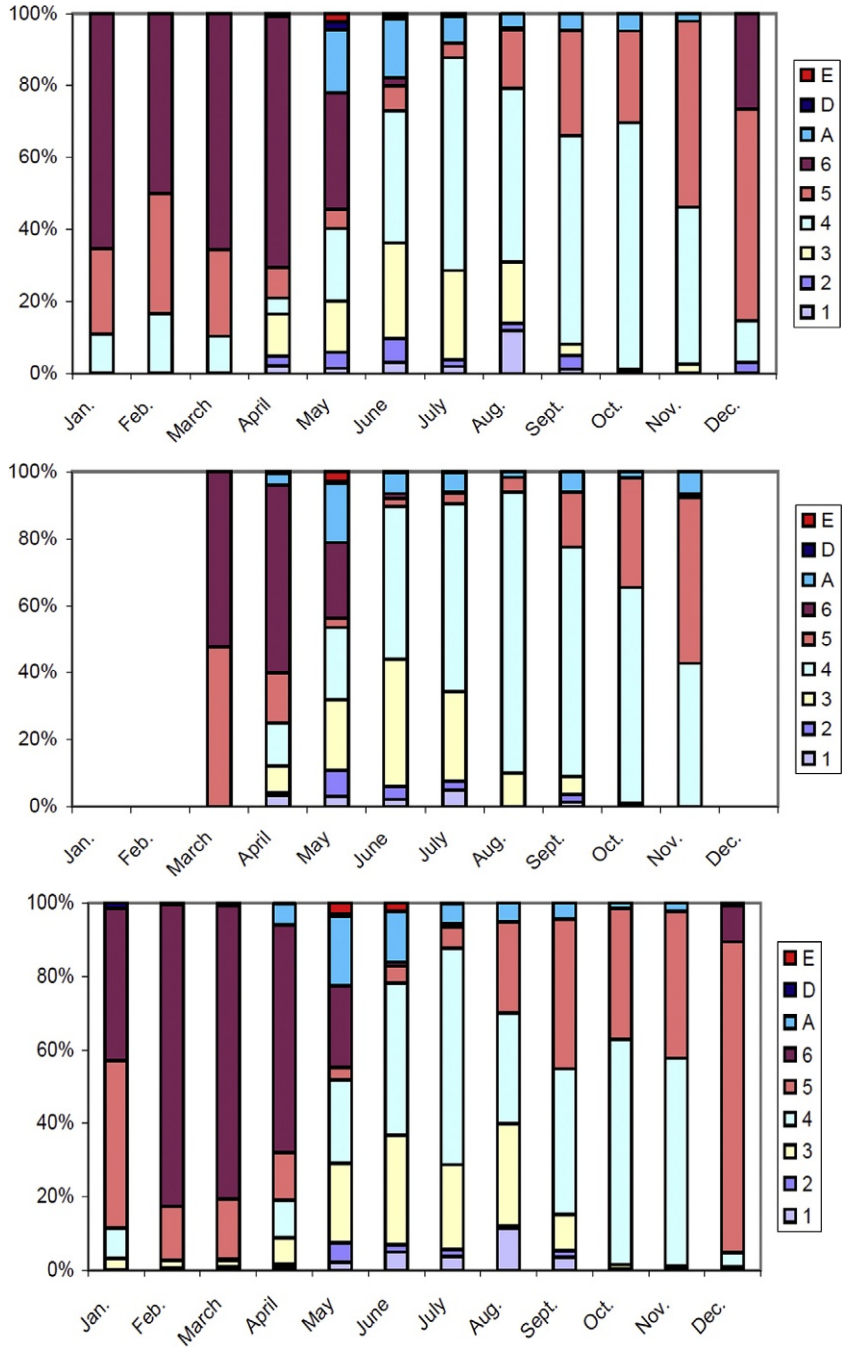


Figure 2.25 Monthly reproductive stages at SW (top), S (middle) and SE Iceland (bottom) during 1965–2010.

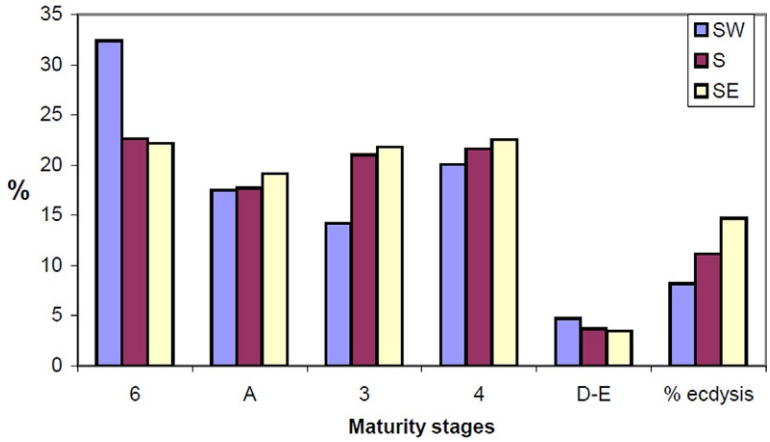


Figure 2.26 Spatial variations in spawning (ovary stage 6, egg stage A) and hatching (ovary stages 3 and 4, egg stage D–E and % ecdysis) at SW, S and SE Iceland during the month of May in 1965–2010.

However, there are quite clear indications of some area variations in the peak of spawning and hatching. Firstly, the overall average for the peak reproduction month of May during the period 1965–2010 shows a much higher ratio of prespawners (ovary stage 6) to that of the recent spawners (egg stage A) in the southwestern area, indicating proportionally later spawning than at the south and southeast (Figure 2.26). Also, a relatively later hatching at southwest Iceland than elsewhere is indicated by a higher percentage of prehatchers (egg stages D–E) accompanied by a lower ratio of posthatching animals with ovary stages 3–4 and a soft-shelled condition (ecdysis), but moulting is known to occur immediately or shortly after hatching.

Moreover, spawning variations are expressed further by the proportionally higher percentage of prespawners (ovary 6) at southwest Iceland in April–May due to a lesser proportion spawning in April and at least early May. This sequence of events ultimately leads to a higher percentage of the recent spawners (egg stage A) in the southwest in June compared to the other areas (Figure 2.27). Likewise, the relatively higher ratio of prehatchers bearing eggs in late incubation stages (D–E) from May to July at southwest Iceland reverberates itself in a smaller proportion of soft-shelled females in May and a delayed higher ratio in July–August, indicating latest hatching off southwest Iceland (Figure 2.28).

A regression analysis of the percentage of berried females (egg stage A), out of the total spawning population (egg stage A + ovary stage 6), plotted against the catch date during May 1 to June 10, indicates a somewhat earliest

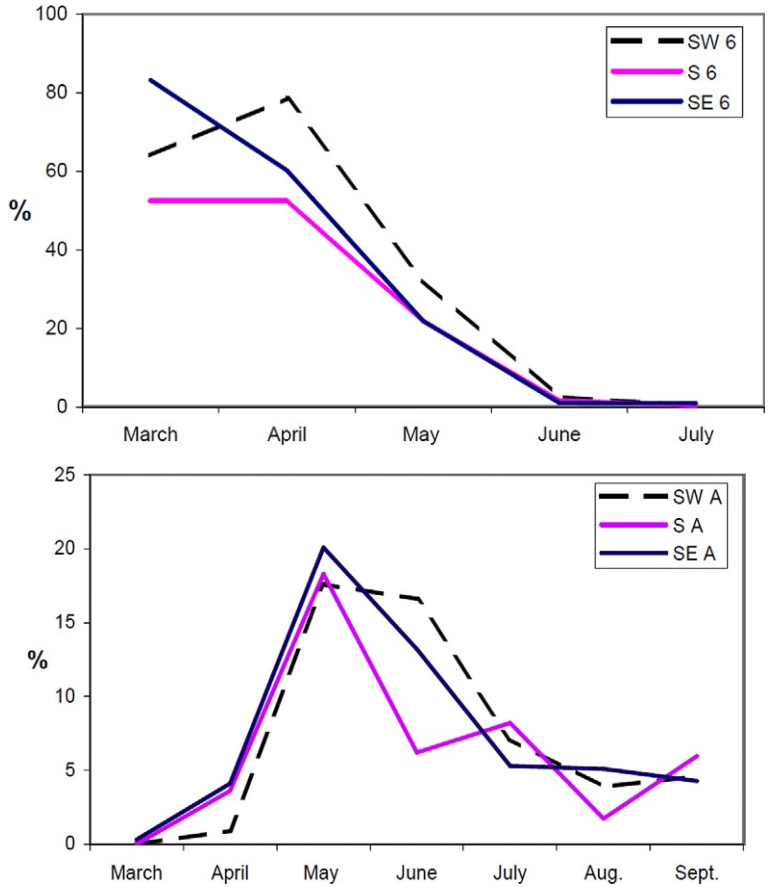


Figure 2.27 Monthly progress of spawning at SW, S and SE Iceland in 1971–2010, indicated by decreasing proportion of prespawning ovary stage 6 females (above) and increasing ratio of postspawning egg stage A females from March to April onwards (below).

spawning at southeast Iceland and latest off the southwest coast. On average, this amounted to 50% of the potential spawners in the catch being ovigerous on May 13 at southeast Iceland compared to May 17 and May 23–24, respectively, off the south and southwest coasts (Figure 2.29). Certain spawning pulses are notable in all areas, possibly linked with some lunar effects although a mere artefact cannot be ruled out.

Considering those reproductive activities, it has to be borne in mind that with the advancement of the month of May, some early spawners may have disappeared from the catch due to the burrowing behaviour and, thus,

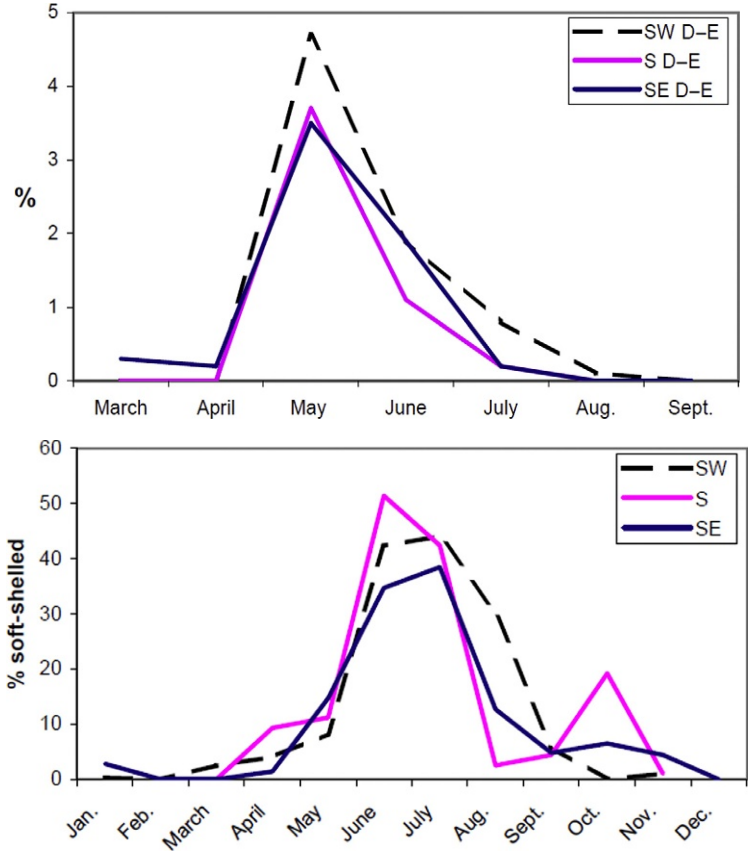


Figure 2.28 Monthly progress of hatching at SW, S and SE Iceland in 1971–2010, indicated by proportion of ready-to-hatch egg stage D–E females (above) and ratio of post-hatching soft-shelled females from March to April onwards (below).

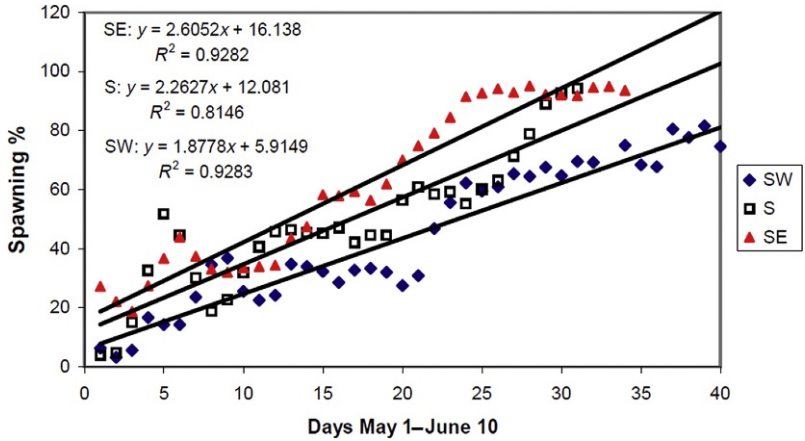


Figure 2.29 Increasing proportion of egg-laying stage A females out of the total spawning population at SW, S and SE Iceland from May 1 to June 10 during 1971–2010, indicating earliest spawning in the southeast and latest in the southwest. Some spawning pulses are apparent, possibly indicating lunar effects.

possibly minimizing the ratio of spawners to prespawners by areas in the catch compared to the actual stock. Also, in the context of soft-shelled post-hatchers, one should be aware of the possible influence of some first-time maturing females that are moulting more frequently and irrespective of the breeding cycle. However, the proportion of soft-shelled females with ovary stages 3–4 that are derived from primiparous animals in May–August was not identified in detail in this study. Therefore, some possible area variations due to primiparous females cannot be ruled out.

4.3.3 Temporal variations

The peak activity of spawning and hatching of *Nephrops* at Iceland seems to be spaced within a relatively short period. Therefore, a sampling programme that has been focused to some extent on an annual *Nephrops* trawl survey, lasting for two weeks within the month of May, may unavoidably have led to some annual variations seen in reproductive parameters.

To give an example, the mean May proportion of prespawning ovary stage 6 and newly spawned egg stage A females in catch samples at southwest Iceland in 1973–2010 amounts to 33.2% (SD = 16.3) and 17.0% (SD = 7.5), respectively. Likewise, the mean proportion of ovary stage 6 and egg stage A amounts to 23.2% (SD = 15.2) and 16.7% (SD = 9.1) and 23.4% (SD = 13.5) and 19.2% (SD = 9.4), regarding the south and southeast areas (Figure 2.30). The relatively higher ratios of spawners on average in the south and especially southeast support the result above on latest spawning on average in the southwest. In addition, the regression of ovary stage 6 and egg stage A females in the southwest in May 1973–2010 (Figure 2.30) is significant at the level of $p = 0.001$ ($r^2 = 0.28$). The ratio of the recent spawners to prespawners appears relatively low in the late 1970s to early 1980s and displays a particularly marked downward trend in the 2000s, indicating relatively later spawning compared to previous years. Moreover, these trends are applicable to a variable extent in all areas (Figure 2.30).

Annual progress of hatching in May 1973–2010 appears notably varied, showing relatively highest peaks of occurrence of the second last egg stage D and overall lower prominence of the last egg stage E at southwest Iceland, indicating very often latest hatching in that area, as previously described. Apart from these spatial variations, a very low incidence of egg stage D and to a lesser degree egg stage E females has been observed in the 2000s in all areas, indicating earlier hatching compared to previous years (Figure 2.31). Yet another indicator of earlier hatching in the recent years

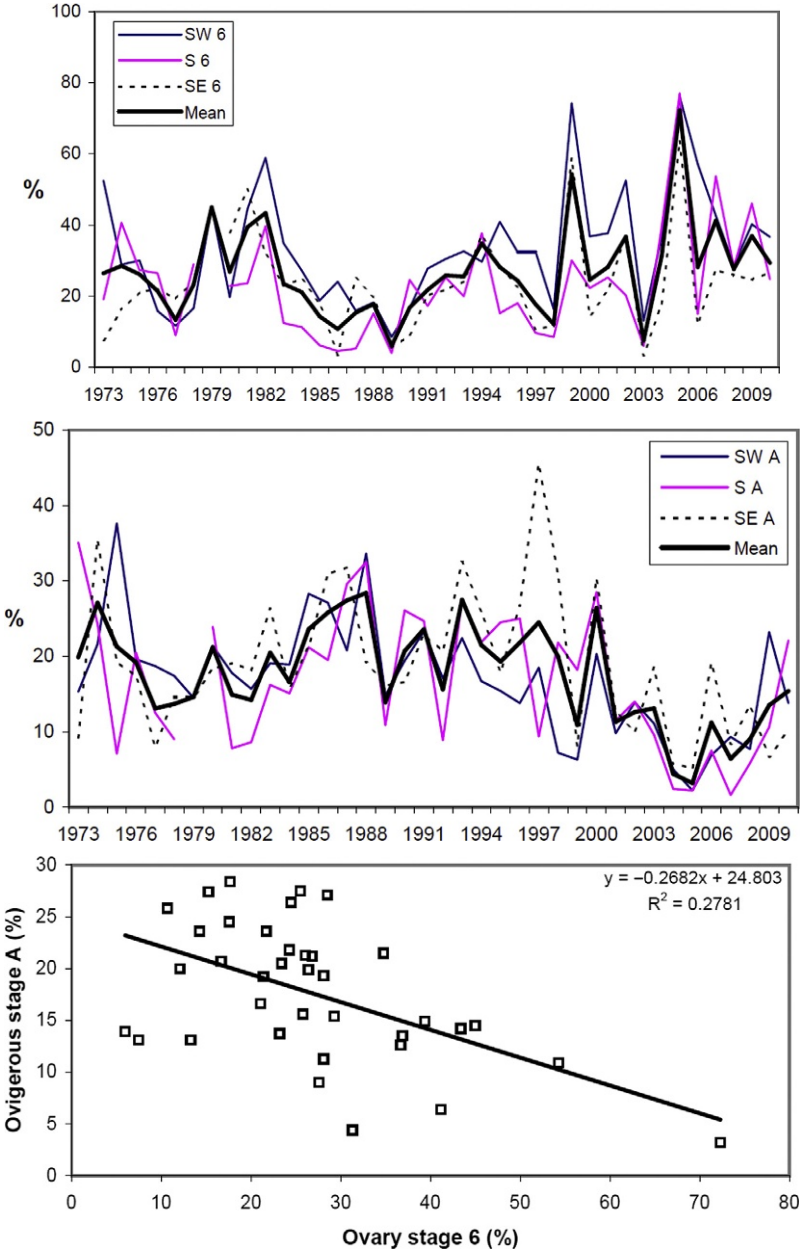


Figure 2.30 Annual and mean proportion of prespawning ovary stage 6 females (top) and postspawning egg stage A females (middle) at SW, S and SE Iceland during May 1973–2010. Correlation between average ratios of prespawning (stage 6) and postspawning (stage A) females during May in 1973–2010 ($p = 0.001$) (bottom).

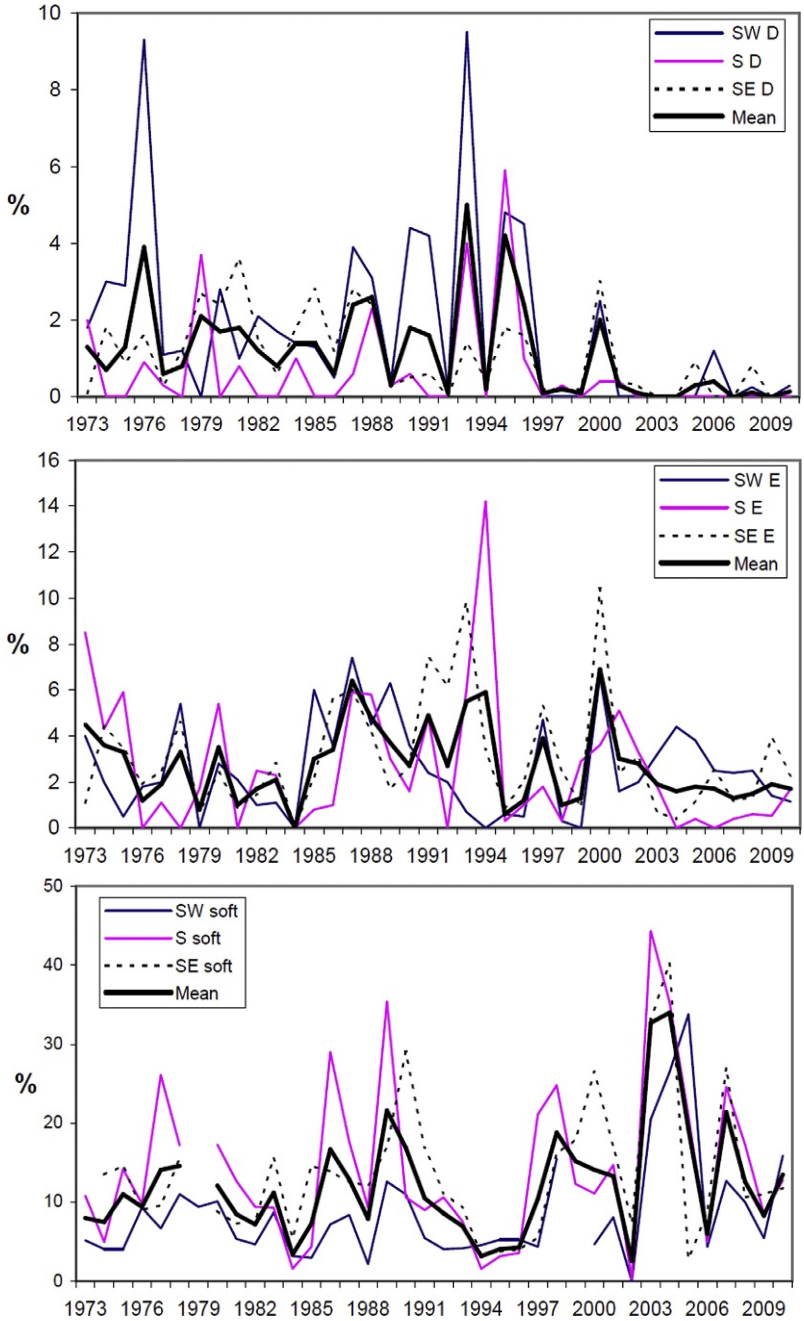


Figure 2.31 Annual and mean proportion of prehatching stage D and E females (top, middle) and posthatching soft-shelled females (bottom) at SW, S, and SE Iceland during May 1973–2010.

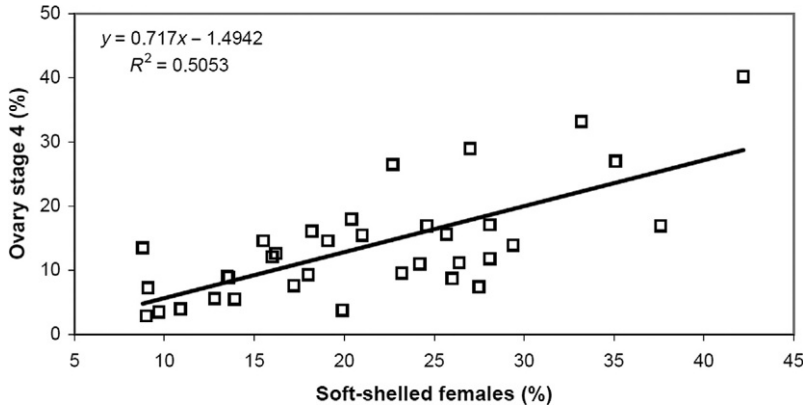


Figure 2.32 Correlation between proportion of ovary stage 4 females and soft-shelled females at SE Iceland ($p < 0.001$) in May 1973–2010 (also SW $p < 0.001$ and S $p = 0.01$).

can be observed in a relatively high, although variable, percentage of soft-shelled females in May, but ecdysis is a prominent biological process among crustaceans following hatching (Figure 2.31). Therefore, the number of soft-shelled females and posthatching ovary stage 4 individuals is a relatively good indicator of the progress of hatching as shown in Figure 2.32 ($r^2 = 0.51$; $p < 0.001$) for southeast Iceland in 1973–2010.

In view of the extreme fluctuations demonstrated above in annual reproduction parameters, the author has also chosen to describe temporal variations in terms of decadal averages for the month of May. Henceforth, Figure 2.33 demonstrates the decadal mean progress of spawning by areas in May 1973–2010. Due to the biennial spawning regime, only some 50% or less of the female population is partaking in spawning each spring, that is, with either ovary stage 6 or egg stage A. Also, as mentioned previously, the southwestern area is generally seen to be lagging behind regarding the progress of spawning with the lowest ratios of the recent spawners. Moreover, most noticeably, spawning is relatively much less advanced in the 2000s compared to previous decades. Likewise, the advancement of hatching appears relatively later in the southwestern area as shown by an overall lower percentage of animals with posthatching ovary stages 3 or 4 and a soft-shelled condition. Moreover, the progress of hatching appears most advanced in the 2000s, as indicated by the lowest ratios of ready-to-hatch egg stages D–E and an increased percentage of soft-shelled animals (Figure 2.34).

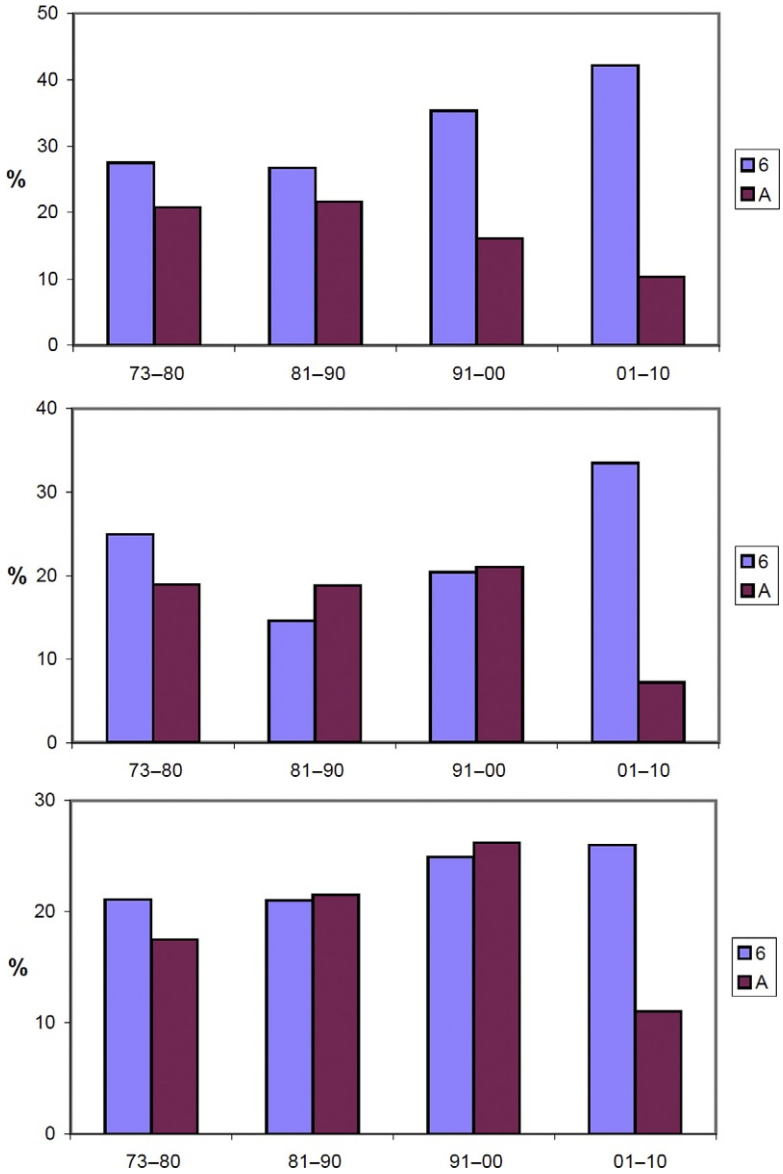


Figure 2.33 Average decadal advancement of spawning, as indicated by the proportion of prespawning females (ovary stage 6) and ovigerous (egg stage A) at SW (top), S (middle) and SE Iceland (bottom) in May 1973–2011.

