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Crustacean Fisheries[☆]

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Introduction	1
Biology and Life History	1
Marine Shrimps and Prawns	2
Crabs	4
Lobsters and Crayfish	5
Fishery Assessment Research	6
Crustacean Management Techniques	8
Recent Developments	11
Conclusions	13
Bibliography and Further Reading	13
References	13
Further Reading	14

Introduction

Crustacea are one of the most diverse groups of aquatic animals, occupying a wide variety of habitats from the shoreline to the deep ocean, tropical to Arctic waters, extending into freshwater and in some cases onto land for part of their life history.

Crustacean species contribute in the order of 14.5 million tonnes annually or about 8% of the total world supply of fish, according to FAO statistics for 2016 FAO. Approximately 50% of this production is from the harvesting wild stocks, with increasing volumes particularly of tropical shrimps being produced through aquaculture. The wild caught crustacean stocks are dominated by the tropical marine and freshwater shrimps, crabs, lobsters, and crayfish species. Owing to their high market value as a sought-after high-protein food, crustaceans make up a disproportionate share of the value of the world's seafood. As a result of their high relative value, crustacean fisheries are generally heavily exploited and require active management to be sustained. Research to underpin management of these resources has been undertaken in many parts of the world, particularly Australia, where, unusually lobsters and shrimps make up a significant proportion of the wild catches and dominate capture fisheries in terms of value.

Fisheries for crustaceans are focused on the more abundant species, particularly those in relatively shallow, accessible areas. Shrimps continue to be the most important wild fishery products, followed by the crabs, lobsters, and krill. Catches recorded in FAO statistics for the crustacean group has increased slightly (12%) from 2010 to 2016, ending around 6.7 million metric tonnes (FAO, 2016).

Biology and Life History

Fisheries research on crustacean stocks is strongly influenced by their unusual life history and biology. A unique feature of crustaceans is that they all must undergo a regular process of molting (casting off their outer shell or exoskeleton) to grow. Once the old shell is cast off, the animal absorbs water to swell or "grow" to a larger size before the new shell hardens. The volume increase at a molt varies between species, but typically results in a gain in the range of 10%–60%. The molting process also allows the animal to regenerate damaged limbs, such as legs, claws or antennae, although regeneration results in lower or even negative growth increments in terms of standard lengths. This molting process occurs throughout all stages of the life history and is often correlated with environmental factors such as moon phase/tidal cycles particularly in shallow waters, and is typically influenced by temperature. Because of this growth mechanism, size increases as a series of discrete "steps" rather than a "smooth" change over time and is complicated to model. Growth rates are typically dependent on water temperature, with tropical and shallow-water crustaceans tending generally to grow much faster than those in cooler and deeper waters. As a result of the molting process, and lack of permanent hard structures it has not been possible to "age" crustaceans using any of the usual methods (growth rings on bones or shells) available for other fished species. However more recently research has been undertaken into the possibility of ageing some crustacean species using pigment granules (lipofuscin) in neural tissues and depositions within the ossicles of the gastric mill (part of stomach) which are not recycled during a molt.

[☆]*Change History:* June 2018. Justin J. Bopp. Updated the text, keywords, Tables 1–3, references, and added the key words, Abstract and Recent Developments section.

The molting process also significantly influences feeding activity and hence the catch rates for all crustaceans. That is, prior to a molt, feeding activity generally reduces, then ceases in the lead-up to the actual molt process. Following a molt, the shell hardens and the animals are particularly hungry, begin active feeding, and are more easily caught in baited traps or trawls. However, at this time there is relatively less muscle (meat) inside the expanded shell size until the animal has fed sufficiently to build up new muscle mass (i.e., the amount of meat early in the cycle corresponds to the much smaller-sized animal prior to the moult). At this stage they are generally of lower market value. These cyclic catches in crustacean fisheries are well known to fishers and are also crucial knowledge in the fisheries stock assessment process needed to support management of harvesting. Significant gains in value of the catch and overall profitability of fishing can be achieved where the fishery management arrangements take into account the molt cycle related variations in product quality and catchability.

The second very important feature of marine crustacean stocks is that they are generally highly fecund, producing large numbers of eggs (millions in some species) which hatch into pelagic larvae, which in turn can be widely distributed by ocean currents. Typically, the early larval stages are of a different form to the adults, but after a series of larval stages the individual molts into a form resembling the adults. Larval stages generally have limited swimming ability, but are able to migrate up and down the water column, and often have behaviors which, in combination with tides and currents, result in active dispersal into “nursery” areas suitable for the later juvenile and adult stages. Because the adult populations often occupy different habitats to juveniles, closed areas to protect stocks usually need to be in a mixture of locations to be effective and generic closures such as marine sanctuaries are less effective. The large numbers of eggs and larvae produced, together with widespread dispersal mechanisms common to most significant marine crustacean species, make them relatively resilient to fishing pressure compared with the freshwater species.

This typical marine larval life history does not generally apply to the freshwater species, where some or all larval development stages occur within a much larger egg and live young are often produced to minimize downstream losses due to river flow. These alternative larval strategies adopted by freshwater crustaceans are efficient but, owing to the relatively low numbers of offspring produced make such species more susceptible to overfishing and environmental changes to habitats than their marine counterparts.

Marine Shrimps and Prawns

This group contains by far the most important crustacean fisheries. In marine waters two major families, the Penaeidae in tropical waters and the Caridea in cold waters, support most of the significant export-based fisheries. In tropical freshwaters, palaemonid shrimps of the genus *Macrobrachium* support the major commercial production.

The terms “shrimp” and “prawn” have no scientific basis and are used interchangeably in different parts of the world. For the purposes of this article, the more commonly applied term “shrimp” will be used for simplicity.

A wide array of penaeid species are harvested from tropical to subtropical waters. These species have a complex life cycle where mated females generally move offshore to spawn in coastal marine waters where hundreds of thousands of eggs are produced at each spawning (Penn, 1980) and hatch as free-swimming planktonic nauplius larvae. After a series of larval molts and stages lasting about 2 weeks, postlarvae typically move toward the coast and are able to actively migrate into estuaries and protected coastal bays. Development through the juvenile stages in coastal nursery areas typically takes several months after which the subadults actively migrate offshore using tidal flows although sometimes river flooding results in forced offshore displacement. This migration into deeper more oceanic waters precedes mating and spawning which generally begins at 6–12 months of age.

Coupled with these relatively short life cycles is rapid growth, but also high levels of natural (predation) mortality such that few individuals survive into their second year, although some individuals may live to 2 or 3 years. This high natural mortality does, however, allow for high but sustainable harvesting rates for most of this group of commercially important species, although there are some exceptions noted later.

Artisanal and sport fishing for these species often occurs in estuary mouths during the offshore migration of subadults, while otter trawling by mechanized vessels in waters offshore from the coastal nursery areas is the main harvesting method for the larger more valuable adult shrimps. These penaeid shrimps are generally not catchable in commercially viable quantities in traps.

Powered otter trawling for shrimp, which evolved in the Gulf of Mexico, has now been adopted worldwide as the main method for industrial-scale fishing of the more valuable larger market-sized adult shrimps. Otter trawling can only occur on smooth bottoms, usually sand or mud adjacent to nursery areas, and typically harvests ~20%–50% of the shrimps in the path of the net. The remaining shrimp not caught in the net have generally burrowed in the sediments, particularly during the day. The exception to this is where some “white” shrimp species with limited burrowing ability (e.g., *Penaeus setiferus*/*Penaeus merguensis*) form dense schools during daylight and can generate turbid mud “boils” as a defense against predators. This behavior, including mid-water swimming, allows very high exploitation rates and catches on some occasions, but has been noted to break down at high levels of exploitation and in areas where river/estuarine habitats and adjacent waters have become increasingly turbid (Penn, 1984).

The major coastal fisheries for shrimps harvest species from the family Penaeidae, and particularly the genus *Penaeus*. (Note: The nomenclature for the genus *Penaeus* was subject to a revision in the late 1990s which elevated subgenera to full genus status, however recent genetic research indicates that the original genus *Penaeus* remains applicable for all of these species (Ma et al., 2011)).

