Biology and Fisheries for the Spot Prawn (*Pandalus platyceros*, Brandt 1851).

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This is to certify that I have examined this copy of a doctoral dissertation by

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and have found that it is complete and satisfactory in all respects,
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Abstract

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In this dissertation I investigate aspects of the biology and fisheries for the spot prawn (*Pandalus platyceros* Brandt 1851). I clarified several basic biological issues, including the geographic range and the length of the planktonic phase of the life cycle. I also improved estimates of the fecundity, growth rate, survivorship and longevity for this species, with reference to stocks in Washington State.

I studied bycatch in spot prawn trawl and pot fisheries, and showed that trawl fisheries had very high levels of bycatch, and likely caused severe damage to benthic habitats. Pot fishery bycatch was much smaller. Partly as a result of these studies, trawl fisheries for spot prawns were closed coast wide by 2003.

I developed three reliable polymorphic microsatellite markers for spot prawns and used them to genotype 525 individuals from 10 locations, mostly within Washington State. However, I was unable to detect any statistically significant differences between samples, probably due to a lack of power caused by the small number of loci and their low level of polymorphism. I did use the markers successfully to analyze the parentage of samples from 14 broods of eggs taken from wild ovigerous females. This showed no evidence for multiple mating in this species

Finally, I modeled the population dynamics of the spot prawn stock off the Washington outer coast. I estimated gear selectivity for pots and trawls and a stock synthesis model was fitted to individual vessel catch per unit effort indices from commercial logbooks and

length frequency data. The results showed that the dynamics of this stock are driven mainly by recruitment, which varied by a factor of 5 over the study period. Heavy fishing in 1997 to 2002 combined with low recruitment in 1997 to 1999 reduced the stock to less than 50% of its virgin level. However, some recovery was subsequently seen due to fairly large recruitments of 2 year old prawns to the fishery in 2001 and 2002, combined with reduced catches associated with the closing of the trawl fishery. Nevertheless, current catch quotas still appear to be higher than this stock will support sustainably.

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Introduction

This dissertation presents a study of the biology, genetics, population structure, and management of the spot prawn (*Pandalus platyceros,* Brandt 1851), a large protandric hermaphrodite shrimp endemic to the Northeastern Pacific Ocean. Although important commercial and recreational fisheries for this species are found throughout its range, it has been comparatively little studied, and management is somewhat ad hoc in many jurisdictions. Many of the fisheries have a fairly short history, and gaps in knowledge of the spot prawn's basic biology complicate management efforts. The objectives of my dissertation are to 1) better describe the species' biology; 2) analyze bycatch in the fishery; 3) use microsatellite markers to assess population structure; and 4) use new and existing data to parameterize and explore a stock assessment model. This work provides a thorough investigation into a previously poorly-described species as well as a foundation for sustainable management for spot prawn fisheries.

In Chapter 1 I present a broad review of the biology and ecology of the spot prawn. This draws on my own work as well as published and grey literature. This chapter summarizes current knowledge, fills in some existing knowledge gaps, and clarifies several areas of controversy about the species' biology. I present the first estimate of the length of the planktonic larval phase of the life cycle, based on a laboratory experiment following the development of wild larvae. I also cover newly compiled information on the range of the species and the diversity of habitat used in different life stages. Data which I collected in the course of other investigations and simulation modeling are also used to improve estimates of the fecundity, growth rate, survivorship and longevity of spot prawns, with a focus on the species in Washington state waters.

Chapter 2 covers investigations into the bycatch in spot prawn fisheries. Before I began this work in 1998, trawl fisheries were active in Washington, Oregon and California and were believed to have a high associated bycatch, based on anecdotal information.   My studies provided the first thorough investigation into the quantity and type of bycatch in

California and Washington, as well as analyses of potential bycatch reduction devices. In Section 1, I describe tests of three types of bycatch reduction devices and provide bycatch data under commercial fishing conditions off Southern California in 1998. Sections 2-4 are observations of bycatch in commercial spot prawn fisheries off the Washington coast. I made two trips with commercial trawl vessels in 1999 and 2000, and one trip with a pot fishing vessel in 2003. I compare the bycatch by fishery area and type and describe the possible damage to sea-floor habitat caused by spot prawn trawling. The chapter closes with a review of the effect of these and other studies on the regulation and development of spot prawn fisheries.

In Chapter 3 I investigate the genetic population structure of spot prawns in Washington waters. A number of lines of evidence such as the relatively short planktonic phase of the life history, relatively sedentary habits as adults and the oceanography of the areas inhabited by spot prawns, indicate the potential for the presence of complex patterns of genetic population structure within the species. In order to test this hypothesis I developed microsatellite markers for spot prawns and used them to investigate the genetic diversity of samples from ten areas in Washington. I also used these markers to study the parentage of broods of eggs being carried by females with the specific aim of determining if these broods were sired by a single or multiple males.

In Chapter 4 I present a case study into the management of a recently developed spot prawn fishery which exploits grounds off the outer coast of Washington state. I also develop a population model to assess the stock size and potential yield of the Washington spot prawn fishery. I used biological data from Chapter 1 to develop model parameters, and used a limited data set consisting primarily of commercial logbook data and length frequency samples to estimate stock size and yield. I end this chapter with a discussion on the implications for the management of the Washington fishery.

Chapter 1: Biology of the spot prawn

1.1 Introduction

This chapter summarizes current knowledge of the biology of the spot prawn. There are many knowledge gaps and conflicting accounts in published literature on topics including species distribution, reproduction, early life history, maximum age, number of times females reproduce, fecundity and growth rate. I have used my own data combined with analyses of existing data to attempt to fill these gaps and resolve some of the conflicts about the biology of the species.

1.2 Spot prawn phylogeny

The spot prawn (*Pandalus platyceros*, Brandt 1851) is a decapod crustacean in the family Pandalidae. The Genus *Pandalus* includes 19 species (Komai 1999), at least 7 of which support commercial fisheries. Pandalid shrimp are distributed throughout the northern hemisphere from subtropical waters to the Arctic. No members of the genus occur south of the equator (Bergstroem 2000). Most members of the genus are found from the lower intertidal down to about 500m depth. Komai (1999) divided the genus into four informal groups of species with similar characteristics (Table 1).

Table 1: Groups and species within the genus Pandalus (After Komai (1999))

P. montagui group	*P. stenolepis* group	*P. hypsinotus* group	*P. platyceros* group
P. montagui	*P. stenolepis*	*P. hypsinotus*	*P. platyceros*
P. borealis	*P. curvatus*	*P. danae*	*P. latirostris*
P. goniurus		*P. prensor*	
P. jordani		*P. gracilis*	
P. tridens		*P. gurneyi*	
P. eous		*P. nipponensis*	
		P. teraoi	
		P. chain	
		P. formosanus	

Komai (1999) considered *P. latirostris* and *P. platyceros* to form a species group within the genus *Pandalus*, based on physical characteristics. However, adults of the two species are unlikely to be confused with each other. *P. latirostris* is distributed in the northwestern Pacific from southeast Siberia to northern Japan and Korea, is a distinctly smaller species (maximum size 30.3 mm CL), and has a distinct coloration of white stripes on a greenish brown background (Komai 1999).

The genus *Pandalopsis* is very closely related to the *Pandalus*, and most closely aligned with the *P. platyceros* group within the genus. In the northeastern Pacific, the most common *Pandalopsis* species is the sidestripe shrimp *P. dispar* (Jensen 1995).

Pandalid shrimp are only distantly related to Penaeid shrimp, which form the bulk of the shrimp and prawn catch from subtropical and tropical waters, and are the mainstay of the farmed shrimp industry (Zetterstrom 2003).This figure also includes phylogeny of *Penaeus monodon*, which is the closest competitor to the spot prawn in seafood marketing terms, and the most commonly farmed species(Zetterstrom 2003). Although attempts have been made to farm pandalid shrimp, especially spot prawns, they have not been successful (Campbell1999, C. Campbell, aquaculture consultant, pers comm. 2006). Pandalids do support major trawl fisheries in both the Atlantic and Pacific oceans. The range of Pandalid shrimp shows little overlap with that of the Penaeid shrimp. Penaeids live in warm, shallow water, whereas Pandalids prefer colder, deeper regions (Baldwin et al. 1998).

Phylum	**Crustacea**	
Order	**Decapoda**	
Suborder	**Pleocyemata**	Dendrobranchiata
Infraorder	**Caridea**	----
Family	**Pandalidae**	Penaeidae
Genus	**Pandalus**	Penaeus
Species	***Pandalus platyceros*** **(spot prawn)**	*Penaeus monodon* (tiger prawn)

Figure 1: Phylogeny of spot prawns (including relationship to tiger prawns)

1.3 Characteristics

The spot prawn is the largest member of the genus *Pandalus*, reaching over 250 mm (8 inches) in total body length (60mm carapace length), and 100 grams (4 ounces) in weight (Butler 1970; Sunada 1984). They reach larger sizes in the southern part of their range.

Typically, spot prawns that are caught commercially are between 20 and 50 grams (33 – 45 mm carapace length) (P. Watanabe, seafood broker, pers comm. 2005). The characteristic features of the spot prawn are two pairs of white spots on the abdomen, one pair behind the head, and one pair in front of the tail. Adult prawns are usually light brown or orange in color, have orange and white banded antennae and often have longitudinal white stripes on the carapace (Figure 2). The species is a sequential hermaphrodite. Individuals mature first as males, breed and then change sex to become females. This life history is referred to as protandric hermaphroditism (Charnov 1979).

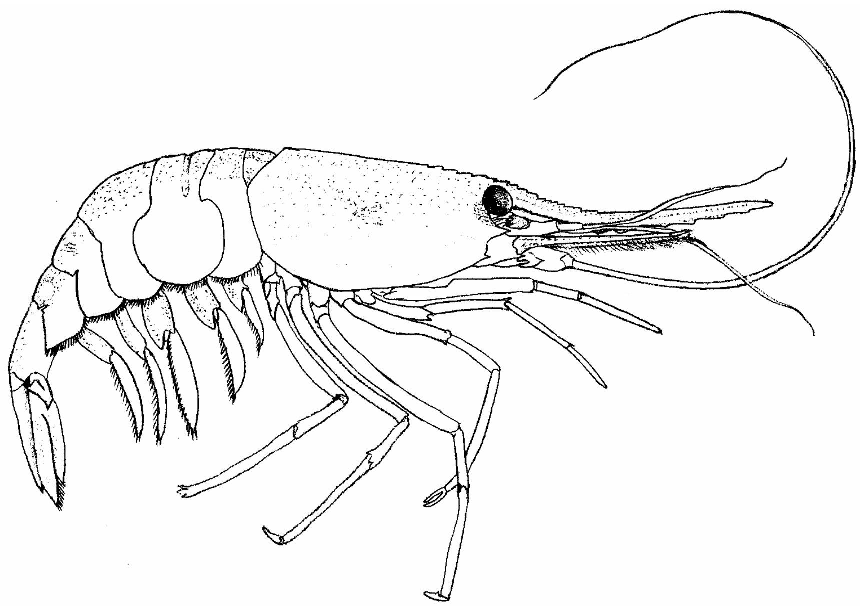


Figure 2: Adult spot prawn (female, 37.6 mm carapace length, San Juan Channel, 2000)

1.4 Distribution

Spot prawns are distributed in the Northeast Pacific ocean, along the west coast of North America from central Baja California to around Unalaska in the Aleutian Islands (Figure 3). The species has a wide bathymetric range from the shallow sublittoral to almost 500m, dependent on life stage (Butler 1970). There has been some disagreement in published literature about the range of spot prawns. Butler (1964) described the range of the spot prawn as being from "Unalaska to San Diego, and off the coast of Japan". He later (Butler 1970; 1980) expands this description to include "Hokkaido, Toyama Bay, Nagasaki, Korea and Vladivostok". Subsequent authors (e.g.Sunada 1986; Marliave and

Roth 1995; Schlining and Spratt 2000; Larson 2001) have cited Butler when describing the range of the spot prawn. However, in some cases they have only described the range as being Alaska to San Diego, without attributing the source for the different information (e.g. Sunada 1986; Marliave and Roth 1995)

Komai (1999) wrote a detailed review of the taxonomy of the genus Pandalus. He states that the range of the spot prawn is from Unalaska, Aleutian Islands, Alaska to San Diego, California. He notes that re-examination of a specimen from the Sea of Japan, which was identified as *P. platyceros* by Yokoya in 1933, is in fact *P. gracilis*. He says "Butler's (1970, 1980) summary on the distribution of the species is in part based on the erroneous record of Yokoya. So far *P. platyceros* has never been found in the Northwest Pacific." Recent publications have tended to follow Komai's lead, and some publications have changed the information they previously used (e.g. Watson 1994; Jensen 1995).

The range of the spot prawn does in fact extend much further south than San Diego. Experimental fisheries for spot prawns were conducted off Northern Baja California between 1999 and 2001 (J. McKay, commercial spot prawn fisher, pers. comm. 2002). Prawns were caught as far south as Ensenada. The programs were sanctioned by the Mexican government and involved spot prawn fishermen from the U.S.A. Catch rates were not as high as those found further north. The final results of the experimental fishing program were not published, and it appears that no commercial fishing has developed. The range of the species probably extends at least as far south as Punta Eugenia near the middle of the Baja California peninsula. This point is a natural biogeographic boundary where the distributional limits of many species occur (Briggs 1974). The region from Vancouver Island in the north to Cabo San Lucas in the south is often referred to as the California current system (Hickey 1979), and is essentially the eastern limb of the Central Pacific Gyre (Field et al. 2006). Within the southern part of this region, three major biogeographic barriers are recognized, at Point Conception, Punta Eugenia and Cabo San Lucas (Terry et al. 2000). As the spot prawn range encompasses the Point Conception boundary, and no records have been found from South of Punta Eugenia, this seems a reasonable estimate for the limit of the southern distribution.

There is no recent published review of the northern limit of the spot prawn range, so it is not possible to confirm whether the limit at Unalaska is correct. However, the northern limit for fisheries has moved south in the recent past, and the range of the species may also have contracted over the last few decades. Populations around Kodiak, Kachemak Bay and Prince William Sound were at one time productive enough to support fisheries, but no longer do so. There have been long term declines in abundance and distribution of Gulf of Alaska Pandalid shrimp stocks in Alaska, beginning in the late 1970's. These declines are thought to be primarily due to unfavorable ocean conditions (Anderson and Piatt 1999). Generally under current conditions the productivity of areas for spot prawns decreases moving north from the Canadian border, with the effective limit for commercial fishing being around Yakutat.