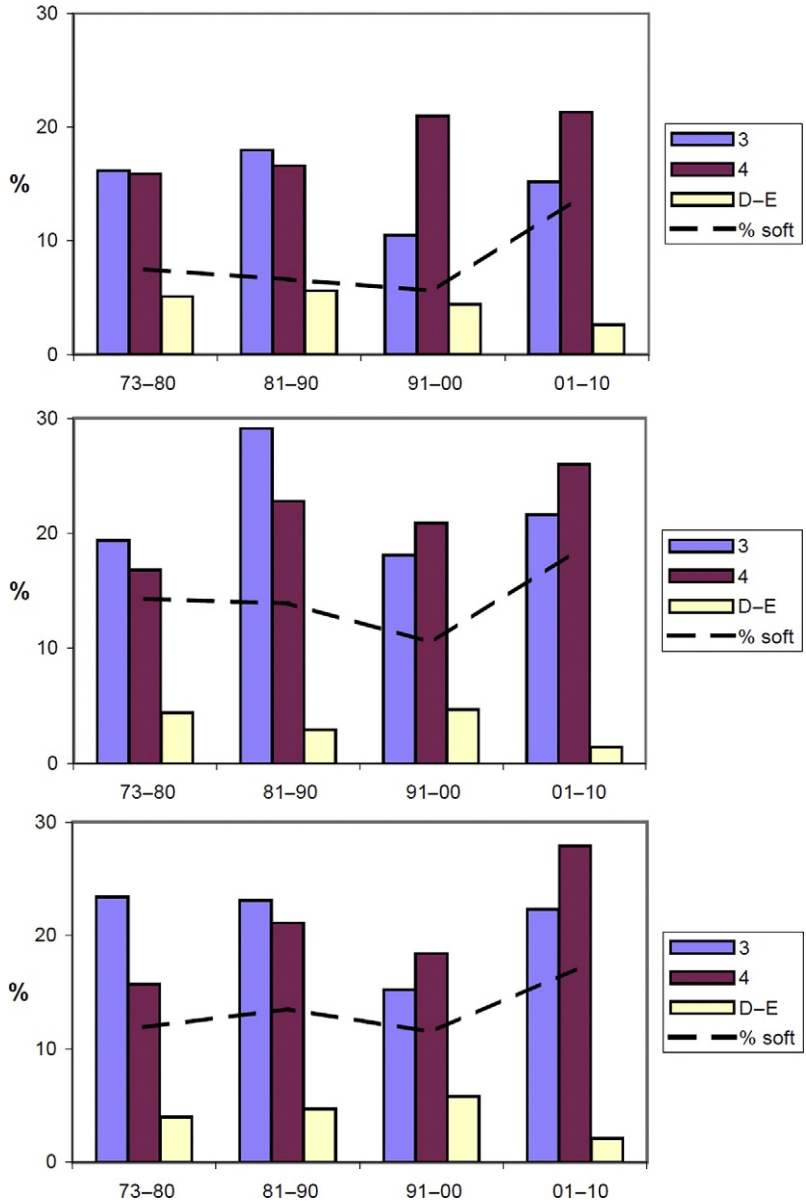


Figure 2.34 Average decadal advancement of hatching, as indicated by the proportion of ready-to-hatch females (egg stages D–E), posthatchers (ovary stages 3 and 4) and soft-shelled posthatchers (% soft) at SW (top), S (middle) and SE Iceland (bottom) in 1973–2010.

4.3.4 Spawning size variations

Data on the spawning population, consisting of females with ovaries at stage 6 and ovigerous at stage A at the peak of spawning in May, show a varying ratio by size, according to both areas and decades. Thus, spawning is sometimes typified by a very high ratio of the recently berried stage A animals, compared to those prespawning ovary 6 females in medium size ranges of approximately 30–40 mm CL, for example, in the 1980s in all areas (Figure 2.35). Larger females are also in many periods seen to be less advanced in the progress of spawning, such as in the southwest in the 1980s. Also, spawning is overall late in all size groups in the 2000s (Figure 2.35). The unusually late progress of spawning identified with the 2000s, most particularly in smaller animals, reflects itself in the extremely low BL_{50} (50% breeding) and high OV_{50} (50% berried) calculations for that decade, as described earlier in Section 4.2.

Since aggregated data are being used for the month of May, thus minimizing the temporal effect of burrowing, the overall results are interpreted as showing most often a slightly earlier spawning by medium-sized females or they are turning less readily than others to their burrows after spawning. In addition, the smallest animals may also be lagging somewhat behind at times due to delayed development of ovaries when spawning for the first time, as is most apparent in the 2000s. Lastly, the largest females may be spawning proportionally late due to an even longer or more irregular breeding cycle that could be related to senility. Therefore, a spawning regime that may occur even less than biennially cannot be ruled out for at least some of the largest animals.

In these data from 1971 to 2010, resorption of ovaries was not recorded as a regular procedure. However, the rate of resorption has been shown to be only minimal (0–4%) in samples in May 1990–1992 and March–September 2004–2010, diminishing the likelihood of ovary stage 6 and egg stage A ratios in May being greatly affected by size-linked resorption rate at Iceland, although previously described for some other geographical areas (Bailey, 1984; Figueiredo, 1982).

The unusually high proportion of small and largely primiparous ovary stage 3–4 females observed in the 1980s resulted in record low L_{50} in that decade indicating good recruitment and/or slow growth. Quite the opposite, however, is seen in the 2000s when record high L_{50} values were calculated in both the southwest and south areas (Figure 2.35).

4.3.5 Reproduction and monthly female size variations

Due to the biennial reproduction regime in Icelandic *Nephrops*, the size composition of female catches changes significantly during the period May–July,

partly as a result of the disappearance of the spawning component into the burrows but even more so by the reappearance of the hatching population from their hideouts. For example, Figure 2.36 demonstrates the length compositions of females in *Nephrops* catch samples obtained at southwest, south

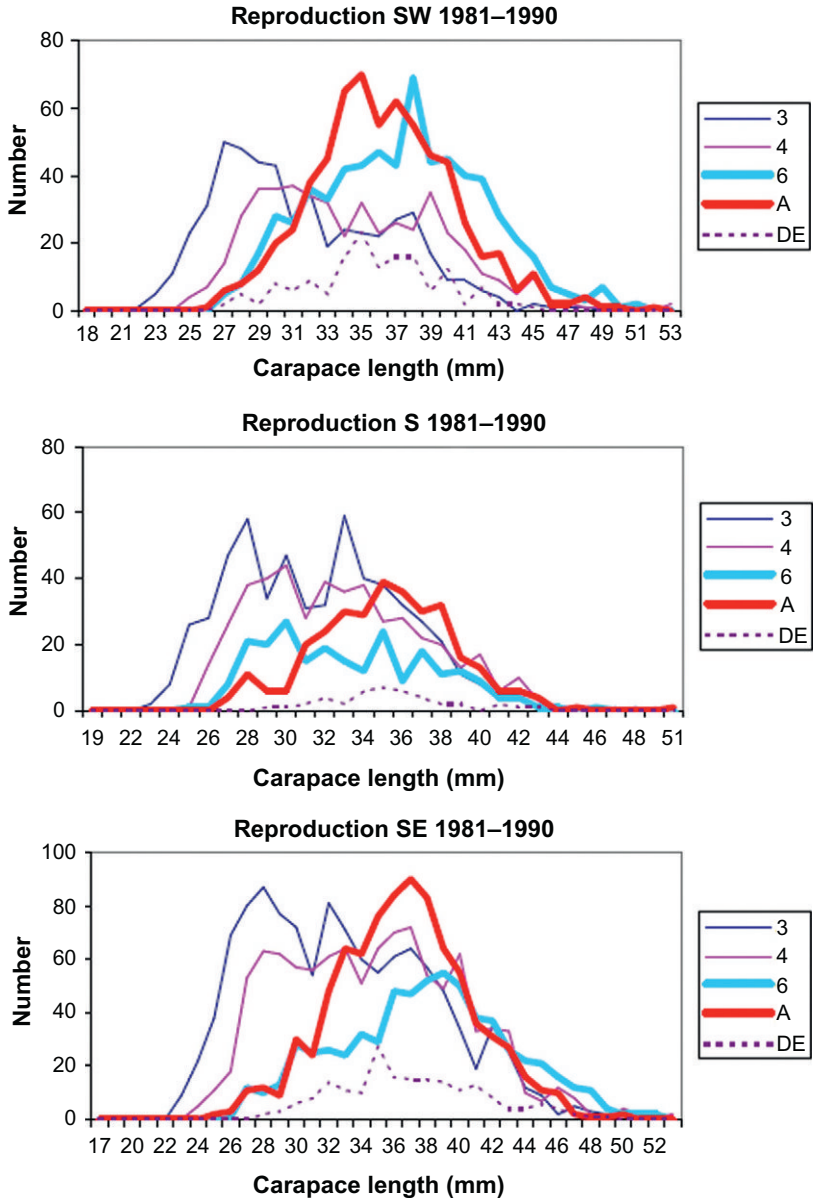


Figure 2.35—Cont'd

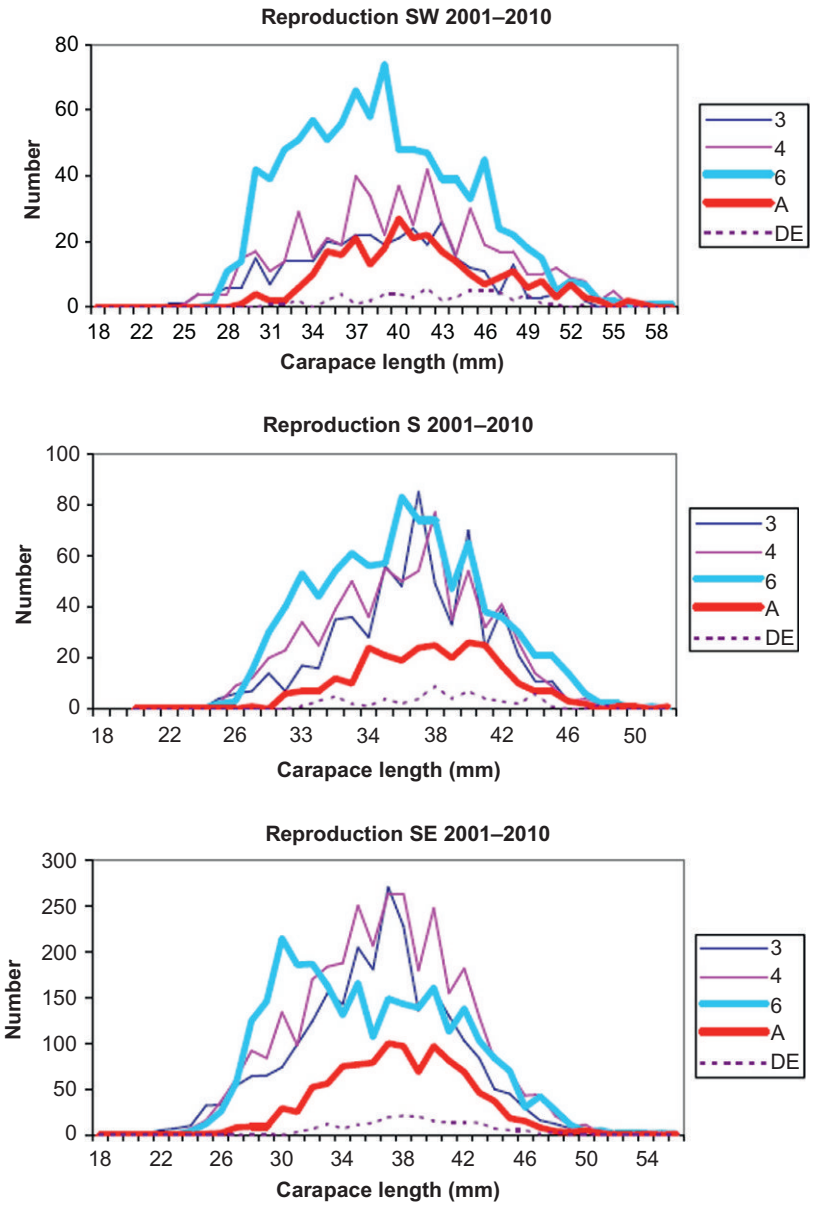
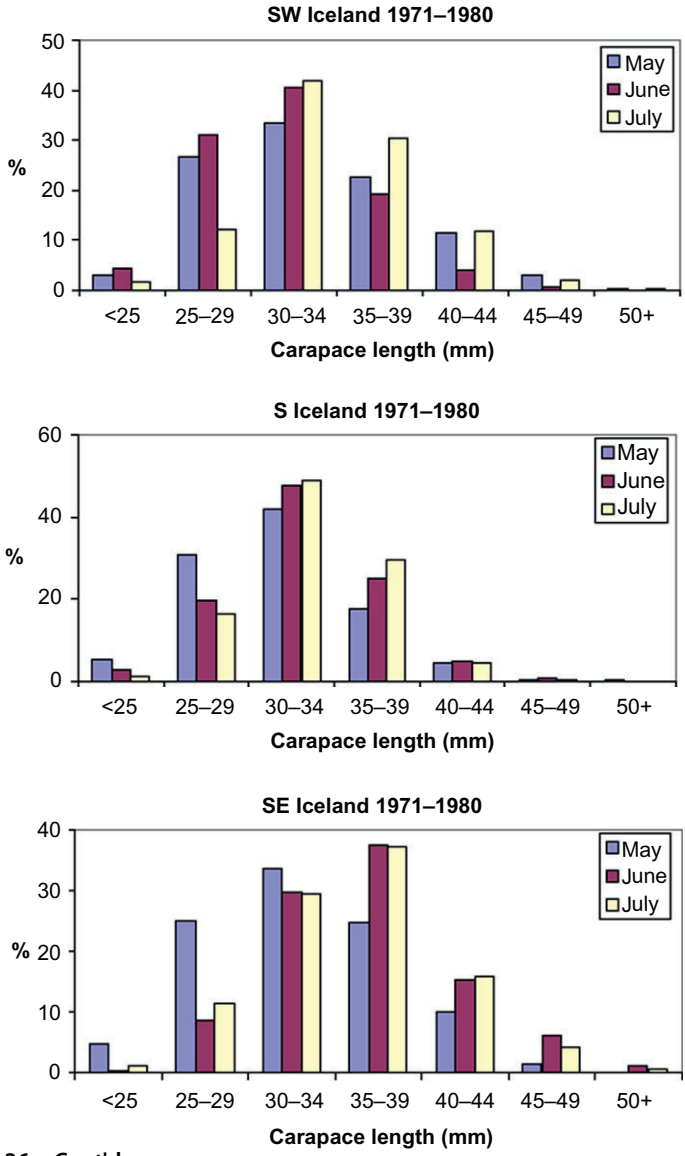


Figure 2.35 Average decadal length distributions of mature female *Nephrops*, shown by number measured and maturity stages at SW, S and SE Iceland during 1981–1990 and 2001–2010.

and southeast Iceland from May to July 1971–1980 and 2001–2010. For clarity, the data are presented as decadal averages of 5 mm CL groups.

The proportion of females in sizes up to 30 mm CL is irrevocably seen to decrease from May to July since a high proportion of these animals are either immature or primiparous, not arriving into the catchable stock as post-hatchers except in relatively small numbers. Medium to small females of



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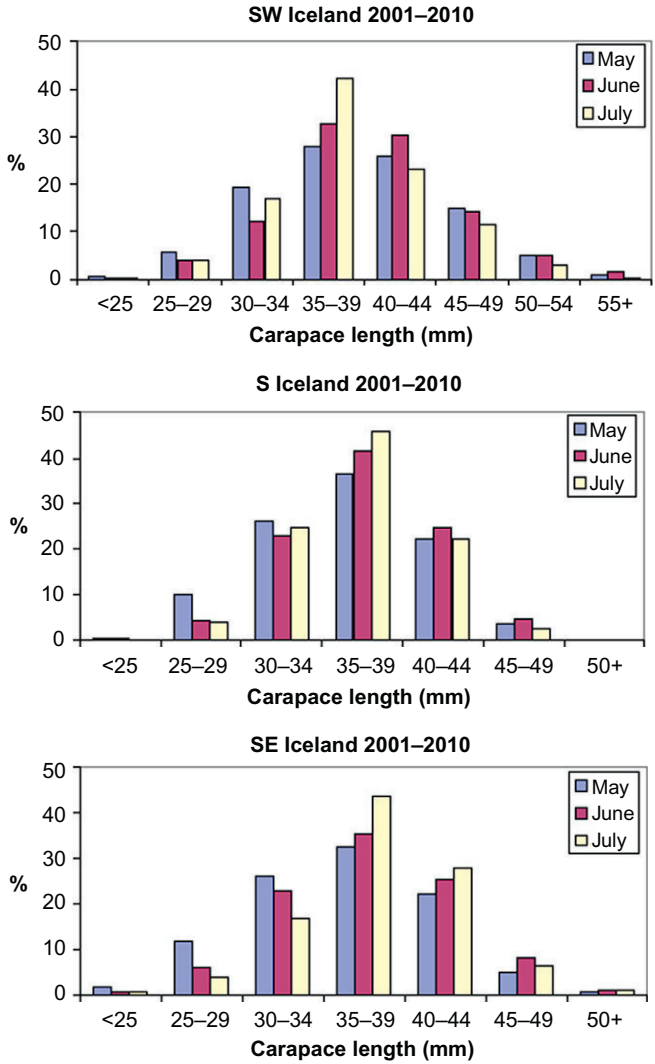


Figure 2.36 Average decadal monthly May to July length distributions (5 mm length groups) of female *Nephrops* at SW, S and SE Iceland during 1971–1980 and 2001–2010.

30–34 mm CL, most of which are engaged in reproductive processes, show an increase in May–July only when they constitute a very large proportion of the female catch, that is, when mean size of females is low as in the 1970s. Therefore, this was only realized in the south and southwest in the 1970s, when both fishing intensity and recruitment were relatively high. Otherwise, the proportion of size group 30–34 mm CL remains similar from May to July or even diminishes when larger individuals make up the bulk

of the catch as in the 2000s. On the other hand, the ratio of the size group of 35–39 mm CL increases ubiquitously from May to June–July due to the increased availability of posthatchers, mostly soft-shelled. Size groups 40–44 mm CL and larger, however, normally show a more similar ratio over the period, possibly reverting more readily to the burrows or the largest possibly partaking in even less than biennial spawning and hatching.

4.3.6 Biennial spawning, growth and size difference between sexes

With maturity and the onset of spawning within a biennial reproduction regime, ecdysis and thus growth in Icelandic female *Nephrops* are prevented for some 12–13 successive months of egg incubation every other year. A possible occurrence of more than one moult during the long non-ovigerous period (11–12 months) is not discernible, however, from the Icelandic data, which show only one clear biennial posthatching moulting peak in June–July (see Figure 2.24). Thus, biennial moulting would imply the retarding of female growth versus that of males to a higher degree than in areas of annual spawning and hatching.

Figure 2.37 demonstrates the mean size of males and females in the catches at southwest Iceland in 1960–2010 and a highly significant relationship of the two parameters ($r^2 = 0.75$; $p < 0.001$). Similar results, although comparatively less significant, are also seen in the south and southeastern areas ($r^2 = 0.64$ and 0.43). However, as indicated by the regressions, heavy exploitation will lead to decreasing mean size in catches of both sexes and an enlarged ratio of female-to-male size due to greater removals of the larger males. Thus, very high exploitation rates are seen to decrease the mean size difference of the two sexes by as much as 50%. Eiríksson (1999) described these changes in catch composition by comparing the mean size of males and females caught at transects of increasing depth at southeast Iceland in 1963 and 1991.

A comparison of the maximum recorded CL should be able to identify the inherent pristine or virgin maximum body size of each sex in *Nephrops* stocks. For that purpose, Figure 2.38 illustrates the maximum annual CL of males and females at southwest Iceland from the early 1960s to 2010 and the relationships of the two parameters. The regression is shown to be highly significant ($r^2 = 0.58$; $p < 0.001$) and similar for the southern area ($r^2 = 0.60$; $p < 0.001$), portraying an average size difference of 15–20 mm CL between the recorded annual maximum CLs of the sexes. Overall, the maximum female-to-male size ratio is around 0.73–1.00, resembling that of mean size of females to males in a virgin or low effort fishery.

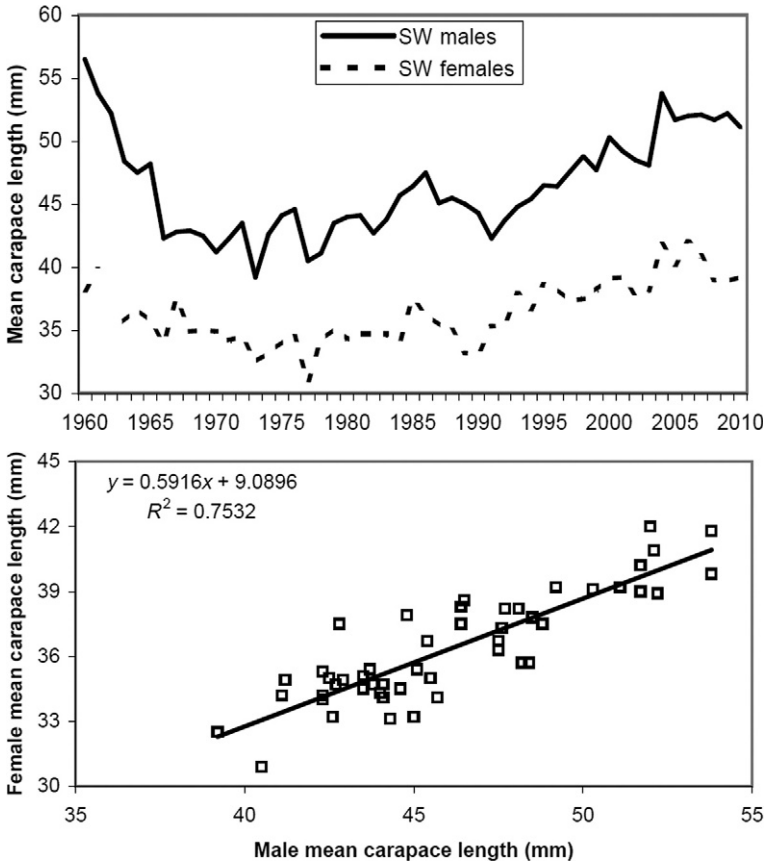


Figure 2.37 Annual average carapace length (mm CL) of males and females at SW Iceland in 1960–2010 (above) and correlation between the two data sets ($p < 0.001$) (below).

A geographical comparison of the maximum recorded CL of females and males within all the 17 *Nephrops* fishery statistical rectangles from west to east is shown in Figure 2.39 ($r^2 = 0.71$; $p < 0.001$). Apparently, both male and female *Nephrops* reach maximum sizes in the southwest and southeast, becoming, however, relatively smaller in the south and near the periphery of the distribution to the far west and east. The relatively smaller individuals found in the southern areas can be easily explained neither by such environmental parameters as sea temperature, depth or sediment type nor by density-dependent growth judging from catch statistics. Overall, however, smaller *Nephrops* have been more prominent on average in the south than elsewhere during the decades from the 1960s to the 2000s (see Figure 2.10).

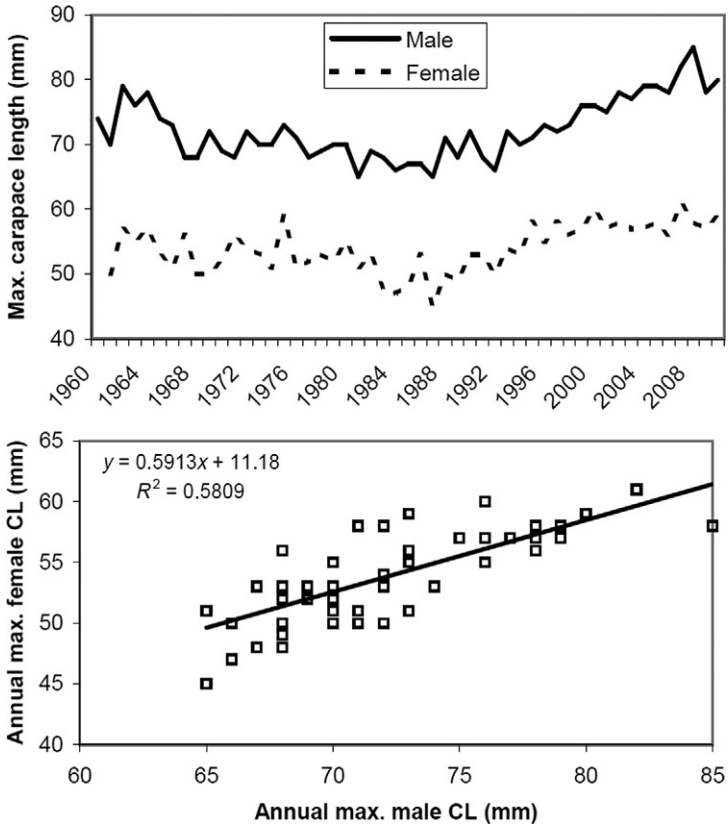


Figure 2.38 Annual maximum recorded carapace length (mm CL) of males and females at SW Iceland during 1960–2010 (above) and correlation between the two parameters ($p < 0.001$) (below).

4.3.7 Geographical and environmental discussion

The breeding cycle of female *Nephrops* in Icelandic waters can best be described as typically biennial with an incubation period of some 12–13 months (Figure 2.24 and Table 2.3). Therefore, each year, one-half of the mature population is spawning in late April or mostly May and the other half hatching their eggs in May to June and vice versa the following year. In spatial terms, spawning and hatching occur a little later at southwest Iceland than off the south and southeast coasts.

Annual/decadal variations are also observed, the most notable being the relatively later peak of spawning in all areas in the 2000s (Figure 2.30). At the same time, however, hatching seems to have been further advanced in the month of May in the 2000s, compared to the 1970s–1990s (Figure 2.31). Moreover, the percentage of moulting and ovary stage 4

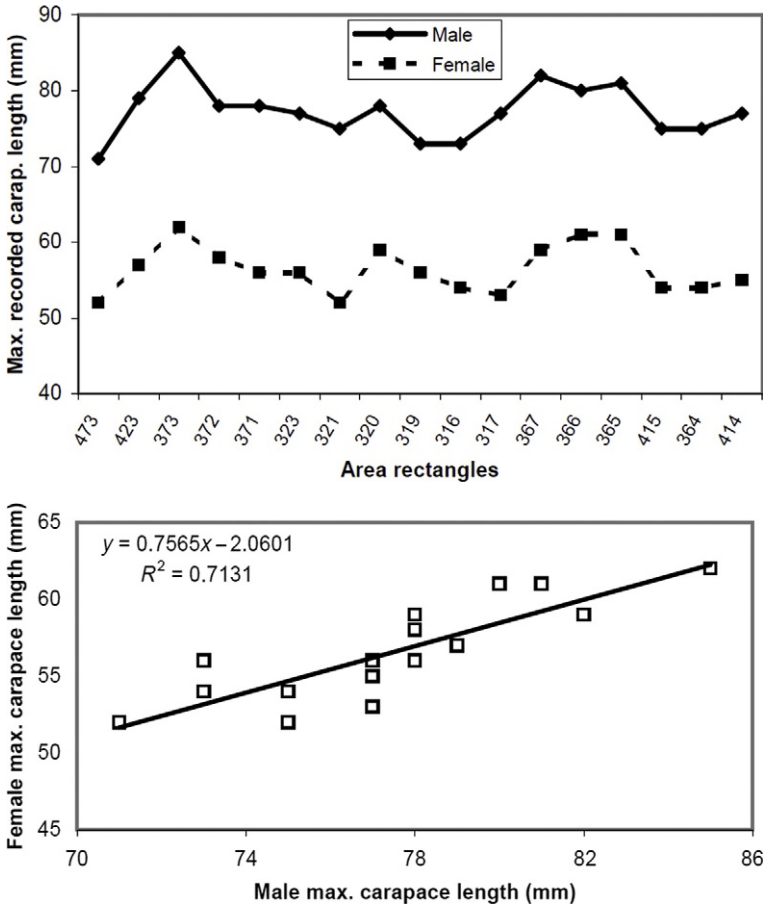


Figure 2.39 Maximum recorded carapace length (mm CL) of males and females from the 17 fishery statistical areas enclosing *Nephrops* fishing grounds off southern Iceland in 1960–2010 (above) and correlation of maximum of males and females shown above ($p < 0.001$) (below).

females in the catch appears a relatively good indicator of the progress of hatching (Figure 2.32).