Major shrimp stocks and coastal fisheries for shrimps, predominantly from the *Penaeus* and *Metapenaeus* species groups occur through the Gulf of Mexico and Central/South American coasts (*P. aztecus*, *P. setiferus*, *P. duorarum*, *P. braziliensis*, *P. californiensis*, *P. vannamei*), off China/Japan/Korea (*P. chinensis*, *P. japonicus*, *P. latissulcatus*), through the Arabian Gulf/Indian subcontinent

(*P. semisulcatus*, *P. indicus*, *P. latisulcatus*, *M. monoceros*, *P. monodon*), through south-east Asia (a wide variety of species), Indonesia–Papua New Guinea (*P. indicus*, *P. merguensis*), Australia (*P. merguensis*, *P. latisulcatus*/plebejus, *P. esculentus*/semisulcatus, *M. endeavouri*/ensis), and the African coasts (*P. notialis*, *P. indicus*, *P. monodon*, *P. japonicus*, *P. latisulcatus*, *Metapenaeus monoceros*).

In addition to the shallow-water tropical to temperate shrimp fisheries, there are small deep-water (mostly 200 m down to 1000 m) fisheries in many parts of the world for species from the families Solenoceridae for example, *Haliporoides sibogae* and *Aristaeidae foliacea*. As a consequence of the depths involved these fisheries are only operated by large industrial vessels who often also harvest deep-water lobster.

While the larger or more valuable penaeids dominate industrial-scale fisheries, large quantities of small *Acetes* and sergestid shrimps are also harvested, by small-scale coastal fisheries particularly in Asian and some African coastal waters.

The second most commercially important group of shrimps being harvested on a large commercial scale is from the taxonomic Caridae group. Within this group, species from the families Pandalidae and Crangonidae support the larger marine fisheries and shrimps from family Palaemonidae are significant in freshwaters. The main marine species are fished predominantly in the Arctic to temperate waters of the Northern Hemisphere, although some species occur further south at greater depths where temperatures correspond to Arctic waters. This group of shrimps is relatively long-lived (up to 4–6 years), spawning at several years of age, and are also typically protandric hermaphrodites. That is, they initially grow into functional males before undergoing a series of molts to become female for the remainder of their life. Females produce larger but fewer eggs than the penaeid species, and carry them after spawning attached under their tail. The eggs remain attached for an extended period, undergoing some developmental stages within the egg before hatching into pelagic larvae which grow for several months before settling onto a wide range of habitat types. *Pandalus borealis* is a typical caridean shrimp for which the life cycle has been well studied and represents the general life history pattern for this important group. Fishing occurs by both otter trawling and trapping using baited traps, which are particularly effective for these species. Major fisheries for these species occur in the Arctic waters of the northern Atlantic and Pacific. Catches of the major species fished, *P. borealis*, increased through the 1980s and 1990s and peaked at 400,000 tonnes in the early 2000s. Some of the increased abundance and catch in the northwest Atlantic followed the decline in stocks of cod which predate on these species.

In freshwater catches of tropical shrimp mostly *Macrobrachium rosenbergii* are significant and currently at around 10,000 tonnes, however this production is now small relative to aquaculture production, which has plateaued at around 200,000 tonnes per year during the 2000s.

In the colder marine waters near the poles, the crustacean fauna includes euphausiid species or krill (see Krill). While krill species occur in both northern Arctic and southern Antarctic waters, the species *Euphausia superba* is particularly abundant in the nutrient-rich Southern Ocean, while other crustacean species like crabs are less abundant. These southern hemisphere krill stocks are highly abundant with biomass estimated to be between 125 and 750 million tonnes. While more recent surveys with better technology have indicated a lower biomass of southern krill, the species still dominates the crustacean stocks in the Antarctic. Krill are small pelagic crustacean species, which swim by way of modified walking legs (swimmerets), and generally undertake a diurnal migration between the surface and significant depths. They form dense schools on the surface, particularly at night, where they are a major source of food for predators including baleen whales, seals, fishes, birds, and cephalopods. As a relatively short-lived species with high natural mortality (predation), krill stocks can be expected to provide significant sustainable fishery yields with estimates ranging to millions of tonnes per year. Fishing has however been limited by their small size and some unique processing difficulties. Recorded catches reached 400,000–500,000 tonnes in the 1980s, before falling to <100,000 tonnes in 1993. Catches then remained low through to 2007, but have increased more recently to above 200,000 tonnes. Table 1 shows recent catches and major species/fishing areas.

Table 1 World wild stock capture production of major shrimp species/groups in 2016 from FAO online database with the recorded catch rounded to nearest 1000 tonnes

Shrimp species/groups	Most significant species	FAO STATS 2016 catch (tonnes)
Northern prawn	<i>Pandalus borealis</i>	241,000
Southern rough shrimp	<i>Trachypenaeus curvirostris</i>	337,000
Banana shrimps	<i>Penaeus merguensis</i>	130,000
Metapenaeus shrimps	<i>Metapenaeus</i> spp.	87,000
Northern brown shrimp	<i>Penaeus aztecus</i>	50,000
Giant tiger prawn	<i>Penaeus monodon</i>	938,000 ^a
Northern white shrimp	<i>Penaeus setiferus</i>	55,000
Common shrimp	<i>Crangon crangon</i>	30,000
Blue shrimp	<i>Penaeus stylirostris</i>	33,000 ^a

^aThese species are the subject of significant aquaculture production and quantities recorded for wild capture fisheries may be over-estimated.

Crabs

Most commercially significant crabs belong to the Brachyura (true crabs) or Anomura (hermit crabs and king crabs) within the order Decapoda. They are generally characterized by a pair of claws, four pairs of walking legs, and a wide, flattened body. Crabs are probably the most highly developed, successful and diverse of the crustaceans. They occupy a wide range of environments, from shallow tropical seas to deep ocean trenches, estuarine and freshwaters, and some tropical species spend the majority of their life on land, only returning to the water to reproduce.

Reproductive patterns in crabs are diverse and often involve intricate courtship behaviors where the male protects the female before she molts and mating occurs. Following copulation, female crabs retain spermatozoa until spawning occurs, with fertilization taking place as the eggs are extruded. Spermatozoa can be retained by the female in a viable condition for considerable periods of time—more than a year in some species. The important swimming crab species are generally resilient to heavy fishing pressure due to their often complex, but efficient reproductive behavior and high levels of fecundity however more recently some stocks of these species have suffered recruitment overfishing (Caputi et al., 2014). Some species carry multiple broods of eggs, which are extruded, fertilized, and attached to the underside of the female during the early development stages. Numbers of eggs produced per year are frequently in the order of 50,000–500,000 per female and over a million eggs are achieved by some species. Crab larval stages are known as zoea and most marine species have four or five zoeal stages before molting into a megalopa, which generally settles out of its planktonic existence onto the sea floor.

In a number of cold-water crab fisheries (e.g., the important Snow, Tanner, King, and Dungeness crab fisheries) where breeding is more restricted, managers have elected to allow harvesting of males only, thereby giving complete protection to the female brood stock. This precautionary approach, whilst useful for some species, has the potential to reduce fertilization rates through sperm limitation but also imposes unusual constraints on research due to the inability to monitor female crabs in the commercial catch.

Most crab fishing worldwide is by use of traps, which are the preferred method because they are simple to use (particularly in deep water), labor-efficient, and the crabs are less likely to be injured. This latter fact is particularly important because it allows the product to be sold live, which guarantees a better market price than received for the frozen forms. However crabs are also caught using other methods including: trawling, tangle netting, dredges, trotlines, and drop/ring nets.

Interestingly, the majority of the large crab fisheries operate in tropical and Northern Hemisphere temperate and Arctic waters.

The three most important commercial crab species are all fast-growing “swimming crabs,” found in shallow tropical or temperate waters and bays (Table 2). These are a family of crabs which have a flattened, paddle-like hindmost leg used to burrow in sand and mud, or to propel them through the water during infrequent occasions when they “swim” over short distances. They reach maturity and are harvested between 1 and 3 years of age. The largest crab catches landed worldwide are those of gazami crab, which has a wide distribution through the western Pacific and lives in shallow inshore waters in sheltered coastal bays. However, a very substantial, but unspecified portion of these reported landings maybe from aquaculture operations and stocking of waters with juvenile gazami crab has become widespread, particularly off the Japanese coast and is considered to be economically effective.