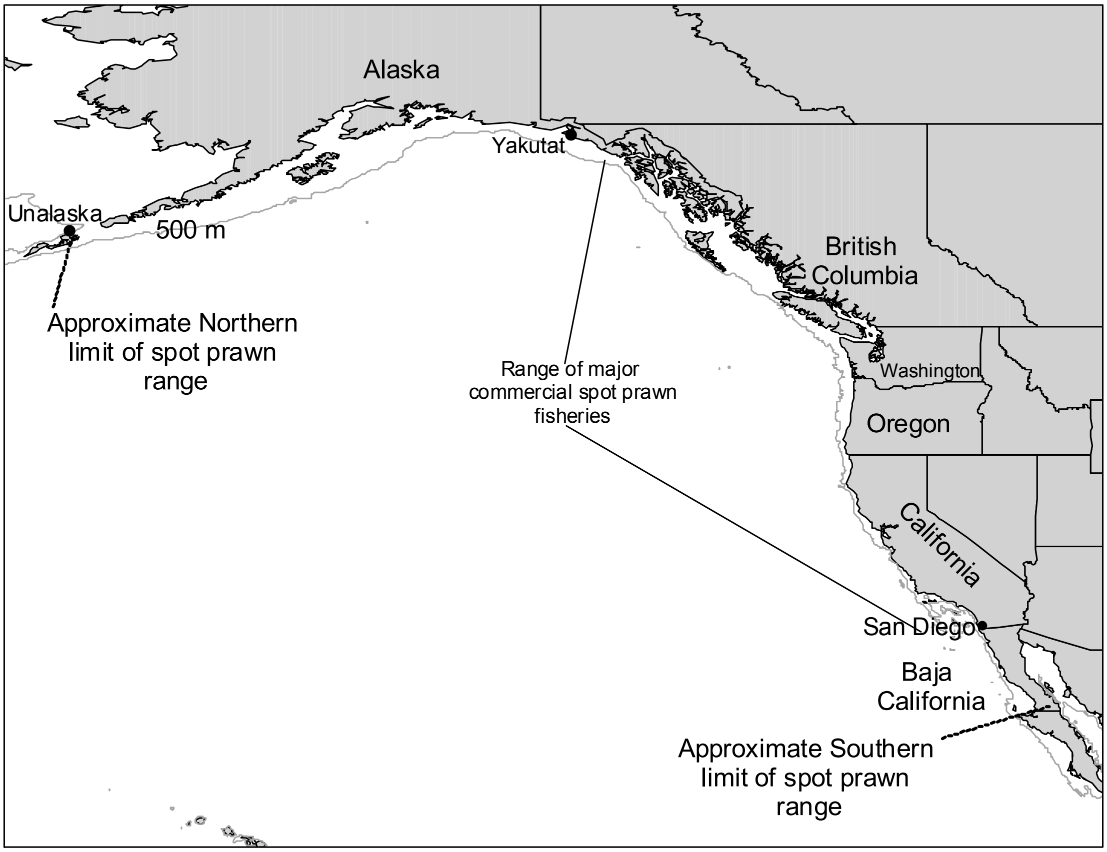


Figure 3: Biological and commercial spot prawn range.

Habitat use (ocean depth and substrate)

Spot prawns spend the first part of their life in shallow water, but then migrate to depth after maturing. The length of the time in shallow water and the depth of the adult grounds vary depending on latitude and habitat availability.

Spot prawns occur in both protected waters and off open coasts, and there appear to be some ecological differences between these two types of populations. In protected waters they are found in channels, sounds and fjords, such as Prince William Sound, the inside waters of the Alaska panhandle, the Queen Charlotte Islands and Straits of Georgia in British Columbia, and the Strait of Juan de Fuca, Hood Canal and Puget Sound in Washington. The Santa Barbara Channel and Channel islands in California are also home to high densities of spot prawns. In the northern part of the range, mature adult spot prawns are most abundant between 45-140 m (25-75 fathoms (fm), with the depth range increasing to the south, to 100–165 m (55-90 fm) in southern British Columbia and Washington. The Santa Barbara channel fishery targets depths from 165-250 m (90–140 fm).

Adults of open coast populations are often found around the shelf break, or at the heads of submarine canyons. Notable concentrations occur in Juan de Fuca and Gray's Canyons off the Washington coast, Monterey Canyon, Carmel Canyon, southern California's offshore islands, and the canyons of the Big Sur coast and the Southern California Bight. They tend to be deeper than protected water populations at similar latitude, and there is a similar change in depth with latitude as seen in inshore populations. Open ocean stocks in Alaska and BC have not been extensively explored, but those in Washington are found at depths from 150-220 m (80-120 fm). Few areas with high concentrations of prawns were found in Oregon, but they were all at depths of 165–230 m (90–125 fm). Fisheries in California are deeper still, 200-400 m (110-220 fm).

Spot prawns appear to be generalists in regard to habitat requirements, preferring some degree of complexity or cover. This seems to be similar in all areas. They are usually found in or near rocky ground (Butler 1980; Sunada 1984), but other sorts of cover are also utilized. Direct observations of spot prawns from submersibles have shown them to be in crevices on rock faces and in lairs under boulders (Butler 1980). Detailed analysis of video transects reported by Schlining (1999) provide the best available analysis of adult spot prawn habitat associations. She showed that prawns were not usually associated with barren sediments, but appeared to actively seek out habitats that are more complex. She also reports that prawns are associated with drift algae (loose kelp on the sea floor) where this habitat type occurs. Prawns have also been observed in areas of shell hash in the San Juan channel (N. Lowry, pers. obs. 2003) or in depressions on muddy bottoms (A. Dalton, Muckleshoot tribal fisheries. pers. comm. 2003).

In protected waters prawns may make diel migrations into shallower water at night with a return to depth during the day. Chew et al. (1974) observed this in Hood canal, and showed movements from approx 30-40 fathoms into 10-30 fathom range. It is not clear if this is the case for all protected water populations, and some believe that it is unique to Hood Canal, Protection Island and Saratoga Passage in Washington (J. McKay, commercial fisher, pers. comm. 2005). Diel migrations do not appear to occur in open coast populations. Little difference is noted in the catch rates and depth range according to time of day off the Washington coast (see Chapter 4).

Once they have settled and migrated to adult grounds, spot prawns appear to remain in a very restricted area throughout the rest of their life, probably limited by the size of the habitat patch they inhabit. Tagging studies have shown that prawns were captured within 1.7 km of their release location over periods of several months (Boutillier and Bond 1999) to years (Kimker et al. 1996). Other evidence of restricted movement of adults is found in parasite loads, which vary considerably between adult patches as close as a few tens of kilometers (Bower and Boutillier 1990; Bower et al. 1996). There is also evidence of isolated patches of spot prawns apparently resulting from single recruitment events, which live out their entire lives in one area without migrating to nearby habitat which is apparently suitable (Boutillier and Bond 1999).

1.5 Life history

The life history of spot prawns is not particularly well understood. There are gaps in the details of early life history, most notably the length of the planktonic larval phase. There is also disagreement in the published literature about the maximum age which the species reaches, how fast they grow, and whether they are iterparous or semelparous.

Reproduction

Spot prawns are protandric hermaphrodites: they are born as males and mature and mate at least once before changing sex to become females. The sexual stage of a spot prawn can easily be determined by examination of the inner part of the endopod of the second pleopod. This has two appendages, the appendix masculina and the appendix interna which vary in size depending on the sexual stage (Figure 4)

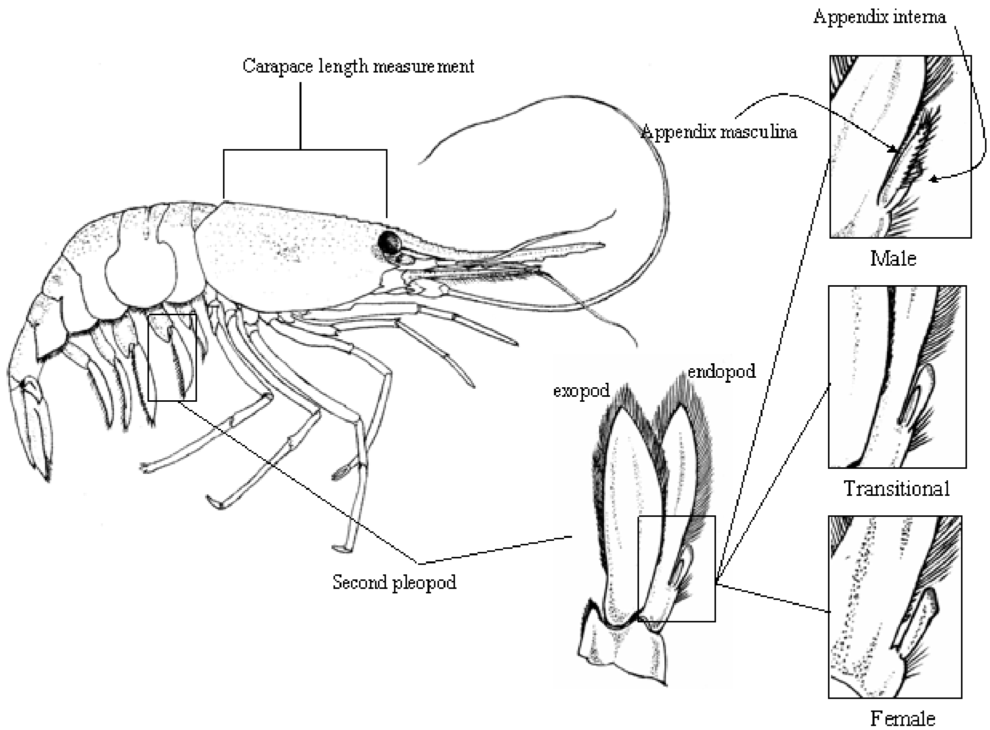


Figure 4: Sex determination for the spot prawn

The sex changing life history strategy has been shown to be an efficient way to maximize the lifetime reproductive output of an individual shrimp (Charnov 1979). In some Pandalids a proportion initially mature as females, but this has not been seen in spot prawns; in addition, the presence of such primary females for a shrimp of this size and longevity is not consistent with Charnov's theory.

Spot prawns mate in deep water in the late summer or early autumn. Mating behavior has not been observed in the wild, but has been seen in a laboratory (Hoffman 1973). However, in Hoffman's (1973) observations, multiple males mated with a single female. Genetic analysis (see Chapter 3) has shown that that broods of eggs carried by a female are likely fathered by a single male, and so it is unlikely that multiple mating happens in the wild. As in most pandalids, mating occurs at night shortly after the female has molted (Bergstroem 2000). The females develop long hair-like setae on the pleopods during this pre-mating molt. Prior to molting and mating the developing eggs can be observed as a dark band inside the thorax of the female. During mating, the males take up a position with the anterior of the abdomen under the posterior of the female's cephalothorax. The male then attaches spermatophores to the abdomen of the female. These are subsequently used in fertilization within a few days when the female extrudes the eggs. The eggs are slightly ovoid and average approximately 1.5 by 2 mm in diameter (Butler 1970). They are a bright orange color when freshly extruded, and become more brownish as they mature (Butler 1970). The eggs of the spot prawn are larger than those of most other pandalid shrimp, (*P. jordani* 0.85 mm (Dahlstrom 1970); *P. montagui* 0.7 mm (Simpson et al. 1970)). The exception is the grass shrimp *P. latirostris,* which has eggs that are similar in size to the spot prawn (Dautov et al. 2004). *P. latirostris* is the species most closely related to the spot prawn (Komai 1999).

Fecundity

The only reliable estimate of spot prawn fecundity was reported by Butler (1970), based on a small sample from British Columbia. In order to get a more reliable estimate for Washington, I estimated the number of eggs carried by 40 females from Gray's Canyon (n=15), central Puget Sound (n=16) and Hood Canal (n=9). Carapace length and total wet weight of each prawn was measured to the nearest 0.1 g. The eggs were separated from the female, and blotted dry before weighing. A sample of 100 eggs was then counted and weighed to the nearest 0.0001 g. The total number of eggs in the brood was calculated by dividing the total weight of the brood by the sample weight *100.

Carapace lengths and weights (without eggs) of ovigerous female shrimp ranged from 36.6 – 58 mm and 28.5 – 99.5 g respectively. The estimated number of eggs ranged from 385 to 9003 (Figure 5). A model fitted to the data by maximizing likelihood was $F=0.000909L^{3.9204}$, with $R^2=0.4875$ (where F=number of eggs and L=carapace length in mm). Although there was no overlap in the adult size range between the Gray's Canyon sample (45 -58 mm) and the other samples (37 – 44 mm), there were no significant differences between deviations from the model for any of the samples. Some individuals in each sample had broods which appeared to be very small, as can be seen in the figure.

The expected brood size by length is slightly lower than that reported by Butler (1970) ($F=0.00878L^{3.39675}$). However, the size range of prawns in Butler's sample only ranged from 33.5 to 41.4 mm, and may not have included individuals with small broods as my samples did.

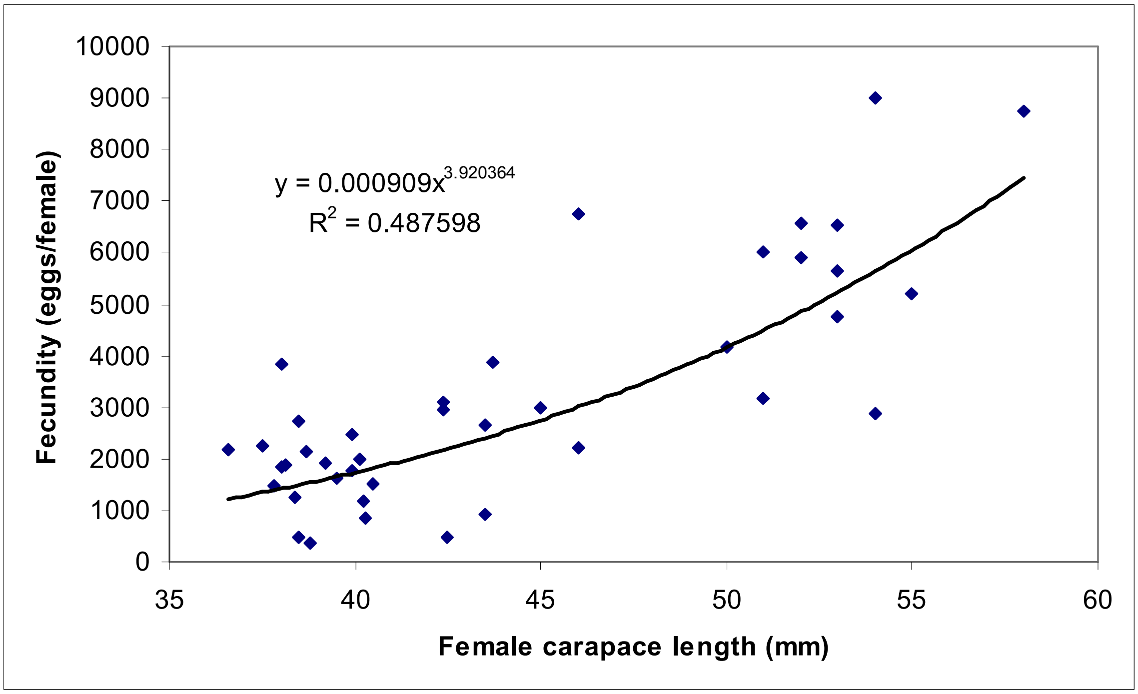


Figure 5: Relationship between fecundity and carapace length for spot prawns.