Medium-sized females of 30–40 mm CL seem to be very often the predominant animals engaged in early spawning with the smallest and largest lagging behind (Figure 2.35). Possibly some of the smallest animals are affected by delayed development of ovaries when spawning for the first time and the largest are spawning relatively late due to a somewhat longer or more irregular breeding cycle that could be related to senility. Therefore, a more irregular or less than biennial spawning regime cannot be ruled out for some of the largest animals in Icelandic *Nephrops* populations.

The length of the incubation period over the range of *Nephrops* distribution in the Northeast Atlantic waters appears to be related to latitude, the most important variable probably being bottom temperature (Chapman, 1980; Figueiredo and Thomas, 1967a). Indeed, observations under experimental conditions have shown that the length of the incubation period increases with decreasing temperature (Dunthorn, 1967; Farmer, 1974b). Thus, the biennial spawning cycle at Iceland can be related to the relatively low bottom sea temperatures in the area where annual monthly means range from 5–6 to 8–9 °C (Anonymous, 2009; Eiríksson, 2009; Stefánsson and Jónsdóttir, 1974). Since the waters off southwest Iceland have somewhat lower bottom temperatures on average than the more southerly and southeasterly areas, sea temperature is considered the most probable explanation for the slight delay in spawning and hatching in that area. It should also be noted that the northwestern limit of *Nephrops* in fishable quantities in the Atlantic is off southwest Iceland (64°30′N) and a viable reproduction cycle in a more northerly distribution is presumably prevented by too low bottom temperatures.

A geographical comparison of the maximum female-to-male CL ratio over the whole range of *Nephrops* distribution in the North Atlantic and the Mediterranean is depicted in Figure 2.40. The female-to-male size ratio for the three Icelandic areas is seen to average around 0.72–0.73 to 1.00. Also, a similar female-to-male size ratio at the Faeroes seems in good conformity with the biennial spawning regime described for that area (Nicolajsen, 1989; Nicolajsen and Eiríksson, 1990). The low ratio for the west of Ireland gives an indication of slow female growth, possibly due to less than annual spawning, although available data are rather limited (O´Riordan, 1964). The maximum female-to-male CL ratio of all other areas, ranging from Northern Scotland to the Aegean Sea, is, however, strongly indicative of preponderant annual spawning with female-to-male maximum size ratio of 0.80–0.85 or more to 1.00. Moreover, the regressions of male-to-female maximum sizes in various European areas, as well as in the present data from Icelandic fishery rectangles, display a highly significant and different relationships ($r^2 = 0.86$; $p < 0.001$ and $r^2 = 0.71$; $p < 0.001$) (Figure 2.40).

The relatively greater difference seen between the indigenous or maximum size of males and females in Icelandic waters can best be described by a particularly slow growth rate of mature females in Icelandic waters as a result of the biennial breeding cycle. Therefore, this size ratio can be considered a relatively clear indication of a different growth pattern of Icelandic female *Nephrops* compared to most other areas, ranging from Scotland and the North Sea south to Portugal and the Mediterranean.

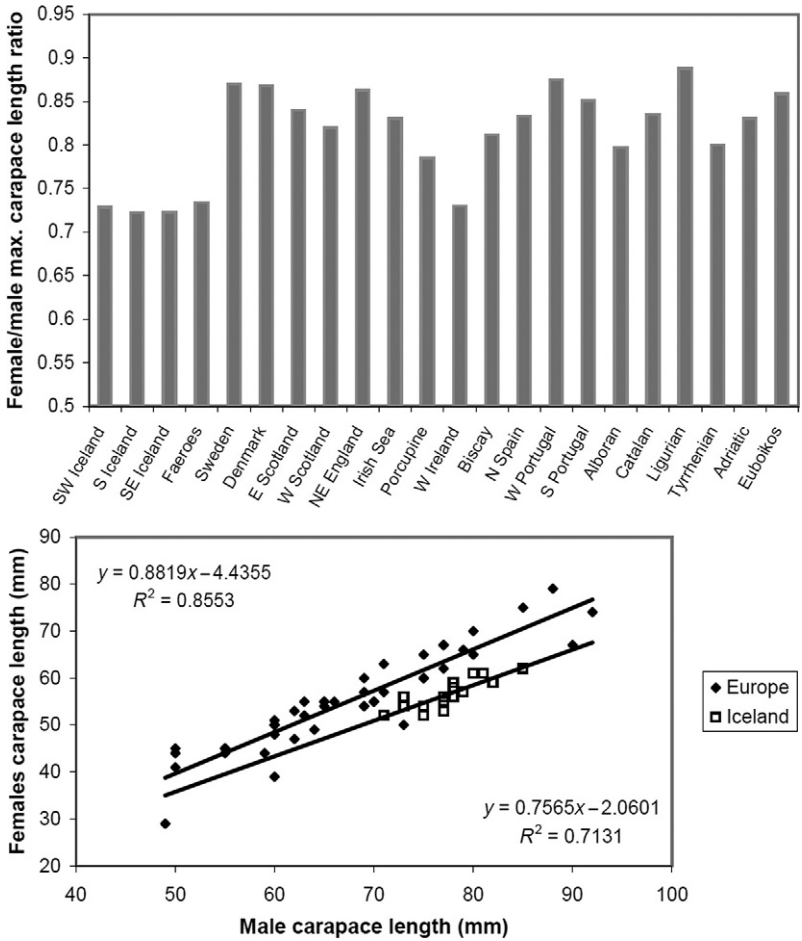


Figure 2.40 Geographical comparison of female-to-male maximum carapace length ratio in the N Atlantic and the Mediterranean (above) and correlations of maximum carapace length of males and females in Iceland ($p < 0.001$) versus other European waters ($p < 0.001$) (below) (see Section 4.3.7 for references).

Nonannual spawning is quite a well-known feature among decapod crustaceans, such as the American lobster *H. americanus* (Templeman, 1936, 1940; Waddy and Aiken, 1991), European lobster *H. gammarus* (Simpson, 1961), edible crab *Cancer pagurus* (Pearson, 1908), blue king crab *Paralithodes platypus* (Jensen and Armstrong, 1989), spider crab *Chionoecetes opilio* (Watson, 1970) and the toad crab *Hyas araneus* and stone crab *Lithodes maja* in Icelandic waters (S. Tr. Einarsson, personal communication). In addition, biennial spawning is a common feature in the northern pink

shrimp *Pandalus borealis* in more northerly latitudes (Skúladóttir, 1991; Skúladóttir et al., 1991). In *H. americanus*, spawning and hatching (followed by moulting) occur in alternate years. Moreover, both low winter temperature and warm summer temperature are essential for proper synchronization of the moult and reproductive cycles. However, if winter temperatures are too high, fewer females spawn and the incidence of moulting increases, whereas if summer temperatures are too low, spawning is delayed or may not occur at all (Waddy and Aiken, 1991).

In a species of such wide distribution as *Nephrops*, area differences in breeding seasons may be expected. Since the length of the ovigerous period is related to latitude, spawning frequency of *Nephrops* appears to be mainly dependent on ambient sea temperature (Chapman, 1980; Figueiredo and Thomas, 1967a). However, it also appears that other factors than temperature may be involved in the control of the reproductive cycle of *Nephrops*, including moulting hormones and photoperiodicity (Sardà, 1991).

The present study corroborates data from southwest Iceland in 1965–1970 (Eiríksson, 1969, 1970b) showing that the reproductive cycle of Icelandic *Nephrops* typically takes 2 years, during which the female moults and mates one summer, spawns the following spring and carries the eggs on her pleopods until the third spring/summer, when they hatch. Shortly after the eggs hatch, the female again moults and mates and the cycle is repeated. Thus, the spawning regime of female *Nephrops* at Iceland can best be described as biennial, although even less than alternate-year spawning in some cases cannot be ruled out, especially in the largest individuals.

Eiríksson (1969, 1970b), describing a 2-year breeding cycle among female *Nephrops* at Iceland, also concluded that a biennial cycle might be typical for some Norway lobsters living at northerly latitudes. Although this had previously been mentioned by some early authors working with limited data, nonannual spawning has been described by the increasing number of authorities in the more recent years.

Andersen (1962), whose data were limited to July–August in 1937 and 1939, stated that the female Norway lobster around the Faeroes has a 2-year breeding cycle. Although he gave no evidence regarding the maturity of the ovary, spawning and hatching were apparently occurring almost simultaneously during these summers. In the absence of more data for other seasons, however, some authors expressed their doubts about the biennial spawning frequency at the Faeroes (Chapman, 1980; Figueiredo, 1982; Thomas and Figueiredo, 1965). Nevertheless, spawning was certainly taking place in midsummer, compared to autumn in nearby areas to the south, such as in

Scotland, thus resembling to some extent the peak of spawning in May at Iceland. The more recent reports by Nicolajsen (1989) and Nicolajsen and Eiríksson (1990), however, strongly support a biennial reproductive cycle in female *Nephrops* at the Faeroes. The data, from the period 1986–1990, revealed the highest average ovary maturity from mid-January to the end of May with females ready to spawn. By mid-June, about one-half of the females had spawned and virtually all by mid-July. From October to January, the ovaries of nonberried females matured, presumably in preparation for spawning the following June–July. Clearly, the non-ovigerous females maturing their ovaries from October to January did not belong to the population that was spawning in June–July, that is, only 3–4 months previously. Although no soft females were caught in the creels that were used for regular monthly sampling, the peak incidence of pinkish-brown external eggs (stage E) in May clearly indicated a springtime hatching. Thus, the most recent data on Faeroe *Nephrops* are strongly supportive of a biennial spawning regime, the period of incubation being on the average from June to May the following year or lasting for 11 months (Nicolajsen and Eiríksson, 1990).

According to Storrow (1912) and Symonds (1972), working on stocks in the Farne Deeps area off Northeast England, the breeding cycle takes 2 years. The low female sex ratios of 6–15% from June to August mentioned by Storrow (1912) and his description of increasing number of females in winter—sometimes equalling that of males—still held true for the Farne Deeps some 50–55 years later (Symonds, 1972). The trend in sex ratios over the year is also somewhat similar to Icelandic waters (see Table 2.8 and Section 4.4), but contrary to the ones observed in other areas around the British Isles such as Scottish waters (Chapman, 1980; Thomas, 1964) and the Irish Sea (Farmer, 1974b; O´Riordan, 1964), where the ratios of females are lowest in winter during the incubation period of a predominantly annual breeding regime. The Farne Deeps, although resembling areas off Iceland in a high proportion of females, almost wholly non-ovigerous in winter, as well as in a rapid fall in female ratio in May, appears, however, to be contradictory in some other respects.

The catch of female *Nephrops*, which at least in theory should rise following hatching in spring, as shown for Icelandic waters and nearby Scottish waters of the Firth of Forth (Chapman, 1980), culminates as late as November–December in the Farne Deeps area (Symonds, 1972). Also, the overall catch increases markedly during the winter months in the Farne Deeps in contrast to not only most British waters like the Firth of Forth but

Table 2.8 Temporal variations in spawning (S) and hatching (H) regimes of *Nephrops norvegicus* in different Atlantic and Mediterranean distribution areas

	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.
North Atlantic															
SW Iceland		S												H	
SE Iceland		S												H	
Faeroes			S											H	
W–E Scotland						S								H	
NE England						S								H	
W Irish Sea						S								H	
Bay of Biscay					S								H		
NW Spain					S							H			
W Portugal					S						H				
S Portugal					S					H					
Mediterranean															
Alboran Sea					S					H					
Catalan Sea					S					H					
Ligurian Sea					S					H					
Tyrrhenian Sea					S					H					
Adriatic Sea				S						H					
Aegean Sea				S						H					

For references, see Section 4.3.7.

also even more so to Icelandic waters where winter catches are mostly comparatively low. This increase in CPUE and proportion of non-ovigerous females in winter has been interpreted by Chapman (1980) to indicate that a substantial proportion of mature females in the Farne Deeps do not spawn every year. Moreover, Chapman (1980) related intermittent spawning to less opportunity for mating and fertilization in summer when *Nephrops* in the Farne Deeps tend to remain in their burrows as shown by a very low CPUE of both sexes. Therefore, a partly nonannual breeding cycle appears to originate from a different pattern of availability of *Nephrops* in the Farne Deeps compared to nearby areas, rather than the inability to complete the ovary maturation cycle for an autumnal spawning. Figueiredo (1982) considered resorption of the ovaries a likely explanation for the high proportion of non-ovigerous females in winter in the Farne Deeps, a situation also described by Bailey (1984) for the Firth of Clyde, west Scotland. Also, Milligan and Nichols (1988), describing results of *Nephrops* larvae surveys off the northeast coast of England in 1976, 1987 and 1988, obtained a very different and lower production of larvae in 1987, which the authors considered supportive of biennial spawning of at least a part of the stock in this area. However, a regular biennial pattern of spawning has not as yet been described for the Farne Deeps, and a great part of mature females is likely to be spawning annually as indicated by peaks of berried animals spawning in autumn and hatching in spring, giving an average incubation period of about 10 months.

Although data are limited from the eastern North Sea areas of Skagerrak and Kattegat, a 2-year breeding cycle has been referred to by Höglund (1942) and Poulsen (1946). Biennial spawning in this area, as described by Storrow (1912) for the Farne Deeps, may, however, be explained by a partly nonannual spawning regime indicated more recently for similar latitudes (Bailey, 1984; Chapman, 1980; Redant, 1987a; Sterk and Redant, 1989).

Redant (1987a,b), investigating reproduction and seasonal behaviour of the *Nephrops* stock in the Botney Gut–Silver Pit area of the central North Sea, described a pattern of availability of *Nephrops* that resembles that of British waters apart from the Farne Deeps. However, his study also revealed relatively large numbers of nonberried females in midwinter landings, indicating that not all sexually mature females spawn every year, this applying especially to the larger animals. Sterk and Redant (1989) further confirmed that some females of different sizes shift to biennial spawning in this area.

Thomas (1964) showed, on the basis of ovary maturities, that 90% of the mature females in Scottish waters spawn annually. However, Bailey (1984) had described a shift from annual to biennial spawning with increasing female size in the Firth of Clyde, west Scotland. His evidence from the proportion of soft females in the catch suggested that at larger female sizes, the summer posthatching moult takes place later, leading to delays in the subsequent spawning and hatching. Finally, a point is reached where resorption occurs for some reason and the females miss out a year of egg-carrying. Although the next spawning of these females is earlier again, this author gives no clear indication of a proceeding biennial spawning pattern.

Therefore, even though spawning is largely annual with an incubation period of some 9 months off W Scotland (Firth of Clyde) and the North Sea (Botney Gut–Silver Pit), there is a tendency, especially among larger or older females, to hatch late and hence miss that year's mating and spawning period. It is, however, uncertain whether these females shift to a biennial spawning regime or to a more or less regular succession of annual and biennial egg-bearing (Bailey, 1984; Redant, 1987a; Sterk and Redant, 1989). In addition, Briggs (1988), examining maturity ogives, suggested that it was possible that a proportion of *Nephrops* in the northwest Irish Sea does not spawn annually.

Sardà (1991) also reported that a substantial proportion of females did not spawn every year in the Catalan Sea, W Mediterranean, which he attributed to a series of random factors and asynchronism in the mating process. However, since the incubation period is very short in Mediterranean waters or 5–7 months (Karlovac, 1953; Mytilineou et al., 1990; Orsi Relini and Relini, 1989; Orsi Relini et al., 1998; Sardà, 1991, 1995), a prevalence of biennial spawning must be considered unlikely although it may for some reason take place asynchronously in certain animals.

In all other areas of *Nephrops* investigations, spawning has been referred to as annual. In Scotland, numerous data exist on annual spawning and an incubation period of about 8–9 months, from mainly September to May (Bailey, 1984; Chapman, 1980; Figueiredo and Thomas, 1967a,b; Thomas, 1964; Thomas and Figueiredo, 1965). An almost identical annual spawning cycle with an incubation period of 8–9 months has also been observed in the Irish Sea (Briggs, 1988; Farmer, 1974b; Hillis, 1972, O´Riordan, 1964).

Moving to more southerly latitudes, the incubation period shortens. In the Bay of Biscay, it lasts for 7.5 months (Fontaine and Warluzel, 1969), with spawning shifting forward to late summer and hatching to late winter

compared to a more typically autumn and spring in the waters around the British Isles (Conan, 1978). Also, off the North Galician coast, Northwest Spain, spawning starts in July–September and incubation lasts for about 7–8 months to March–April (Farina, 1989; Farina et al., 1999).

In the waters off Portugal, spawning is at its peak in August–September and hatching culminates in February–March after an incubation period of only 6–7 months (Figueiredo, 1965; Figueiredo and Barraca, 1963; Figueiredo and Thomas, 1967a,b). However, unlike in other areas, a few large female *Nephrops* have been observed spawning out of season in January–February or just previous to the typical hatching season (Figueiredo, 1965). Thus, a more rapid rate of ovary development with increasing size seen in Portugal differs from what has been noted for some other areas such as the Firth of Clyde (Bailey, 1984).

In the Alboran and Catalan Seas, off the Mediterranean coast of Spain, spawning begins in August and hatching in January–February, incubation lasting for only 5–6 months (Orsi Relini et al., 1998; Sardà, 1991, 1995; Sardà and Caballín, 1977). Similarly, berried females are found in the Ligurian Sea and Tyrrhenian Sea off western Italy from August–November to December–March, that is, an ovigerous period of 4–7 months (Orsi Relini and Relini, 1989; Orsi Relini et al., 1998).

A relatively short incubation period of some 6–7 months has also been described for the High Adriatic (Froglia and Gramitto, 1979; Karlovac, 1953; Orsi Relini et al., 1998), with spawning, however, shifting forward by approximately 1–2 months compared to Portuguese and West Mediterranean waters or to June–July.

Moreover, in the Gulf of Euboikos, West Aegean Sea, spawning seems to be shifted a little forward to July and hatching appears mostly finished within about 6-month incubation period (Orsi Relini et al., 1998).

A schematic summary of the spawning and hatching periods in all the above regions is given in Table 2.8 and the approximate incubation length in the number of days according to latitude in the Atlantic and the Mediterranean is displayed in Figure 2.41. The latitudinal incubation time gradient as estimated from the literature is less obvious in the Mediterranean or in accordance with a more uniform annual temperature regime than in similar or more northerly latitudes of the Atlantic. The minor differences seen are apparently related to lesser depth in the shelf populations of the Adriatic and Aegean (Euboikos) Seas than in the mainly slope habitats of other areas (Orsi Relini et al., 1998) and thus a somewhat greater annual temperature gradient. The positive correlation between latitude and the duration of the

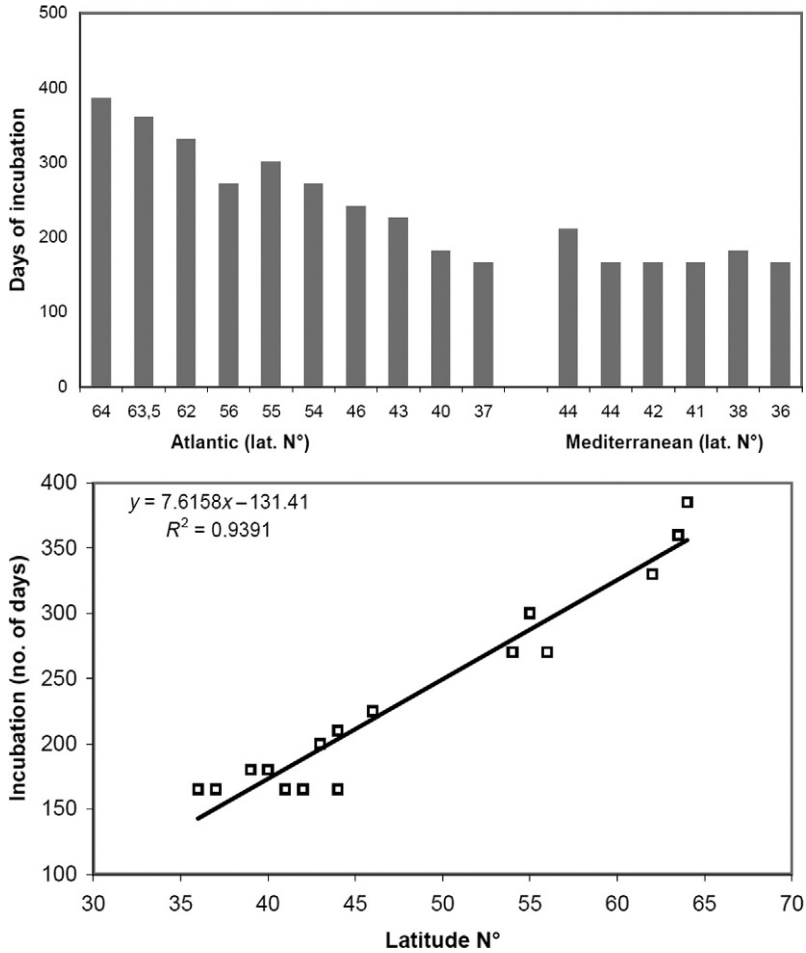


Figure 2.41 Approximate number of incubation days of *Nephrops* eggs according to latitude in the North Atlantic and Mediterranean distribution areas (above). Correlation between latitude and number of incubation days of *Nephrops* eggs in the North Atlantic waters ($p < 0.001$) (below) (see Section 4.3.7 for references).

incubation period is shown in Figure 2.41, relating a highly significant regression ($r^2 = 0.94$; $p < 0.001$). The relationship between latitude and incubation periods estimated from literature by Powell and Eriksson (2013), that is, $y = 6.97x - 120.33$, conforms well to the present result.

The latitudinal shortening of the incubation period and thus speedier larval development is clearly related to increasing regional ambient temperature as previously described by Dunthorn (1967) and Farmer (1974b) in laboratory experiments and described for a number of areas by other authors

(e.g. Chapman, 1980; Figueiredo and Thomas (1967a); Sardà, 1995). Figure 2.42 portrays still further a highly significant correlation between ambient bottom temperature of the areas in question and the duration of the incubation period ($r^2 = 0.99$; $p < 0.001$). Therefore, one can approximate that for every 1 °C rise in ambient temperature, the duration of the incubation period is shortened by some 30 odd days.

As previously described, spawning is a very uniform feature in August–September over the whole range of stocks from Scotland to the western Mediterranean, only occurring a little earlier or June–July in the Adriatic and the Gulf of Euboikos, Aegean Sea. On the other hand, the peak of spawning at Iceland is typically around mid- to late May but a little later or in June–July at the Faeroes, since Icelandic and most probably Faeroese waters are characterized by a regular biennial spawning cycle—the post-hatching females being unable to complete the maturation of ovaries before the onset of winter due to lower sea temperatures. Springtime spawning should, however, favour to a certain degree the early developmental stages of external eggs since those stages are coinciding with the highest sea temperatures of summer to autumn. Certainly, recent observations indicate that

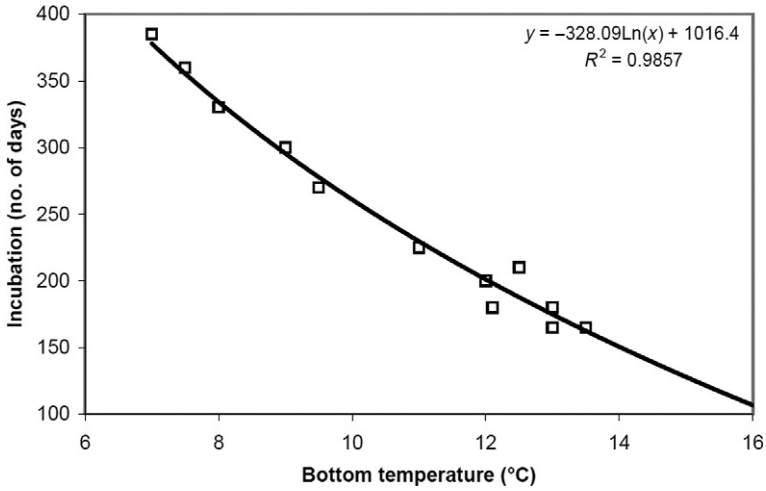


Figure 2.42 Correlation between approximate average bottom temperature and number of incubation days of *Nephrops* eggs ($p < 0.001$) in 15 North Atlantic and Mediterranean areas. *Temperature data from Aliverti et al. (1968), Anonymous (2007), Anonymous (2009), Balopoulos and Papageorgiou (1991), Farmer (1972), Fontaine and Warluzel (1969), Hillis (1972), Karlovac (1953), Mori et al., 1998, Morizur (1980), Orsi Relini and Relini (1989), Papathanossiou et al. (1992), Sardà (1998), and Stefánsson and Jónsdóttir (1974).*

the second maturity egg stage B was occurring to some extent in October–November at Iceland in 2010.

The peak of hatching in Icelandic waters in May–June coincides well with the spring blooming on offshore (120–230 m depth) *Nephrops* grounds, on average at its maximum between late April and early June (Gudmundsson, 1998; Thordardottir, 1986). Similarly, the spring blooming of March–May identified with regions in the Atlantic located between 45°N and 55°N (D'Ortenzio and Ribera d'Alcala, 2009) is equally concurring with that of *Nephrops* hatching around the British Isles south to the Bay of Biscay (March–April to May–June). However, moving southwards to 35°N–45°N, towards west and south Portugal, the spring blooming would likewise be a little earlier in the year (February–April) (D'Ortenzio and Ribera d'Alcala, 2009), again in concordance with *Nephrops* hatching off the Atlantic Iberian coast (see Table 2.8). The relationship of estimated hatch day of year and latitude as well as bottom temperature (Figure 2.43) in the Atlantic *Nephrops* grounds from SW Iceland to S Portugal is shown to be highly significant or $r^2 = 0.97$ ($p < 0.001$) and $r^2 = 0.98$ ($p < 0.001$), respectively. A worthwhile study would be to extend this further by using satellite chlorophyll data for regressions of hatching time and latitude as described for *P. borealis* in the North Atlantic (Koeller et al., 2009).

Moving to the Mediterranean areas, hatching is dominantly in winter months (December/January–February/March) when mean chlorophyll-like pigment concentrations by the SeaWiFS satellite have been shown to be maximal (Barale et al., 2008). However, blooming is an increasingly more intermittent event compared to similar latitudes in the Atlantic (D'Ortenzio and Ribera d'Alcala, 2009), and bottom temperatures are quite stable throughout the year in the deeper or slope *Nephrops* grounds, 12–14 °C (Sardà, 1998). These oligotrophic conditions are possibly one of the factors relating to the normally smaller *Nephrops* stock biomass that is realized in large parts of the Mediterranean compared to the Atlantic from the Bay of Biscay northwards (Anonymous, 1996a; Sardà et al., 1998). Nevertheless, an appropriate exception from this would presumably be the shallower northern Adriatic with its more seasonal temperature range of 10–14(15) °C influenced by relatively cold water masses from the northern part of the area (Karlovac, 1953; Sardà, 1998).