Blue crabs occur in the western and central western Atlantic. The vast majority of the landings are made off the United States coastline from states in the Gulf of Mexico and mid-Atlantic. The commercial fishery targets both hard crabs and peeler/soft crabs, with soft-shelled crabs being considered a delicacy in the United States. These soft-shelled crabs have very recently molted and have a shell that has yet to become hard. While some of the peeler/soft crab product is taken with crab scrapes and other specialized methods capable of taking nonfeeding animals, the majority of the product is produced in commercial operations which hold peelers in shedding tanks until molting occurs.

The Snow, Tanner, and King crabs, which are on the list of important species in Table 2, are examples of moderately deep-water species occurring in cold water conditions. The distributional range of these species encompasses water <400 m deep (and, particularly for King and Snow crabs, usually <200 m and colder than 10°C). These species are very slow growing when compared with the inshore warmer water species mentioned earlier. Their age at maturity is generally upward of 5 years and in most cases they enter into the commercial fishery over 8 years after settlement.

Table 2 World wild stock capture production of major crab species/groups in 2016 from FAO online database with the recorded catch rounded to nearest 1000 tonnes

Crab species/group	Most significant species	FAO STATS 2016 catch (tonnes)
Gazami crab	<i>Portunus trituberculatus</i>	558,000
Blue swimming crab	<i>Portunus pelagicus</i>	266,000
Blue crab	<i>Callinectes sapidus</i>	98,000
Edible crab	<i>Cancer pagurus</i>	54,000
Dungeness crab	<i>Cancer magister</i>	32,000
King crabs	<i>Paralithodes</i> spp.	7000
Red crab	<i>Geryon/Chaceon</i> spp.	1000
Tanner Crab	<i>Chionoecetes bairdi</i>	5300

Note: The mud crabs (*Scylla* spp.) are not included as the majority of the production is from aquaculture.

Over the long history of crab production in the north Pacific, large catches of King, Tanner, and Snow crabs have been made. Despite stock collapses of some species, this area is still important for its crab production and for the research efforts that have been made to understand the biology and develop management systems to sustain these important stocks.

Crabs belonging to the *Geryon* and *Chaceon* genus (Table 2) are commercially important deep-water crabs. They have a wide depth range, but most of the commercially exploited populations tend to be in the 500–1000 m depth range. Water temperatures at these depths are typically <10°C and these animals are therefore slow growing taking ~8 years to reach maturity.

Lobsters and Crayfish

Lobster and crayfish species support significant and high-value fisheries. The major commercially fished lobsters are marine species taken from tropical to cold temperate waters, while freshwater crayfish are mostly taken from tropical and subtropical regions. Most of the marine species have similar life history patterns, where females carry fertilized eggs externally under their abdomens. Following hatching, the larvae undergo a series of molts before taking up a benthic habitat and growing to adulthood, a process which can take many years. Freshwater crayfish species generally have a reduced larval life and hatch as small juveniles.

Unlike many other crustacean groups there is little aquaculture production of marine lobster species due to their typically long and complex larval stages with some spiny lobster species requiring a year or more to reach the puerulus or stage which settles onto the sea floor. While the life cycle for many lobster species has been closed, the only significant aquaculture production is currently from grow-out of wild caught post larvae (puerulus) or juveniles of tropical species, mostly *Panulirus ornatus* in Vietnam. In contrast, many of the freshwater crayfish are relatively easily grown and there is increasing aquaculture production.

Wild fisheries production is dominated by three groups, the north Atlantic cold water *Homarus* species (large-clawed lobsters), the tropical shallow water *Panulirus* group (spiny or rock lobsters, without claws) and the temperate to cold water *Nephrops* group (small-clawed lobsters). The *Jasus* species group (rock lobsters) from temperate southern hemisphere waters, the *Scyllarid* group (slipper lobsters) found in all warm temperate oceans and the *Palinurus* group species (rock lobsters) typically found in temperate waters in both north Atlantic and south-west Indian Oceans where catches are taken from depths down to around 600 m make up the bulk of the remaining recorded catch. Catches from these six groups in 2016 were the order of 313,000 tonnes (Table 3).

Lobster fishing is generally by baited traps (*Homarus*, *Jasus*, and *Palinurus* groups), although the *Nephrops* and *Scyllarid* groups are mostly taken by trawl. In contrast many of the tropical *Panulirus* species do not readily enter traps and are taken by diving or by use of artificial shelters (mostly known as “casitas” in the Caribbean) which are used to concentrate the lobsters typically living in shallow seagrass habitats. Nets are used to take the lobsters sheltering under casitas, when they are lifted or disturbed and the lobsters leave their shelter. *Palinurus* species are also taken by trammel netting and sometime as trawl bycatch. Most freshwater crayfish are taken by baited traps.

The major clawed lobster fishery is for *Homarus americanus* off eastern Canada and the United States, where trap catches have increased significantly since the 1980s. This followed the collapse of the ground fish (cod) stocks in the 1990s, which were considered to be predators of lobsters. The largest fishery for *Nephrops norvegicus* occurs off the European Atlantic coasts and through the Mediterranean where they are taken primarily by trawling but also by trapping. Spiny lobster fisheries for the *Panulirus* species occur through the tropics, with major fisheries in the Caribbean (*P. argus*) and in temperate waters off Western Australia (*P. cygnus*). Smaller but significant fisheries for *Jasus* species occur in the cooler waters off southern Australia, New Zealand, South Africa and Chile. The largest fisheries for *Palinurus* species (*P. gilchristi*, *P. delagoae*) occur off southern Africa and in the NE Atlantic (*P. elephas*). The major freshwater crayfish fishery occurs in the southern states of the United States.

Stocks of the marine species appear to have generally been resilient to fishing, with the exception of some lobster species off southern Africa and some seamounts, which have been significantly reduced over time. These catch reductions appear to have resulted from a combination of environmental changes and fishing impacts. More recently (2008–09), a major fishery for the rock lobster *Panulirus cygnus* off Western Australia suffered a significant recruitment decline related to environmental changes affecting the time of spawning (de Lestang et al., 2015), despite breeding stocks being within historic levels, however the recruitment has since recovered.

Table 3 World wild stock capture production of major lobster groups in 2016 from the FAO online database with the recorded catch rounded to nearest 100 tonnes.

Lobster species/group	Most significant species	FAO STATS catch (tonnes)
<i>Homarus</i>	<i>Homarus americanus</i>	167,260
<i>Panulirus</i>	<i>Panulirus argus</i>	77,700
<i>Nephrops</i>	<i>Nephrops norvegicus</i>	59,000
<i>Jasus</i>	<i>Jasus edwardsii</i>	9000
<i>Scyllarid</i>	<i>Ibacus ciliatus</i>	1100
<i>Palinurus</i>	<i>Palinurus gilchristi</i>	300

For each lobster group, the most significant species is listed.

Fishery Assessment Research

There are two fundamental biological issues to be addressed in the management of fish stocks generally and including crustaceans. The most important problem is to control the level of fishing such that there is sufficient breeding stock is maintained to provide an adequate supply of new recruits to the fishery. This is generally tackled by utilizing catch records from a fishery to define the relationship between breeding stock levels and the resulting recruitment of new individuals into the fished population. The second issue facing fisheries is to maximize the overall catch (and value) within sustainability limits. This problem is traditionally examined using yield-per-recruit models which examine the trade-off between the increase in biomass through growth over time and the decrease in survival through natural and fishing mortality. The other biological studies undertaken, such as evaluating growth rates, migration, reproduction and mortality, are generally the building blocks to enable the assessment of these two key issues.

The main differences in the assessment of fished crustacean stocks compared with the more conventional finfish stocks and fisheries are the unusual growth, catchability and migrations exhibited by many crustacean stocks. Growth by molting and the associated catchability changes are the key difference between crustaceans and other marine species. Thus stock assessment needs to take into account the timing of the growth, which is often coordinated and the size increment at each molt. The frequency and size increment of molting usually decreases with age, especially after reaching maturity and some species undergo a final terminal molt, after which no further growth in length occurs.