Female spot prawns carry their eggs on the first 4 pairs of pleopods between fertilization and hatching. Most females are ovigerous (carrying eggs) by late October in BC (Butler 1964), and they carry the eggs throughout the winter months. During this 5 to 5½ month period, the females continue to feed and move about and hence are vulnerable to fishing. The eggs are released by the female and hatch in the late spring. This happens at night in deep water. The female raises her abdomen and flaps the pleopods until the eggs are free, and they hatch immediately (Figure 6). Eggs are hatched in late March or early April throughout the range, although larger females seem to shed their eggs later than smaller females within any particular area. An individual female will typically release her brood over three or four successive nights.

Figure 6: Female spot prawn releasing eggs in the laboratory.

Larval biology

The larvae are very large and well developed in comparison with other pandalids when they hatch, and are approximately 8mm in length (Figure 7), compared with only 4-5mm for *P. borealis* (Shumway et al. 1985). Growth stages were fully described by Price and Chew (1972). The first two larval stages are planktonic and positively phototrophic (Price and Chew 1972) and probably swim to the surface. They are found in the water column over deep water near the locations at which the adults are found (Berkeley 1931; Dunagan and Lowry in review). The amount of time the larvae spend as plankton before settlement has not yet been accurately determined in the wild. Recent work (Dunagan and Lowry in review) showed that in laboratory conditions larvae settle at the third larval stage in less than 20 days at a temperature of 8.5 $^{\circ}$C. In this experiment a preference was shown for seaweed as a settlement substrate. A series of plankton tows in an area of the San Juan islands with a high concentration of spot prawns during the period at which larvae would be in the water column caught no larvae beyond stage 3. In experiments done to assess the suitability of spot prawns for aquaculture, Campbell (1999) stated that the larvae sought hiding places after 10 days and 2 molts, i.e. at stage 3. Berkeley (1931) also stated her belief that migration to nursery habitat and settlement occurred at the third larval stage. Price and Chew (1972) stated that the 5^{th} stage was the first postlarval stage (i.e. the settlement stage) reached after approximately 40 days, but the conditions in their experiments were apparently not ideal. The temperature in their rearing chamber was highly variable (7-22 °C), growth rate per stage (9days) was slower than I observed, and no substrate for settlement was provided. A paper circulated by the Canadian Department of Fisheries and Oceans (Anon 2001) states that the larval period is 12 weeks. In the light of the above works, this seems to be incorrect, and is probably based on a note by Butler (1964) which states that he first collected juveniles in midsummer. The relatively short (10-20 days) planktonic larval period has major implications for population structure of spot prawn stocks, and is likely to lead to greater separation of stocks than would be expected for other crustaceans with longer larva duration (see Chapter 3).

Figure 7: Stage 1 spot prawn larva.

Juvenile biology

Settlement of larvae out of the plankton occurs in shallow water. The juveniles remain in this shallow water habitat until shortly before they mature. It is not known if the larval prawns actively swim to seek out settlement habitat or if their movement from deep to shallow water is driven by wind and tides. Marliave and Roth (1995) observed post-larval prawns in shallow (10-15m) water *Agarum* kelp beds in May and June in British Columbia. Barr (1973) observed that the principal habitat requirement for juveniles in Alaska was for some kind of cover, including kelps such as *Laminaria* or *Agarum*, sunken wood debris or even artificial materials. The average depth at which they were observed was 13m. I also found juvenile spot prawns in the San Juan Islands in kelp beds, as well as green algae (*Ulva* sp.) and eelgrass beds (Lowry, pers. obs. 2000, 2002). In the latter habitats the juveniles are a distinct green color which matches the substrate, while in kelp beds they tend to be brown. Other than this they closely resemble the adults. The 17mm CL juvenile shown in Figure 8 was caught in eelgrass in October, and had a bright green coloration. In the nursery area off San Juan Island, the depth range inhabited by the prawns was approximately 2-10 m. Exploration using a video camera showed that suitable habitat was not available at greater depths in this bay. Sunada (1984) notes that juvenile prawns are also found in shallow water in the Santa Barbara channel. Juvenile prawns in these nursery areas are nocturnal, hiding from predators in cover during the day and venturing out to feed at night.

Figure 8: Juvenile spot prawn 17 mm carapace length.

Young prawns follow a well established pattern of migration from shallow nursery areas into deeper water (Butler 1970; Sunada 1984). The cue for emigration out of the nursery is probably size-related, occurring as they reach a carapace length of about 20mm. This appears to be relatively constant across the range, and has been noted by Barr (1973), in Alaska, Marliave and Roth (1995) in British Columbia and by personal observations in the San Juan Islands, Washington (2000, 2002). The smallest prawns noted by Sunada (1986) in an analysis of commercial catches in the Santa Barbara channel were 18-21 mm, which indicates them leaving nursery areas at similar size to more northerly populations.

However, there is a wide variation in growth rates across the range, which leads to some variation of the age at which the juveniles leave the nursery. Growth rate in Pandalid shrimp has been shown to be closely linked to water temperature (Parsons et al. 1989; Hansen and Aschan 2000; Wieland 2004), so a latitudinal gradient in growth rates can be expected. Barr (1973) reported that all juveniles in southeast Alaska over-wintered in the nursery area and recruited to the adult population in their second summer. In contrast, Marliave and Roth (1995) observed that most of the prawns in British Columbia remained in shallow nursery habitat until early fall, but some slower growing individuals over-wintered in the nursery habitat and emigrated the following summer. This potentially complicates the estimation of age structure from population length frequencies in this area, since each length mode could consist of more than one age class. In the San Juan Islands, juveniles collected in November averaged 17-19 mm. The length frequencies in these samples appear truncated at around 20-22 mm (Figure 9), indicating that juveniles are migrating at about this time. No juvenile prawns were seen in the same area in April. It seems likely that the vast majority of the prawns reached the threshold size and migrated before the end of the year in this area (Lowry, pers. obs. 2000, 2002).

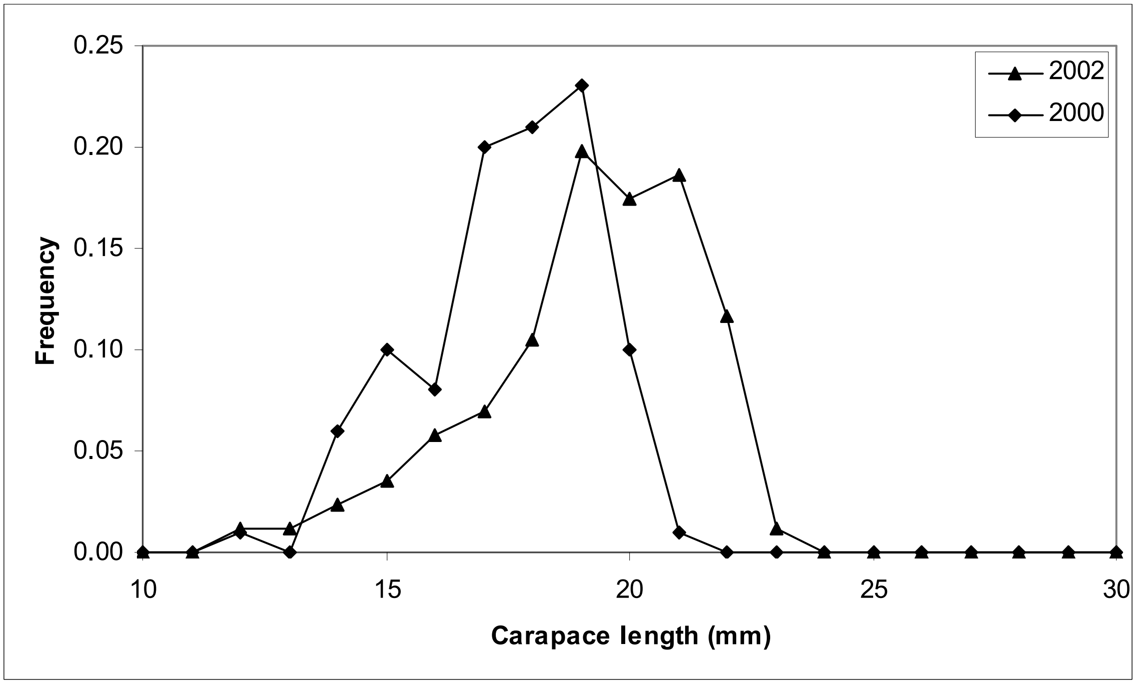


Figure 9: Length frequency of juvenile spot prawns caught in Griffin Bay, San Juan Island in 2000 and 2002.

Few prawns less than 30 mm carapace length were seen in catches made with small-mesh (12.5 mm) pots deployed on commercial fishing grounds (155 to 247 m) off the Washington coast in 2001(pers obs. 2001), or trawls with a mesh size of 50 mm. It is possible that prawns in these coastal stocks remain in nursery habitats until they reach a larger size than those in sheltered waters. The distances between where the nurseries for these stocks are presumed to be and the adult grounds are greater than other areas, so an alternative explanation is that the prawns are staging in some intermediate areas and growing during this time.

Maturation and growth

After migrating to the adult habitat areas, the prawns mature and become functional males. Pandalid shrimp have a very plastic life history, and have been shown to have very variable size and age at maturity and at sex change (Charnov and Anderson 1989; Bergstroem 2000; Koeller et al. 2000). Spot prawns in British Columbia first begin to mature (as males) at a minimum of 1.5 yrs of age. By this time they measure about 28 mm carapace length (CL) (Butler 1970). They remain as males for a year and mate in late summer. Sex reversal occurs the following winter and spring. These prawns are between 2.5 and 3.5 years (33-38 mm CL). The prawns mature as females in time to mate for the first time in the late summer. Mature females are 3.5 years and older (>42 mm).

In Washington there is wide variation in size at transition from about 35 mm CL in Hood Canal to 40 mm CL in the Strait of Juan de Fuca (pers. obs. 2000, 2001). Prawns off the Washington coast are slightly larger, changing sex at about the same size as those observed in California (40 - 45 mm CL)(Sunada 1986). There is also some variation in the size at sex transition reported in Alaska, ranging from 37-39 mm CL to 43-44 mm CL (Love and Bishop 2005). In the northern part of the range, growth rates are slower and each life stage may be reached a year or more later than in more southerly areas. Sunada (1986) reports that in the Santa Barbara channel (California), males mature at a larger size (40 mm), transition at 45 mm and mature as females at 50 mm. He concluded that these life stages were reached a year later than in Washington populations (male at 3.5 years, transition at 4, female at 4.5). However, his assumptions on growth rates of juveniles may have been incorrect, and the ages may be the same, with a faster growth rate in California related to higher water temperatures.

Charnov and Skuladottir (2000) described a relationship between maximum size and size of sex change which was constant over multiple populations and years for *Pandalus borealis* populations off Iceland. Within each population, the average size at sex change was 0.80 of the maximum size. This type of relationship appears to also hold for spot prawn populations. Figure 10 shows the relationship between maximum size (L_{max}) and the size at which 50% of the prawns became mature females (L_{50}) for 7 populations in Washington. The resulting proportionality constant (0.82) is very close to that found by Charnov (0.80). The sample sizes in this analysis are smaller than would be desired and may slightly underestimate L_{max}. The actual ratio in the population may be very close to that estimated by Charnov.

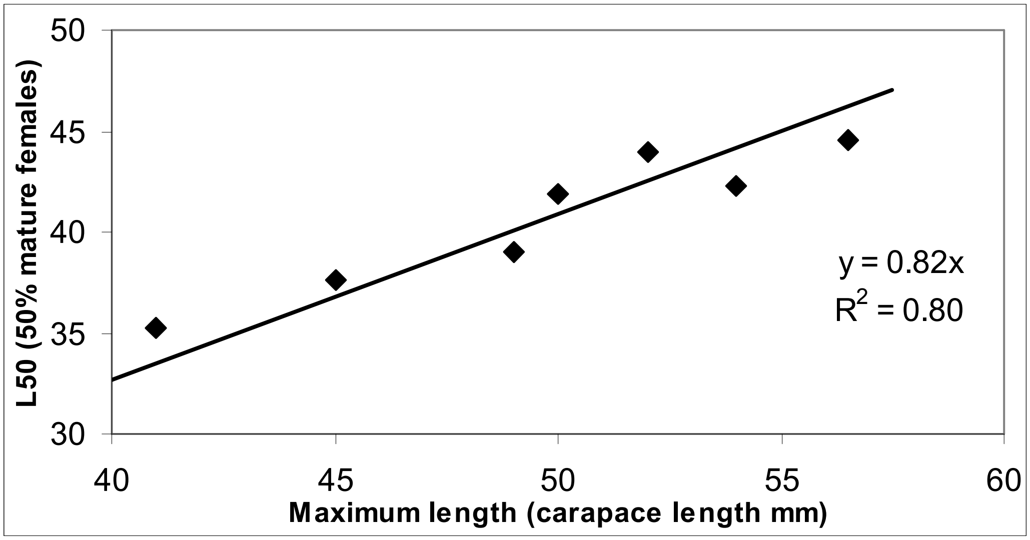


Figure 10: Relationship between size at sex change (L_{50}) versus maximum size for 7 spot prawn populations in Washington.

It has been suggested that the size at sex change is influenced by fishing in some pandalids, with more heavily fished populations changing sex earlier, at a smaller size (Charnov 1981; Charnov and Hannah 2002). This is particularly notable with the increasing proportion of primary females (individuals which first mature as females, skipping the male stage) in some heavily fished populations of *P. jordani* (Hannah and Jones 1991). In Figure 10, the two leftmost points on the figure represent samples from Discovery Bay and Hood Canal respectively, which are the most heavily exploited spot prawn fisheries with the longest histories of exploitation in the state. In contrast, samples from open coast fisheries which have only recently been exploited show higher L_{50} and L_{max}, but at a similar ratio. However, an alternative explanation is that the variations in the size at each life stage simply reflect variations in growth rates (Koeller 2006). This is the more likely explanation here as there is no indication that there are any primary females in any of the populations, or of any other change in the age at which each life stage is reached.