At Iceland, hatching among female *Nephrops*, followed by the post-hatching moult from May to July, is almost invariably accompanied by yellowish to mostly light green ovaries or stages 3–4 on the scale used in this study (from Figueiredo and Barraca, 1963) (Table 2.1). Although various

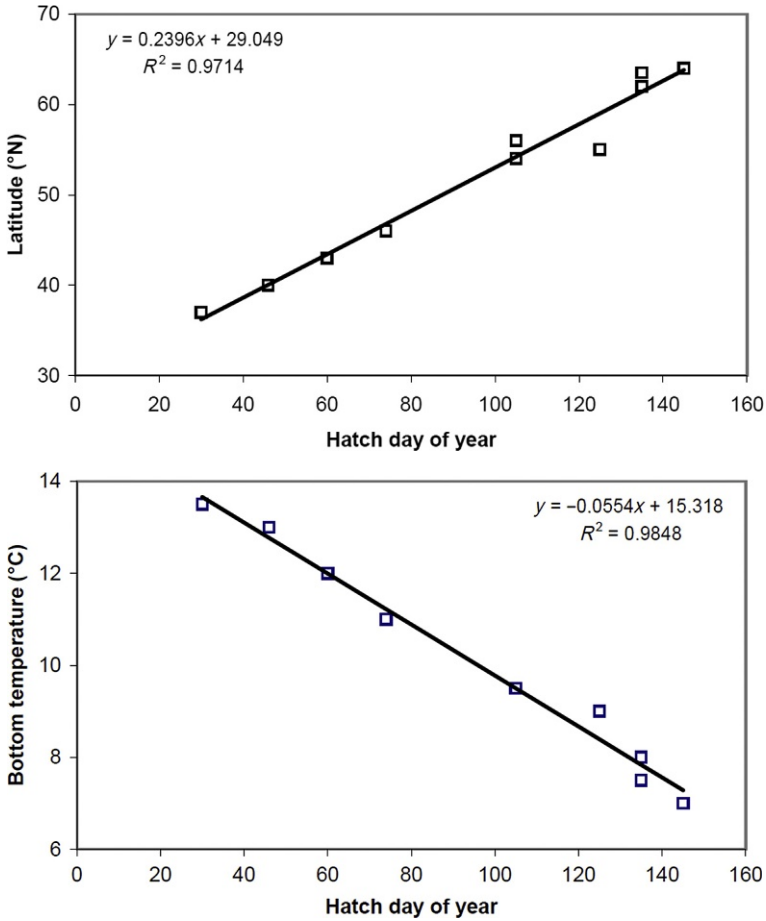


Figure 2.43 Correlations between approximate hatch day of a calendar year and latitude ($p < 0.001$) (above) and average bottom temperature ($p < 0.001$) (below) in 10 North Atlantic *Nephrops* areas ranging from SW Iceland to S Portugal.

investigators have used different maturity scales, hatching appears to be uniformly accompanied by a rather similar ovary maturity stage in hatching females within a great part of the geographical range, that is, most often pale green to green (Bailey, 1984; Farmer, 1974b; Figueiredo, 1965, 1982; Figueiredo and Barraca, 1963; Morizur, 1980, 1981b; Symonds, 1972; Thomas, 1964). Furthermore, hatching is prevalently a spring to early summer (April–June) feature of all stocks ranging from Iceland to the Bay of Biscay, shifting forward in the year, however, in Portuguese and Mediterranean waters where it occurs as early as January–February.

The varying length of the incubation period, where spawning is generally annual, poses a number of questions. Firstly, with the shortening of the incubation period, the interim non-ovigerous season of moulting, mating and ripening of ovaries becomes longer. Thus, the rate of ovary development of non-ovigerous females may decrease southwards from the British Isles to Portugal and the Mediterranean. Secondly, since the mating process can be assumed to differ little geographically, more energy may therefore be diverted to growth in the more southerly latitudes. Indeed, Bailey (1984) had suggested that a high growth rate could retard the maturation of ovaries. This is certainly implied by the large maximum size of females in some Portuguese and Mediterranean waters and the generally larger size at maturity in Portugal and the Mediterranean than, for example, around the British Isles (Figueiredo and Thomas, 1967a,b; Orsi Relini et al., 1998; see also Figure 2.22). This is also in accordance with the results from studies on *H. americanus*, which have shown that although higher sea temperatures normally stimulate both ovarian and moulting development, moulting usually takes precedence over ovary maturation (Waddy and Aiken, 1991).

Relatively later progress of spawning in May at Iceland in the 2000s compared to previous decades may also be linked with higher rate of growth and delayed ovary maturation and relatively earlier hatching, since the 2000s have been endowed with the highest sea temperatures since the early 1960s. Growth taking precedence over ovary maturation is also a likely explanation for an increase in L_{50} in the 2000s and an apparent change in the phase of 50% breeding (BL_{50}) and 50% berried size (OV_{50}), although further studies on these aspects would be valuable.

Thus, low sea temperature plays a major role in delaying ovary maturity in Norway lobster at Iceland, the most northerly stock found in fishable concentrations, although the times of hatching, moulting and thus presumably mating correspond rather well with other northerly or intermediate areas of distribution. Therefore, females at Iceland are unable to spawn like those of the more southerly stocks before the onset of winter. Instead, they mature their ovaries gradually from the posthatching period of summer through the autumn and winter, eventually to spawn at an opportune and relatively short period the following April or mostly May.

The time of hatching, following an incubation period of some 12–13 months, is inherently linked with that of favourable larval phytoplankton food supply in spring/early summer. Although some slight delay in spawning and hatching is apparent in the coldest area at southwest Iceland, it is clear that the reproductive cycle has been predominantly biennial among females at Iceland since investigations began in the mid-1960s, from mainly May to

May–June the following year. In the 2000s, however, which have been typified by a May bottom temperature of around 8 °C in south Icelandic waters, some 0.5–1.0 °C higher than on average in 1970–1995 (Eiríksson, 2009), there appears to have been a slight shift in the reproduction phase, showing a delay in spawning but a little earlier hatching, possibly amounting to some 2–4 weeks shorter incubation time. Yet, there have been no signs of individual females reverting to an annual spawning cycle. Nevertheless, if North Atlantic warming continues at the rate of that seen in Icelandic waters during the last 15 years, future researchers may, however, experience a partial reversion to an annual cycle within only a few decades or less.

4.4. Sex composition

Thomas and Figueiredo (1965) showed that in Scottish waters, the percentage of females in the catch followed the breeding cycle, egg-bearing being less easily caught than nonberried females. Furthermore, they pointed out that the sex ratio of *Nephrops* catches will depend on the size at maturity of females, the difference in annual growth rates between the sexes and the level of total mortality of each sex. Eiríksson (1968a,b) described an increase in the average proportion of females in the catch over the months May to August 1962–1967 in all the main fishing areas at Iceland. This was invariably accompanied by a decrease in CPUE during the same months.

As a result of the biennial spawning regime at Iceland and an incubation period of around 12–13 months, approximately half of the mature female stock is partly berried at all times and therefore less available to sampling by trawl. For that reason alone, the overall female ratios at Iceland are as a rule lower than those of non-ovigerous seasons in *Nephrops* areas of annual spawning. Also, sex ratios, which are influenced by a combined effect of the biennial reproductive cycle and fishing mortality and seasonal variation in availability of males, do not appear to show appreciably different monthly trends by areas or years. For instance, the monthly increase in female sex ratio from May to August (largely the main fishing season over the study period) is mainly related to an increasing proportion of mature females entering the catch following hatching and greater removals of males during the fishing season, although some disappearance of the spring spawners due to burrowing must also be realized.

4.4.1 Annual and seasonal variations in sex ratio

Not unexpectedly, there have been considerable variations in the sex ratio of *Nephrops* catches during the 50-year period from 1961 to 2010. Overall, there have been significant annual and equivalent monthly changes in the

course of time not to mention those on a much finer scale, for example, pertaining to locality, fishing effort, environmental conditions and diurnal variations in availability by sex. An important parameter such as minimum mesh size has been relatively constant over the whole period, being legalized at 80 mm in 1965 with a 2-year period of grace allowed for using up smaller-meshed gear of around 70 mm (Eiríksson, 1970a). Still, other parameters possibly affecting the sex ratio, such as variable amount of *Nephrops* and/or by-catch, can only be dealt with in a more detailed short-term study.

Figure 2.44 demonstrates the historical average monthly female sex ratio in *Nephrops* catches at southwest, south and southeast Iceland from May to August 1961–2010, the prevalent season of the fishery during the whole era. Almost ubiquitously, the female sex ratio increases from May to August, partly due to the entrance of posthatching and primarily soft females into the catch and a greater removal of larger-bodied males due to the fishery and/or dissipation of those owing to lesser availability (see Figure 2.48). In cases of missing monthly data, values have been interpolated from the regression of available monthly data for May–June ($r^2 = 0.18$; $p = 0.01$), June–July ($r^2 = 0.24$; $p < 0.01$) and July–August ($r^2 = 0.27$; $p < 0.01$).

The seasonal behaviour of *Nephrops*, as reflected in the overall mean monthly sex ratio of females in the catch at all study sites during the period 1961–2010, is depicted in Figure 2.45. The highest average ratio of females is seen in August to February, almost invariably surpassing 25–30%, mainly

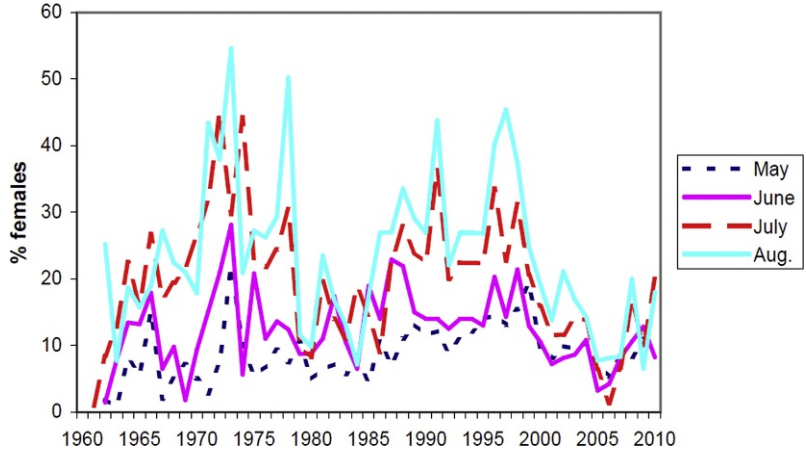


Figure 2.44 Overall monthly mean female sex ratio (%) in *Nephrops* catches from May to August during 1961–2010.

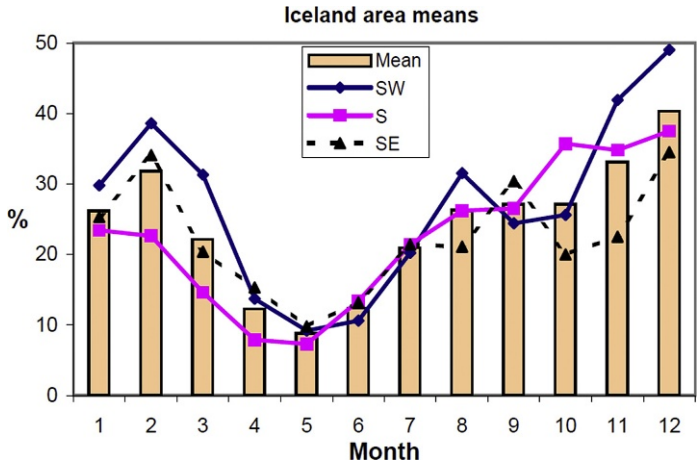


Figure 2.45 Monthly mean female sex ratio (%) in *Nephrops* catches at SW, S and SE Iceland as well as overall during 1961–2010.

composed of non-ovigerous animals maturing increasingly from ovary stages 4 to 6 in preparation for spawning the following May (see Figure 2.24). The behaviour of the berried half of the female population is, on the other hand, identified by its almost total disappearance in winter catches due to the burrowing behaviour. In addition, the ratio of females in winter appears to be further enhanced by an overall decreasing activity of males in autumn, as indicated by a low CPUE of *Nephrops* in winter (shown for 1997–2009 in Figure 2.46), as well as in older winter fisheries and winter research survey data (Eiríksson, 1970a; Sigurðsson, 1965; Skúladóttir, 1965). Thus, the highest female ratios in November–December to January–February are partly realized by the low availability of males.

The female sex ratio drops rapidly in March–April and reaches its minimum of 10% or less in May. This appears to be mainly the result of increasing availability of males by late winter to spring since CPUE (around 95% or more based on males) is normally at its height in April–May, sometimes rising very dramatically at a certain stage during this period (Figure 2.46). Likewise, the early-spring spawners may somewhat accentuate this decrease in sex ratio due to burrowing. The enhanced availability of male *Nephrops* is most probably associated with the spring blooming of phytoplankton production and concurring increase in light attenuation that has been monitored to a certain extent in annual *Nephrops* surveys in May, showing significant negative correlation between CPUE and light penetration as demonstrated in Figure 2.47 ($r^2 = 0.67$; $p < 0.001$; from Eiríksson, 2009).

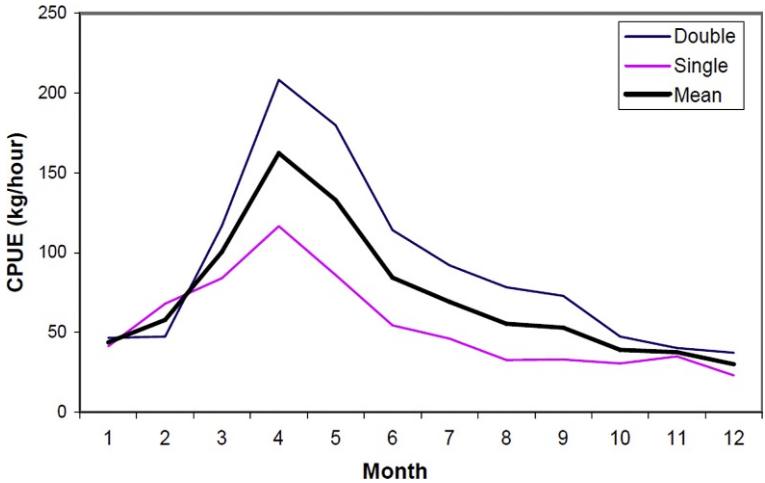


Figure 2.46 Monthly CPUE (kg h^{-1}) of *Nephrops* during the years 1997–2009, indicated for single- and double-rigged vessels.

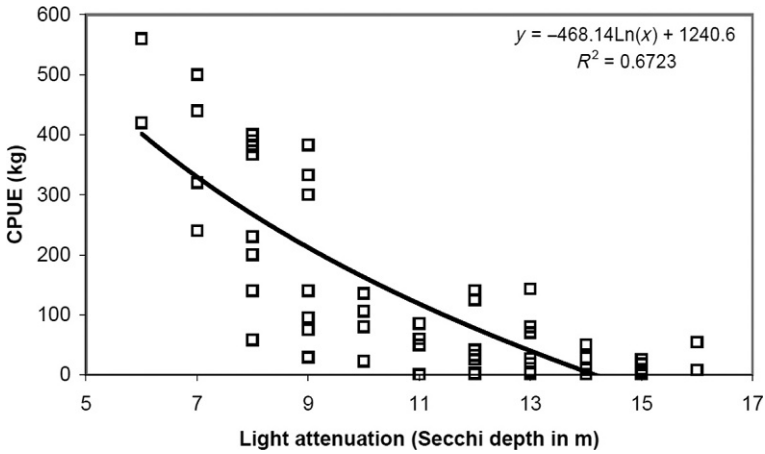


Figure 2.47 Correlation between light attenuation (Secchi depth, m) and catch of *Nephrops* (kg) in 60 individual hauls at Selvogsbanki, S Iceland. *From Eiríksson (2009)*.

Only three times in the period 1961–2010 has the average CPUE not peaked in spring, that is, in 1968, 1979 and 2005, when abnormally low values were recorded for sea temperature and phytoplankton density, especially at southeast Iceland (Anonymous, 2009; Eiríksson, 2009; Malmberg, 1980, 1983; Stefánsson, 1972).

Following the low level in May, the female sex ratio rapidly increases again from less than 10% up to over 25% by August–September or on

average about three times during this 3-month period. The main reason lies in the increasing appearance of posthatchers that have recently hatched their eggs. These females are to a large extent soft-shelled (see Figure 2.24), ready for mating, and thus more accessible to the fishery although mostly discarded. The rise in proportion of females from May to late summer may, however, be partly alleviated by the disappearance of newly berried females from the catch due to their burrowing behaviour. Although one-half of the mature population is ovigerous and largely hiding in the burrows in winter, the female sex ratio stays maximal owing mainly to a relatively high availability of non-ovigerous females, actively maturing their ovaries in preparation for spawning. In addition, the increasing summer and the high winter percentage of females is further enhanced by lesser availability and accumulated removals (F) of males (Figure 2.48).

Eiríksson (1968a,b) suggested that the increase observed in the proportion of females from May to August was due to fishing effort during the period and due to the breeding cycle of females. In a fishing season that has normally extended from the month of May to about August, one would expect fishing mortality to be much higher in males, since they constitute on the average some 90% down to 70% of the numbers caught during these months. Therefore, the partial disappearance of males over the fishing season, as indicated by the ubiquitous decrease in CPUE, certainly favours the sex ratio of females, whether being solely the result of removal due to the

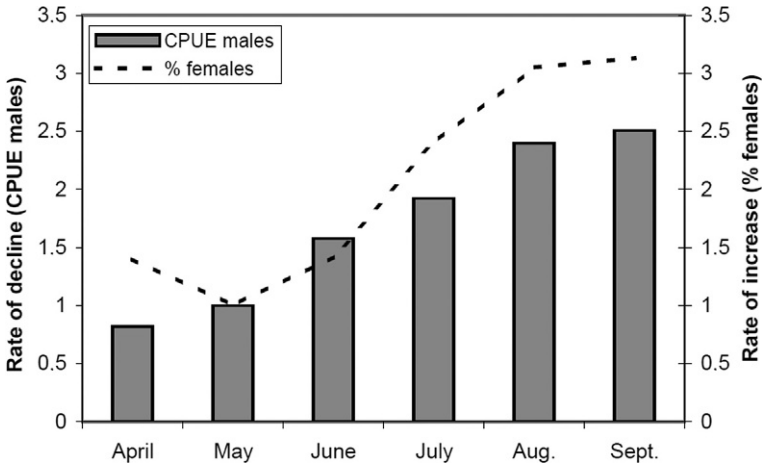


Figure 2.48 Overall rate of depletion of males (CPUE) along with rate of increase in female ratio (% by numbers) during April to September in the *Nephrops* fishery at Iceland (May = 1).

fishery or also because of decreasing availability of males. However, as shown in Figure 2.48, the rise in proportion of females during the period May to September would maximally amount to about 80% of the observed levels, were it alone for the dissipation of males due to mortality or less availability, based on monthly CPUE and sex ratio trends (May = 1). At least the remaining 20% of the increase observed in female sex ratios can, on the other hand, be attributed to the reproductive cycle as the posthatching population passes in increasing numbers into a more catchable state. Nevertheless, the increase in female percentage is somewhat diminished by increased burrowing of the spring spawners.

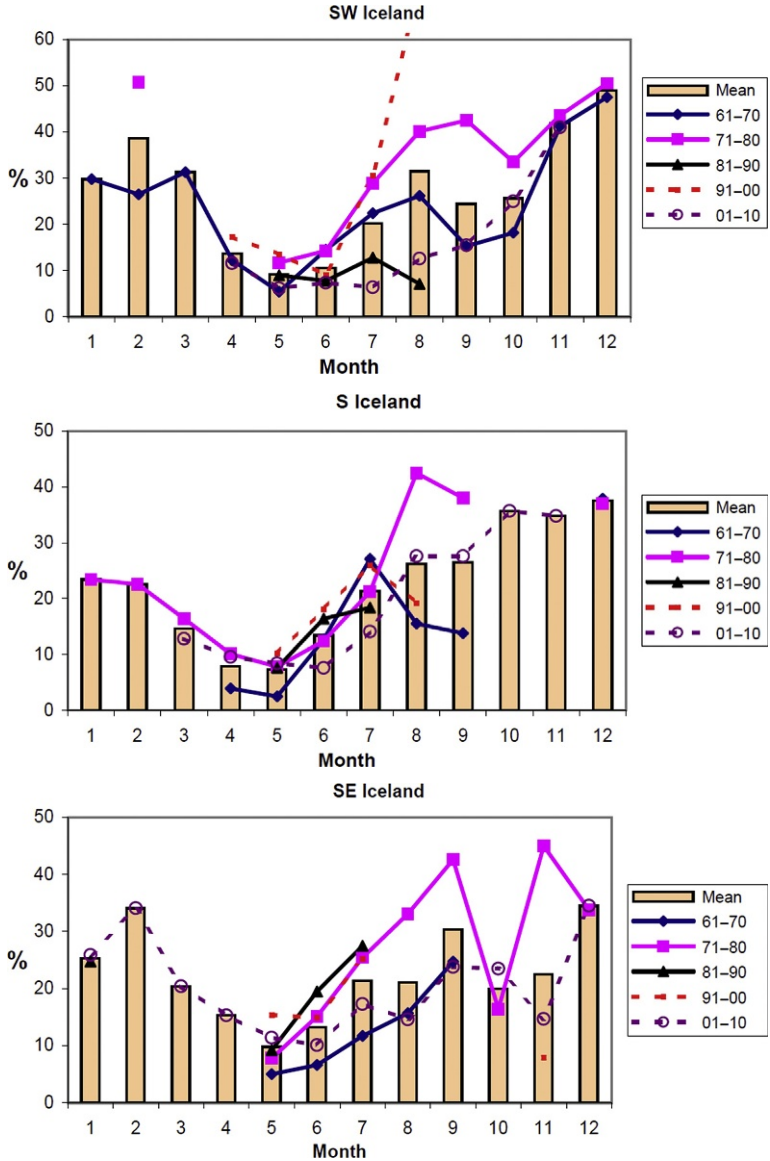
4.4.2 Temporal, spatial and fishery-induced variations in sex ratio

Figure 2.49 demonstrates the temporal and spatial female sex ratio of the catches at southwest, south and southeast Iceland in the five decades 1961–2010 and overall decadal means for the three areas. The average monthly female sex ratio in catches shows identical trends in all areas and periods. However, sex ratio variations appear to follow fishery trends such as mean size of animals, CPUE and fishable stock size assessment of males.

Thus, relatively high May–August female sex ratios shown overall in the 1970s and 1990s are concurring with low mean size of animals and low CPUE and vice versa in the 1960s, 1980s and 2000s, displaying significant regressions for both variables ($r^2 = 0.44$; $p < 0.001$ and $r^2 = 0.28$; $p < 0.001$) (Figures 2.50 and 2.51). In addition, low fishable stock size in the larger part of the 1970s, late 1980s and the 1990s, as described by Eiríksson (1976, 1979, 1982, 1992, 2009) and Anonymous (2010), is reflected in high May–August female sex ratio in those decades, whereas the pristine years of the 1960s, the early 1980s and the 2000s show reversely much lower female ratios (Figure 2.52). The relationship of the two variables, fishable stock size/May % of females, is also highly significant ($r^2 = 0.59$; $p < 0.001$). Thus, good monitoring of female sex ratio in conjunction with CL and CPUE can give valuable information on stock trends and evolution along with analytical stock assessments.

A rise in sea temperatures in the latter half of the 1990s and in the 2000s has been favouring increased distribution and abundance of various commercial species at their northern limit of distribution, such as monkfish (*Lophius piscatorious*), haddock (*Melanogrammus aeglefinus*) and lemon sole (*Microstomus kitt*) (Astthorsson and Palsson, 2006; Astthorsson et al., 2007) and, in the most recent years, Atlantic mackerel (*Scomber scombrus*) (Astthorsson et al., 2012). Therefore, favourable sea conditions in the last

decade may have induced *Nephrops* catch rates and sustained lower sex ratio of females, resembling somewhat the years of the early 1960s. Also, a larger stock and low prevailing fishing intensity in conjunction with a TAC management strategy of $F=0.15$ have benefitted the fishery in the 2000s with increased mean size and value of catches and a lesser proportion of low-value soft-shelled females that are mostly discarded.



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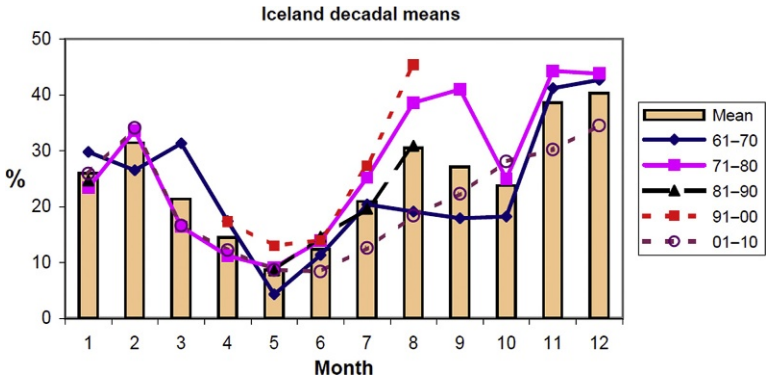


Figure 2.49 Monthly mean female sex ratio (%) in *Nephrops* catches during the five decades 1961–1970 to 2001–2010 at SW, S and SE Iceland and Iceland overall as well as decadal area and overall means. Areas and decades indicated in figures.

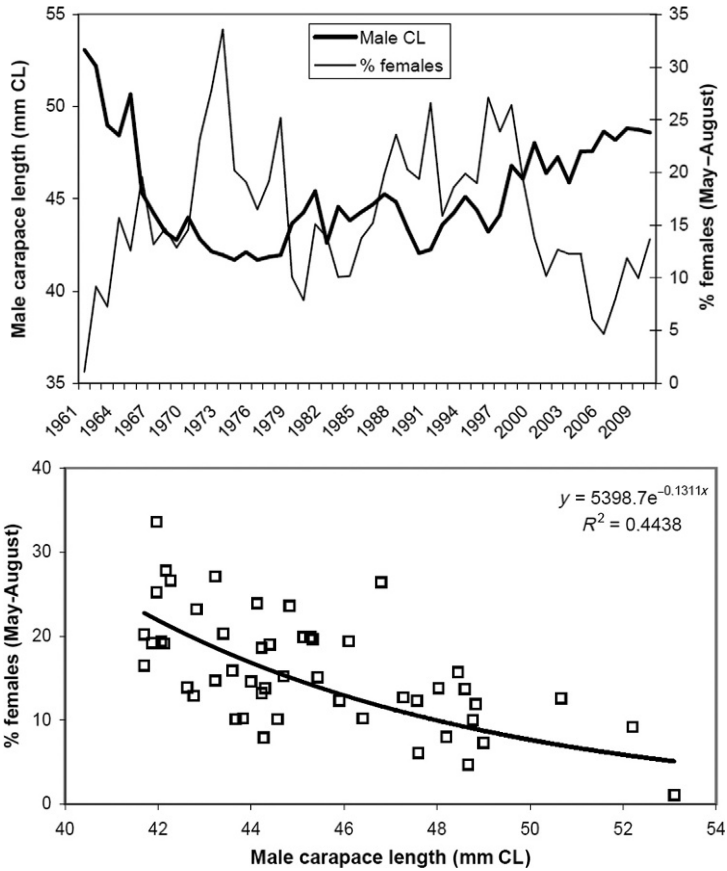


Figure 2.50 Mean annual carapace length (mm CL) of males and mean percentage of females in *Nephrops* catches during May–August 1961–2010 (above) and relationship between the two data sets ($p > 0.001$) (below).