Crustacean growth by molting results in size changing as a series of steps which contrasts with that of more common finfish species, where size increases steadily and can generally be modeled using a continuous growth model. Secondly, because crustaceans replace their outer shell at each molt and do not have an internal skeleton which is maintained, they cannot be easily aged by counting growth rings in their bones or hard parts, which creates specific problems for their stock assessment. This molting process and frequent loss of tags attached through the exoskeleton also makes recapture data as a means of measure growth, less reliable for crustacean species. As a consequence, crustacean age is usually estimated by following changes in the size frequency modes of particular year-classes, although this is often possible for only the younger year-classes. In recent decades, a number of innovative ways to age crustaceans using soft tissues which are retained through the molt have been developed, however none of these have been used in broad scale crustacean stock assessments needed to support fishery management.

The second feature of crustaceans which sets them apart from finfish and affects their stock assessment is their often intermittent migration events. While generally poor in swimming ability, crustacean species can undergo significant migrations linked to specific stages in their life cycle. For example, tropical shrimps and swimming crabs have specific behavioral characteristics which enable them to actively migrate offshore from coastal nursery areas, utilizing ebb tidal flows, typically as they approach sexual maturity.

Many spiny lobster species also undergo extensive directional migrations as juveniles, usually following a coordinated molt, after which they march in columns from their shallow nurseries to offshore spawning areas before reaching sexual maturity. These migration “events” are often of short duration, usually unidirectional and with the lobsters typically walking into the prevailing currents.

Such, short-term interruptions to the normal, relatively sedentary behavior of crustaceans poses special constraints on stock assessment. That is, crustacean migration typically causes erratic changes in stock distribution and catches, contrasting with most finfish fisheries where the regular, more consistent swimming movements of the fish result in continuous redistribution and mixing of stocks.

Because molting is often synchronized with environment factors (e.g., temperature and lunar cycles), the catchability of many crustaceans is also typically inconsistent and often cyclic. Specifically, the molting process alters their feeding behavior and therefore vulnerability to fishing gear particularly traps and trawls. That is, crustaceans are hungry and very active immediately after the molt (once their shell hardens), but then feeding activity slows as they build up their internal organs and approach the next molt, then effectively ceases during the period immediately prior to the next molt. For these reasons, short-term variations in catch rates for crustacean stocks do not necessarily reflect changes in the abundance of the stock and these factors which alter “catchability” must be corrected for in the data sets which are utilized in stock assessments. For all of these reasons, the assessment of the status of exploited crustacean stocks with these inherent data issues, often need to rely on the long time series data sets, which are particularly useful where the relationship between catch rate and true abundance (catchability) is fully understood and the data can be used to establish the linkages between different life history stages and subsequent catches.

These time series data are also typically necessary for the assessment of the relationship between spawning stock and subsequent recruitment to the fishery (spawning stock–recruitment relationships), which are critical to being able to distinguishing between the effects of fishing and climatic changes to recruit survival on fished crustacean stocks (Caputi et al., 1998, 2013). Long time series of catch and fishing effort data, are additionally useful where they include standardized (for location and environmental/catchability factors) survey-based prerecruit indices of abundance. These linked measures of abundance have proved to be key element in the success of management of the crustacean fisheries in Western Australia (Caputi et al., 2014).

For example, the long time-series of fishery data was fundamental in assessing the cause of the collapse of brown tiger prawn stocks in Shark Bay, Western Australia (Fig. 1). This relatively unique time series encapsulating all catches and fishing effort (standardized) since the start of the fishery, were able to be used to evaluate the impact of fishing on spawning stocks and in the assessment of the fishing effort reduction required for the stock to be recovered back to its optimal sustainable biomass.

Fig. 2, derived from the historical data, shows the relationship between spawning stock levels and subsequent recruitment to the Shark Bay tiger prawn stock. This relationship, together with the reverse relationship between annual recruitment and the

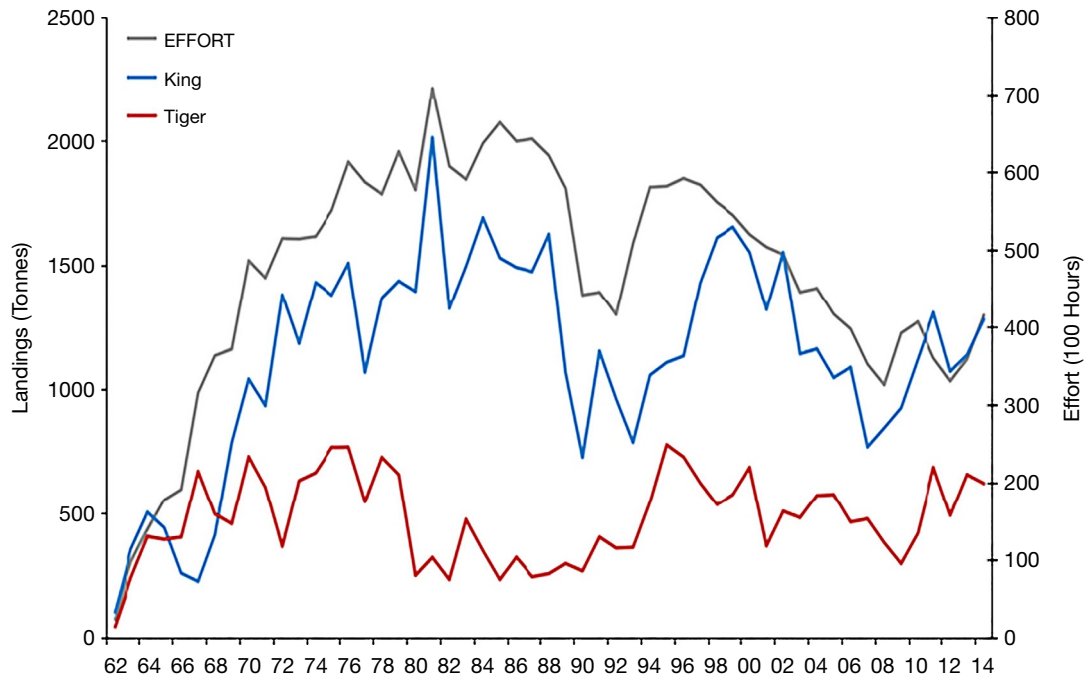


Fig. 1 The time-series data on catch, fishing effort (unstandardized hours trawled) for western king (*Penaeus latissulcatus*) and Tiger (*Penaeus esculentus*) prawns since the inception of the Shark Bay (Western Australia) prawn fishery in 1962. Note management changes since the late 1980s has reduced fishing effort to increase the sizes and total value of the prawns (shrimps) caught and has reduced the average catches for both stocks. Data from Sporer, E., Kangas, M., Koefoed, I., and Oliver, R. (2014). Shark Bay prawn and scallop managed fishery report. In: Fletcher, W. J. and Santoro, K. (eds.) *Status reports the fisheries and aquatic resources of Western Australia 2013/14: The State of the Fisheries*. Western Australia: Department of Fisheries (<http://www.fish.wa.gov.au/About-Us/Publications/Pages/State-of-the-Fisheries-report.aspx>).

abundance of spawning stock surviving to the spawning season (later in the same year) relative to variations in fishing effort targeting the stock, has been used to construct a simple combined model (Fig. 3) to determine optimal levels of tiger prawn fishing effort. Management changes to reduce and redirect effort away from the species based on this modeling have resulted in an improvement in spawning output and a recovery of the tiger prawn stock and catches in the mid-1990s (Fig. 1).

The management system for this and other key shrimp stocks in Western Australia now utilizes prerecruit surveys to determine the abundance and shrimp size structure to adjust fishing effort so that the shrimps are harvested at an optimum size and to ensure sufficient shrimp survive to the spring spawning season (Caputi et al., 2014). These prerecruit surveys also provide an ability to forecast catches, which allows management and fishers to adjust the fishing strategy to optimize the value of the available catch each year (Caputi et al., 2014). Spawning stock surveys are also undertaken to confirm that the “harvest strategy” has achieved its objective (Kangas et al., 2015). These harvest strategies have a target, threshold and limit reference point for the spawning stock with appropriate management control rules aimed at maintaining the spawning stock within the target range (Fig. 4).