All crustaceans grow by molting and therefore growth is a discontinuous process. Growth rate depends on the frequency of molting and the amount of growth at each molt. An individual prawn that is well fed will grow more, and if it has endured severe stress, it will either not molt or grow less at each molt. The stress of spawning probably has an effect on growth. I observed growth of post-spawning prawns held at Friday harbor laboratory in 2004 and 2005. Ovigerous females were captured by trawling in the San Juan Channel, maintained in tanks, and allowed to spawn. Each female was subsequently held in an individual tank for up to three months, during which time most molted once. During this three month holding period, the prawns were regularly fed on pieces of fresh fish, and temperature was maintained at the ambient temperature of the water in the San Juan Channel (approximately 11 °C). Multiple measurements were made of these prawns before and after molting. Measurements of a total of 18 prawns showed a range of growth during this molt from -0.55 mm to 0.90 mm (i.e. some were actually slightly smaller after molting than before). Average growth was 0.26 mm. After molting, these prawns were effectively indistinguishable from virgin females[1]. The post spawning females would be expected to molt once more before mating in the fall and would grow somewhat during that molt, perhaps by 1-2 mm. They then would not be able to molt and grow any more until after releasing the eggs the following April. This represents a slower average annual growth rate for females after their first breeding episode than would be expected based on their growth rates before breeding.

Kimker et al. (1996) tagged prawns in Prince William Sound, Alaska to study their growth rate. Some of these prawns showed no growth over 3 years. Epiphytic organisms often grow on prawn carapaces (Childers et al. 2004), and would be likely to create a lethal burden in three years (R. Childers, WDFW. pers. comm. 2004), so the most likely conclusion is that these prawns had molted but not grown. As noted above, this makes estimation of growth rates and maximum age from length composition alone very difficult. The growth rate estimated by Kimker et al. (1996) is not reflective of the entire population, as they only used data from those prawns that had grown between release and

[1]McCrary (1971), noted that sternal spines located on the ventral surface of the abdomen could be useful for distinguishing between virgin females and older age groups that had previously spawned in a number of species of *Pandalus*. However, in spot prawns, the sternal spines of virgin females and recently molted post spawning females are identical (C. Dolphin, Lummi fisheries Pers. Comm, 2005)

recapture. As approximately half of the recaptured prawns had not grown, the actual average growth rate for prawns in Prince William Sound would have been substantially less than their estimate.

Estimation of growth rate of spot prawns in Washington

There is substantial variation in individual growth of prawns, but the von Bertalanffy growth curve should describe the average growth of a cohort adequately.

$$L_a = L_{inf} * (1-\exp(-K*(a-t_0)) \qquad (1)$$

Where L_a is length at age a, L_{inf} is the average maximum length, K is a rate constant, and t_0 is the age at zero length.

The few published estimations of growth rate show substantial variation across the range of the species (Table 2). To some extent this reflects the wide variation in conditions such as water temperature experienced by the prawns across the range. As noted above, the amount of time that juveniles spend in nursery areas varies with latitude, and growth rates are affected by water temperature.

Table 2: Published spot prawn growth data. Size at age represents the average size of prawns, assuming a birthdate of April 1. Von Bertalanffy parameters marked with an asterisk are estimated from the size at age data, others are published values.

Source	Area	Size at age				Von Bertalanffy parameters			
		1	2	3	4	K	L_{inf}	t_0	
Sunada 1986	Santa Barbara Channel	16	28	37	46	0.157	96.0	-0.18	
Butler 1964	East Vancouver Island	21	29	34	40	0.266	55.6	-0.84	*
DFO 2007	British Columbia	23	34	40	42	0.651	46.3	-0.06	*
Kimker 1996	Prince William Sound	12	22	29	34	0.290	49.2	0	

No estimation of growth rate of spot prawns has been published for Washington waters. However, a reasonable amount of length frequency data is available which can be used for this purpose.

Spot prawns in Washington follow a similar life history to that described above for BC. They spend their first years as males, mate at age 2.5, change sex at approximately age 3, mature as females at age 3.5 and remain as females for the rest of their lives. During the late winter and spring the 3 year olds are in a transitional stage, which can easily be identified by examination of the second pleopods (Figure 4). Therefore data sets in which length and sex information is collected during the transitional period effectively have three stages identified. These stages are not strictly year classes, males are age 1 and 2, transitionals 3 and females 4 and older. Outside of the transitional period, the two sexes represent two stages, males age 1.5 and 2.5, females 3.5 and older. Figure 11 shows the length frequency of a sample in which four age groups can easily be identified.

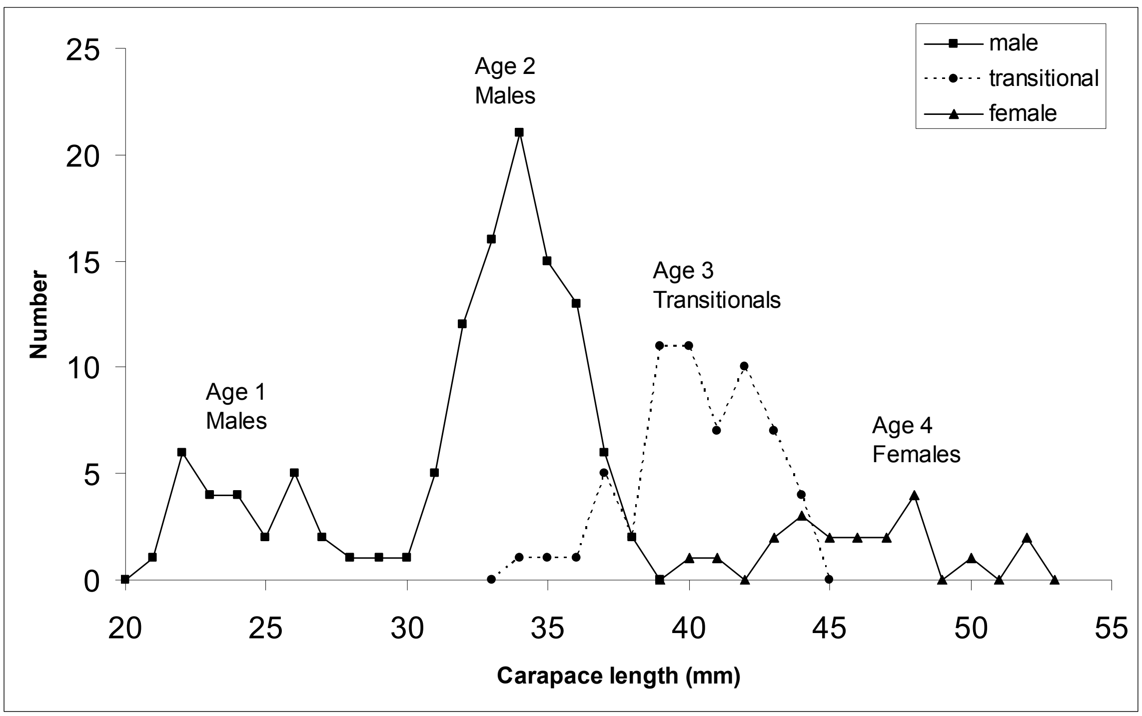


Figure 11: Spot prawn length frequency, Strait of Juan de Fuca, spring 2000.

To estimate a growth curve from this data, the population was modeled assuming that each age group could be represented by a normal distribution (eq. 2), with the mean size of each age group described by the Von Bertalanffy growth function (eq. 1). The modeled age groups were matched with the stages described above. For samples taken in spring, where males, females and transitionals could be identified, a 3 stage model was fitted with age 1 and 2 as male, 3 as transitional and 4, 5 and 6 as female. A 2 stage model was used for summer and fall samples when only mature males and females are present. In this case ages 3, 4, 5 and 6 were combined for the female group.

$$N_{al} = C_a * N_0 * S^a * (1/\sqrt{(2*\pi*(\sigma*a)^2)} * e(-((l-Vbl)^2/(2*\sigma*a)^2))) \quad (2)$$

N_{al} = number of individuals in age group a at length l

N_0 = abundance at age 0

S = annual survival

a = age

σ = CV of normal distribution representing the population at each age group.

Vbl = length at age predicted by Von Bertalanffy equation

C_a = catchability at age a

In cases like that shown in Figure 11, where the catchability of the smallest age group was clearly less than that of older age groups a catchability constant was fitted for those age groups. This was only used for ages 1 and 2. For age groups over age 2 $C_a = 1$. A birth date of April 1 was assumed for all samples, in line with observations of the timing of larval hatching in Washington. The value of t_0 was fixed at -0.15. This reduces the number of estimated parameters and ensures that the model gives a reasonable estimate of the larval size at hatching (within the range 2.5-5 mm, (Price and Chew 1972). A total of 6 age classes were included in the model, i.e. there were three age classes of females.

The model was fitted by maximizing the likelihood between predicted and observed numbers for each life stage at each length. The fits of the model to the data were generally good (r-squared =0.64-0.97). Figure 12 shows a typical example of the fit of the model. As can be seen from Table 2, the parameters estimated were relatively consistent between samples taken from the same area, with more variability between areas (Table

3). Elliott Bay is an exception to this, due to the size range of prawns caught at different times of year being very variable.

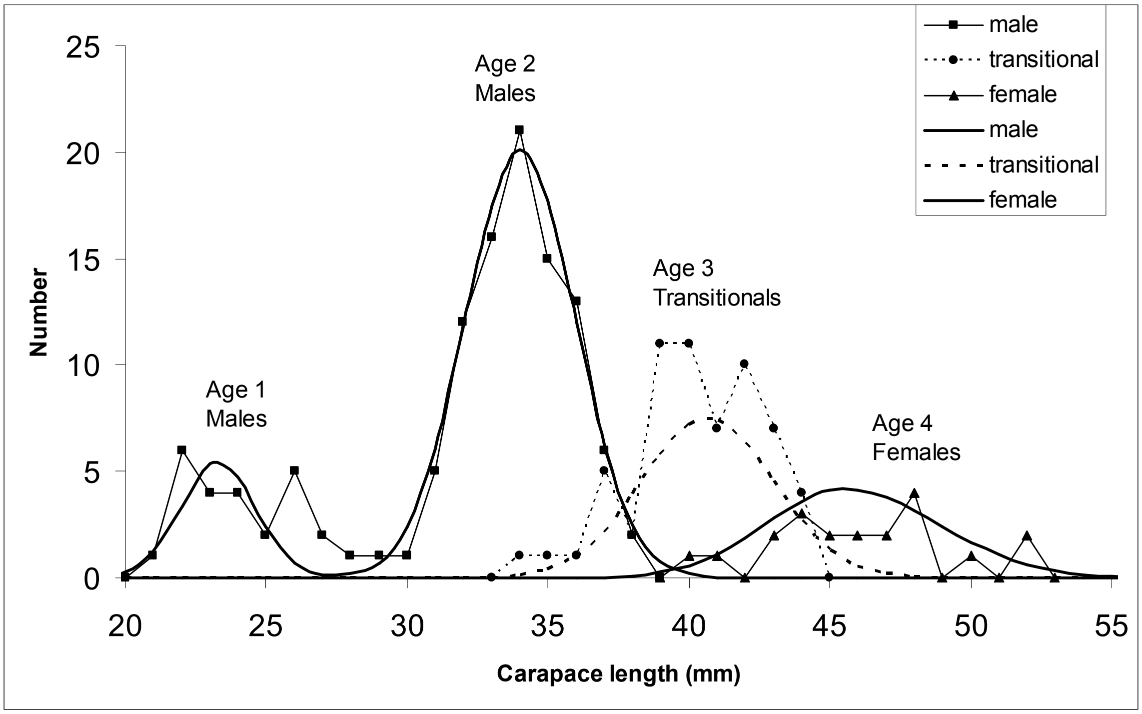


Figure 12: Spot prawn length frequency with fitted curves.

Table 3: Parameter estimates for growth models for spot prawn samples in Washington. The 3 stage model (3s) is fitted to samples taken in spring when males, females and transitionals can be identified. 2 stage models (2s) are based on summer and fall samples when only mature males and females are present. Parameters shown in the table are L_{inf} = average maximum length, K = Von-Bertalanffy rate constant, t_0 = age at zero length, σ = CV for normal distribution representing the population at each age group, S = annual survival, C_1 and C_2 = catchability at ages 1 and 2, R^2 = goodness of fit.

Area	date	N	model	L_{inf}	K	t_0	σ	S	C_1	C_2	R^2
Strait of Juan de Fuca	5/10/00	198	3s	51.5	0.478	-0.15	0.057	0.445	0.083	1.000	0.895
Eastern Strait	8/18/03	447	2s	46.2	0.505	-0.15	0.055	0.603	0.010	1.000	0.848
Eastern Strait	8/20/03	515	2s	47.6	0.540	-0.15	0.058	0.601	0.010	1.000	0.919
Eastern Strait	8/20/03	374	2s	46.9	0.586	-0.15	0.041	0.500	0.010	0.246	0.975
Northern Puget Sound	8/20/03	345	2s	55.0	0.333	-0.15	0.061	0.486	0.000	0.654	0.644
Saratoga Passage	8/17/00	110	2s	55.7	0.380	-0.15	0.035	0.335	0.010	1.000	0.899
Hood Canal	4/18/00	188	3s	40.6	0.586	-0.15	0.055	0.489	0.000	0.070	0.934
Edmonds	4/1/02	1195	3s	40.4	0.668	-0.15	0.062	0.198	0.000	0.031	0.932
Edmonds	4/16/02	585	3s	40.2	0.706	-0.15	0.064	0.333	0.000	0.093	0.934
Edmonds	6/12/02	925	2s	41.1	0.680	-0.15	0.038	0.674	0.010	0.565	0.965
Elliott Bay	4/1/01	711	3s	38.5	0.915	-0.15	0.052	0.038	0.000	0.022	0.968
Elliott Bay	7/27/01	346	2s	49.7	0.493	-0.15	0.031	0.141	0.000	0.053	0.965
Elliott Bay	8/22/01	369	2s	49.0	0.499	-0.15	0.039	0.209	0.000	1.000	0.973
J d F canyon	4/1/01	46	3s	47.5	0.641	-0.15	0.026	0.800	0.000	0.859	0.764

Estimated average size at age calculated from the parameters in table 2 is given in Table 4. Spot prawns in Hood Canal show the slowest growth rates and smallest size at maturity as females (age 4). This result was also supported by analysis of a larger dataset (not presented here) of Hood Canal prawns which did not include sex data. Prawns at Edmonds also grew slowly, whilst those in the Strait of Juan de Fuca reached a slightly larger size by age 4 and a larger maximum size. These variations in growth rate may be due to density dependent effects. Hood Canal and the Edmonds area are known to have high density populations of spot prawns, and density dependent effects on growth have been shown for other pandalid species (Hannah and Jones 1991). Overall, the growth rates for spot prawns in Washington are similar to those reported from British Columbia (Table 2).