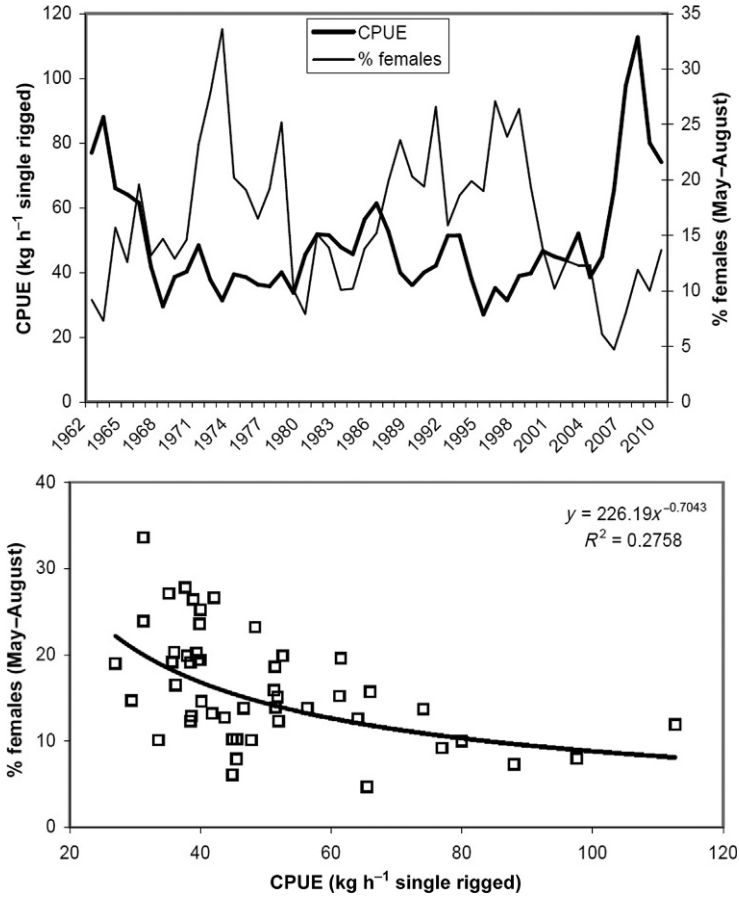


Figure 2.51 Mean annual CPUE (kg h^{-1}) and percentage of females in *Nephrops* catches during May–August 1962–2010 (above) and relationship between the two data sets ($p < 0.001$) (below).

4.4.3 Monthly length distributions by sex and size

An example of monthly length frequency distributions of males and females is displayed by months in Figure 2.53 for the southwestern area in the 1960s. From January to May, the female ratio decreases as a result of increased availability of males and the nature of burrowing by early female spawners in April–May. Thus, female numbers only resemble or surpass those of males in the lowest size categories of largely immature females. Males, however, exceed female numbers as early as sizes 28–30 mm CL due to slower female growth following maturity. In summer (June–August), female ratios increase again as the larger-bodied hatching population enters the catch, although

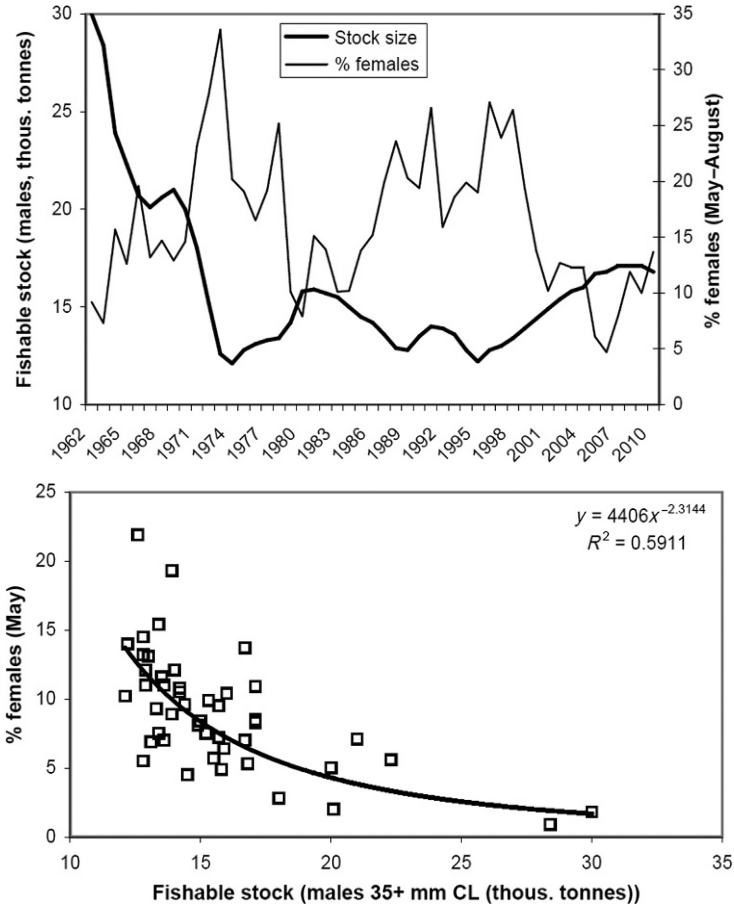
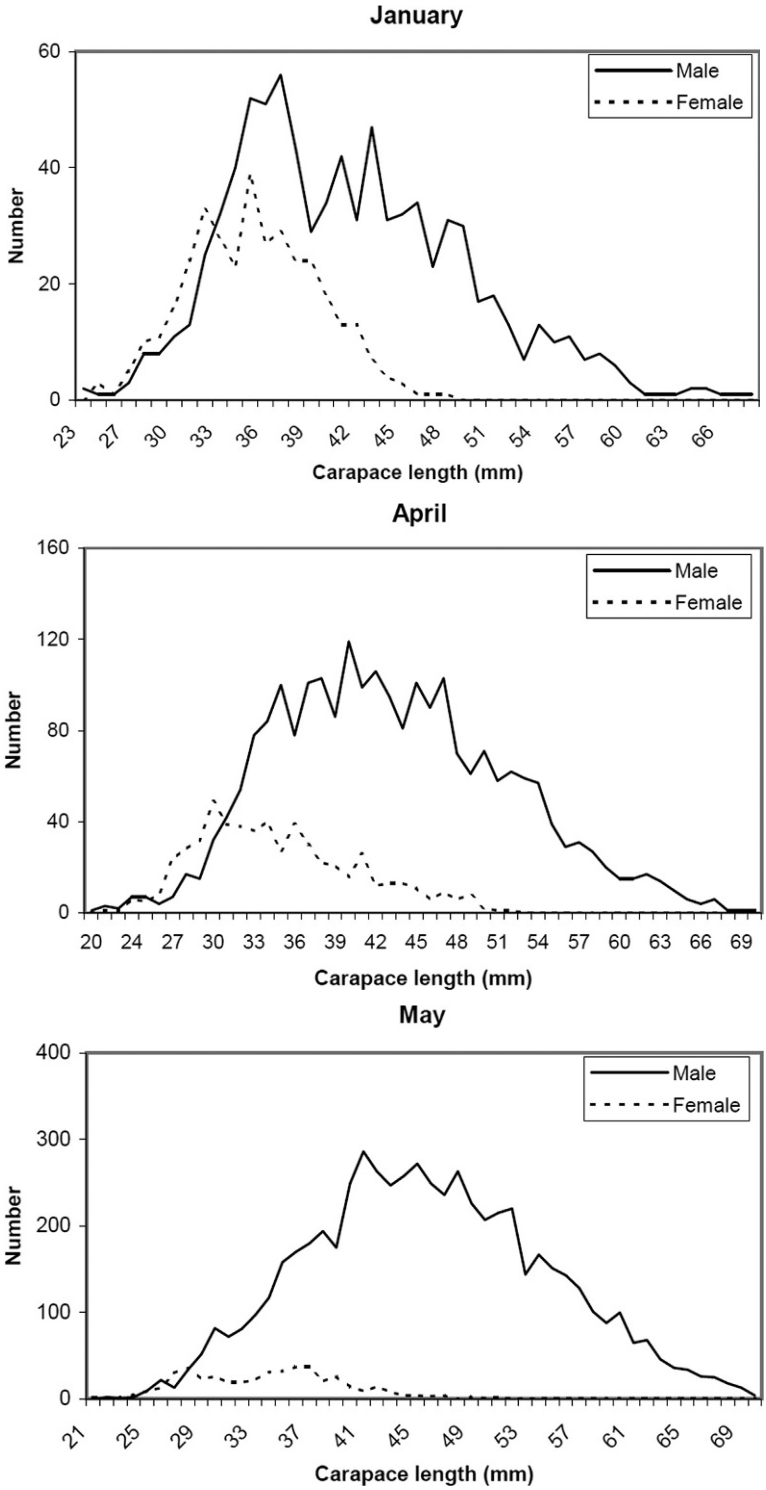


Figure 2.52 Fishable stock size assessment of males (thousand tonnes) and proportion of females (%) in *Nephrops* catches during May–August 1962–2010 (above) and relationship between fishable stock size and % of females in May 1962–2010 ($p < 0.001$) (below).

overtaken by males in numbers at around 35 mm CL in July–August. In autumn and early winter (September–December), the proportion of females continues high, constituting the female population actively maturing their ovaries in preparation for spawning next spring. Berried females, however, present a minor proportion since they are largely buried in their hideouts. Furthermore, female sex ratio is further enhanced by the normally low availability of males in winter as reflected by very high female proportion in November–December.

The decrease in the percentage of females at larger sizes was first noted by Storrow (1912), who attributed it to a lower moulting frequency of females



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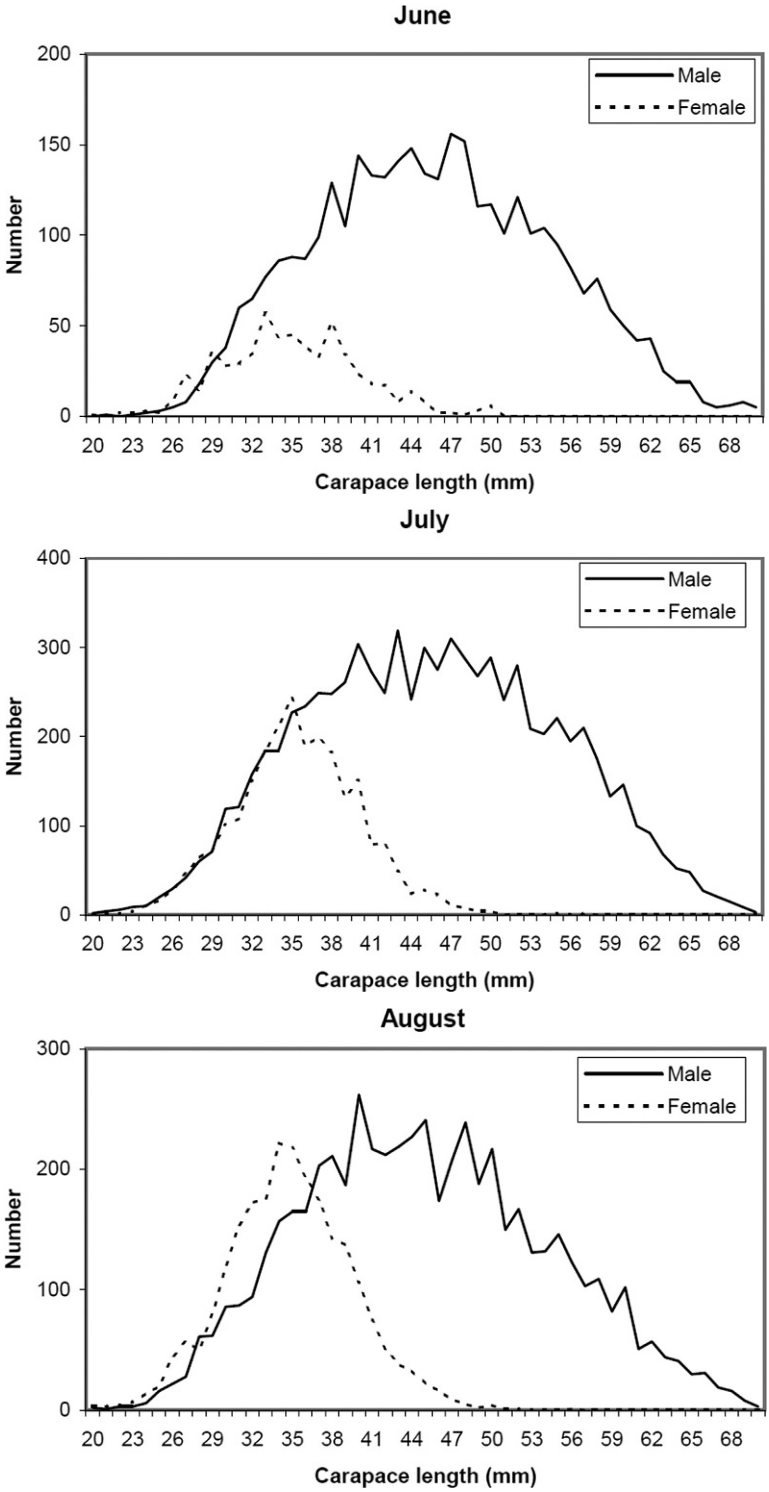

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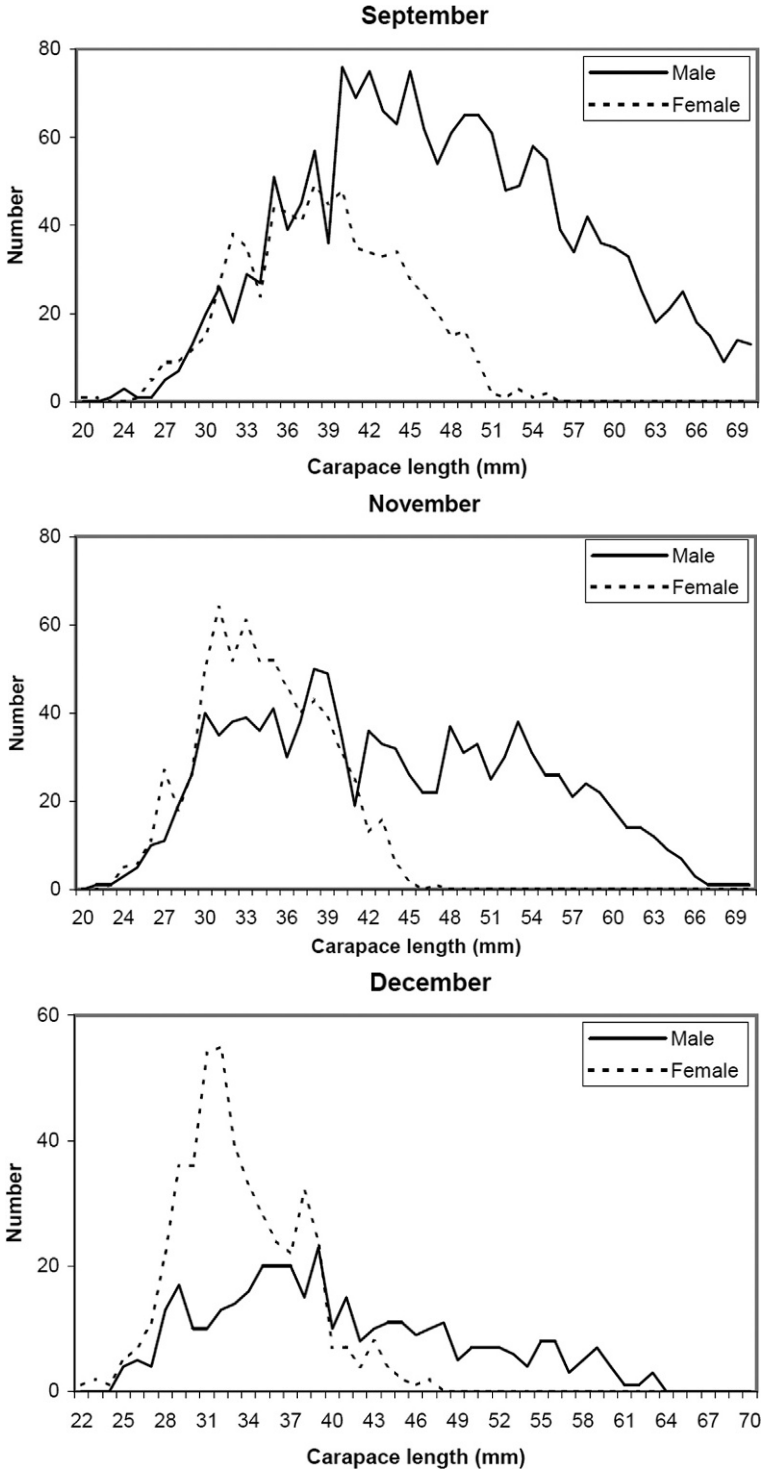


Figure 2.53 Length frequency distributions of males and females by stated months in *Nephrops* catches at SW Iceland in the 1960s.

compared with males and therefore a slower rate of growth. Barnes and Bagenal (1952) considered this a result of different mortality and Karlovac (1953) suggested a combination of mortality and lower moulting frequency. Thomas (1954) related this to less frequent moulting of mature females in addition to lesser percentage increase in size at each moult among mature females in comparison with males. Figueiredo and Thomas (1967a,b) outlined it by stating that in all areas, females are most abundant relative to males in the smallest size groups. Following maturity, however, the female sex ratio decreases markedly with size, being lowest during the incubation period.

In general, the ratio of females in the *Nephrops* stock at Iceland, even in the lower size groups, never exceeds appreciably that of males during the main fishing season May–August. However, monthly or annual sex ratios can vary according to the year-class strength and recruitment and can be influenced by different fishing mortality patterns and dissimilar size/age structure of the male and female stock components. In addition, varying availability of both sexes is of major importance in determining monthly sex ratios.

4.4.4 Discussion

The results of this study on sex ratios of *Nephrops* at Iceland are considered corroborative to previous data concerning biennial spawning (see Section 4.3), since female ratios at Iceland are as a rule relatively lower than observed in other areas of *Nephrops* distribution (Anonymous, 1982) (Table 2.9). It should be noted, however, that these geographical stock variations in sex ratios could also be the product of different levels of sustained fishing effort, as discussed above for Icelandic waters.

A monthly pattern of sex ratio, similar to the one described above for Iceland, is seen only in the Faeroes and can best be described by the biennial reproductive cycle (Nicolajsen and Eiríksson, 1990) (Figure 2.54). Also, the sex ratio experienced in the Farne Deeps off Northeast England (Storrow, 1912, 1913; Symonds, 1972) and to a lesser degree in Skagerrak–Kattegat waters (Anonymous, 1980; Poulsen, 1946) and the central North Sea area of Botney Gut–Silver Pit (Redant, 1987a; Sterk and Redant, 1989) may be due to a partly biennial or nonannual spawning cycle in these areas.

Lower availability of berried females within populations that spawn annually is well known in Scottish and Irish waters, characterized by decreased female ratios during the incubation period in winter (Anonymous, 1984; Briggs, 1981, 1988; Farmer, 1972; Hillis, 1972;

Table 2.9 Monthly proportion of females (%) in *Nephrops* catches, by areas and periods studied

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Period	References
Iceland	26	32	22	12	9	12	21	26	27	27	33	40	1961–2010	This study, overall
SW Iceland					6	11	17	27					1962–1967	Eiríksson (1968a,b)
SE Iceland					4	11	12	14						Eiríksson (1968a,b)
SW Iceland	30	39	31	14	9	11	20	32	24	26	42	49	1961–2010	This study
S Iceland	23	23	15	8	7	13	21	26	27	36	35	38	1961–2010	This study
SE Iceland	25	34	20	15	10	13	21	21	30	20	23	35	1963–2010	This study
Faeroes	60	64	25		22	17	17		26	21	57		1988–89	Nicolajsen and Eiríksson (1990)
Kattegat				19		37	20	41			25	38	1935–1938	Poulsen (1946)
Skagerrak	33	29	43	46		37		29	35	48	44	25		Anonymous (1980)
NE England	21	47	43	43	22	6	8	15	20	42	43	49	1911–1913	Storrow (1912, 1913)
Farne Deeps	34	38	35	57	18	15	13	15	28	36	43	41	1962–1968	Symonds (1972)
Central North Sea				18	16	11	12	27	40	29	23	12	1984–1986	Redant (1987a); Sterk and Redant (1989)
Scotland	26	23	16	41	27	44	37	35	40	35	15	22	1960–1969	Overall data
Clyde			11		18	32	44				20		1960–1963	Thomas and Figueiredo (1965)
South Minch			12			44	39				6		1960–1963	Thomas and Figueiredo (1965)

Continued

Table 2.9 Monthly proportion of females (%) in *Nephrops* catches, by areas and periods studied—cont'd

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Period	References
North Minch			12			51	28	20			12		1960–1963	Thomas and Figueiredo (1965)
Moray Firth			18			57	51	56	46	42			1960–1963	Thomas and Figueiredo (1965)
Firth of Forth					33		31	19	30	22	14	24	1960–1963	Thomas and Figueiredo (1965)
Firth of Forth	26	23	29	41	30	37	29	45	45	40	21	20	1966–1969	Thomas (1969)
Irish Sea	23	23	30	28	32	50	54	49	43	33	31	26	1958–1983	Overall data
W Irish Sea	9	11	8	16	24	45	52	32	35	20	20	18	1958–1962	O'Riordan (1964)
W Irish Sea	2	8	16	24	8	52	60	49		18	21	19	1961	O'Riordan (1965)
W Irish Sea				22	27	23	43						1966	Gibson (1966)
W Irish Sea	25	21	34	28	42	69	59	54	44	37	36	34	1968–1971	Hillis (1972)
W Irish Sea	19	23	35	20	28	33	37	61	42	34	32	16	1969–1972	Farmer (1972)
W Irish Sea	38	31	36	31	44	55	68	43	44	40	36	28	1970–1980	Briggs (1981)
W Irish Sea	31	34	43	39		62	50	49	44		37		1980–1984	Anonymous (1984) (data from Hillis)
W Irish Sea	39	34	37	44	51	61	61	57	51	46	38	40	1983	Briggs (1988)
Bay of Biscay		26	44	54	57	41	51	35	29	36	30	31		Conan (1975, 1978)
NW Spain	27	28	34	48	49	53	50	40	35	38	40	37	1981–1985	Farina (1989) (extrapolated data)

Portugal	25	24	33	32	39	45	49	34	34	36	28	23	1959–1985	Overall data
W coast	14	21	24	10	23	31	36	33	28	26	19	30	1959–1964	Figueiredo (1963); Figueiredo and Thomas (1967a,b)
W coast	15	21	23	12	22	34	35	32	28	24	16	13	1962–1963	Figueiredo and Barraca (1963)
Central coast	41	22	30	42	43	55	67		50	55	59	33	1973–1974	Jorge (1975)
S coast, Algarve	29	30	37	42	44	43	40	34	28	27	25	24	1979–1980	Arrobas (1982)
SW coast		25	43				50	37	30	48	17	22	1981–1985	Figueiredo (1986)
S coast, Algarve	26		42	53	63	61	55	33	39	35	29	15	1981–1985	Figueiredo (1986)
W Mediterranean	37	39	52	65	54	57	52	35	36	30	17	23		Overall data
East coast of Spain	24	42	52	65	54	62	48	33	38	14	17	23		Vives and Suau (1963) (extrapolated data)
Catalan Sea	50	35		65	53	52	56	37	35	45			1974	Sardà and Caballín (1977); Sardà (1995)
Adriatic Sea	41	62	65	56	57	48	43	41	38		39		1948–1949	Karlovac (1953)
Aegean Sea														
Pagasitikos Gulf	14	18	48	57	61	65	52	62	61	50	48	39	2007	Mente et al. (2009) (extrapolated data)

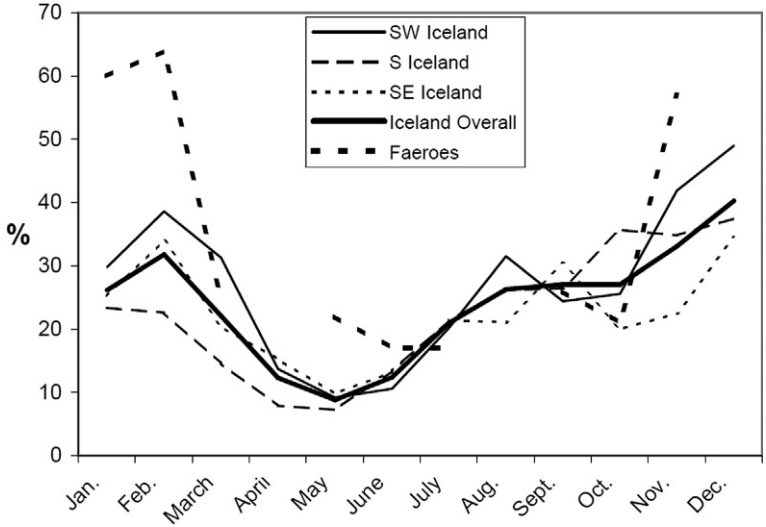
Thomas, 1969; Thomas and Figueiredo, 1965). As seen in Table 2.9, considerably higher female ratios were observed in the Irish Sea in the 1970s–1980s (Anonymous, 1984; Briggs, 1981, 1988) than in the period 1958–1962 (Gibson, 1966; O´Riordan, 1964, 1965), most likely due to increased fishing intensity.

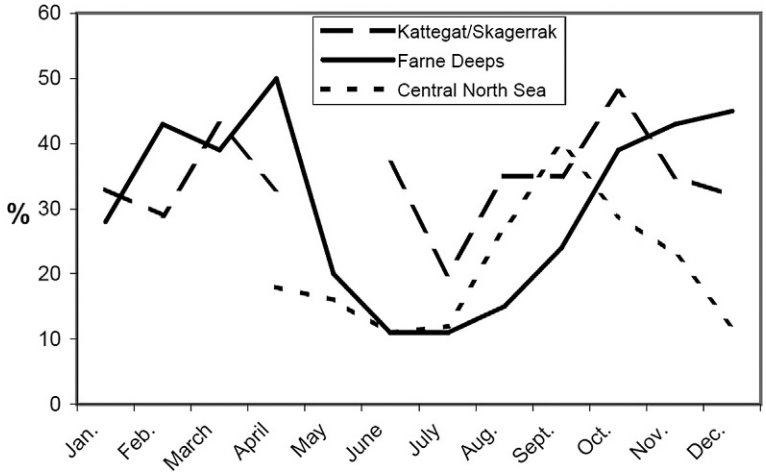
Seasonal variations in sex ratio are also reflected quite well in the main spawning and hatching seasons in the Bay of Biscay, Northwest Spain and west and south Portugal, although sex ratio data are showing some tendency towards earlier spawning in late summer–autumn and earlier hatching in spring (Arrobas, 1982; Conan, 1975, 1978; Farina, 1989; Figueiredo, 1963, 1986; Figueiredo and Barraca, 1963; Figueiredo and Thomas, 1967a,b; Jorge, 1975). The overall female sex ratio in Portugal was much higher in 1973–1974 than in 1959–1964 as reported by Jorge (1975) (see Table 2.9), possibly related to increased fishing mortality, although not mentioned by this author. Moreover, the effect of fishing is also demonstrated in decreasing size of *Nephrops* and a higher ratio of females off south Portugal according to the data from 1960 and 1980 (Arrobas, 1982). In addition, berried females are as a rule more readily caught in Portuguese waters than elsewhere in the N Atlantic, possibly due to the egg-bearing period being less concentrated into a single season than in more northerly areas (Figueiredo, 1965; Figueiredo and Thomas, 1967a,b).

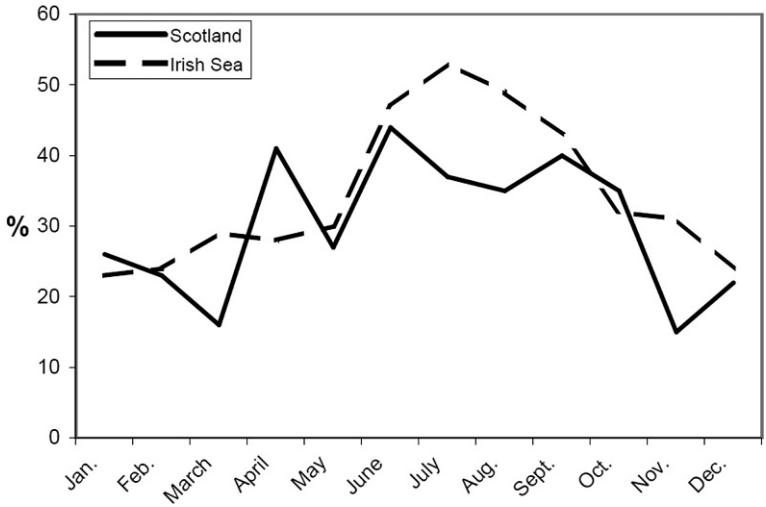
In the West Mediterranean and in Adriatic and Aegean waters, the female sex ratio rises early in the year, possibly in a phase with earlier spring blooming and hatching of *Nephrops* larvae in relatively isothermal conditions. Subsequently, decreasing female ratios in midsummer to autumn indicate relatively earlier spawning than elsewhere in areas of annual spawning (Karlovac, 1953; Sardà, 1995; Sardà and Caballín, 1977; Vives and Suau, 1963). The recent sex ratio data from the Pagasitikos Gulf, western Aegean Sea, depict a clear rise in female ratio from January to March, although continuing relatively high for most of the year (Mente et al., 2009). Therefore, in many cases, lesser concentration into a pronounced ovigerous season could be expected in some most southerly latitudes.