Similarly, the development of catch predictions in the western rock lobster (*Panulirus cygnus*) fishery up to 4 years ahead using an index of abundance of settling puerulus (first post larval-stage) and fishing effort has enabled fisheries management to be proactive rather than reactive to changes in stock abundance.

These forecast catches and actual catches for each management zone in the fishery between the mid-1980s and 2010/11 (when catch quotas were implemented and catch forecasts no longer relevant) are shown in Fig. 5. Such predictive relationships were used in Western Australia to adjust fishing levels in advance to ensure that breeding stock levels were maintained. The puerulus abundance is no longer used to forecast the recruitment to legal-size catch 3–4 years ahead, but is incorporated in a length-structured stock assessment model used to set the total allowable catch (TAC), since the fishery was converted to a catch quota management system (Penn et al., 2015).

This development of predictive relationships based on long-run prerecruitment abundance data sets also enables environmental factors which may influence survival of larval stages, and catchability in crustacean stocks, to be examined. Fig. 6, showing the relationship between rock lobster puerulus settlement and the combination of environmental factors (timing of spawning, water temperature and winter storm index) that explain the variation in puerulus settlement including the recent downturn, is an example of this type of analysis. The availability of this type of relationship is particularly valuable to researchers attempting to distinguish between the effects of fishing and short-term “natural” variations in recruitment to the fishery caused by environmental influences. This is an important distinction as if the downturn in abundance is due to the spawning stock being below optimum levels then urgent management action is required. However even if the poor year-class is due to environmental factors, but high fishing effort is allowed to continue, it can combine to produce a very low breeding stock and trigger a long-term stock decline.

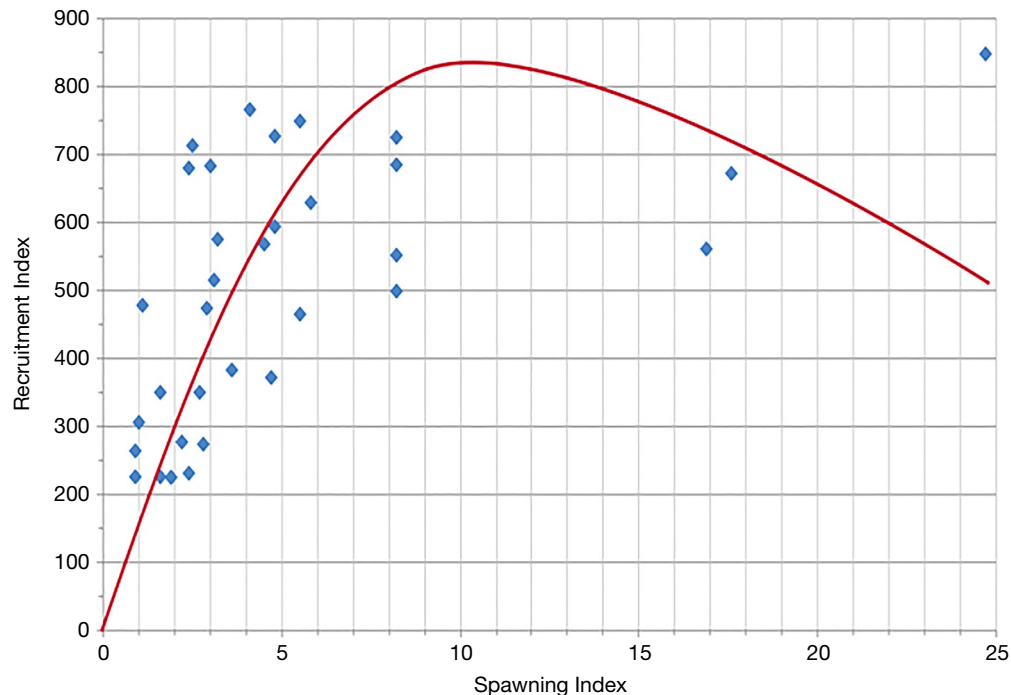


Fig. 2 The relationship between spawning stock abundance and abundance of recruits 1 year later (both indices are standardized catch rates—kg/h) for the tiger prawn (*P. esculentus*) stock in Shark Bay (Western Australia). Fitted line is best fit to the data points and the scatter of points around the line reflect the impact of the environment on recruit survival in the inshore nursery areas between spawning in spring and recruitment in the following autumn. Reproduced from Penn, J. W., Caputi, N., and Hall, N. G. (1995). Spawner-recruit relationships for the tiger prawn, *Penaeus esculentus*, stocks in Western Australia ICES Symposium on Shellfish Life Histories and Shell Fishery Models (1990). *ICES Marine Science Symposium* **199**, 320–333.

Understanding environmental factors affecting the stock has become particularly important under changing climate conditions. These changes can occur as long-term trends in the environment such as water temperature increases, decadal shifts in climate, or due to extreme events occurring such as cyclones or the marine heat wave that affected the lower west coast of Australia in 2010/11 (Caputi et al., 2015b). These have the potential to cause major changes to the recruit abundance of stocks as well as affecting other biological parameters such as size at maturity and growth. The environmental changes may also indirectly affect the stock via their effect on a species' habitat, prey or predators. This highlights the importance of monitoring environmental conditions that are likely to affect the species, early detection of changes in abundance of stocks and having flexible management harvest strategies that are responsive to changes in abundance.

The second most important fisheries problem, optimizing yield per recruit to the fishery, is also particularly difficult to assess for crustacean stocks owing to the molting process. The resulting inability to age or reliably tag some of these species makes estimation of natural mortality and growth of prerecruit year-classes relatively unreliable.

This has led to an “adaptive” management approach using adjustments to sizes at first capture over a number of years to directly assess the resulting impact on catch. The alternative approach has been to develop complex stock assessment simulation models based on length rather than age. These model-based assessments have improved significantly the ability to manage crustacean fisheries, but again where successful have relied heavily on long-run, detailed fishery databases for their testing and validation.

Crustacean Management Techniques

Management techniques applied to the significant tropical shrimp fisheries focus mainly on minimum trawl mesh sizes, accompanied by area and seasonal closures to optimize the quantity and size of shrimps caught. Many of these trawl fisheries also involve specific gear regulations to minimize unwanted by-catch and avoid the capture of protected species. Owing to the highly variable annual recruitment to these mostly short life cycle stocks, the most common and successful management approaches have involved controls on fishing inputs for example, limits on vessel numbers, gear size/number and fishing time. More recently, some of these basic input controls have been developed into sophisticated total allowable effort (TAE) with individually transferable effort (ITE) quotas systems with capacity for both biological and economic management (Penn et al., 2015). For the longer-lived, cold-water pandalid shrimp and krill fisheries with less variable recruitment, total allowable catch (TAC) quotas with individually transferable catch (ITQ) quotas are often utilized to manage the trawl and trap fisheries harvesting these resources.