Table 4: Estimated length at age for Washington spot prawn samples.

Area	Date	Size at age (mm carapace length)				
		1	2	3	4	6
Strait of Juan de Fuca	5/10/2000	21.8	33.1	40.1	44.4	48.8
Eastern Strait of JdF	8/18/2003	20.4	30.6	36.8	40.5	44.1
Eastern Strait of JdF	8/20/2003	22.0	32.7	38.9	42.5	45.9
Eastern Strait of JdF	8/20/2003	23.0	33.6	39.5	42.7	45.6
Northern Puget Sound	8/20/2003	17.5	28.1	35.7	41.2	47.9
Saratoga Passage	8/17/2000	19.7	31.1	38.9	44.2	50.3
Hood Canal	4/18/2000	19.9	29.1	34.2	37.0	39.5
Edmonds	4/1/2002	21.7	30.8	35.5	37.9	39.7
Edmonds	4/16/2002	22.4	31.4	35.9	38.1	39.7
Edmonds	6/12/2002	22.3	31.6	36.3	38.6	40.5
Elliott Bay	4/1/2001	25.1	33.1	36.4	37.7	38.4
Elliott Bay	7/27/2001	21.5	32.5	39.2	43.3	47.3
Elliott Bay	8/22/2001	21.4	32.2	38.8	42.8	46.7
Juan de Fuca canyon	4/1/2001	24.8	35.5	41.2	44.2	46.6

Survival

Natural mortality needs to be known in order to construct a model of spot prawn population dynamics. This parameter can be estimated by the model used in the previous section to estimate growth rate, for samples from un-fished populations if the assumption of equal recruitment each year is made, and the selectivity of the gear is known. Four of the samples were taken from areas in Northern Puget Sound and the Eastern Strait of Juan de Fuca which had not been fished to any great extent prior to the collection of the samples (D. Sterrit, WDFW, 2003). If it is assumed that the gear used is unselective for prawns over age 3, then the mortality estimates from these samples represent natural mortality.

The annual proportion surviving for age 2 to 6 prawns in these samples ranged from 0.49 to 0.60 with an average of 0.55, (representing instantaneous mortality rates of 0.72 to 0.51, average 0.60). For the other samples, which are all from fished areas, only total mortality can be estimated. Survival for these samples ranged from 0.04 to 0.80, with an average of 0.37 (instantaneous rates 0.23 to 3.26, average 1.00). All but two of the estimates from fished areas were higher than those from the unfished areas, which gives some indication that the results may be reasonable.

Boutillier and Bond (2000) estimated natural mortality from abundance indices taken at multiple times during the year in an area which was closed to all fishing. Their estimates (instantaneous rates) ranged from 0.42 to 1.46, with an average of 0.88. This is reasonably close to the average estimate from unfished Washington areas.

Longevity

Maximum lifespan of prawns is not clearly defined across the range. Butler (1964) states that “following hatching of eggs in the spring, practically all females evidently leave these (rocky) grounds, and the conclusion is that most die”. This assertion has been widely interpreted as a definition of maximum age as no more than 4 years, implying that prawns only breed once as females during their lives and led to their being treated as a semelparous species in management in British Columbia.

There is ample evidence that prawns are capable of surviving and breeding multiple times. The reason for Butler's findings may be that the prawns continue to migrate into deeper water after first spawning and older individuals were outside the range of his sampling, or it may be that they did not grow as he expected. Ontogenic migrations are common in Pandalid shrimp, average size of shrimp caught often increases with depth (Shumway et al. 1985), and a clear reduction in growth rate after the first breeding event is detailed above.

Rensel and Prentice (1977) observed multiple breeding events for prawns in captivity. All spawners survived at least four months after the eggs were released, 40% survived until the breeding season in October and 85% percent of these prawns were observed to spawn. These prawns were held in net pens in very much shallower, warmer, water than they would normally inhabit. Survival (75%) and breeding frequency (100%) were higher in prawns held in laboratory tanks. Multiple spawning in such sub-optimal habitats and the large size of some females captured indicates that it is probably common in wild populations.

The work by Kimker et al. (1996) clearly shows longer lifespan in Prince William Sound. Tagged mature prawns were captured after more than four years at liberty, indicating a minimum lifespan of at least 6-7 years. Unpublished data from the same study showed that individual females spawned multiple times in successive years. However, this study was based near the northern limit of the range of the spot prawn, and given the wide range of conditions inhabited by prawns, the results may not be applicable in all areas. Sunada (1986) estimated the maximum age to be 6+ years in Southern California from analysis of length frequencies, but as noted above, he may have overestimated age by one year. The presence of extremely large prawns in coastal waters and lightly fished areas also implies a longer possible lifespan.

Recruitment

Recruitment can be highly variable in marine animals with planktonic life stages, and is often correlated with oceanographic conditions (Botsford 2001). Hannah (1993) showed a correlation between pink shrimp (*Pandalus jordani*) recruitment levels off Oregon and environmental variables; the strength and timing of the "spring transition" between downwelling dominated winter conditions and upwelling dominated summer conditions was strongly correlated with subsequent recruitment to the stock. Years with El Niño events had a reduced recruitment (to near zero) and this led to greatly reduced catches in the fishery for this species in the subsequent years. Koeller (2000) also showed environmental effects on recruitment of *P. borealis* in the northwest Atlantic. Hannah (1999) subsequently showed that once these environmental effects (which were the major drivers of recruitment strength) were accounted for, an underlying stock-recruitment relationship existed, especially at low stock levels. The implication of this is that management should endeavor to maintain stocks over some threshold level, below which average recruitment would be reduced.

Little information is available on recruitment in spot prawn stocks. Barr (1973) reported a six fold difference between years in the abundance of juveniles in Auke Bay, Alaska. Larson (2001) reported strong recruitment of spot prawns in California associated with the 1997 El Niño event, although this was not noted in other areas. Boutillier and Bond (2000) fitted a Ricker spawner-recruit relationship to data from an experimentally monitored population of spot prawns in Howe Sound, British Columbia. This suggested that there was a density dependent mechanism operating in this area, which resulted in slightly lower recruitment at high spawning stock levels. Howe Sound is a semi-enclosed fjord, so the dynamics that operate there may be similar to those in places like Hood Canal. However, the dynamics may be different in more open areas such as the Washington coast.

Predators and prey

Analysis of stomach contents indicates the diet of the spot prawn is composed of crustaceans, polychaetes, and siliceous sponges (Butler 1970). This and the fact that prawns are captured in trawls with large quantities of sponge bycatch in some areas (Lowry, pers. obs.) may indicate a habitat preference for areas with sponges as a food source, or that sponges are used for cover by the prawns. Other observations have shown that spot prawns are generalist benthic scavengers, consuming dead fish, mollusks and crustaceans ((Butler 1970)). A large number of spot prawns were observed via remote operated vehicle, scavenging on the carcass of a whale which was sunk for an experiment in the San Juan Channel in 2004 (Lowry, pers. obs, 2004). There is little definitive information about what eats spot prawns. Butler (1970) notes that adult prawns are probably eaten by a variety of fish such as lingcod (*Ophiodon elongatus*), dogfish (*Squalus acanthias*) and Pacific cod (*Gadus macrocephalus*). Octopi are also a predator, and are frequently caught in prawn pots where they are attracted to the prawns which have already been captured. Predator abundance may have an effect on spot prawn abundance. This effect has frequently been seen for other pandalid shrimp. For example, Hannah (1995) noted that predation by Pacific hake impacted the stock of pink shrimp off Oregon.

1.6 Conclusion

Spot prawns are large, long-lived shrimp with a complex life history. As they spend much of their life span in inaccessible places (deep water, open ocean planktonic phase) current knowledge about details of their reproduction, growth, survivorship, etc has many gaps. Here I have summarized previous work on the species, both in peer-reviewed literature, grey literature, and unpublished data. I have added results from my work where relevant. This included clarification of the full range of the species, which extends much further south than reported in published work, further details of the habitat types used by juveniles and the first estimate of the length of the planktonic larval phase of the life history. I also collected data and used simulation modeling to improve estimates of the fecundity, growth rate, survivorship and longevity of this species.

Chapter 2: Bycatch in spot prawn fisheries

2.1 Introduction

Bycatch and damage to sea floor habitats are major problems in most trawl fisheries. Prawn trawl fisheries in particular suffer from large quantities of bycatch. The Food and Agriculture Organization of the United Nations (FAO) recently estimated that nearly 7 million tonnes of fish bycatch was discarded each year, and over a quarter of this was taken in prawn trawl fisheries (Kelleher 2005). Damage to sea floor habitats is also a major issue in some habitat types (Løkkeborg 2005). The quantity of bycatch and severity of seafloor damage in the spot prawn fishery was unknown in 1998 at the start of this study, but some anecdotal evidence raised cause for concern. Over the course of this study, I found that the spot prawn trawl fishery off California and Washington suffered from both these issues. The bycatch included large quantities of fish, some of which were of commercial importance or listed as overfished. The areas fished by the trawlers were of a type which is susceptible to damage by trawl gear. Partly due to the results of the studies reported here, trawl fisheries for spot prawns were closed coastwide by 2004. The trawl fisheries were partially replaced by pot fisheries which were perceived as having lower bycatch and causing less habitat damage. This chapter presents results of studies related to bycatch and bycatch minimization in spot prawn fisheries, conducted over several years. Here I present a comparison of bycatch reduction devices (BRDs) in the California spot prawn trawl fishery (Section 1, page 34), analysis of bycatch in the Washington trawl fishery (Section 2, page 54 and Section 3, page 61), and analysis of bycatch in the Washington spot prawn pot fishery (Section 4, page 68). Results of each study are presented, and a brief discussion follows each section. Implications of the results and their impact on fishery regulation are discussed in a general discussion on page 78.

Bycatch in fisheries is defined as the unintentional capture of non-target species (Harrington et al. 2005). It is characteristic of most trawl fisheries, as trawl gear is generally fairly unselective as to the types of fish that it captures. Prawn and shrimp trawls in particular catch large quantities of bycatch (Kelleher 2005) as the target species are usually relatively small and so small mesh sizes are used. The major issues associated with bycatch are wastage of natural resources, threats to rare species or stocks that are already overexploited, and changes in the overall structure and function of ecosystems caused by the removal of large quantities of biomass (Harrington et al. 2005; Kelleher 2005). The catch of juveniles of species that are important to other commercial or recreational fisheries is often a major force causing change in trawl fisheries. Substantial efforts have been made to reduce bycatch by means of alterations to trawl gear. These have concentrated to a great extent on shrimp and prawn fisheries where the problem is greatest, and were greatly accelerated by the need to conserve endangered sea turtles (Broadhurst 2000; Eayrs 2005).

Damage to benthic habitat is the second major issue driving changes in bottom trawl fisheries worldwide. The degree of damage caused by a particular fishery depends on the type of seafloor that the fishery operates over and the type of ground gear used on the nets. Fisheries using light gear over shallow areas with frequent natural perturbations (e.g., wave action) appear to cause relatively little damage (Løkkeborg 2005). Fisheries which drag heavy trawls over hard substrates dominated by large emergent fauna such as sponges and corals can cause extremely severe damage and have long lasting effects on the associated benthic ecosystems (Roberts and Hirshfield 2004; Løkkeborg 2005). Coastal spot prawns prefer to live in a depth range between 100 and 400 m on or near hard bottom sites in habitats with some form of cover (see Chapter 1). Areas at this depth experience little natural disturbance, favoring the growth of large, long lived sessile invertebrates which add structure and provide habitat for other invertebrates and fishes (Tissot et al. 2006). During the development of the spot prawn trawl fishery, the size and type of ground gear used changed from relatively light gear of a small diameter to much larger, heavier gear such as rockhopper gear (See page 67 for a description of rockhopper gear) in order to target spot prawns on harder substrates of higher relief. Thus, the degree of damage caused by the fishery probably increased over time as new areas were exploited.

Prior to 1998 when this study began, there had been no published studies of bycatch in spot prawn fisheries. Only anecdotal information was available; a few studies had recorded some bycatch information incidental to other objectives (Reilly and Geibel 2002), but data were not yet released. The bycatch had been described anecdotally as including a large volume of rockfish of all sizes and types, and the existence of a problem was acknowledged by some of the people involved with the fishery (L. Massey, Pacific Trawl co. Eureka CA. pers. comm. 1998). The only reliable report available to me in 1998 described six hauls using experimental bycatch reduction devices (BRD) on a vessel sailing from Eureka, in which 204 kg of spot prawns were caught along with an estimate of approximately 5450 kg of fish (approximately 4550 kg of rockfish, mainly sharpchin (*Sebastes zacentrus*), and 900 kg of flatfish).

Management concerns in 1998 were centered on the bycatch of overfished species of rockfish (*Sebastes spp.*). Six species of rockfish were determined to be overfished (boccacio, canary, cowcod, darkblotched, Pacific ocean perch and widow rockfish) and all of these were thought to be present to a greater or lesser extent in spot prawn fishery bycatch. The relatively small mesh used in the fishery was also thought to present a threat to juveniles of these and other species of rockfish. The issue of damage to benthic habitat by the spot prawn trawl fishery had received little exposure by 1998.

Given these concerns, the original objective of this study was to reduce the quantity of bycatch taken in the spot prawn fishery, especially rockfish bycatch, with the use of appropriate bycatch reduction technology. At that time, the trawl fishery was presumed to be a permanent fixture in the regulatory landscape. Bycatch reduction devices had been shown to be effective in fisheries for large penaeid prawns in many parts of the world, including Australia and the Gulf of Mexico (Eayrs 2005). They have also proved effective in fisheries for small pandalid shrimp worldwide (Broadhurst 2000). My challenge in applying bycatch reduction technology to the spot prawn fishery was to combine approaches which are effective in deep water pandalid fisheries with those that are effective for larger species of prawns. This study is presented in Section 2.2 (page 34).

Results and observations made during the bycatch reduction study showed that the bycatch in the spot prawn fishery off southern California was much more diverse than had been previously thought, with likely damage to benthic habitats in areas where trawling was conducted over rocky ground with large amounts of structure forming invertebrates. Further study concentrated on quantifying the bycatch in the spot prawn trawl fishery off the Washington coast, and these studies are presented in Sections 2.3 and 2.4 (pages 54 and 61). As a direct result of these two studies, the spot prawn trawl fishery off Washington was closed at the end of 2002, and the Oregon fishery followed suit at the end of 2003. The results of my BRD study prompted further study in California by the California department of fish and game (CDFG), and the Californian spot prawn trawl fishery was closed in April 2003.

The closure of the trawl fisheries for spot prawns allowed pot fisheries to expand. Although these fisheries were thought to have a very low level of bycatch, no definitive studies had been conducted. The final study is an analysis of the bycatch in the spot prawn pot fishery which continues in the same area as the trawl fishery occurred off the Washington coast. This is presented in Section 2.5 (page 68).