4.5. Fecundity

Some early investigators, including Gauss-Garady (1912), Storrow (1912) and Poulsen (1946), presented ranges of egg numbers carried by *Nephrops* females on the pleopods. The number of eggs was shown to vary from 800 to 5000, but no specific relationships were given between female size







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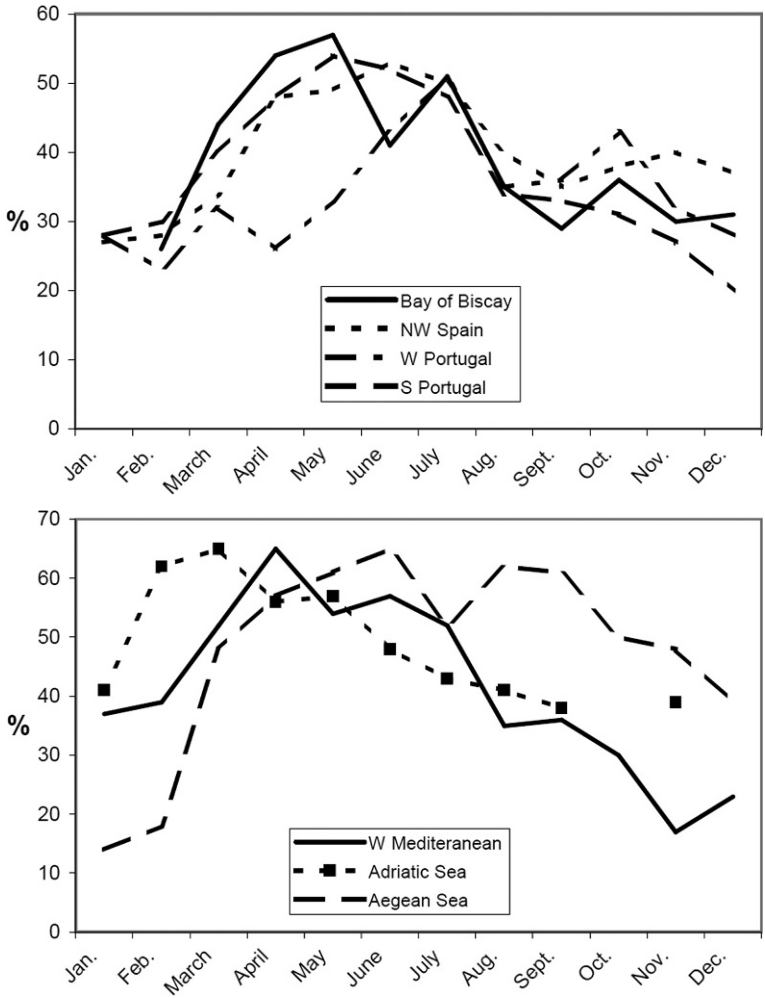

Figure 2.54 Monthly female sex ratio (%) by denoted geographical areas ranging from SW Iceland to the Aegean Sea (for references, see Table 2.9).

and egg number. More recently, a number of authors have studied fecundity and female size relationships at one or more stages of external egg development (Abelló and Sardà, 1982; Allonso-Allende, 1979; Briggs et al., 2002; Chapman and Ballantyne, 1980; Farina et al., 1999; Farmer, 1974b; Froglia and Gramitto, 1979, 1981, 1982; Gramitto and Froglia, 1980; Nichols et al., 1987; Orsi Relini et al., 1998), while others have estimated the fecundity from the number of oocytes of mature ovaries (Fontaine and Warluzel, 1969; Morizur and Rivoalen, 1982; Smith, 1987; Thomas, 1964; Tuck

et al., 2000). Some authors have used both ovaries and one or more ovigerous stages for fecundity estimates (Eiríksson, 1970b; Figueiredo and Nunes, 1965; Figueiredo et al., 1982; Gramitto and Froglia, 1980; McQuaid et al., 2009; Mori et al., 2001; Morizur, 1980; Morizur et al., 1981).

Preliminary results on fecundity of *Nephrops* in Icelandic waters were previously described by Eiríksson (1969, 1970b) and showed that the number of both ovary and external eggs in Icelandic *Nephrops* is directly related to CL. Furthermore, although apparently undamaged recently berried animals had been sampled, the study revealed that the loss of eggs from ovary stage 6 to external egg stage A amounted to approximately 33% in average-sized females of 35 mm CL. In addition, fecundity at southwest Iceland was much lower than previously documented for Scottish and Portuguese waters (Figueiredo and Nunes, 1965; Thomas, 1964).

4.5.1 Oocyte and early egg-bearing fecundity

The number of ripe ovary stage 6 oocytes and developmental stage A eggs in Icelandic *Nephrops* was seen to be proportional to the female CL and expressed by the power function $F = a \times \mathrm{CL}^b$ or by the following equations:

$$F(6) = 0.0407 \times \mathrm{CL}^{2.9483}, \quad r^2 = 0.84 \tag{2.1}$$

$$F(A) = 0.0523 \times \mathrm{CL}^{2.7719}, \quad r^2 = 0.70 \tag{2.2}$$

where $F(6)$ denotes the fecundity of ripe oocytes of ovary stage 6, $F(A)$ the fecundity of abdominal eggs (stage A) and CL the CL in millimetre with a and b as parameters representing, respectively, the intercept and the slope.

Both these curvilinear regressions (Figure 2.55) reveal a highly significant correlation ($p < 0.001$), although slightly less so for the abdominal egg data, possibly owing to a variable loss of eggs at adherence to pleopods at spawning, abrasion during sampling by trawl and/or other reasons. In addition, as indicated in the figure, an exponential regression seemed to fit even marginally better to the fecundity data in case of the ovary oocytes.

Ovary oocyte number (potential fecundity) range from 538 in 25 mm CL females up to 4156 in females of 50 mm CL, whereas newly extruded eggs (realized fecundity) only number from about 392 to an estimated 2678 within the same size range. For an average-sized female of 35 mm CL, the eggs number 1452 and 997 for the ovary and spawn, respectively, a considerably less fecundity than recorded for other areas (Table 2.10 and Figure 2.56).

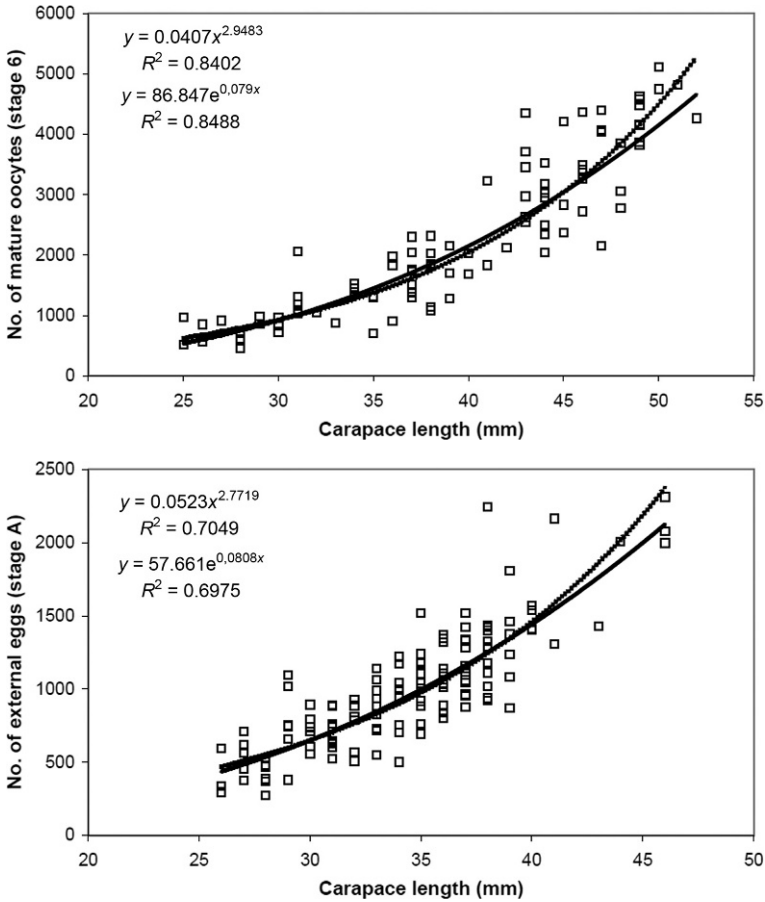

Figure 2.55 Relationships between potential fecundity (mature stage 6 oocytes) (above) and realized fecundity (newly extruded stage A eggs) (below) and carapace length at SW Iceland.

Over the size range 25 to 50 mm CL, the loss of eggs between potential and realized fecundity, terms described by Figueiredo et al. (1982) and Stechey and Somers (1995), was seen to be ranging from 27% to 35%, increasing with size. Thus, with a greater mass of ova, more eggs may fail to adhere at the time of spawning due to technical or biological reasons. One could consider mechanically greater loss of eggs due to abrasion in larger animals during intermittent movements or the fishing operation by trawl. Also, a small number of ripe oocytes remain in the ovaries and are possibly resorbed. In addition, the low fecundity observed in Icelandic waters seems to be accompanied by not only a longer incubation period

Table 2.10 Fecundity of *Nephrops* by areas, methods and authorities

Area/method	Equation									References
	$F = a \times CL^b$ $F = a + b\ CL$		Carapace length (mm)							
Late ovary										
	a	***b***	**25**	**30**	**35**	**40**	**45**	**50**	**30–40**	
North Atlantic										
SW Iceland	0.0407	2.9483	538	922	1452	2153	3046	4156	1509	Eiríksson (1970b) (this study)
Scotland										
Overall (5 areas)	0.526	2.350	1014	1557	2236	3061	4037	5171	2285	Thomas (1964)
Clyde	0.353	2.423	861	1339	1946	2489	3577	4617	1925	Thomas (1964)
Clyde	0.191	2.644	949	1537	2310	3288	4489	5931	2378	Smith (1987)
Clyde (St. 2)	0.1501	2.697	884	1446	2191	3141	4316	5735	2259	Tuck et al. (2000)
Clyde (St. 3)	0.2001	2.697	1179	1928	2921	4188	5754	7645	3012	Tuck et al. (2000)
Sound of Jura	0.201	2.644	999	1620	2431	3450	4724	6241	2500	Smith (1987)
W Irish Sea	0.076	2.930	948	1617	2541	3757	5305	7224	2638	McQuaid et al. (2009)
E Irish Sea	0.0069	3.599	741	1429	2489	4024	6148	8983	2569	McQuaid et al. (2009)
Celtic Sea	0.196	2.576	782	1251	1861	2625	3556	4664	1912	Morizur and Rivoalen (1982)
Bay of Biscay	0.108	2.797	878	1462	2250	3269	4544	6102	2327	Fontaine and Warluzel (1969)

Continued

Table 2.10 Fecundity of *Nephrops* by areas, methods and authorities—cont'd

Area/method	Equation									References
	$F = a \times CL^b$ $F = a + b\ CL$		Carapace length (mm)							
Late ovary										
	a	***b***	**25**	**30**	**35**	**40**	**45**	**50**	**30–40**	
Bay of Biscay	0.133	2.700	791	1294	1963	2815	3868	5141	2024	Morizur (1980); Morizur et al. (1981)
S Portugal	0.04249	3.0557	794	1387	2221	3340	4786	6604	2316	Figueiredo and Nunes (1965)
W Portugal	0.3234	2.5045	1025	1619	2382	3327	4469	5818	2443	Figueiredo et al. (1982)
Mediterranean										
N Tyrrhenian Sea	0.00522	3.5998	562	1077	1875	3032	4665	6817	1995	Mori et al. (2001)
NW Adriatic	0.0575	2.942	745	1275	2006	2971	4202	5728	2084	Froglia and Gramitto (1979); Gramitto and Froglia (1980)
Stage A eggs										
	a	***b***	**25**	**30**	**35**	**40**	**45**	**50**	**30–40**	
North Atlantic										
SW Iceland	0.0523	2.7719	392	650	997	1443	2000	2678	1030	Eiríksson (1970b) (this study)
Scotland										
Moray Firth	−1918.9	108.11	784	1324	1865	2406	2946	3487	1865	Chapman and Ballantyne (1980)
Loch Torridon	−3888.9	148.15		556	1296	2037	2778	3519	1296	Chapman and Ballantyne (1980)

W of Kintyre	−2520.8	129.66	721	1369	2017	2666	3314	3962	2017	Chapman and Ballantyne (1980)
Clyde	−1261.0	81.25	770	1177	1583	1989	2395	2802	1583	Chapman and Ballantyne (1980)
Irish Sea	−1376.42	1 78.204	579	970	1361	1752	2143	2534	1361	Farmer (1974b)
W Irish Sea	0.080	2.86	797	1342	2085	3055	4278	5783	2161	Nichols et al. (1987)
W Irish Sea	0.259	2.566	1001	1598	2373	3343	4523	5927	2438	Briggs et al. (2002)
Irish Sea	0.0311	3.1309	741	1311	2124	3226	4291	6487	2220	McQuaid et al. (2009)
Galicia, NW Spain	1.20	2.11	1069	1570	2174	2881	3694	4613	2208	Allonso-Allende (1979)
Galicia, NW Spain	0.050	2.96	687	1178	1860	2761	3913	5345	1933	Farina et al. (1999)
S Portugal	0.0229	3.0557	428	747	1197	1800	2580	3559	1248	Figueiredo and Nunes (1965)
W Portugal	0.0563	2.8924	622	1054	1647	2423	3406	4620	1708	Figueiredo et al. (1982)
NW Portugal	0.0246	3.125	575	1016	1645	2497	3608	5014	1719	Abelló and Sardà (1982)
Algarve	−3795.5	160.83	225	1029	1834	2638	3442	4247	1834	Orsi Relini et al. (1998)
Mediterranean										
Alboran Sea	−5851.4	204.2		274	1296	2316	3338	4358	1295	Orsi Relini et al. (1998)
Catalan Sea	0.2103	2.488	632	995	1460	2036	2729	3547	1497	Abelló and Sardà (1982)
Catalan Sea	−2852.6	113.46		551	1119	1685	2253	2820	1118	Orsi Relini et al. (1998)

Continued

Table 2.10 Fecundity of *Nephrops* by areas, methods and authorities—cont'd

Stage A eggs

	a	*b*	25	30	35	40	45	50	30–40	
Ligurian Sea	−7519.9	258.07		222	1513	2803	4093	5384	1513	Orsi Relini et al. (1998)
Tyrrhenian Sea	−3311.4	132.27		657	1318	1979	2641	3302	1318	Orsi Relini et al. (1998)
N Tyrrhenian Sea	0.00077	4.0560	360	755	1410	2424	3908	5991	1530	Mori et al. (1998)
Adriatic Sea	0.019	3.14	466	826	1340	2038	2950	4107	1401	Froglia and Gramitto (1979); Gramitto and Froglia (1980)
Adriatic Sea	0.0177	3.1635	468	833	1357	2071	3005	4194	1420	Froglia and Gramitto (1982)
NW Adriatic	−2862.5	120.79	165	761	1365	1969	2573	3177	1365	Orsi Relini et al. (1998)
Aegean Sea										
Gulf of Euboikos	−1752.4	90.117	501	951	1402	1852	2303	2753	1402	Orsi Relini et al. (1998)

Stage D–E eggs

	a	*b*	25	30	35	40	45	50	30–40	
Scotland										
Moray Firth	(−2863	120.8)		640	1060	1490	1910	2340	1063	Chapman and Ballantyne (1980)
Irish Sea	0.0189	3.170	510	910	1483	2265	3290	4594	1553	McQuaid et al. (2009)
Bay of Biscay	0.016	3.194	467	836	1367	2095	3051	4272	1433	Morizur (1980); Morizur et al. (1981)

NW Spain	0.002	3.68	279	546	962	1573	2426	3575	1027	Farina et al. (1999)
S Portugal	0.015076	3.0557	282	492	788	1185	1698	2343	822	Figueiredo and Nunes (1965)
W Portugal	0.0647	2.6215	299	482	722	1025	1396	1839	743	Figueiredo et al. (1982)
Ligurian Sea	0.046	2.69	265	433	655	938	1288	1710	675	Orsi Relini and Relini (1989)
N Tyrrhenian Sea	0.05137	2.6004	222	356	532	753	1023	1345	547	Mori et al. (2001)
Adriatic Sea	0.033	2.81	280	467	720	1048	1459	1962	745	Froglia and Gramitto (1979); Gramitto and Froglia (1980)

but also an increased diameter of the ova compared to available data from more southerly regions with shorter incubation time (see Sections 3.1 and 4.1 and Table 2.1).

4.5.2 Geographical variations and discussion

A clear north to south variation has been described in the duration of the incubation period of *Nephrops* larvae, linked with sea temperature (see Figures 2.41 and 2.42). Likewise, as in various female biological parameters, fecundity by female size would be expected to differ somewhat by areas. Thus, a latitudinal gradient of increase is slightly indicated for data sets of newly extruded eggs (realized fecundity) in 30–40 mm females from areas

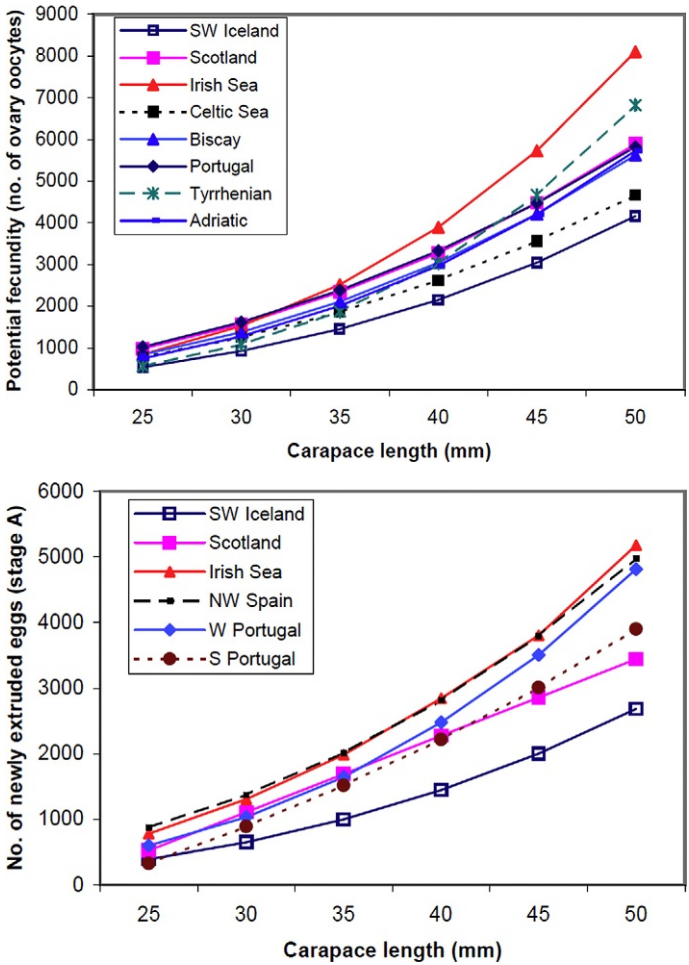

Figure 2.56—Cont'd

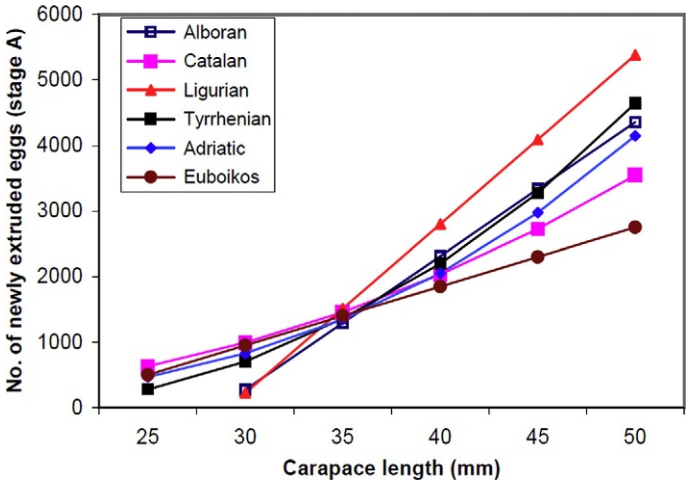

Figure 2.56 Relationships between potential fecundity and carapace length in denoted geographical areas ranging from SW Iceland to the Adriatic Sea (top) and realized fecundity (newly extruded eggs) and carapace length in denoted N Atlantic waters ranging from SW Iceland to S Portugal (middle) and Mediterranean areas ranging from the Alboran Sea to the Gulf of Euboikos, Aegean Sea (bottom) (for references, see Table 2.10).

ranging from Iceland to Galicia, NW Spain and a decrease from the Irish Sea and NW Spain to S Portugal (Figure 2.57). Although such a gradient is not wholly apparent for the overall distribution from Iceland to the Aegean Sea, the fecundity seems considerably lower in south Portuguese and Mediterranean waters than in the North Atlantic apart from Iceland, indicating some latitudinal tendency (Figure 2.57; $r^2 = 0.34$; $p = 0.05$). Additionally, considerable variation on a much smaller scale has been observed by Tuck et al. (2000) in the Firth of Clyde. Moreover, a decrease for ready-to-hatch stage D(E) eggs (effective or actual fecundity) is noted from the Irish Sea south to Portugal and the Mediterranean Ligurian and Tyrrhenian waters (Figure 2.58).

It should be mentioned that some variations between studies tend to be methodological, for example, based on regression equations used (curvilinear/linear) or possibly time-elapsed between spawning and sampling of animals and variable individual egg loss or failure to adhere to the pleopods (Smith, 1987). Also, according to Chapman and Ballantyne (1980), trawling may cause 11–22% loss of eggs compared to creel-caught animals, although Tuck et al. (2000) pointed out that such a comparison had to be repeated at the same geographical location. That may also apply to the same season since

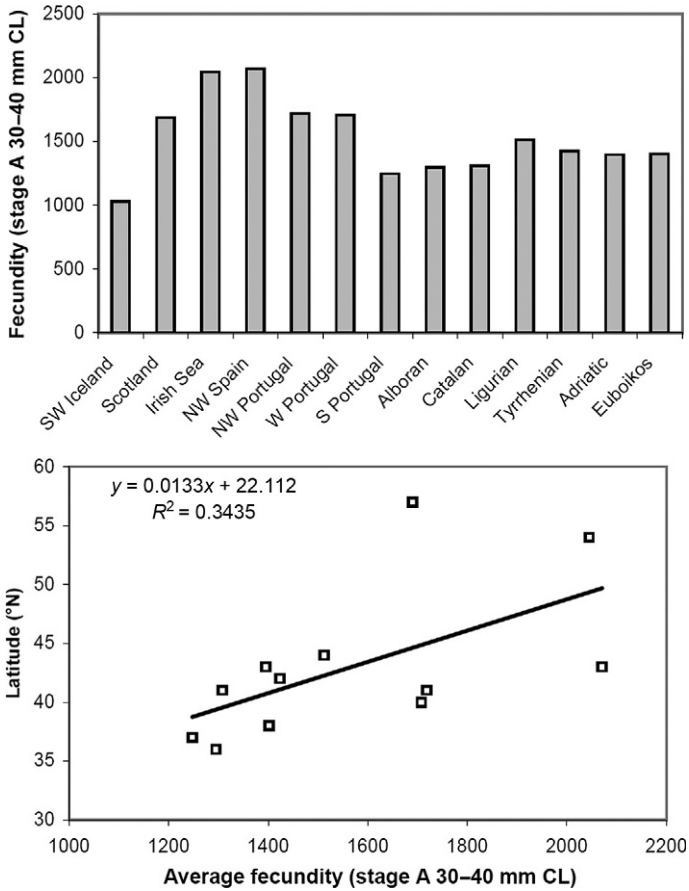

Figure 2.57 Realized fecundity (30–40 mm CL) in various geographical areas ranging from SW Iceland to the Gulf of Euboikos (above) and relationship between realized fecundity (30–40 mm CL) and latitude (N°) in various N Atlantic and Mediterranean waters apart from Iceland ($p = 0.05$) (below) (for references, see Table 2.10).

annual variations in fecundity have been described in the Irish Sea and between the western and eastern stocks of the area (McQuaid et al., 2009).

At Iceland, the northwestern limit of *Nephrops* distribution in Europe, the fecundity is clearly much lower than elsewhere, amounting to around 60–80% of the average for other study areas as regards the number of ovary oocytes and 45–90% for newly extruded eggs. The anomaly observed in fecundity at Iceland is seemingly associated with the long incubation period of eggs in waters of relatively low sea temperatures. Moreover, a biennial reproductive cycle, incorporating an incubation period of some 12–13

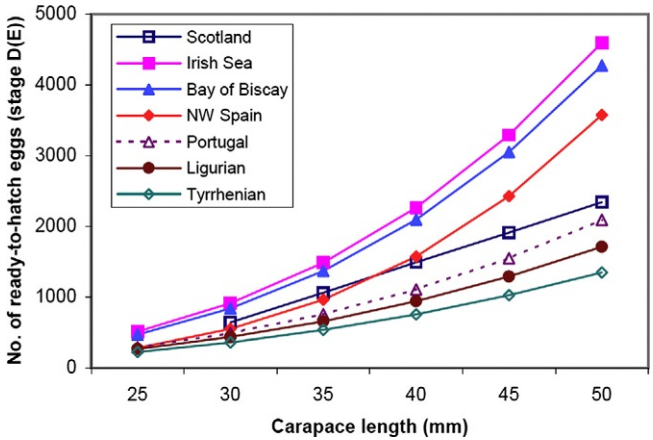

Figure 2.58 Effective fecundity (ready-to-hatch eggs) in denoted geographical areas ranging from Scotland to the Tyrrhenian Sea, west of Italy (for references, see Table 2.10).

months, produces fewer but relatively larger eggs. Loss in number of newly extruded eggs compared to ovary oocytes that can be accounted for by mechanical reasons such as the fishing operation should apply to any population, depending on the sampling methods, fishing gear, duration of trawling, total catch composition and possibly weather. However, authors dealing with trawl data are most likely calculating some underestimates of fecundity (Chapman and Ballantyne, 1980). Apparently, this anomaly is not a major issue when studying geographical variations, although it has to be corrected for when fecundity estimates are used in stock recruitment and biomass models (Nichols and Thompson, 1988; Nichols et al., 1987; Tuck et al., 1997).

Physiological reasons for the loss of eggs, such as the failure of eggs to be fertilized or adhered to the pleopods at spawning or simply the failure to be extruded from the ovary, appear to vary somewhat between areas and size of animals. That could depend on the variable rate of resorption before spawning (Bailey, 1984; Figueiredo, 1982) or simply relatively less adherence of larger egg masses or increased abrasion in larger animals when caught by trawl as indicated above for the Icelandic data.