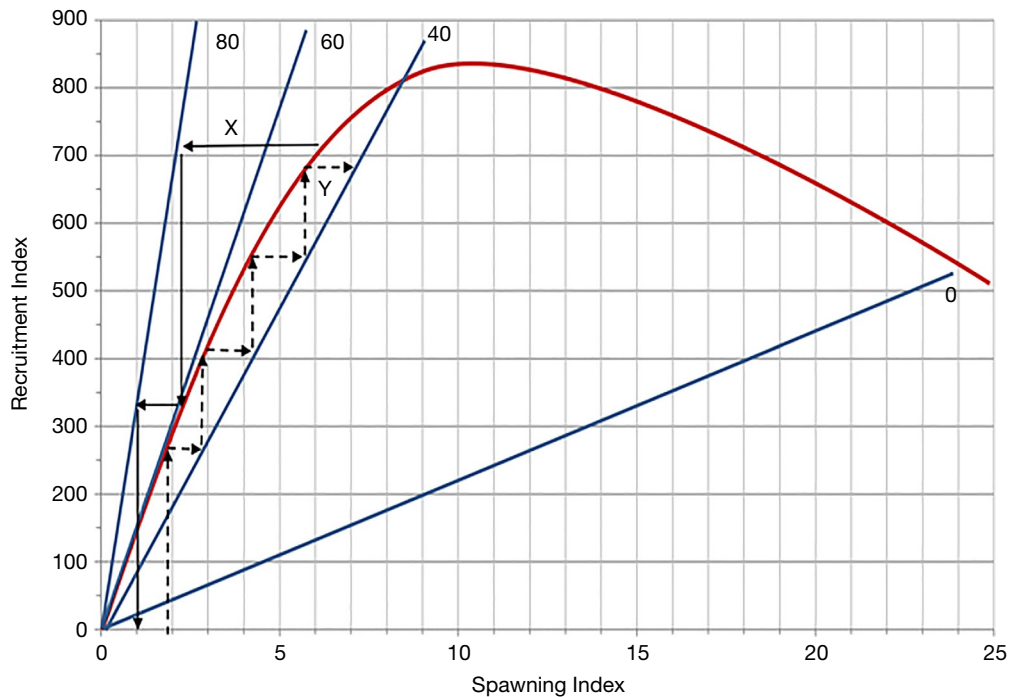


Fig. 3 A model combining the spawn stock-recruit relationship (red line) and the reverse recruitment to spawning stock relationship (as affected by fishing effort—blue lines) for the Shark Bay tiger prawn stock, which has been utilized to estimate optimal fishing effort levels. Trajectory “X” shows the expected annual decline in recruitment and spawning stock at an unsustainable level of fishing effort that is, at 80,000 of effective trawling hours. Trajectory “Y” shows the converse stock recovery from low levels when fishing occurs at optimal levels of about 40,000 h of trawling effort. Reproduced from Penn, J. W., Caputi, N., and Hall, N. G. (1995). Spawner-recruit relationships for the tiger prawn, *Penaeus esculentus*, stocks in Western Australia ICES Symposium on Shellfish Life Histories and Shell Fishery Models (1990). *ICES Marine Science Symposium* **199**, 320–333.

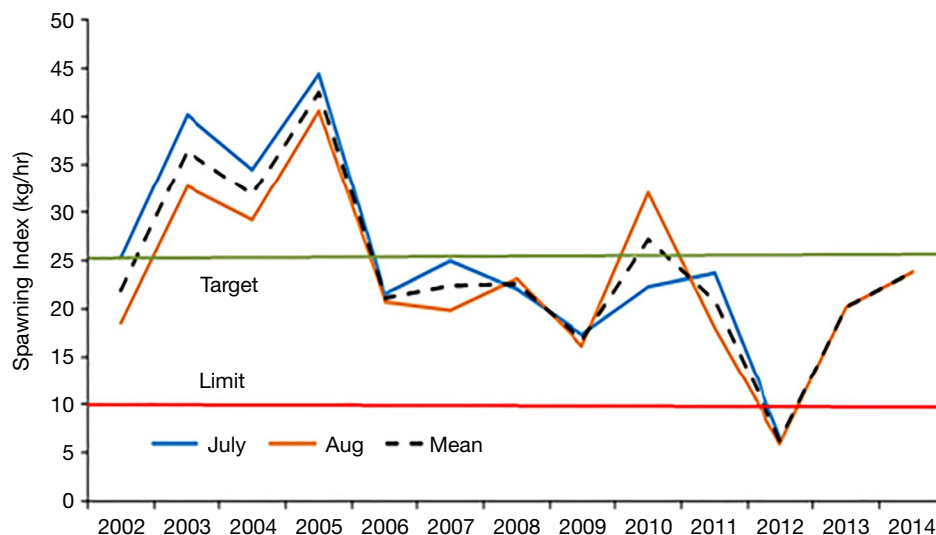


Fig. 4 The tiger prawn spawning stock index (catch rate, in standardized kg/h) from fishery independent surveys (2002–14) in Shark Bay with the “Target” and “Limit” reference point catch rate levels set in the management plan for the fishery to maintain sustainability. Reproduced from Kangas, M. I., Sporer, E. C., Hesp, S. A., Travaille, K. L., Brand-Gardner, S. L., Cavalli, P., and Harry, A. V. (2015). Shark Bay Prawn Managed Fishery. *Western Australian Marine Stewardship Council Report Series No. 2*, 294 pp. Western Australia: Department of Fisheries (http://www.fish.wa.gov.au/Documents/wamsc_reports).

For crab fisheries where the dominant capture method is by traps, the basic management focus is on legal minimum size regulations and protection for spawning females. These methods are particularly appropriate for crabs, which are typically larger in size (and value) and illegal animals can be discarded safely with limited mortality. Gear design rules specifying “escape gaps” to reduce the capture of undersize crabs have also become a common management tool for these fisheries. Overall management of the

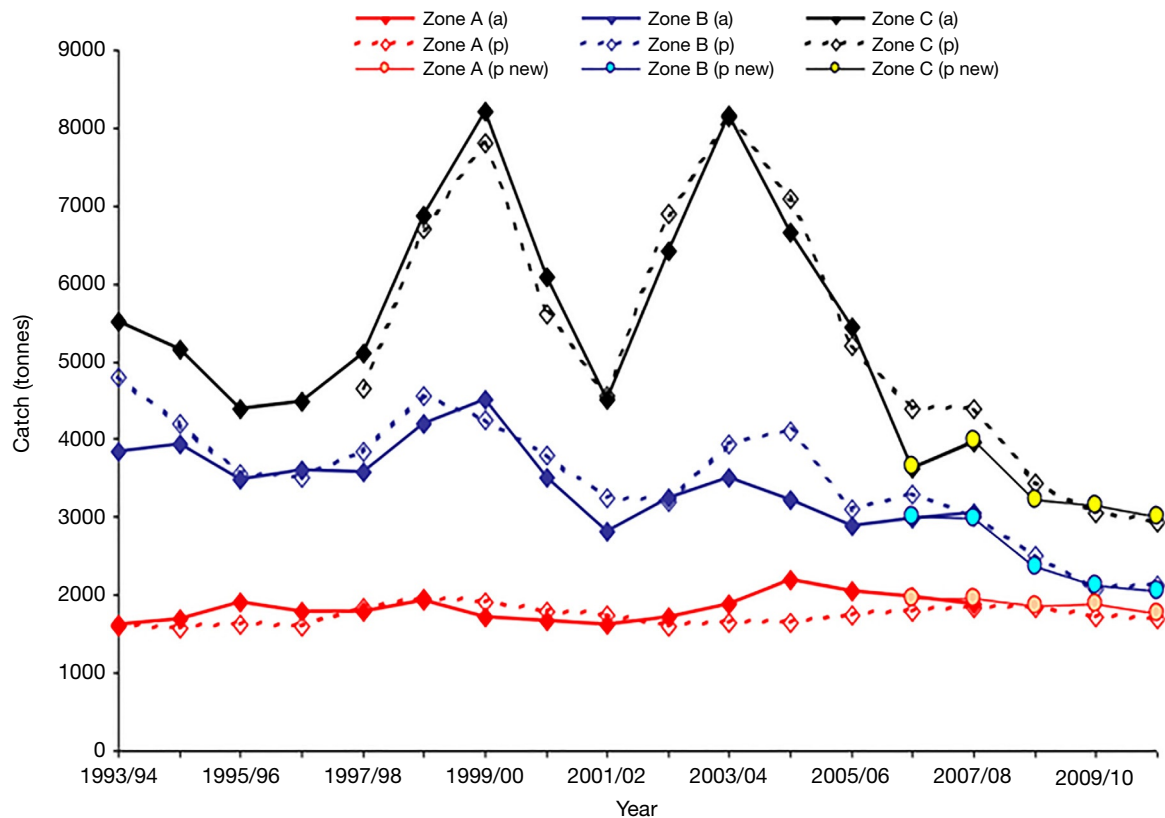


Fig. 5 Catches and catch forecasts (based on puerulus settlement 3–4 years prior) taking into account effort levels for the three fishing zones in the western rock lobster fishery from 1986/87 to 2007/08. Forecasts from 2008/09 onward assume the effort levels of 2007/08 continued; however, the catches achieved reflect the significant management changes to the TAE in 2008/09, 2009/10, and the implementation of a TAC in 2010/11. Reproduced from Penn, J. W., Caputi, N., and Hall, N. G. (1995). Spawner-recruit relationships for the tiger prawn, *Penaeus esculentus*, stocks in Western Australia ICES Symposium on Shellfish Life Histories and Shell Fishery Models (1990). *ICES Marine Science Symposium* **199**, 320–333.

longer-lived temperate and deep-water crabs often involves catch quotas to ensure maintenance of breeding stocks and economic performance of fisheries. This methodology is more difficult to apply to the faster-growing tropical crab stocks with more variable recruitment, unless there is a reliable method to predict recruitment or the catch quota is set conservatively. In many of these fisheries, effort controls through limited entry are more common.