2.2 Bycatch reduction experiments off Southern California, June 1998.

Research objectives

This study compared the effectiveness of 3 different types of bycatch reduction devices (BRDs) on a commercial vessel off southern California in June of 1998. It also provided the first data on the quantity and type of bycatch in the spot prawn trawl fishery.

Methods and equipment

Study area and vessel

The bycatch reduction experiments were performed on a commercial fishing vessel during normal fishing operations. The captain of the vessel which agreed to do the study was paid a small fee for participation, but it was a cooperative agreement, not a full charter. This limited the scope of the data collection as it was necessary to fit in the experimental hauls within a normal program of commercial hauls. The weather conditions that prevailed during the period of the charter were generally extremely poor, which also affected the scope of the data collection. Fishing was only possible on 9 days of the 18 initially planned for the tests.

The vessel used was the F/V Nita H, based in Pt. Hueneme, California. This boat is a large shrimp trawler, approximately 32 m in length. The vessel was set up to use a double rig, towing two identical trawls simultaneously from booms on each side of the vessel. Each net had a single towing warp, attached to a bridle which connected to a pair of wooden otterboards. The otterboards were connected directly to the wings of the trawl without intervening sweeps. The nets were a simple two seam Gulf of Mexico type. Rockhopper ground gear with 25 cm discs was used. The use of a double rigged vessel allowed direct comparisons to be made between a net fished normally on one side and a net with a BRD on the other.

Monitoring equipment

The first part of the work used underwater cameras and electronic net monitoring equipment to attempt to assess the optimal design and configuration of each of the BRD types. Prior to starting the experimental part of the work, a calibration of the two nets used by the vessel was carried out to ensure that their fishing performance was as close to identical as possible. Subsequently, video observations were made of the performance of each BRD in turn and the reactions of fish and prawns to it.

Instruments used to measure gear parameters were "Scanmar" sensors, which communicate acoustically with each other and with a transponder onboard the vessel to give real time measurements of gear geometry (in meters). Gear variables that were measured included wing end spread, otterboard spread (indicators of swept width) and headline height. The instrumentation used on each net was identical, which enables direct, simultaneous comparison of fishing performance of each net.

Video observations were made with an in situ SIT (silicon image intensifier) camera. This camera was mounted on the trawl inside a protective frame, aimed to allow observation of the part of the gear being studied – usually the BRD. Floats were added as necessary to make the camera unit neutrally buoyant. Recordings were made on 8mm-video tape using an integrated submersible recording unit. Artificial lights were used as necessary. These were green LED lights (approximately 510 nm wavelength). This color of light was chosen as it has high transmissibility in sea water, allowing very low power lights to be used. The major disadvantage is that this color is visible to the majority of fish and potentially will change their behavior relative to the gear. Catch composition was not measured during hauls when the video camera was installed due to the time constraint on getting the camera, recording unit and lights out of the net before shooting again.

Catch and bycatch estimation

The catch composition was measured during the experimental hauls to assess the degree of separation and catching performance for target species using these devices. Data collected from each net for each haul was the total catch weight, catch of each species (or species group where precise identification was difficult), and length frequency of major bycatch species when time permitted. The catch sorting procedure was to dump the catch from each cod end on one side of the deck. The spot prawn catch was then sorted out from the bycatch, weighed and placed in live tanks. The bycatch was placed in baskets which were individually weighed to give the total catch before sorting and weighing individual species. When catches were too large to sort completely, a representative sample of 25-50 kg (1-2 baskets) of the bycatch was taken after spot prawns were sorted from the entire catch. Species composition of the bycatch in this sample was measured and a raising factor applied according to the ratio of the sample weight to the total catch weight. An electronic marine scale (Ryco) was used for weight measurement initially, followed by a mechanical scale after the electronic one was damaged (data from 6 hauls were lost due to malfunctioning of the electronic scale after it was damaged). Lengths were measured and recorded using an electronic fish measuring board.

For the analysis of catch data, the amount of bycatch of individual species was too small to be meaningful. The catch was divided into four species groups by general type: large rockfish, small rockfish, flatfish and other roundfish. Large rockfish were: greenblotched, blackgill, bank, chillipepper, boccacio, cowcod and darkblotched rockfish. Small rockfish were: stripetail, greenstriped, splitnose, shortbelly, halfbanded, flag and pinkrose rockfish. Flatfish were primarily Dover, English, rex, petrale and slender sole. Roundfish were: Pacific hake, ratfish, various cottids, grenadiers, eelpouts, and dogfish.

<u>Bycatch reduction devices</u>

Three different types of BRDs which have shown potential in shrimp/prawn fisheries elsewhere in the world were tested. These were a separator panel, a Nordmøre grid and a "fish eye" (Figures 13-15, respectively). Commercial net makers familiar with the fishery provided the BRD’s tested in this experiment. No new BRD designs were tested, as the intent was to use existing designs and alter them as necessary. The separator panel was supplied by Astoria Net Shop, Astoria, Oregon (George McMurrick), and the Nordmøre grid from Seattle Marine and Fishing Supply, Seattle, Washington. As these are commercial products, the precise details of the designs are proprietary and are not presented here. The “fish eye” BRDs were manufactured by Robert P Driscoll Net Services, Warrenton, Oregon, according to a standard design. The elliptical openings were 25 cm high and 38 cm wide.

<u>Separator panel</u>

The separator panel used (Figure 13) was an adaptation of the Gulf of Mexico turtle excluder devices and was made entirely of netting or with only a few rigid parts. The concept is similar to the Nordmøre grid, i.e., shrimp pass through an angled mesh panel and fish are deflected upwards and out through an escape hole. Panel mesh sizes are normally 8-20 cm in USA fisheries. Performance of these devices tends to be less consistent than rigid grids. Shrimp losses have been reported between 2 and 30% and fish exclusion 30-80 % for small fish. They have advantages over rigid grids in being easier to handle on small vessels and cheaper to produce and repair. The separator panel has the most potential for performance problems caused by incorrect setup.

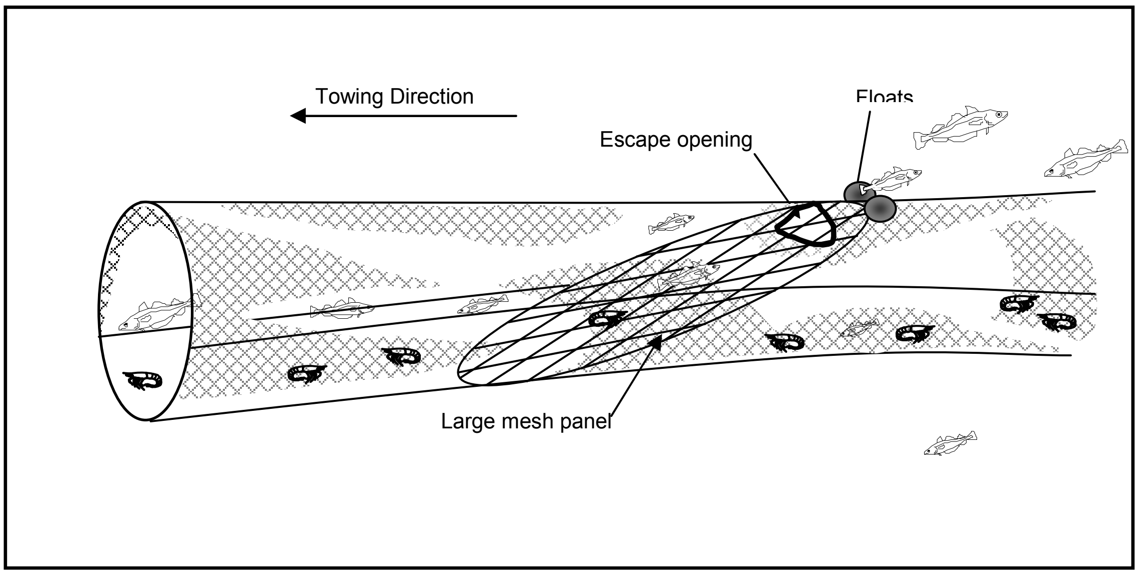


Figure 13: Separator panel bycatch reduction device.

The separator panel was made from 14 cm (5 1/2") polyethylene mesh and framed with a loop of 1/2" steel cable, which was wrapped with nylon cord to protect from abrasion. A crosspiece of 1/2" steel cable was also installed to help the panel retain its shape. The panel was installed in a section of 5 cm (2") mesh size netting, 160 meshes in circumference. Three 10 cm (4") floats were installed inside the net at the back of the panel to help it retain its shape and ensure that it would fish the right way up.

Nordmøre grid.

This system was developed in Norway for separating shrimps from fish in pink shrimp (Pandalus borealis) trawls (Figure 14). It consists of a rigid grid, made of stainless steel or plastic, mounted at a 45-50 degree angle in the aft section of a shrimp trawl. The grid has a netting funnel in front of it to ensure that all catch initially comes to the bottom of the grid to increase the chance of small objects (i.e. shrimp) passing through the grid and into the trawl cod-end. Above the grid, the top panel of the net has an opening to allow large fish to escape. Normal bar spacing is a maximum of 19 mm for shrimp fisheries in Norway. The performance of this device tends to be good in pink shrimp fisheries, with an average shrimp loss is 1-3% by weight and fish bycatch reduction up to 95% for small fish, 100% for larger species (Isaksen et al. 1992). The Nordmøre grid is a device that has been extensively studied and has been shown to be effective. However, it is not popular in some fisheries due to its cost and perceived difficulties in handling.

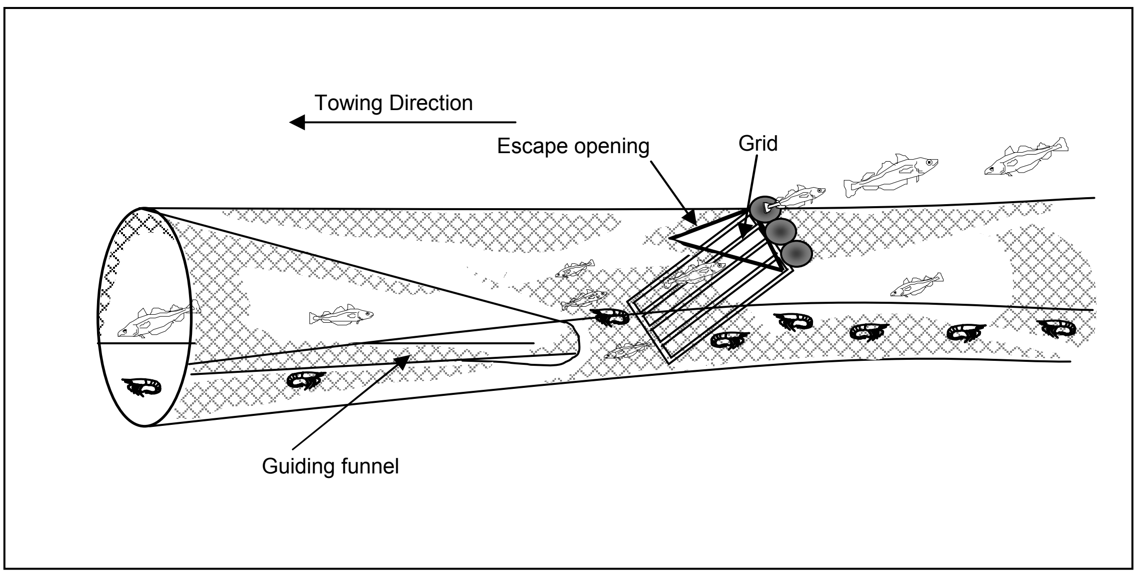


Figure 14: Nordmøre grid bycatch reduction device

The grid used was manufactured from a 12 cm thick polyethylene sheet, into which the grid openings were cut using a milling machine. The openings were 7.5 cm in width. This was determined by estimation of the differences between the sizes of the pink shrimp targeted in fisheries using the grids and the size of spot prawns. The overall grid dimensions were 1.2 m in height and 0.6 m in width. It was mounted at a 45-degree angle in a 160 mesh round extension section (2" mesh size), complete with an 85-mesh-long guiding funnel. Four 15 cm floats were mounted on the top corners to ensure that it fished in the correct orientation, and the bottom edge was reinforced with nylon twine to avoid abrasion damage from contact with the sea floor.

Fish eye.

This device consists of one or a pair of elliptical framed openings, which are inserted in the top panel of the aft part of the trawl (Figure 15). The frames are made from stainless steel and have bars attached to ensure that they remain vertical and that the openings point forwards relative to the towing direction of the net. For a fish to escape it has to swim forwards and upwards from the back of the net and then exit. This device is the simplest of the three tested, and devices of this type were required to be used in some spot prawn trawl fisheries. There are few variables that can be adjusted with this type of BRD, and the major question is where it should be positioned in the cod-end. Workers in the Gulf of Mexico have researched the position of this in the net for those fisheries (Watson et al. 1993), and the supplier suggested a similar position. Two fish eyes were mounted in the top of the net, 88 meshes from the end of the cod-end, with a single 30 cm float attached between them to ensure that they would remain on the top of the extension.

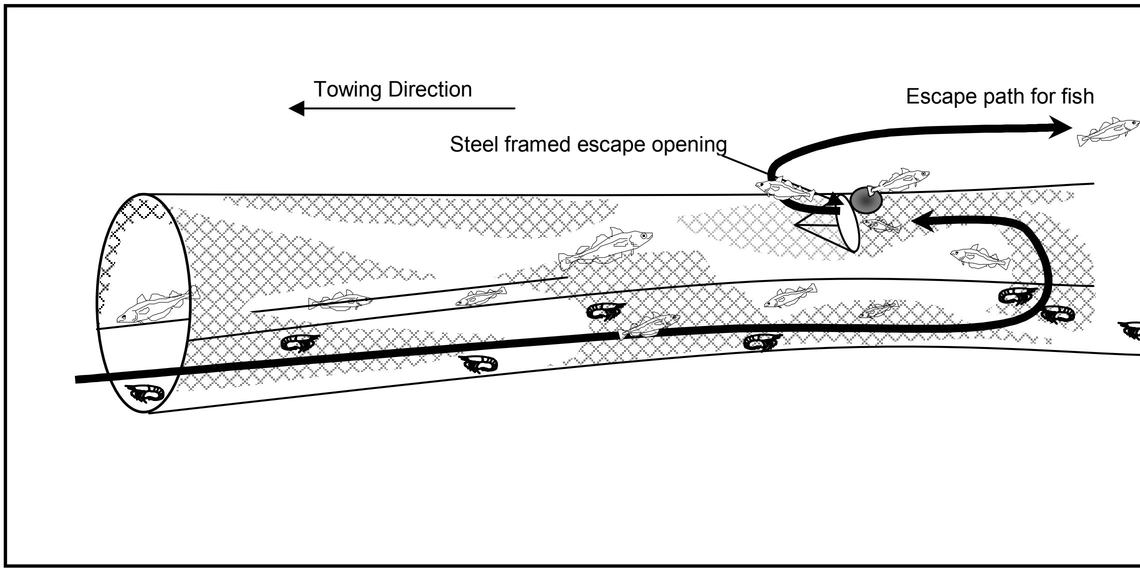


Figure 15 Fish eye bycatch reduction device

Results

General conditions

During the trial period, the weather conditions were generally poor, with mostly strong winds from the north. This limited the amount of time which we could spend fishing on the more productive grounds. The 24-hour non-stop fishing schedule kept by the captain also made it difficult to achieve the objectives as little time was available for altering the gear between hauls. The use of the trawls hung from extended booms on the sides of the vessel made it difficult to get access to the gear for making changes and for positioning cameras and trawl monitoring equipment.