Figueiredo et al. (1982) and Stechey and Somers (1995) described the terms for oocyte, newly extruded and ready-to-hatch egg numbers, respectively, as potential, realized and effective (or actual) fecundity. Some authors have described this progressive loss of eggs during the spawning, incubation and hatching development. Most comprehensive studies of different stages of

fecundity progression include those of Figueiredo and Nunes (1965) and Figueiredo et al. (1982) in Portuguese waters, Gramitto and Froglia (1980) in the Adriatic Sea, Mori et al. (1998) in the Tyrrhenian Sea and McQuaid et al. (2009) in the Irish Sea. Others describe the loss of eggs from the potential or realized to the effective fecundity stage including Chapman and Ballantyne (1980) and Smith (1987) in Scottish waters, Morizur (1979b, 1981a) and Morizur et al. (1981) in the Bay of Biscay, and Farina et al. (1999) in Galicia, NW Spain. As indicated in Figure 2.58, the progressive loss of eggs during incubation seems to be in the range of 20–45% in those more northerly Atlantic waters. However, in more southerly areas, such as Portuguese, Ligurian, Tyrrhenian and Adriatic waters, the loss of eggs is apparently in the range of 45–70% (Figueiredo and Nunes, 1965; Figueiredo et al., 1982; Gramitto and Froglia, 1980; Mori et al., 1998; Orsi Relini and Relini, 1989; Orsi Relini et al., 1998). The reasons for the loss of eggs from spawning to hatching may include predation (Morizur, 1981a) or abrasion due to tail beats as described by Newland and Chapman (1985, 1989). Moreover, higher rates of loss in more southerly regions could be ascribed to more activity and movement in search of food and therefore possibly also more predation of eggs. Potential or realized fecundity, which may be similar for individual females over the geographical distribution, may therefore end up with less effective fecundity in more southerly areas as shown in Figure 2.59. This occurs in spite of shorter incubation period and may be one reason for an apparently higher fishery potential of Scottish, Irish Sea and Bay of Biscay stocks than those of Portuguese and most Mediterranean waters.

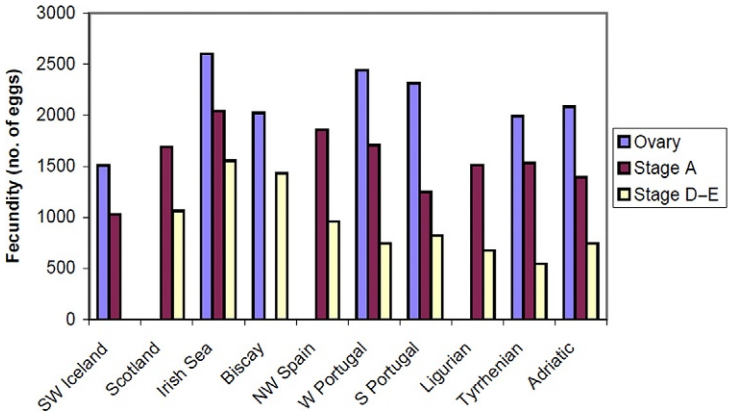

Figure 2.59 Variability in reported potential, realized and effective fecundity in various *Nephrops* areas ranging from Iceland to the Adriatic Sea (for references, see Table 2.10).

The Icelandic area, having by far the lowest potential fecundity, also has the longest recorded incubation period of 12–13 months, as discussed previously. Females carrying newly extruded eggs that are readily caught in May–June, at or just after the peak of spawning, largely disappear from the catch from about August and are only caught again in appreciable numbers when they moult after hatching, that is, peaking in June to July the following year. Females with abdominal eggs in the later developmental stages (D–E) are only caught in small quantities in Icelandic waters and those in the middle stages (B–C) have only been recorded on rare occasions in winter. Therefore, this prolonged inactivity when berried could minimize the loss of eggs during the long incubation period and in turn lead to a comparatively high effective fecundity at Iceland in comparison with the initially low potential number of progeny.

5. SUMMARY AND CONCLUSIONS

The chapter contains studies on 1275 thousand individual *Nephrops* from the Marine Research Institute's (MRI) Reykjavík database, including 185,000 females. However, data containing biological parameters that have been collected for up to 50 years (1960–2010), or almost over the whole historical era of the Icelandic *Nephrops* fishery, are prone to be somewhat disaggregated at times. Therefore, in many cases, data have been dealt with on decadal terms and for areas denoted as SW, S and SE Iceland, regarding three fishery statistical rectangles each.

Studies on ovary oocyte and abdominal egg maturity stages indicate a relatively larger egg diameter in Icelandic waters than at more southerly latitudes. However, there are strong indications that a geographical comparison of ovary oocyte and external egg diameter has to be based on similar sizes of females since a significant positive relationship was found between the diameter of newly extruded eggs and female CL at Iceland ($p < 0.001$).

All three scenarios based on the state of ovary maturity and presence of external eggs that were used for estimating female size of maturity indicate that both temporal and spatial variations are relatively minimal. At the height of the spawning season in May, the conventional L_{50} (primiparous females included) or average SOM calculated by a least-squares sigmoid logistic curve was seen to range from 24.9 mm CL at SE Iceland during the 1980s up to 28.1 mm CL at SW Iceland in the 2000s. Thus, the overall area and decadal range of L_{50} amounted to 24.9–28.1 mm (SD = 0.89).

Since first-time maturing females will not, however, spawn until springtime the year after, it was decided to include calculations of the real-time 50% breeding stock ogives (denoted BL_{50}) and 50% ovigerous stock ogives (OV_{50}). This resulted in the BL_{50} and OV_{50} ogives elevating some 3.1 and 5.1 mm, respectively, to the right due to the omission of primiparous females and growth for a whole year between first maturity and spawning. Therefore, the overall decadal and spatial variations in BL_{50} were seen to have a maximum range of 27.1–32.4 mm CL (SD = 1.67), respectively, in the 2000s and 1980s (southeast) and overall OV_{50} estimations ranging from 28.0 to 34.4 mm CL (SD = 1.77), respectively, in the 1970s and 2000s (south). Unusually large size at L_{50} in the southwestern and southern area in the 2000s is considered firstly the result of high growth rate of immature females taking some precedence over ovary maturation followed by slower growth of primiparous females (L_{50} to BL_{50}). In addition, the following anomalously large size difference between BL_{50} and OV_{50} is the result of delayed spawning of smaller and largely first-time spawners (BL_{50} to OV_{50}). An increased first maturity size (L_{50}) in an age-related maturity scenario followed by a delay in first extrusion of eggs (OV_{50}) in the 2000s may therefore be a direct effect of the warmer sea temperatures experienced in Icelandic waters during the late 1990s and the 2000s, bringing on enhanced growth rate up to first maturity.

Good recruitment with large numbers of small immature females, impinging on growth rate and age-related maturity, appears to play a role in relatively low values observed in L_{50}, for example, in the 1970s and 1980s and, vice versa, high values seen in the 2000s, apart from SA Iceland where recruitment rates were higher. Thus, significant positive correlations are observed between L_{50} and CL of both males and females ($p < 0.02$ and $p = 0.10$), in addition to OV_{50} correlating with female and male CL ($p > 0.05$). Lastly, significant relationship is seen between OV_{50} and average monthly May–July % of females in *Nephrops* catch samples ($p < 0.01$).

A relatively easy method for approximating minimum size of maturity is that of studying minimum size of berried females. Thus, annual time series for this parameter is presented by location for the period 1964–2010. Annual minimum ovigerous size relates positively and highly significantly to average annual CL of both males and females ($p < 0.001$). However, this is least so at SA Iceland ($p = 0.001$) where more regular recruitment and larger year classes seem to have influenced density-dependent growth rate and size of first maturity. Therefore, not wholly unexpectedly, decadal average minimum ovigerous size by areas correlates with the average percentage of females

and average OV_{50}, the regressions being at the $p > 0.001$ and $p = 0.01$ levels of significance. Although the size of maturity estimations seem to indicate relatively small variations in both space and time, more detailed and localized studies may reveal further differences, for example, according to depth, temperature and growth rate.

The fifth and final scenario in the study of size at maturity of female *Nephrops* in Icelandic waters relates to relative growth of the carapace (CL) and maximum width of the second abdominal segment (AW). The relationship between AW and CL showed a high level of allometry in juvenile female *Nephrops* with a reduction of the allometry level and inflection points at 23.90 mm CL when using log-transformed CL and log-transformed AW and 25.35 mm CL, when using untransformed values of CL and log-transformed values of AW, thus corresponding reasonably well with L_{50} values described by ovary maturity analyses.

The fact that the size of maturity estimates in Iceland (L_{50}, OV_{50} and minimum annual ovigerous size) relates positively to both female and male CL and OV_{50} relating to % females in the catch strongly indicates the effect of fishing intensity and/or recruitment on these maturity assessments. Therefore, one is likely to compute a lower maturity estimate with increasing ratio of smaller animals and % females in the catch, be it due to periods of higher fishing effort and/or stronger recruiting year class and slower growth. Although higher fishing mortality (F) may lead to lowering of L_{50} and in some cases improved recruitment, relatively stringent limitations of F values in Iceland are still likely to increase the value per recruit and overall value of the fishery due to the much higher-priced larger *Nephrops*.

A latitudinal gradient in the size of maturity within the geographical range of *Nephrops* distribution is by no means evident. However, L_{50} and minimum berried size are, as a rule, lowest in areas of medium latitudes between 47°N and 57°N, that is, around the British Isles and in the Bay of Biscay, areas of the largest *Nephrops* fisheries and overall highest recruitment rates. On the other hand, the highest reported values for maturity size were found in the slope populations of the Mediterranean that support relatively smaller fisheries.

Within the Atlantic geographical range of *Nephrops* distribution from Iceland to Portugal, the author also found a positive correlation between female L_{50} and maximum reported CL of both males and females ($p < 0.001$ and $p < 0.01$).

The reproductive cycle of female *Nephrops* at Iceland is preponderantly biennial. One-half of the mature population, which hatches their larvae in

spring and first-maturing (primiparous) individuals, actively matures their ovaries (stage 3–4) from the moulting and mating period in summer to the final maturity stage 6 in late winter to spring next year with extrusion and fertilization of stage A eggs occurring from April to mainly May. The ovigerous (stage A) population in spring disappears in increasing numbers due to the burrowing behaviour from May to autumn. Although data are rather limited from winter months, it appears that egg stages B and even some C start appearing in October–November and the final prehatching stages D–E eventually occurring in April–May when hatching initiates, followed by moulting and mating. Therefore, a concurring peak of spawning and hatching takes place in spring each year, without any relevant deviations, and thus a reproductive cycle of 2 years.

Spatial and temporal variations appear rather minimal with 50% spawning, on average, some 10 days earlier at SE Iceland than in the southwest. The same applies to a little later hatching and moulting at SW Iceland. However, some anomalous results were observed in the 2000s when spawning appears to have occurred a little later in May and hatching followed by moulting relatively earlier. This apparent curtailment of the incubation period and development of larvae coincides with increasing ambient sea temperatures since the late 1990s. Yet, a much greater rise in temperature is needed for a possible future development of annual spawning and hatching cycle of some 8–9 months (September–May), similar to that reported, for example, around the British Isles.

Apart from the overall trend towards later spawning and earlier hatching in the 2000s, the annual variations since the early 1970s have been considerable, with average proportion of ovary stage 6 being 23.2–33.2% (SD = 13.5–16.3) and egg stage A 16.7–19.2% (SD = 7.5–9.4), by areas in May. Comparable variations have been observed within the hatching population in numbers of prehatching egg stage D–E females and ovary stage 3–4 and soft-shelled moulting animals. Such fluctuations may partly be related to the main sampling effort within the 2- to 3-week annual *Nephrops* survey in May. Moreover, the peak activity of spawning and hatching appears to be spaced within a relatively short period and the progression of both spawning and hatching are proportional values of total number of females sampled. Still, the high percentage of ovary stage 6 and low ratio of egg stage A females in the 2000s as well as the low numbers of prehatching egg stage D–E females and a high ratio of posthatching moulting animals (ovary stages 3–4) seem sufficient for stating that a change has occurred in the progression of these important biological activities. Also, the correlations

of ovary stage 6 and ovigerous stage A female ratio and ovary stage 4 and percentage of soft-shelled female ratio are good indicators of the progress of spawning and hatching ($p < 0.001$ and $p = 0.01$).

Overall, medium-sized females are apparently the earliest spawners with smallest animals lagging somewhat behind, particularly when there is a strong recruitment of primiparous females. In addition, the mean size of females increases during May to July when mature posthatchers enter into the catch.

Irrefutably, a biennial reproduction regime prevents growth for some 12 successive months of egg incubation every other year. Thus, biennial moulting cycle retards female growth versus that of males to a higher degree than in areas of annual spawning and hatching. As a consequence, the maximum female-to-male size ratio averages only 0.73 to 1.00 in Iceland versus that of some 0.80–0.85 to 1.00 in various reported studies from both Atlantic and Mediterranean areas. Thus, the slopes of the regression between maximum male and female CL in all the 17 statistical *Nephrops* fishery rectangles at Iceland are significantly different to those of more southerly Atlantic and Mediterranean waters ($p < 0.001$).

A geographical overview of main spawning and hatching periods in different North Atlantic and Mediterranean waters reveals clearly a north to south latitudinal gradient involving shortening of the incubation period of larvae with increasing temperature ($p < 0.001$). An increase in ambient temperature of 1 °C could apparently pave the way for a 30-day shortening of the incubation time. Although the latitudinal gradient is much clearer for the Atlantic than Mediterranean waters, the overall correlation is significant ($p < 0.001$). In addition, hatching time of year, apparently synchronized with spring blooming, clearly moves forward in the year with decreasing latitude and increasing sea temperature ($p < 0.001$).

Seasonal variations in sex ratio have been widely reported in areas of mostly annual spawning with lowest ratios of females being observed during the ovigerous season when females are largely in their burrows.

The biennial spawning regime at Iceland, however, involves that approximately half of the mature female population is partly berried at all times and therefore less available to sampling by trawl. Thus, overall female sex ratios at Iceland are as a rule lower than in non-ovigerous seasons in *Nephrops* areas of annual spawning. Also, sex ratios are influenced by a combined effect of biennial spawning and hatching and higher fishing mortality rates and seasonal variation in the availability of males.

Monthly trends in sex ratio have been relatively homogenous by areas during the 50-year period of study, 1960–2010, with lowest female ratios

in spring (April–May) at the peak of spawning and highest CPUE of males. Maximum ratios of females are displayed from late summer to winter (August–March) when CPUE of males is normally lower, berried females in their burrows and the non-ovigerous part of the population actively maturing the ovaries in preparation for spawning in spring. The intervening period from May to August is characterized by an increasing female sex ratio from around 10% to 25–30% due to the posthatching population of females entering the fishery and increased depletion of the larger-bodied males due to the fishery.

Temporal and spatial sex ratio variations have been considerable in *Nephrops* catches, with highest proportions of females very often clearly fishery-induced and displaying itself in low CPUE, small mean size of animals and low fishable stock assessments of males. Significant correlations were shown between the percentage of females in catches and these three variables above ($p < 0.001$).

A geographical study of seasonal variations in sex ratio in other fishing areas ranging from the Faeroes to the Aegean Sea largely demonstrates the availability state of the female population in context with spawning and hatching. In areas of biennial spawning regimes such as the Faeroes, the seasonal variations in sex ratio resemble that of Iceland. Somewhat similar pattern is observed in the Farne Deeps and, although less clearly, other North Sea areas, giving an indication of at least a partly biennial reproductive cycle. In Scottish areas and in the Irish Sea, a typical annual cycle is observed with the female sex ratio rising in spring and falling again in autumn in phase with hatching and spawning activities. Also, a similar seasonal pattern is reflected in data from the Bay of Biscay to south Portugal and the Mediterranean, although there is a clear southward tendency towards the female sex ratio rising earlier in the year, probably in step with earlier spring blooming and hatching of *Nephrops* larvae in relatively warmer and sometimes more isothermal conditions. In addition, the diminishing ratio of females is apparently earlier and more widespread in time, probably indicating a longer spawning season and/or more activity and less burrowing behaviour in more southerly warmer waters.

Fecundity of Icelandic female *Nephrops* is curvilinearly and highly significantly related to CL, for both numbers of ripe last stage ovary oocytes (stage 6; potential fecundity) and newly extruded fertilized eggs (stage A; realized fecundity) ($p < 0.001$). For a medium-sized female of 35 mm CL, the eggs number 1452 and 997 for the ovary and spawn, respectively, a considerably less fecundity than reported from other areas. For females of 25–50 mm CL,

the loss of eggs between potential and realized fecundity was seen to range from 27% to 35%, increasing with size due to some biological or technical reasons, such as variable fertilization and/or adherence to the pleopods at spawning or greater size-related loss of eggs due to abrasion during intermittent movements or the fishing operation by trawl.

A latitudinal gradient in fecundity, similar to that shown in the duration of the incubation period of *Nephrops* larvae, is only partly apparent ($p = 0.05$), although a relevant comparison may be somewhat camouflaged by methodological reasons such as sampling procedures and regression calculations.

Although potential or realized fecundity may be somewhat comparable for similar-sized individuals over a great part of the geographical distribution, the most southerly areas, those off Portugal and in the Mediterranean, appear to end up with less effective (actual) fecundity at time of hatching. That could be ascribed to more activity and movement in areas of higher sea temperatures involving greater loss of eggs due to abrasion and tail beats as well as possibly more predation of eggs. Thus, less effective fecundity may relate to the overall low fishery potential of the slope populations of southern Europe, although other stock and environmental components undoubtedly play an important role.

Southern Icelandic waters, the northwestern limit of *Nephrops* distribution in Europe, are seemingly bestowed with minimum sea temperatures for the survival of *Nephrops*, making possible the progress of growth, maturity, spawning and hatching. However, the biennial spawning regime and low fecundity unavoidably limit the number of progeny and play a major part in the vulnerability of the Icelandic *Nephrops* stock to high fishing intensity. Therefore, sustainable yields of *Nephrops* at Iceland are realized at relatively lower fishing mortality (F) than in areas of annual spawning. Also, notable increases in fishing intensity reverberate quickly in diminishing stock size, lesser mean size and CPUE. This has on occasions led to economical overfishing and may have resulted in localized recruitment overfishing during certain periods in the history of the fishery. Consequently, good data not only on the male population but also on female biological parameters, such as size at maturity, proportion of females in the catch and overall size distribution and mean size of animals, can give valuable indications of stock trends as a whole.

ACKNOWLEDGMENTS

The author expresses his sincere thanks to all colleagues involved in the collection of *Nephrops* data since the 1960s, especially the late Þorsteinn Jónsson (1920–1999) who worked as a

research assistant at the Marine Research Institute for 26 years (1967–1993). His compilation of invertebrate data includes some in this chapter, mostly in precomputer years. Many thanks also to my colleague Gunnar Pétursson for his invaluable assistance in later years in the compilation of data from the MRI database. Thanks are also due to my colleagues Gudrún Þórarinsdóttir and Jónas P. Jónasson for reading the manuscript at an earlier stage and their valuable recommendations. Finally, merited thanks are due to Sigurborg Jóhannsdóttir whose assistance in the final formatting of text figures was invaluable and Jónas P. Jónasson for assisting with the geographical maps of Iceland and Europe.

REFERENCES

Abelló, P., Sardà, F., 1982. The Fecundity of the Norway lobster (*Nephrops norvegicus*, L.) off the Catalan and Portuguese coasts. Crustaceana 43 (1), 13–20.

Aliverti, G., Picotti, M., Trotti, L., De Maio, A., Lauretta, O., Moretti, M., 1968. Atlante del Mar Tirreno: Isoterme ed isoaline. Consiglio Nazionale Ricerche, Roma, p. 6 Ser. A.

Allonso-Allende, J.M., 1979. Estudio sobre la biología y pesca de la gigala Nephrops norvegicus (L.) de la costas de Galícia. Thesis doctoral, 1979, Universidad de Salamanca (unpublished).

Andersen, F.S., 1962. The Norway lobster in Faeroe waters. Medd. Danm. Fisk. Havunders (N.S.) 3, 265–326.

Anonymous, 1980. Report of the *Nephrops* working group. International Council for the Exploration of the Sea CM 1980/K:2 (mimeo).

Anonymous, 1982. Report of the *Nephrops* working group. International Council for the Exploration of the Sea CM 1982/K:3 (mimeo).

Anonymous, 1984. Report of the *Nephrops* working group. International Council for the Exploration of the Sea CM 1983/K:4 (mimeo).

Anonymous, 1992. Working group on *Nephrops and Pandalus* stocks. International Council for the Exploration of the Sea CM 1992/Assess:8 (mimeo).

Anonymous, 1996a. Report of the working group on *Nephrops* stocks. International Council for the Exploration of the Sea CM 1991/Assess:12, parts 1 and 2 (mimeo).

Anonymous, 1996b. State of marine stocks in icelandic waters 1995/96. Prospects for the Quota year 1996/97: Hafrannsóknastofnunin Fjölrit 46, pp. 73–79.

Anonymous, 2007. State of marine stocks in icelandic waters 2006/2007. Prospects for the Quota year 2007/2008: Hafrannsóknastofnunin Fjölrit 129, pp. 72–74.

Anonymous, 2008. State of marine stocks in Icelandic waters 2007/2008. Prospects for the Quota year 2008/2009: Hafrannsóknastofnunin Fjölrit 138, pp. 76–78.

Anonymous, 2009. Environmental conditions in Icelandic waters 2008: Hafrannsóknir. Marine research in Iceland 145, pp. 1–74.

Anonymous, 2010. State of marine stocks in Icelandic waters 2009/2010. Prospects for the quota year 2010/2011: Hafrannsóknir. Marine research in Iceland 153, pp. 73–74.

Arrobas, I., 1982. Some aspects on the biology and fishery of *Nephrops norvegicus* (L.) from the south Portuguese coast. International Council for the Exploration of the Sea CM 1982/K:27, 28 pp (mimeo).

Astthorsson, O.S., Palsson, J., 2006. New fish records and records of rare southern fish species in Icelandic waters in the warm period 1996-2005. International Council for the Exploration of the Sea CM 2006/C:20, pp. 1–22.

Astthorsson, O.S., Gislason, A., Jonsson, S., 2007. Climate variability and the Icelandic marine ecosystem. Deep-Sea Res. II 54, 2456–2477.

Astthorsson, O.S., Valdimarsson, H., Gudmundsdottir, A., Óskarsson, G.J., 2012. Climate-related variations in the occurrence and distribution of mackerel (*Scomber scombrus*) in Icelandic waters. ICES J. Mar. Sci. 69 (7), 1289–1297.

Attard, J., Hudon, C., 1987. Embryonic development and energetic investment in egg production in relation to size of female lobster (*Homarus americanus*). Can. J. Fish. Aquat. Sci. 44, 1157–1164.

Ayza, O., Tuset, V.M., Gonzalez, J.A., 2011. Estimation of size at onset of sexual maturity and growth parameters in Norway lobster (Nephrops norvegicus) off the Portuguese coast. Fish. Res. 108, 205–208.

Bagenal, T.B., 1953. The biology of *Nephrops norvegicus* (L.) in the Clyde area. Ann. Biol. Copenh. 9, 212.

Bagge, O., 1988. The Development of the Fishery on Norway Lobster in the Kattegat, 1970-87. International Council for the Exploration of the Sea CM 1988/K:11 (mimeo).

Bagge, O., Munch-Petersen, S., 1979. Some possible factors governing the catchability of Norway lobster in the Kattegat. Rapp. P.-V. Réun. Cons. Int. Explor. Mer. 175, 143–146.

Bailey, N., 1984. Some aspects of reproduction in *Nephrops*. International Council for the Exploration of the Sea CM 1984/K:33 (mimeo).

Bailey, N., 1986. Why does the size of *Nephrops* vary? Scottish Fish. Bull. 49, 31–36.

Bailey, N., Chapman, C.J., 1983. A comparison of density, length composition and growth of two Nephrops populations off the west coast of Scotland. International Council for the Exploration of the Sea CM 1983/K:42 (mimeo).

Balopoulos, E., Papageorgiou, E.J., 1991. Water masses and flow features in the North Euboikos Gulf (Eastern Mediterranean) an initial assessment. Vie Milieu 41, 69–176.

Barale, V., Jaquet, J.M., Ndiaye, M., 2008. Algal blooming patterns and anomalies in the Mediterranean Sea as derived from the SeaWiFS data set (1998-2003). Remote Sens. Environ. 112, 3300–3313.

Barnes, H., Bagenal, T.B., 1952. Observations on *Nephrops norvegicus* (L.) and on an epizoic population of *Balanus crenatus* Brug. J. Mar. Biol. Assoc. U.K. 30, 369–380.

Bell, M.C., Redant, F., Tuck, I., 2006. *Nephrops* species. In: Phillips, B.F. (Ed.), Lobsters: Biology, Management, Aquaculture and Fisheries. Blackwell Publishing Ltd, Oxford, UK, pp. 412–461 (Chapter 13).

Bianchini, M.L., Di Stefano, L., Ragonese, S., 1998. Size and age at onset of sexual maturity of female Norway lobster *Nephrops norvegicus* L. (Crustacea: Nephropidae) in the Strait of Sicily (Central Mediterranean Sea). Sci. Mar. 62 (1–2), 151–159.

Boulton, G.S., Thors, K., Jarvis, J., 1988. Dispersal of glacially derived sediment over part of the continental shelf of south Iceland and the geometry of the resultant sediment bodies. Mar. Geol. 83, 193–223.

Briggs, R.P., 1981. Trends in the Northern Ireland *Nephrops* Fishery 1970-1980. International Council for the Exploration of the Sea CM 1981/K:9 (mimeo).

Briggs, R.P., 1988. A preliminary analysis of maturity data for Northwest Irish Sea *Nephrops*. International Council for the Exploration of the Sea CM 1988/K:21, pp. 1–16 (mimeo).

Briggs, R.P., Armstrong, M.J., Dickey-Collas, M., Allen, M., McQuaid, N., Whitmore, J., 2002. The application of fecundity estimates to determine the spawning stock biomass of Irish Sea *Nephrops norvegicus* (L) using the annual larval production method. ICES J. Mar. Sci. 59, 109–119.

Chapman, C.J., 1980. Ecology of juvenile and adult *Nephrops*. In: Cobb, S., Phillips, B. (Eds.), In: The Biology and Management of Lobsters, vol. II. Academic Press, New York, pp. 143–178 390 pp.

Chapman, C.J., Howard, F.G., 1979. Field observations on the emergence rhythm of the Norway lobster *Nephrops norvegicus* (L.), using different methods. Mar. Biol. 51, 157–165.

Chapman, C.J., Priestley, R., Robertson, H., 1972. Observations on the diurnal Activity of the Norway lobster, *Nephrops norvegicus* (L.). International Council for the Exploration of the Sea CM 1972/K:20 (mimeo).

Chapman, C.J., Ballantyne, K.A., 1980. Some observations on the Fecundity of Norway lobsters in Scottish Waters. International Council for the Exploration of the Sea CM 1980/K:25 (mimeo).

Conan, G.Y., 1975. A growth model for Nephrops norvegicus from Biscay Bay in function of periodicity of moult. International Council for the Exploration of the Sea CM 1975/K:10 (mimeo).

Conan, G.Y., 1978. Life history, growth, production and biomass modelling of *Emerita analoga*, *Nephrops norvegicus* and *Homarus vulgaris* (Crustacea, Decapoda). Ph.D. thesis, University of California, San Diego, pp. 1–349.

D'Ortenzio, F., Ribera d'Alcala, M., 2009. On the trophic regimes of the Mediterranean Sea: a satellite analysis. Biogeosciences 6, 139–148.

Dunthorn, A.A., 1967. Some observations on the behaviour and development of the Norway lobster. International Council for the Exploration of the Sea CM 1967/K:5 (mimeo).

Eiríksson, H., 1968a. Áhrif veiða á aflamagn, stærð og kynhlutfall leturhumarsins við Ísland á árunum 1962–67. Ægir 61, 9, p. 8.

Eiríksson, H., 1968b. The effect of fishing on catch per effort, size and sex-ratio of the Norway lobster (*Nephrops norvegicus* L.) in Icelandic waters during the years 1962-1967. International Council for the Exploration of the Sea ICES CM 1968/K:4, pp. 1–11 (mimeo).

Eiríksson, H., 1969. Rannsóknir á leturhumri (*Nephrops norvegicus* L.) árið 1968. Tímgun leturhumars við Ísland (On the breeding cycle of Norway lobster at Iceland). Hafrannsóknir 1968. Smárit Hafrannsóknastofnunarinnar 1 (Annual Report of the Marine Research Institute 1968), pp. 66–75.