The management techniques for high-value lobster stocks are generally similar to those for crabs, focusing on legal minimum sizes, associated gear controls, and female protection in the trap fisheries which dominate this crustacean sector. Limited-entry arrangements remain the most common overall management strategy for lobster fisheries, although these have been developed into TAE with ITEs based on tradable trap quota management systems in some spiny lobster fisheries (Penn et al., 2015). These more sophisticated management systems are required in high value species lobster fisheries to continually adjust for technology improvements which would otherwise result in excessive exploitation rates and ultimately overfishing. These systems with automatic fleet reduction capacity (Fig. 7) have been able to protect lobster spawning stocks when there has been a downturn in recruitment (Penn et al., 2015) through significant environmental perturbations and also facilitate a smooth transition to TAC based management if required.

Notably, more restrictive TAC management strategies with ITQs are now being applied successfully to some longer-lived cold-water lobster stocks, particularly New Zealand and Australia, to generate improved economic performance. In these fisheries there has been an increased focus on achieving the maximum economic yield (MEY) rather than maximum sustainable yield (MSY), which in turn requires more conservative TAC settings. This strategy maintains higher stock abundance, reduces the costs of fishing, increases profitability and also results in increased residual spawning stock levels (Caputi et al., 2015a). This situation is in contrast to the historically common management target of maximizing sustainable yield (MSY) that results in a higher catch, but can also lower profitability and create a higher risk to spawning stock levels particularly when it is applied under catch quota management systems.

The research and management systems developed for the Western Australian lobster fishery allowed it to become the first fishery certified under the now common Marine Stewardship Council third-party certification systems (Penn et al., 2015) and has led to a number of other crustacean fisheries in the state being certified (Kangas et al., 2015).

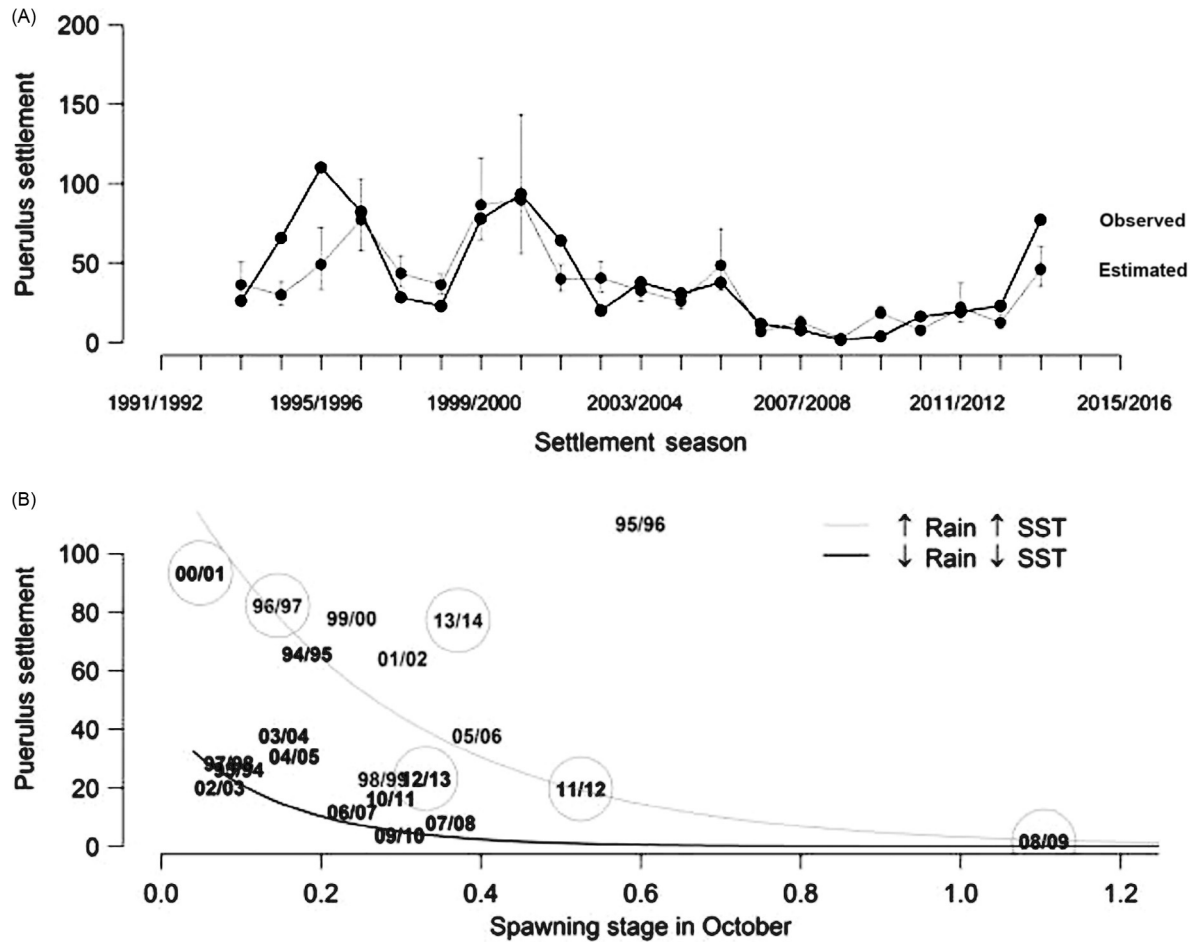


Fig. 6 (A) Observed (black) and estimated ± 1 s.d. (grey) standardized puerulus settlement between 1993/94 and 2013/14 seasons. (B) The relationship between the timing of spawning (year t) and the subsequent level of puerulus settlement (year $t + 1/t + 2$) under good environmental conditions (high rainfall and SST in year $t + 1$) and poor environmental conditions. Seasons shown represent the puerulus settlement seasons in high (grey) and low (black) rainfall years, with high SST years identified by grey circles. Reproduced from de Lestang, S., Caputi, N., Feng, M., Denham, A., Penn, J., Slawinski, D., Pearce, A., How, J. (2015). What caused seven consecutive years of low puerulus settlement in the western rock lobster fishery of Western Australia? *ICES Journal of Marine Science* **72**, i49–i58

Recent Developments

Knowledge regarding the effects of ocean acidification on many commercial crustacean fisheries is currently scarce, although concerns have been raised regarding the viability of crustaceans that require calcium carbonate for shell formation under future ocean acidification projections. Surface ocean pH is expected to decrease by 0.3 to 0.32 units by 2100 under the IPCC RCP8.5 scenario, primarily a result of rising anthropogenic atmospheric carbon emissions (IPCC, 2013). Ocean acidification can adversely impact calcium carbonate bearing organisms by lowering the saturation rate of calcium carbonate, and can engender reduced growth rates, and thinner shell formation (Cooley and Doney, 2009; Doney et al., 2012). Most marine crustaceans harden their chitinous and proteinaceous exoskeletons by depositing CaCO_3 with calcite, a less soluble form of calcium carbonate. Many crustaceans regulate extracellular pH through active ion exchange, and may therefore, possess a higher tolerance to acidification (Kroeker et al., 2010). The additional energy allocated toward extracellular pH regulation under acidified conditions, however, might result in reductions in metabolism, growth, and immunity. It is important to account for these energetic tradeoffs and consequences exhibited by some crustaceans under acidified conditions when formulating current and future management decisions, especially when considering the high value commercial stocks.