Great difficulty was found in adjusting the nets to fish similarly. This was partly because the vessel's nets were not identical. Due to the nature of the fishery, nets are damaged frequently, resulting in them needing repair, and whole nets are lost occasionally. The vessel was using three nets interchangeably. Two had been manufactured identically but had subsequently been extensively repaired. The third was similar but not identical in design, including slightly different ground gear configuration, and was therefore not used in experimental hauls. Five hauls were made with Scanmar gear attached to the nets, and the nets were adjusted after each by adding/removing floats, and altering the length of headlines and footropes in order to achieve equal wing spread and headline height. Groundgear tension relative to the footrope was also adjusted so that the rockhoppers would make reasonably equal amounts of contact with the seafloor, and in an attempt to reduce the amounts of debris and benthic organisms entering the nets. Bycatch during these hauls was not sorted, and only the total amount estimated. Extreme variability was seen between the catches from haul to haul, and also between the catches from the two nets being fished simultaneously. Side to side variation made it impossible to determine if the catching performance of the two nets were the same, although their geometry was similar. Wing spread was approximately 17.5 m and headline height approximately 2.5 m.

Fishing was carried out in three general areas, dependent on the prevailing weather conditions and catches (Figure 16). The first three hauls were made north of San Nicolas Island, but catches were small, and so the captain decided to move to around Tanner Banks. Fishing continued there until the weather worsened and we were forced to return to port because of vessel damage caused by extreme weather conditions. The rest of the hauls were made further to the north, in the Santa Barbara channel, which was more sheltered from the wind. Unfortunately, these changes in area coincided with the changes in the gear type tested, with the result that most of the Nordmøre grid tests were made at the Tanner banks and most of the fish eye tests in the Santa Barbara channel. The Tanner banks area has never been heavily exploited by commercial bottom trawling. Prior to this study, the area had only been lightly fished by the spot prawn trawl fishery. In contrast, the Santa Barbara channel had been extensively trawled for both groundfish and spot prawns.

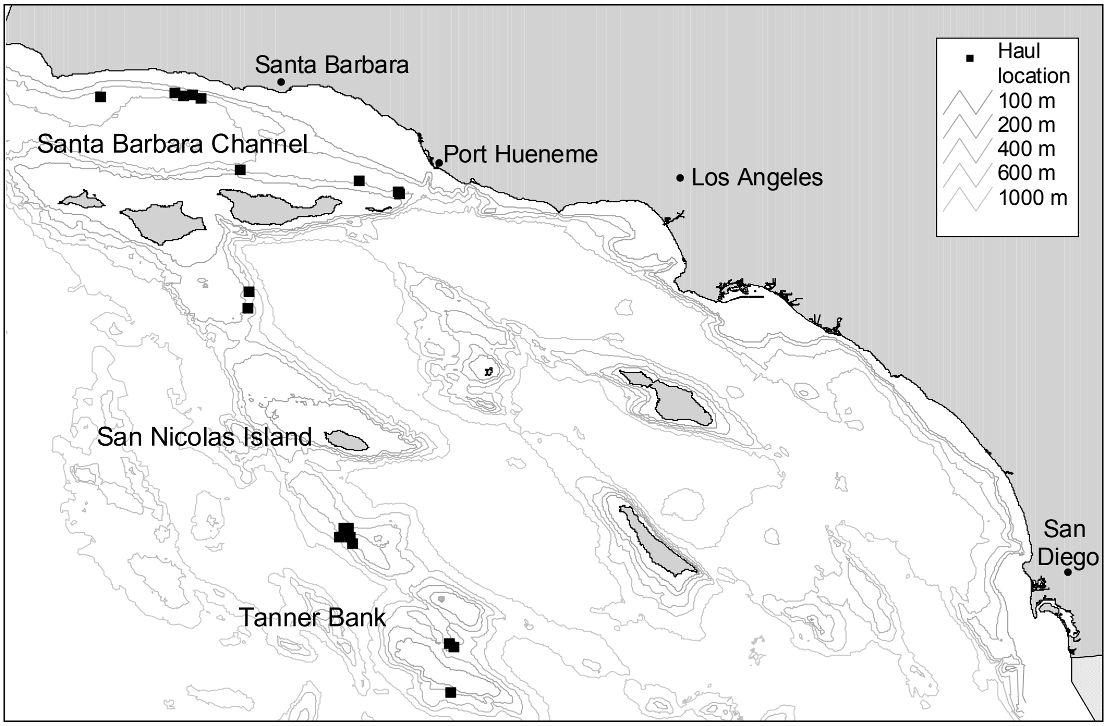


Figure 16 Haul locations for bycatch reduction experiments off southern California.

<u>Bycatch reduction devices</u>

<u>Separator panel</u>

The first tests were with the separator panel. The aim in the first experimental haul was to see both if the panel was functioning and to test the potential of the video system to work with natural light. Results of these were somewhat unimpressive. The video system gave excellent pictures on the surface and down to substantial depth, but there was insufficient light when the net got to the fishing depth at >200 meters. The surface video pictures clearly show that the panel did not take up the anticipated shape but was bowed downwards like a spoon. It also appeared to be at too shallow an angle (approximately 30° from horizontal) for fish or prawns to easily penetrate the meshes. Some prawns which had been caught in the meshes further up the trawl were seen to leave the exit hole as the net was hauled back. The mesh size used may also have been too small to allow spot prawns to penetrate through to the cod-end easily. Very few spot prawns were caught in either net during this haul - approximately 2.5 kg of prawns were caught in each side.

A second haul was attempted with this gear, without the video camera. There was a substantial quantity of hard invertebrates (mostly sponges, corals and sea urchins) and inorganic debris caught during this haul. This material stuck on the meshes of the separator and had completely blocked them by the time the net was hauled. Fewer prawns were caught in the side with the BRD (11 kg vs 16 kg). Because this was a commercial fishing trip, the experiments with the separator panel were discontinued at this time. The initial performance was seen by the captain as reducing the catch too much to be a viable fishing option.

Nordmøre grid

The second set of tests was with the Nordmøre grid. Video observations were made of the grid during 5 hauls using lights. These showed that the angle of the grid during towing was approximately 45 degrees from horizontal, and that the grid was performing as designed. Prawns were seen passing down the extension straight through the grid without seeming to be significantly impeded. A number of small fish were also observed to pass straight through the grid and into the cod-end. Some fish were seen holding station in front of the grid. There was sufficient flow down the net that it seemed to be necessary for these fish to make a definite upward escape attempt to exit through the escape hole. The majority of them did not do this, and were eventually exhausted and passed through the grid towards the cod-end. Some large fish were observed being deflected by the grid and out of the escape hole. Fish were observed escaping when the net pulsed, presumably due to being snagged temporarily on some bottom obstruction. This is further evidence that the water flow held the fish in the area in front of the grid and discouraged escape attempts. However, as it was necessary to make all of these observations with the aid of lights, the behavior of the fish cannot be considered completely typical of that under normal fishing conditions. The fish may have been holding station relative to the light rather than to the grid or other net components, thus reducing the proportion that would go through the exit hole.

Some prawns were observed passing down the extension and through the grid. They all stayed right at the bottom of the net where they were directed by the funnel, and passed easily through the grid. These observations, combined with the fact that only the largest fish were deflected by the grid, show that the bar spacing chosen was too large. Better results in terms of fish exclusion would be expected with a smaller bar spacing, without very much cost in terms of catch loss.

A major problem with the Nordmøre grid, as with the soft panel BRD, was that any large sponges or other pieces of debris were stopped by the grid and remained there, blocking passage through into the cod-end. This may cause loss of prawn catch if the blocked grid creates an upward flowing current that sweeps the prawns out of the exit hole. It was also somewhat difficult to clear the grid when it was hauled. This was partly due to the way it was handled on board the vessel. The second problem with the grid was associated with the funnel used to direct the catch to the bottom of the grid. This became blocked with sponges and debris, and occasionally large rockfish were caught in the meshes by their spines, presumably as they were falling back down the net when they were exhausted. To alleviate these problems, the length and taper of the guiding funnel was altered. It was shortened to 40 meshes (approximately 2.25 m), and opened to approximately half the diameter of the extension. Using this different taper on the funnel reduced some of these problems, but did not avoid them completely. Removing the funnel altogether risks a loss in prawn catch and was not tested.

The weight of fish and prawn catches obtained with the Nordmøre grid were compared with the other trawl with no BRD installed. Paired t-tests were used in order to control for the high degree of haul to haul variation. A total of 10 hauls were available for this comparison (Table 5). Eight of these hauls were made in the Tanner Banks area, with one each in the Santa Barbara channel and north of San Nicolas Island. These were hauls which were made without video camera installed to avoid fish behavior differences caused by the lights, and on which there were no gear problems such as damage to the nets which would bias the catches on one side or other. Half of these hauls were made with the grid installed in the port side net and half with it in the starboard net, which should compensate any bias caused by net differences. These comparisons showed that there was no significant difference in the prawn catch with or without the grid. It was also very effective at releasing large fish. No large fish were caught in the cod end of the net with the BRD installed, although some large rockfish were caught lodged in the funnel in front of the grid. The difference in catch of large rockfish is of marginal significance (paired t-test; P (one tailed) = 0.0539). Catches of small rockfish were variable. For instance, on one haul over 250 kg of shortbelly rockfish were caught in the side with the BRD, as opposed to less than 85 kg in the side without. Overall, the Nordmøre grid did not seem to have much effect on catches of small rockfish, flatfish or roundfish, and none of these comparisons were significant.

Table 5: Direct comparisons of paired catches (kg, side by side) with and without bycatch reduction devices during bycatch reduction experiments off Southern California. (Data were not collected on hauls with the separator panel excluder as video equipment was used on these hauls, and this may have affected the performance of the BRD).

	Haul area	**BRD spot prawns**	**No BRD**	**BRD large rockfish**	**No BRD**	**BRD small rockfish**	**No BRD**	**BRD flatfish**	**No BRD**	**BRD roundfish**	**No BRD**	**BRD invertebrates**	**No BRD**
Nord more Grid	Tanner Bank	15.7	20.2	3.3	28.4	15.7	35.0	7.5	10.1	6.4	12.9	4.0	3.5
	Tanner Bank	7.6	10.2	3.0	15.6	53.5	86.1	6.5	12.0	6.9	15.6	1.6	7.9
	Tanner Bank	18.2	19.8	0.5	5.8	15.0	9.5	4.2	4.1	4.6	7.9	1.8	0.7
	Tanner Bank	18.8	15.9	0.1	0.0	0.2	0.3	1.2	1.3	2.6	4.7	2.0	2.3
	Tanner Bank	19.1	17.7	0.4	0.1	4.7	2.7	2.0	0.8	6.0	2.2	0.8	0.5
	Tanner Bank	18.2	20.5	0.5	0.1	0.6	0.1	2.5	2.6	2.7	3.9	2.2	2.0
	Tanner Bank	49.0	34.7	1.3	0.8	9.1	6.0	21.7	10.1	10.2	5.7	3.7	1.9
	S.B.channel	19.5	18.9	0.0	0.0	10.2	6.1	5.8	21.9	34.1	37.9	4.5	2.7
	San Nicolas is.	17.3	10.9	3.3	0.3	281.9	122.4	13.4	1.7	11.7	14.0	25.9	31.4
	Tanner Bank	42.5	37.3	3.0	14.0	2.3	0.8	1.5	1.4	4.9	2.4	6.5	6.4
	AVERAGE	22.6	20.6	1.5	6.5	39.3	26.9	6.6	6.6	9.0	10.7	5.3	5.9
Fish eye	S.B.channel	12.7	14.7	0.0	0.0	27.0	28.0	18.9	22.0	86.5	60.5	24.3	41.3
	S.B.channel	17.7	19.5	0.0	0.0	4.1	31.7	4.4	4.4	41.8	55.4	17.7	2.7
	S.B.channel	10.3	10.0	0.0	0.0	9.9	6.2	1.1	1.8	90.3	168.2	3.1	0.9
	S.B.channel	12.0	11.2	1.0	2.1	18.0	20.3	2.2	7.5	41.8	37.1	9.7	7.6
	AVERAGE	13.2	13.9	0.2	0.5	14.8	21.5	6.7	8.9	65.1	80.3	13.7	13.1

Fish eye

The third device tested was the fish eye. Video observations of this BRD during six hauls showed that there were clear openings in the top panel of the trawl which were held open by the fish eye frame. There appeared to be significant water flow through the fish eye in the direction of the cod end, which served to keep prawns in the cod end during towing. Large numbers of fish (mostly flatfish) were seen escaping through the fish eyes by swimming against the current. The catches during the hauls observed consisted primarily of flatfish, with only a few small rockfish, so conclusions on the escape of rockfish through the fish eyes cannot be drawn from these observations. Some events where large numbers of fish escaped were seen when the trawl pulsed due to snags, as was seen with the Nordmøre grid. Again, this is evidence that the water flow down through the fish eye was holding the fish back in the cod-end and preventing escape. It again seems that the behavior of the fish may have been influenced by the presence of the lights. Some fish were seen to bump the light before swimming off after escaping from the net.

Catch comparisons could only be made for four hauls, all of which were made in the Santa Barbara Channel (Table 5). None of these comparisons produced a significant result, as would be expected with such a small sample size. Even though many flatfish and some small rockfish were seen escaping on the video hauls, this effect was not pronounced in the comparison between nets with and without the BRD (paired t test: flatfish P (one tailed) =0.0761, small rockfish P (one tailed) =0.2040). The fish eye did not appear to have a consistent effect of reducing bycatch of any of the other species groups.

The fish eyes used in the experiment were manufactured from 6.4 mm (1/4") stainless steel rod. This appeared to be very strong, but nonetheless all the fish eyes became bent after a few hauls of use, mainly due to their being caught on the rail as they were brought on board. Use of a stronger material and greater care during hauling would seem to be advised in the light of this experience.