Eiríksson, H., 1970a. The Nephrops fishery of Iceland 1958–1969. International Council for the Exploration of the Sea C.M. 1970/K:5, pp. 1–9 (mimeo).

Eiríksson, H., 1970b. On the breeding cycle and fecundity of the Norway lobster at South-West Iceland. International Council for the Exploration of the Sea CM 1970/K:6, pp. 1–4 (mimeo).

Eiríksson, H., 1976. A study of the Icelandic *Nephrops* fishery with emphasis on stock assessments. In: International Council for the Exploration of the Sea. Special Meeting on Population Assessments of Shellfish Stocks No. 22, pp. 1–10.

Eiríksson, H., 1979. A study of the Icelandic *Nephrops* fishery with emphasis on stock assessments. Rapp. P.-V. Réun. Cons. Int. Explor. Mer. 175, 270–279.

Eiríksson, H., 1980. Humarinn við Ísland. Ægir 73, 187–192.

Eiríksson, H., 1982. A trial VPA on the *Nephrops* stock at Iceland with comparisons to catch and effort data. International Council for the Exploration of the Sea CM 1982/K:17, pp. 1–9 (mimeo).

Eiríksson, H., 1992. A synopsis of age based assessments and predictions on *Nephrops* at Iceland during 1977-1992. International Council for the Exploration of the Sea CM 1992/K:20, pp. 1–20.

Eiríksson, H., 1993. On the biennial breeding cycle of *Nephrops* at Iceland and how it relates to the fishery. International Council for the Exploration of the Sea CM 1993/K:5, pp. 1–18.

Eiríksson, H., 1999. Spatial variability of CPUE and mean size as possible criteria for unit stock demarcations in analytical assessments of *Nephrops* at Iceland. *Rit Fiskideildar* (Journal of the Marine Research Institute Reykjavík) 16, 239–245.

Eiríksson, H., 2009. Humarstofninn, aflabrögð og umhverfisþættir/The Nephrops stock, fishery and the environment. Environmental conditions in Icelandic waters 2008. Hafrannsóknir. Marine Research in Iceland 145, pp. 42–47.

Farina, A.C., 1989. The North Galician *Nephrops* fishery. International Council for the Exploration of the Sea CM 1989/K:20, pp. 1–5 (mimeo).

Farina, A.C., Freire, J., González_Gurriarán, E., 1999. Fecundity of the Norway lobster *Nephrops norvegicus* in Galicia (NW Spain) and a review of geographical patterns. Ophelia 50 (3), 177–189.

Farmer, A.S.D., 1972. The general biology of *Nephrops norvegicus* (Linnaeus, 1758) (Decapoda: Nephropidae) off the Isle of Man. Ph.D. Thesis 307 pp.
Farmer, A.S., 1974a. The development of the external sexual characteristics of *Nephrops norvegicus* (L.) (Decapoda: Nephropidae). 8, 241–255.
Farmer, A.S.D., 1974b. Reproduction in *Nephrops norvegicus* (Decapoda: Nephropidae). J. Zool. (Lond.) 174, 161–183.
Farmer, A.S.D., 1974c. Relative growth in *Nephrops norvegicus* (L.) (Decapoda Nephropidae). J. Nat. Hist. 8, 605–620.
Farmer, A.S.D., 1975. Synopsis of biological data on the Norway lobster *Nephrops norvegicus* (Linnaeus, 1758). FAO Fish. Synop. 112, 1–97.
Figueiredo, M.J., 1963. Note sur la composition des stocks langoustines (*Nephrops norvegicus* L.) de la côte portugaise en 1959/63. In: International Council for the Exploration of the Sea CM 1963/No. 43, pp. 1–2.
Figueiredo, M.J., 1965. The spawning of the Norway lobster, *Nephrops norvegicus* (L.) in Portuguese waters. International Council for the Exploration of the Sea CM 1965/No. 133, 6 pp (mimeo).
Figueiredo, M.J., 1982. The occurrence of resorption in the ovaries *Nephrops norvegicus* (L.) in Portuguese waters. International Council for the Exploration of the Sea CM 1982/K:28, pp. 1–7.
Figueiredo, M.J., 1986. Length and sex composition of *Nephrops* stocks in several areas off the Portuguese coast. International Council for the Exploration of the Sea CM 1986/K:8, pp. 1–5 (mimeo).
Figueiredo, M.J., Barraca, I.F., 1963. Contribuiçao para o Conhecimento da Pesca e da Biologia do Lagostim (*Nephrops norvegicus* L.) na Costa Portuguesa. Inst. Biol. Marit., pp. 1–44 Notas e Estudos. No. 28.
Figueiredo, M.J., Nunes, M.C., 1965. The fecundity of the Norway. Lobster, Nephrops norvegicus (L.) in Portuguese waters. International Council for the Exploration of the Sea CM 1965/No. 34, pp. 1–5 (mimeo).
Figueiredo, M.J., Thomas, H.J., 1967a. *Nephrops norvegicus* (Linnaeus, 1758) leach—a review. Oceanogr. Mar. Biol. Ann. Rev. 5, 371–407 Notas e Estudos Inst. Biol. Marit. 33.
Figueiredo, M.J., Thomas, H.J., 1967b. On the biology of the Norway lobster, *Nephrops norvegicus* (L.). J. Cons. Perm. Int. Explor. Mer. 31 (1), 89–101.
Figueiredo, M.J., Margo, O., Franco, M.G., 1982. The fecundity of *Nephrops norvegicus* (L.) in Portuguese waters. International Council for the Exploration of the Sea CM 1982/K:29, pp. 1–10.
Fontaine, B., Warluzel, N., 1969. Biologie de la langoustine du Golfe de Gascogne *Nephrops norvegicus* (L.). Rev. Trav. Inst. Pêches Marit. 33 (2), 223–246.
Fraser, J.H., 1965. Larvae of *Nephrops norvegicus* in the Scottish Area, 1935-1964. International Council for the Exploration of the Sea CM 1965/No. 10, pp. 1–4 (mimeo).
Froglia, C., Gramitto, M.E., 1979. An estimate of the fecundity of Norway lobster (*Nephrops norvegicus*) in the Adriatic Sea. Rapp. Comm. Int. Mer Médit. 25/26 (4), 227–229.
Froglia, C., Gramitto, M.E., 1981. Summary of biological parameters on the Norway lobster, *Nephrops norvegicus* L., in the Adriatic. FAO Fish. Rep. 253, 165–178.
Froglia, C., Gramitto, M.E., 1982. Effeti della crisi di ossigeno del 1977 sulla pesca degli Scampi in Adriatico. Boll. Musei inst. Biol. Univ. Genova 50(Suppl.), 195–201.
Gauss-Garady, V., 1912. Über die Lebensgeschichte der adriatischen Scampi (*Nephrops norvegicus*). Öst. Fisch Ztg 9, 42–79.
Gibson, F.A., 1966. *Nephrops norvegicus* in the Irish Sea. International Council for the Exploration of the Sea CM 1966/M:4, pp. 1–7 (mimeo).
Gibson, F.A., 1967. Stocks of *Nephrops norvegicus* off the south coast of Ireland. Ir. Fish. Invest. (1a), 1–11. Department of Agriculture and Fisheries, Dublin.

Gramitto, M.E., Froglia, C., 1980. Osservazioni sul potenziale riproduttivo dello scampo (*Nephrops norvegicus*) in Adriatico. Mem. Biol. Mar. Oceanogr. 10, 213–218.
Gudmundsson, K., 1998. Long-term variations in phytoplankton productivity in spring in Icelandic waters. ICES J. Mar. Sci. 55, 635–643.
Hallbäck, H., Ulmestrand, M., 1990. Havskräfta I Kattegat. Fauna och Flora (Stockholm) 85, 186–192.
Hartnoll, R.G., 1974. Variation in growth pattern between some secondary sexual characters in crabs (Decapoda Brachyura). Crustaceana 27, 131–136.
Hartnoll, R.G., 1978. The determination of relative growth in Crustacea. Crustaceana 34 (3), 281–293.
Hartnoll, R.G., 1982. Growth. In: Bliss, D.E. (Ed.), The Biology of Crustacea. In: Abele, L.-G. (Ed.), Embryology, Morphology and Genetics, vol. 2. Academic Press, New York, pp. 111–196.
Havinga, B., 1929. Krebse und Weichtiere. Handb. Seefisch. Nordeuropas. Bd. 3, 1–147.
Hillis, J.P., 1968. Larval distribution of *Nephrops norvegicus* (L.) in the Irish Sea and North Channel. International Council for the Exploration of the Sea CM 1968/K:6 (mimeo).
Hillis, J.P., 1972. Studies on the biology and ecology of the Norway lobster *Nephrops norvegicus* (L.) in Irish waters. Ph.D. Thesis, University College, Galway, National University of Ireland, pp. 1–294.
Hillis, J.P., 1974. Field observations on larvae of the Dublin Bay Prawn *Nephrops norvegicus* (L.) in the Western Irish Sea. Irish Fisheries Investigations, Series B (Marine), vol. 13. Dublin.
Hillis, J.P., 1979. Growth studies on the prawn, *Nephrops norvegicus*. Rapp. P.-V. Reun. Cons. Int. Explor. Mer. 175, 170–175.
Höglund, H., 1942. Havskräftan eller Kejsarhummern, *Nephrops norvegicus*. In: Anderson, K.A. (Ed.), In: Fiskar och Fiske i Norden, vol. 1, pp. 293–296.
Höglund, H., Dyber, B.I., 1965. Diurnal and seasonal variations in the catch composition of *Nephrops norvegicus* (L.) at the Swedish West Coast. International Council for the Exploration of the Sea Shellfish Committee No. 146 (mimeo).
Jensen, G.C., Armstrong, D.A., 1989. Biennial reproductive cycle of blue king crab, *Paralithodes platypus*, at the Pribilof Islands, Alaska and a comparison to a congener *Paralithodes camtschatica*. Can. J. Fish. Aquat. Sci. 46, 932–940.
Jorge, I.M., 1975. Catches, length and sex compositions of trawl and tangle nets landings of Norway lobster *Nephrops norvegicus* (L.) from the central Portuguese coast. International Council for the Exploration of the Sea CM 1975/K:17, pp. 1–6 (mimeo).
Jorgensen, O.M., 1925. The early stages of *Nephrops norvegicus*, from the Northumberland plankton, together with a note on the post-larval development of *Homarus vulgaris*. J. Mar. Biol. Assoc. U.K. 13, 870–879.
Karlovac, O., 1953. An ecological study of *Nephrops norvegicus* (L.) of the High Adriatic. Izv. Inst. Oceanogr. 5(2C) 50 pp.
Koeller, P., Fuentes-Yaco, C., Platt, T., Sathyendranath, S., Richards, A., Ouellet, P., Skúladóttir, U., Wieland, K., Savard, L., Aschan, M., 2009. Basin-scale coherence in phenology of shrimps and phytoplankton in the North Atlantic Ocean. Science 324, 791–793.
Leloup, E., Gilis, C., 1965. Les Apports de Langoustines dans les Ports Belges. Rapp. P.-V. Réun. Cons. Int. Explor. Mer. 156, 139–141.
Lizàrraga-Cubedo, H.A., Tuck, I., Bailey, N., Pierce, G.J., Kinnear, J.A.M., 2003. Comparisons of size at maturity and fecundity of two Scottish populations of the European lobster, *Homarus gammarus*. Fish. Res. 65, 137–152.
Malmberg, S.-Å., 1980. Hydrographic conditions in Icelandic waters in May-June 1979. International Council for the Exploration of the Sea ICES CM 1980/ C:28, 10 pp (mimeo).

Malmberg, S.-Å., 1983. Hydrographic conditions in Icelandic waters in May/June 1979 and 1980. Ann. Biol. Copenh. 37, 47–56.

Matta, F., 1959. Lo scampo del Mar Tirreno. Nota 1. Boll. Pesca Piscic. Idrobiol. 14 (2), 189–205.

McIntosh, D.C., 1908. Variation in the Norway lobster (*Nephrops norvegicus*). Proc. R. Phys. Soc. Edinburgh 17, 129–142.

McQuaid, N., Briggs, R.P., Roberts, D., 2006. Estimation of the size of onset of sexual maturity in Nephrops norvegicus (L.). Fish. Res. 81 (1), 26–36.

McQuaid, N., Briggs, R.P., Roberts, D., 2009. Fecundity of *Nephrops norvegicus* from the Irish Sea. J. Mar. Biol. Assoc. U.K. 89 (6), 1181–1188.

Mente, E., Karapanagiotidis, I.T., Logothetis, P., Vafidis, D., Malandrakis, E., Neofitou, N., Exadactylos, A., Stratakos, A., 2009. The reproductive cycle of Norway lobster. J. Zool. 278, 324–332.

Milligan, S.P., Nichols, J.H., 1988. *Nephrops* larvae surveys off the north-east coast of England in 1987. International Council for the Exploration of the Sea CM 1988/K:5, pp. 1–13 (mimeo).

Mori, M., Biagi, F., Ranieri, S., 1998. Fecundity and egg loss during incubation in Norway lobster (*Nephrops norvegicus*) in the North Tyrrhenian Sea. J. Nat. Hist. 32, 1641–1650.

Mori, M., Modena, M., Biagi, F., 2001. Fecundity and egg volume in Norway lobster (*Nephrops norvegicus*) from different depths in the northern Tyrrhenian Sea. Sci. Mar. 65 (2), 111–116.

Morizur, Y., 1979a. Utilisation de critéres fonctionnels (présence de spermatophore, maturation des ovaires) pour la détermination de la taille et l´age á maturité sexuelle de *Nephrops norvegicus* femelles dans la région Sud-Bretagne. International Council for the Exploration of the Sea ICES C.M. 1979/K:41, pp. 1–18 (mimeo).

Morizur, Y., 1979b. Evaluation de la perte d'oefs lors de l'incubation chez *Nephrops norvegicus* dans la region de Sud-Bretagne (Loss of eggs during incubation period in *Nephrops norvegicus* from the South-Brittany area). International Council for the Exploration of the Sea ICES C.M. 1979/K:45, pp. 1–9 (mimeo).

Morizur, Y., 1980. Reproduction de la langoustine, *Nephrops norvegicus*, dans la région Sud-Bretagne. Thèse du Diplome de Docteur de 3ème cycleL´Université Pierre et Marie Curie, Paris 6, France, pp. 1–115.

Morizur, Y., 1981a. Evaluation de la perte d´oeufs lors de l´incubation chez *Nephrops norvegicus* (L.) dans la région Sud-Bretagne, France. Crustaceana 41 (3), 301–306.

Morizur, Y., 1981b. Évolution du taux de présence de spermatophore chez les femelles de *Nephrops norvegicus* (L.) (Decapoda: Reptantia) et développement ovarien. J. Exp. Mar. Biol. Ecol. 52, 15–24.

Morizur, Y., 1983. Utilisation de critères fonctionnels (présence de spermatophore, maturation des ovaires) pour la détermination de la taille et de l´âge à maturité sexuelle des *Nephrops norvegicus* femelles de la région sud-Bretagne. J. Cons. Int. Exp. Mer. 41, 28–36.

Morizur, Y., Rivoalen, J.J., 1982. Fécondité de *Nephrops norvegicus* en Mer Celtique: approche quantitative et qualitative. International Council for the Exploration of the Sea CM 1982/K:9, pp. 1–11 (mimeo).

Morizur, Y., Conan, G., Cuénolé, A., Omnés, M.H., 1981. Fécondité de *Nephrops norvegicus* dans le golfe de Gascogne. Mar. Biol. 63, 319–324.

Mytilineou, C., Papaconstantinou, C., Fourtouni, A., 1990. Some aspects of the biology of Norway lobster *Nephrops norvegicus* in the N. Euvoikos Gulf (Greece). Rapp. Comm. Int. Mer. Mèdit. 32(1), 34 pp.

Newland, P., Chapman, C., 1985. Some observations on orientation and swimming behaviour of *Nephrops* in relation to trawling. International Council for the Exploration of the Sea ICES C.M. 1985/K:7, pp. 1–8 (mimeo).

Newland, P.L., Chapman, C.J., 1989. The swimming and orientation behaviour of the Norway lobster, *Nephrops norvegicus* (L.), in relation to trawling. Fish. Res. 8, 63–80.
Nichols, J.H., Thompson, B.M., 1988. Quantitative sampling of crustacean larvae and its use in stock size estimation of commercially exploited species. In: Symp. Zool. Soc. Lond.59, 157–175.
Nichols, J.H., Bennett, D.B., Symonds, D.J., Grainger, R., 1987. Estimation of the stock size of adult *Nephrops norvegicus* (L.) from larvae surveys in the western Irish Sea in 1982. J. Nat. Hist. 21 (6), 1433–1450.
Nicolajsen, Á., 1989. Hummaraveiðan. Fiskirannsóknarstovan. Smárit 3, 1–13.
Nicolajsen, Á., Eiríksson, H., 1990. A preliminary report on the reproductive cycle of *Nephrops norvegicus* at the Faeroes. International Council for the Exploration of the Sea CM 1990/K:3, pp. 1–7, (mimeo).
O´Riordan, C.E., 1964. *Nephrops norvegicus*, the Dublin Bay Prawn, in Irish waters. Sci. Proc. R. Dublin Soc. Ser. B 1 (13), 131–157.
O´Riordan, C.E., 1965. *Nephrops norvegicus* fishing Grounds around the Irish Coast. Rapp. P.-V. Réun. Cons. Int. Explor. Mer. 156, 161–163.
Orsi Relini, L., Relini, G., 1989. Reproduction of *Nephrops norvegicus* (L.) in isothermal Mediterranean waters. In: Ryland, S., Tyler, P.A. (Eds.), Reproduction, Genetics and Distributions of Marine Organisms. International Symposium Series. Olsen & Olsen, Fredensborg, Denmark, pp. 153–160.
Orsi Relini, L., Zamboni, A., Fiorentino, F., Massi, D., 1998. Reproductive patterns in Norway lobster *Nephrops norvegicus* (L.), (Crustacea Decapoda Nephropidae) of different Mediterranean areas. In: Sarda, F. (Ed.), Sci. Mar. 62, 25–41 (Suppl. 1).
Ouellet, P., Plante, F., 2004. An investigation of the sources of variability in American lobster (*Homarus americanus*) eggs and larvae: female size and reproductive status, and interannual and interpopulation comparisons. J. Crustac. Biol. 24 (3), 481–495.
Pampoulie, C., Skirnisdottir, S., Hauksdottir, S., Olafsson, K., Eiríksson, H., Chosson, V., Hreggvidsson, G.O., Gunnarsson, G.H., Hjorleifsdottir, S., 2011. A pilot genetic study reveals the absence of spatial genetic structure in Norway lobster (*Nephrops norvegicus*) on fishing grounds in Icelandic waters. ICES J. Mar. Sci. 68 (1), 20–25.
Papathanossiou, E., Anagnostou, C., Voutsinou-Taliadouri, F., 1992. Environmental study of the North Euboikos Gulf: Final Tech. Report. NCMR 243 pp.
Pearl, R., Reed, L., 1920. On the rates of growth of the population of the United States since 1790 and its mathematical representation. Proc. Natl. Acad. Sci. U.S.A. 6 (6), 275–288.
Pearson, J., 1908. Cancer (the edible crab). Liverpool Mar. Biol. Comm. Mem. 16, 1–217.
Phillips, B.F., Cobb, J.S., George, R.W., 1980. General biology. In: Cobb, J.S., Phillips, B.F. (Eds.), The Biology and Management of Lobsters. In: Physiology and Behavior, vol. 1. Academic Press, New York, pp. 1–82.
Poulsen, E.M., 1946. Investigations on the Danish fishery for and the biology of the Norway lobster and the deep-sea prawn. Rep. Dan. Biol. Stn. 48, 27–49.
Powell, A., Eriksson, S.P., 2013. Reproduction: life cycle, larvae and larviculture. Adv. Mar. Biol. 64, 201–245.
Redant, F., 1987a. Reproduction and seasonal behaviour of the Norway lobster, *Nephrops norvegicus*, in the Central North Sea. International Council for the Exploration of the Sea C.M. 1987/K:32, pp. 1–12 (mimeo).
Redant, F., 1987b. The states of exploitation of the Norway lobster stock, *Nephrops norvegicus*, in the Central North Sea. International Council for the Exploration of the Sea C.M. /K:33, pp. 1–10 (mimeo).
Redant, F., De Clerck, R., 1984. Diurnal variations in CPUE and length compositions of the catches in a *Nephrops* Directed Fishery in the Central North Sea. International Council for the Exploration of the Sea C.M. 1984/K:03, pp. 1–9 (mimeo).

Sæmundsson, B., 1937. Tífættir skjaldkrabbar íslenzkir (Thoracostraca decapoda Islandiae). Náttúrufræðingurinn VI 3, 123.
Sardà, F., 1991. Reproduction and moult synchronism in *Nephrops norvegicus* (L.) (Decapoda Nephropidae) in the Western Mediterranean: is spawning annual or biennial? Crustaceana 60 (2), 186–199.
Sardà, F., 1995. A review (1967-1990) of some aspects of the life history of *Nephrops norvegicus*. ICES Mar. Sci. Symp. 199, 78–88.
Sardà, F., 1998. *Nephrops norvegicus* (L.): comparative biology and fishery in the Mediterranean Sea. Introduction, conclusions and recommendations. Sci. Mar. 62 (Suppl. 1), 5–15.
Sardà, F., Caballín, I., 1977. Some aspects on the biology of Norway lobster (*Nephrops norvegicus*) from the Catalan area. International Council for the Exploration of the Sea C.M. 1977/K:15, 9 pp (mimeo).
Sardà, F., LLeonart, J., Cartes, J.E., 1998. An analysis of the population dynamics of *Nephrops norvegicus* (L) in the Mediterranean Sea. In: Sarda, F. (Ed.), *Nephrops norvegicus:* Comparative Biology and Fishery in the Mediterranean Sea, In: Sci. Mar.62, 135–143 (Suppl. 1).
Sigurðsson, A., 1965. A preliminary report on the Norway lobster (*Nephrops norvegicus*) in Icelandic waters. Rapp. P.-V. Réun. Cons. Int. Explor. Mer. 156, 142–146.
Simpson, A.C., 1961. A contribution to the bionomics of the lobster (*Homarus vulgaris* Edw.) on the coast of north Wales. Fish. Invest. Lond. Ser. 2, 23,1–23,28.
Simpson, A.C., 1965. Variations in the catches of *Nephrops norvegicus* at different time of day and night. Rapp. P.-V. Réun. Cons. Int. Explor. Mer. 156, 186–189.
Skúladóttir, U., 1991. Stærð rækju við kynskipti og eggburðartímabil við mismunandi sjávarhita. Ægir 84 (3), 160–166.
Skúladóttir, U., 1965. The *Nephrops* Fisheries of Iceland. International Council for the Exploration of the Sea C.M. 1965/Shellfish Committee No. 63, pp. 1–9 (mimeo).
Skúladóttir, U., Pálsson, J., Bragason, G.S., Brynjólfsson, S., 1991. The variation in size and age at change of sex, maximum length and length of ovigerous periods of the shrimp, *Pandalus borealis*, at different temperatures in Icelandic waters. ICES C.M. 1991/K:5, 16 pp (mimeo).
Smith, R.S.M., 1987. The biology of larval and juvenile *Nephrops norvegicus* (L.) in the Firth of Clyde. PhD ThesisUniversity of Glasgow.
Stechey, D.P.M., Somers, K.M., 1995. Potential, realized, and actual fecundity in the crayfish *Orconectes immunis* from southwestern Ontario. Can. J. Zool. 73, 672–677.
Stefánsson, U., 1972. Near-shore fluctuations of the frontal zone southeast of Iceland. In: Physical Variability in the North Atlantic, Proceedings of a Symposium, Dublin, 25–27 September 1969. In: Rapp. P.-V. Réun. Cons. Int. Explor. Mer., vol 162, pp. 201–205.
Stefánsson, U., Jónsdóttir, S., 1974. Near-bottom temperature around Iceland. Rit Fiskideildar 5 (2), 1–73.
Stephensen, K., 1939. The Zoology of Iceland **III**, Part 25, Crustacea Decapoda. p. 23.
Sterk, W., Redant, F., 1989. Further evidence on biennal spawning of the Norway lobster, *Nephrops norvegicus*, in the Central North Sea. International Council for the Exploration of the Sea CM 1989/K:2, 13 pp (mimeo).
Storrow, B., 1912. The prawn (Norway lobster, *Nephrops norvegicus*), and the prawn fishery of North Shields. Rep. Dove Mar. Lab. N.S. 1, 10–31.
Storrow, B., 1913. The prawn (Norway lobster, *Nephrops norvegicus*), and the prawn fishery of North Shields. Rep. Dove Mar. Lab. N.S. 2, 9–12.
Symonds, D.J., 1972. The fishery for the Norway lobster, *Nephrops norvegicus* (L.), off the north-east coast of England. Fish. Invest. Lond. Ser. 2 27, 1–35.
Teissier, G., 1960. Relative growth. In: Waterman, T.H. (Ed.), In: The Physiology of Crustacea, vol. 1. 537–560.

Templeman, W., 1936. Local differences in the life history of the lobster (*Homarus americanus*) on the coast of the Maritime provinces of Canada. J. Biol. Bd. Can. 2, 41–87.
Templeman, W., 1940. Embryonic developmental rates and egg laying of Canadian lobsters. J. Fish. Res. Board Can. 5, 71–83.
Thomas, H.J., 1954. Some Observations on the distribution, biology and exploitation of the Norway lobster (*Nephrops norvegicus* L.) in Scottish waters. Mar. Res. 1, 1–12.
Thomas, H.J., 1961. The Norway lobster. World Fish. 10 (6), 45–46 53–54.
Thomas, H.J., 1964. The spawning and fecundity of the Norway lobsters (*Nephrops norvegicus* L.) around the Scottish Coast. J. Cons. Perm. Int. Explor. Mer. 29, 221–229.
Thomas, H.J., 1969. Recent fluctuations in the Norway lobster fishery in the Firth of Forth. International Council for the Exploration of the Sea C.M. 1969/K:31, 10 pp (mimeo).
Thomas, H.J., Figueiredo, M.J., 1965. Seasonal variations in the catch composition of the Norway lobster, *Nephrops norvegicus* (L.) around Scotland. J. Cons. Perm. Int. Explor. Mer. 30 (1), 75–85.
Thordardottir, Th., 1986. Timing and duration of spring blooming south and southwest of Iceland. In: Skreslet, S. (Ed.), The Role of Freshwater Outflow in Coastal Marine Ecosystems, In: NATO ASI Series G, vol. 7, pp. 345–360 453 pp.
Tuck, I.D., Chapman, C.J., Atkinsson, R.J.A., 1997. Population biology of the Norway lobster, *Nephrops norwegicus* (L.) in the Firth of Clyde, Scotland. I: Growth and density. ICES J. Mar. Sci. 54, 125–135.
Tuck, I.D., Atkinsson, R.J.A., Chapman, C.J., 2000. Population biology of the Norway lobster, *Nephrops norwegicus* (L.) in the Firth of Clyde, Scotland. II: fecundity and the size at onset of sexual maturity. ICES J. Mar. Sci. 57, 1227–1239.
Tully, O., Roantree, V., Robinson, M., 2001. Maturity, fecundity and reproductive potential of the European lobster (*Homarus gammarus*) in Ireland. J. Mar. Biol. Assoc. U.K. 81, 61–68.
Vives, F., Suau, P., 1963. Note on the biology of *Nephrops norvegicus* (L.) var. meridionalis Zar. off the coasts of Vinaroz (west Mediterranean). Proc. Gen. Fish. Coun. Mèdit. 7, 329–335.
Waddy, S.L., Aiken, D.E., 1991. Egg production in the American lobster, *Homarus americanus*. In: Wenner, A., Kuris, A. (Eds.), Crustacean Egg Production. A. A. Balkema, Rotterdam, Holland, pp. 267–290 (Crustacean issues 7).
Watson, J., 1970. Maturity, mating, and egg-laying in the spider crab, *Chionoecetes opilio*. J. Fish. Res. Board Can. 27, 1607–1616.

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