Several deleterious impacts of ocean acidification have been observed in crustaceans, particularly during more vulnerable larval and juvenile life history stages which could have direct management implications. For instance, larval American lobsters (*Homarus americanus*) exhibit smaller carapace lengths and slower molting cycles under acidified waters (pH = 7.7) (Keppel et al., 2012). Moreover, juvenile red king crabs (*Paralithodes camtschaticus*), tanner crabs (*Chionoecetes bairdi*), and larval blue crabs (*Callinectes sapidus*) have been known to suffer high mortality rates when subjected to pH concentrations predicted at the end of the 21st century (Long et al., 2013; Giltz and Taylor, 2017). Ocean acidification has been observed to not only compromise growth, but immune

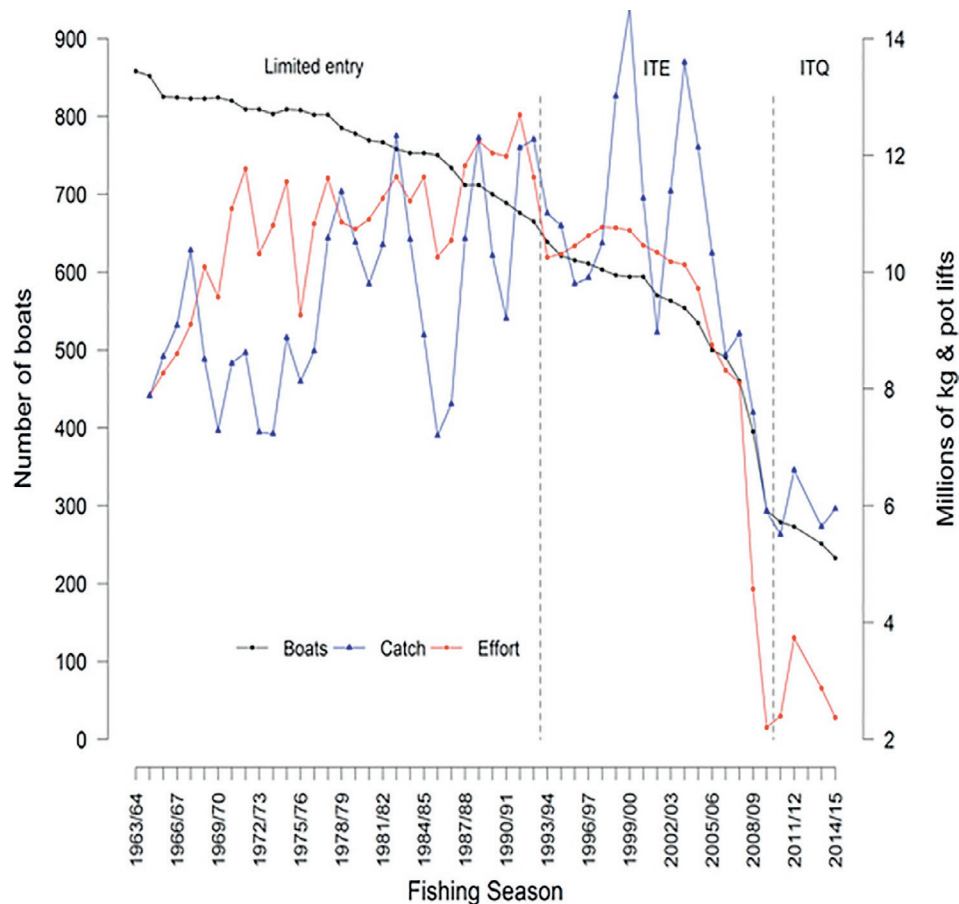


Fig. 7 Boat numbers, catches (millions of kilograms) and effort (millions pot lifts) in the West Australian rock lobster fishery in three periods: 1963/64–1992/93 when limited entry operated, 1993/94–2009/10 when ITE management was developed, and 2010/11 onwards following adoption of ITQ management. Adapted from Penn, J. W., Caputi, N., and de Lestang, S. (2015). A review of lobster fishery management: The Western Australian fishery for *Panulirus cygnus*, a case study in the development and implementation of input and output-based management systems. *ICES Journal of Marine Science* **72**, i22–i34. <https://doi.org/10.1093/icesjms/fsv057>.

response in several marine crustaceans. Suppressed hemocyte and phagocyte production, two proxies of immune response, is common for Norway lobsters (*Nephrops norvegicus*) when exposed to projected ocean acidification levels for the year 2100 (Hernroth et al., 2012). Reduced immune response expressed in crustaceans in acidified waters could enhance their susceptibility to disease, potentially conferring higher mortality rates and lower recruitment into fisheries. Outside of crabs and lobsters, the impact of ocean acidification on other taxa is not well understood. Only a handful of marine prawns and shrimp are noted to exhibit lower growth rates when residing in more acidic waters (low pH). Currently, few stock assessments have integrated ocean acidification impacts on crustacean fisheries yields and recruitment (Punt et al., 2014). The quantification of synergistic and additive effects of ocean acidification, temperature, and other environmental variables on fisheries yield, recruitment and stock dynamics is currently being emphasized in crustacean fisheries research.

Over the past two decades, the application of size-integrated models in stock assessments has become more common in crustacean fisheries management and has primarily been employed to enhance biomass and fishing mortality estimates (Punt et al., 2013). As aforementioned, the “stepwise,” discontinuous growth and lack of an innate internal structure that persists between molts creates a challenge for accurately quantifying age in crustaceans, so size structured models are often preferred for parameter estimation across multiple cohorts within a population or stock (Punt et al., 2013). Size-structured crustacean fisheries models incorporate similar parameters as catch-at-age models such as growth, recruitment, selectivity, environmental variables, age-at-maturity, catch and fishing and natural mortality estimates. Recruitment is commonly fit using classical stock-recruitment relationships and the proportion of the stock contributing to recruits (i.e., mature stock) is either prespecified or estimated by least squares or maximum likelihood methods (Punt et al., 2013). Growth among and within crustacean species varies considerably and is influenced by multiple factors, such as hormones, temperature, food provisions, and photoperiod. Blue crab and American lobster for instance, experience fast growth during high summer water temperatures which tend to induce molting (Chang et al., 2012). To account for growth variability, some modeling efforts include time-steps that account for multiple molting events in a year, latitudinal growth rate disparities within a species, and changes in gear selectivity across age classes (Punt et al., 2013). Despite

the advantages of using size-structured models for management purpose, the complexity of size-structured models can be difficult to interpret, predetermined priors are commonly mis-specified, and these models require a substantial amount of data (Punt et al., 2013). Overall, size-structured analyses have been implemented in many crustacean fisheries stock assessments around the world, including the United States, New Zealand, Australia, and South Africa (Punt et al., 2013).

Conclusions

The high value of crustaceans has led to increasing exploitation pressures and the need for improved research assessments to underpin management. Stock assessment methods for crustacean fisheries, however, provide significant scientific challenges owing to the unique crustacean method of growth through molting. This mode of growth prevents the use of the long-established age-based methods applied to the more generic finfish and some molluscan fisheries.

The crustacean stock assessment approach adopted has therefore focused on size (rather than age) based methods, direct measurement of recruitment and spawning stocks and the use of long-run fishery catch and effort databases. The importance of having long-run fishery-based data sets and associated stock prediction systems to validate and test length-based models has been critical to the more recent improvements in crustacean fisheries assessment needed for the management necessary to ensure sustainable harvest levels (Caputi et al., 2014).

Bibliography and Further Reading

The stock assessment and management examples provided are largely from extensive published work on Western Australian crustacean stocks. These single jurisdiction fisheries for tropical to temperate crustacean stocks are relatively unique in having all been subject to continuous research and detailed monitoring programs since their inception. The detailed time series data sets created by this process now extending to over 50 years in some cases, together with associated scientific review processes has allowed the development of a range of innovative stock assessment systems, specifically for crustacean fisheries which dominate this region. These crustacean case study fisheries were also some of the earliest subject to management using limits on entry, which subsequently evolved into sophisticated bio-economic control systems with detailed annual assessment and reporting (Fletcher and Santoro, 2014—<http://www.fish.wa.gov.au/About-Us/Publications/Pages/State-of-the-Fisheries-report.aspx>). These include the first fishery worldwide to achieve MSC third party environmental certification.

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