Catch and Bycatch

16 hauls were completely or partially sampled for bycatch composition. The total catch during these hauls was 554 kg of spot prawns, 1898 kg of fish and 498 kg of invertebrates. The rate of spot prawn catch was variable by area. The lowest catch rate (14.1 kg/hour for both sides combined) was north of San Nicolas Island where the first hauls were made. According to the skipper, this is too low to be commercially viable for this vessel. Catch rates at Tanner banks and in the Santa Barbara Channel were 27.9 and 33.7 kg/hour respectively, which are commercially viable catch rates. The breakdown of the fish bycatch was 917 kg of rockfish (92 kg of large species of rockfish and 826 kg of small species), 196 kg of flatfish and 761 kg of other fish. The overall ratio of bycatch to spot prawn catch was 4.3:1.

Species composition of the fish bycatch was highly variable from area to area (Table 6). On the Tanner banks, the catches contained a greater proportion of rockfish, fewer flatfish, more corals, sponges, and a higher proportion of prawns to total catch. The most common species were shortbelly, splitnose and cowcod rockfish and spotted ratfish. The Santa Barbara channel area catches had a greater proportion of bycatch, and this consisted primarily of California argentine, Pacific hake, small rockfish (stripetail, shortbelly and splitnose rockfish) and flatfish (Dover, English, rex and slender sole).

At least 35 species of fish, including 19 species of rockfish (*Sebastes sp.*) were caught during the trip. This is a minimum estimate as it was not possible to identify all individuals to species. Eighteen of the rockfish species were caught in the Tanner banks area, with only five species seen in the Santa Barbara Channel. Of the six species of rockfish which have been designated as overfished by the National Marine Fisheries Service (NMFS), boccacio, cowcod and darkblotched rockfish were caught during this trip. The quantity of each of these caught during the monitored hauls was fairly small; 38.1 kg of cowcod, 7.3 kg of boccacio. Darkblotched rockfish were only caught during hauls where the catch was not sorted to species. Cowcod and boccacio were also caught during these hauls.

Table 6 Average catch (kg) per haul by area during bycatch reduction experiments off Southern California.

Area		**Santa Barbara Channel**			**San Nicolas Island**			**Tanner banks**		
Number of hauls		5			1			9		
Bycatch reduction device		no	yes	total	no	Yes	total	no	yes	Total
spot prawn	*Pandalus platyceros*	14.9	14.5	29.3	10.9	17.3	28.2	21.2	23.6	44.8
ridgeback	*Sicyonia ingentis*	7.8	7.8	15.6	0.0	0.0	0.0	0.0	0.0	0.0
pink shrimp	*Pandalus jordani*	15.5	17.8	33.3	0.0	0.0	0.0	0.0	0.0	0.0
shortbelly	*Sebastes jordani*	9.2	4.3	13.5	84.7	256	341	9.7	6.9	16.6
splitnose	*Sebastes diploproa*	5.7	6.2	11.9	30.2	16.7	47.0	3.6	2.2	5.8
stripetail	*Sebastes saxicola*	3.3	1.3	4.7	7.4	9.2	16.6	1.1	1.2	2.3
greenstriped	*Sebastes elongatus*	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.7	1.9
halfbanded	*Sebastes semicinctus*	0.3	2.0	2.2	0.0	0.0	0.0	0.0	0.0	0.0
pinkrose *	*Sebastes simulator*	0.0	0.0	0.0	0.0	0.0	0.0	2.1	1.6	3.7
greenblotch	*Sebastes rosenblatti*	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.2	0.5
blackgill	*Sebastes melanostomus*	0.0	0.0	0.0	0.3	3.3	3.6	1.6	0.9	2.5
bank	*Sebastes rufus*	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.2	0.8
chillipepper	*Sebastes goodei*	0.4	0.2	0.6	0.0	0.0	0.0	0.5	0.3	0.8
cowcod	*Sebastes levis*	0.0	0.0	0.0	0.0	0.0	0.0	4.2	0.0	4.2
boccacio	*Sebastes paucispinis*	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.8
shortspine thornyhead	*Sebastolobus alascanus*	0.0	0.0	0.0	0.0	0.0	0.0	1.1	1.7	2.7
Pacific hake	*Merluccius productus*	18.1	16.7	34.8	6.6	3.3	9.9	1.8	1.4	3.1
spotted ratfish	*Hydrolagus colliei*	2.3	1.7	4.0	7.1	4.2	11.3	2.7	1.3	4.0
Pacific argentine	*Argentina sialis*	44.2	33.9	78.1	0.0	0.0	0.0	0.0	0.0	0.0
bigfin eelpout	*Aprodon cortezianus*	0.5	0.7	1.2	0.0	0.0	0.0	0.0	0.0	0.0
dogfish	*Squalus acanthias*	1.5	0.3	1.8	0.0	0.0	0.0	0.0	0.0	0.0
petrale sole	*Eopsetta jordani*	2.2	0.0	2.2	0.0	9.2	9.2	0.4	0.0	0.4
unidentified flatfish		9.3	6.5	15.8	1.7	0.0	1.7	4.6	5.9	10.4
unidentified sculpins	*(cottidae)*	5.3	5.6	10.9	0.3	4.2	4.5	1.2	1.1	2.3
total fish		102	80	182	138	310	449	37	26	63.
benthic invertebrates		11.0	11.9	22.9	31.4	25.9	57.3	5.9	2.8	8.8
total catch		151	131	283	181	354	534	65	52	117
large rockfish		0.4	0.2	0.6	0.3	3.3	3.6	8.1	1.5	9.6
small rockfish		18.5	13.9	32.3	122.4	281.9	404	17.7	12.6	30.3
flatfish		11.5	6.5	18.0	1.7	13.4	15.1	4.9	5.9	10.8
roundfish		71.8	58.9	130.7	14.0	11.7	25.7	5.7	3.9	9.6

* pinkrose rockfish (*Sebastes simulator*) was one component of a group of similar species of red rockfish with white spots. This also included rosy (*S. rosaceus*), rosethorn (*S. helvomaculatus*), swordspine (*S. ensifer*) and pink (*S. eos*) rockfishes. Other rockfish species caught which are not recorded in the table were flag (*S. rubrivinctus*) and darkblotched rockfish (*S. crameri*) and California scorpionfish (*Scorpaena guttata*). Unsorted flatfish included rex sole (Errex zachirus), Dover sole (Microstomus pacificus), and hornyhead turbot (*pleuronichthys verticalis*).

Invertebrates caught during this sea trial also varied according to area. Invertebrates were not sorted to species, so these are only qualitative observations. In the Tanner bank area a large number of sponges were caught, and were the most common invertebrate bycatch. The sponges were of many species and morphological types, including barrel sponges, flat sponges, foliose sponges and shelf sponges (Tissot et al. 2006). Basket stars (*Gorgonocephalus eucnemis)*, crinoids (*Florometra serratissima*), anemones (*Metridium* sp), sea pens (*subselliflorae*) sea urchins (*Allocentrotus fragilis* and *Lytechinus anamesus*), tanner crabs (*Chionoecetes sp.*), sea whips (*Halipteris californica*), and a small amount of coral (probably *Antipathes dendrochristos* (Opresko 2005) which was at the time an undescribed species) were also caught. Some large boulders and items of anthropogenic trash that were covered in epifauna were also brought up in the nets. In the Santa Barbara Channel the main invertebrates caught were sea urchins (*Allocentrotus fragilis*) and crabs, although a few starfish and sponges (possibly including the hexactinellid *Aphrocallistes vastus*) were also caught.

Discussion

I tested three types of bycatch reduction device in the spot prawn fishery off southern California. None of the three produced large reductions in bycatch, although the Nordmøre grid was effective at releasing large rockfish. The overall level of bycatch was high, including a diverse array of fish species and habitat forming sessile invertebrates.

<u>Bycatch reduction devices</u>

The separator panel did not function adequately in the configuration in which it was installed. This may have been an inherent design flaw in the panel supplied, but it seems more likely to have been due to the aft part of the trawl collapsing. It is likely that mounting the panel in a pre -made extension section as was done here is not appropriate. For this sort of design to work it needs to be in a part of the net which is more open than the aft part of the extension, and the meshes need to be under some tension to retain the shape of the panel. The most potential for this sort of separator is if it is designed as an integral part of the net and mounted in the aft of the belly where these conditions are met. However, for the spot prawn fishery, where there is often a substantial catch of benthic organisms such as sea urchins and sponges, there needs to be a way to avoid the panel becoming blocked. It is possible to achieve this objective by using a buoyant flapper on the bottom panel so that any heavy objects will fall out before they reach the panel. Alternatively, the panel could be installed to slope down from the top of the net to the bottom, which would direct heavy objects out of the escape hole. It would probably be necessary to use a guiding funnel with this arrangement, and that would have some additional problems.

The Nordmøre grid produced more encouraging results than the separator panel. However, it seems that the 7.5 cm bar spacing chosen was quite significantly too large to be optimal in this fishery. The choice of bar spacing has to be a compromise between the risks of losing part of the target catch or blocking the grid and the benefits of deflecting bycatch. Further work would need to use much smaller grid spacing. Five cm or less would be an appropriate starting point.

The use of a grid with smaller spacing does, however, increase the chance of the grid becoming blocked by some of the larger invertebrates (corals, sponges, kelp mats). This was a relatively serious problem in some of the hauls made during this experiment. Various solutions exist to combat this. Workers in Australia have used grids that are inclined downwards, and let fish out of the bottom rather than the top ((Brewer et al. 2006)) and shown that these are more effective at getting rid of debris that reaches the grid. Alternatives include using a buoyant flapper over an escape opening in the bottom of the net so that the weight of heavy debris causes it to drop out, but lighter prawns will not have this option. The problem of blocking of the funnel in front of the grid still exists. This can be mostly eliminated by attaching the funnel further up the net where it is more open, rather than in the collapsed extension section. It may be necessary on some vessels to slightly change shooting and hauling procedures to accommodate these changes in the rig.

As it was necessary to make all of the observations of fish behavior in relation to the grid and the fish eye with the aid of lights, the behavior observed cannot be considered completely typical of that under normal fishing conditions. Many of the fish observed holding station in front of the grid may have been entrained to the lights and not reacting to the grid at all. However, it seems to give an indication that the fish which are caught in prawn trawls are not inclined to make escape attempts in an upward direction in the manner of for instance haddock and whiting in the Atlantic (Wardle 1993). Some Pacific hake were observed from within the cod-end to attempt to escape through the lower panel of the net. This seems to give further impetus to the use of escape panels in the lower, rather than the upper panel of the trawl.

The fish eye was the simplest of the devices used, and the video observations seemed to suggest that it worked to a certain extent. It is clear however, even from the small number of hauls tested, that it is not a particularly efficient means of getting bycatch species out of the trawl. Improvements to its performance may be possible by moving it further back in the cod-end, although this risks loss of prawns. Its simplicity in use and installation are the main factors in its favor.

Other solutions, such as square mesh panels, may be an equally simple way to exclude small fish from the catch, although they will not release the large rockfish which are one of the species groups which are significantly impacted by the spot prawn fishery. The optimum solution, if the aim is simply to reduce the quantity of bycatch in the net, is probably some sort of combination device. This could use a grid to let out the large bycatch and a second device such as a square mesh panel or fish eye to let out the rest of the small bycatch. This sort of combination of devices has been used successfully in the Australian northern prawn fishery (Brewer et al. 2006). The size of the target prawns is sufficiently large that a panel of rather large mesh could be used without risking loss of prawns. The use of a grid/panel combination would reduce the volume of bycatch and divert some of the water flow away from the end of the cod-end, potentially reducing damage to the prawns and thus increasing their value.

Bycatch

The total amount of bycatch and the composition of the bycatch presented a cause for concern with this fishery. More than four times as much bycatch was caught as target spot prawns, and all of this was discarded.

Some rockfish were caught on every haul in the Tanner Banks area, and included cowcod, darkblotched rockfish and boccacio. These species have been listed as overfished and in need of rebuilding by the National Marine Fisheries Service (NMFS). Although the numbers observed on any particular haul were not very large, if these numbers are expanded by the number of hauls made annually by the spot prawn fleet, they would represent a substantial proportion of the annual allowable catch levels set by NMFS. The total catch in the California spot prawn fishery south of Pt. Conception in 1998 was 373,588 kg of prawns. If cowcod were caught at the same rate as was seen during this trip (0.0688 kg per kg prawns) then the total catch of cowcod would have been 25,688 kg. This is greater than the total catch currently allowed for the species (24,000 kg in 2005). The Nordmøre grid used in many of the hauls was very effective at releasing cowcod; so many more would have been caught if this gear had not been in use.

The quantity of attached, structure forming invertebrates such as sponges and corals caught in the Tanner Banks area was quite large, with some being caught on almost every haul. This was unexpected. Prior to this study, little mention had been made of invertebrate bycatch or the effect of spot prawn trawling on structure forming species and habitat. These organisms could be excluded from the catch by the use of BRD's, but their fate after this is probably not significantly different than being caught and discarded overboard. They are unlikely to survive after being uprooted and even if they do, they are unlikely to settle in a suitable place for continued survival. Some of these species are very slow growing in the deep water environment in which the fishing took place, and their removal may have a significant effect on the ecosystem. The Tanner banks area where part of this study took place was included as part of the Cowcod Conservation Area

(CCA) which was established off southern California in 2001. These areas are now closed to groundfish harvest and the use of any bottom tending gear.

The invertebrate bycatch taken in the SBC was much less diverse, and consisted mostly of organisms that thrive on flat or disturbed seabeds. The grounds fished in the SBC were not as rocky as those fished on Tanner banks, so there would be expected to be fewer structure forming invertebrates, but some rocky reefs were trawled over (seen on sonar traces), so the lack of these classes of invertebrates is probably an indication of long term changes caused by extensive trawling in the area.

2.3 Observations of bycatch in commercial spot prawn trawling operations off Washington, September 15-16 1999.

Research objectives

Prior to 1999, no observations had been made of the bycatch in the spot prawn trawl fishery off the Washington coast. Concerns about the bycatch and habitat damage caused by the trawl fishery had been raised as early as 1994 by pot fishers exploiting the same resource (S. Barry WDFW, pers. comm. 1999). The objective of this trip was to describe and quantify the bycatch in this spot prawn trawl fishery.

Methods and equipment

<u>Study area and vessel</u>

Spot Prawn trawling operations were observed on board a commercial vessel during a two-day trip in September 1999. The "Miss Mary" is a 23 m, 90 tonne, 500hp shrimp trawler, built in 1968 of a design typical of steel vessels used in the Gulf of Mexico and off the West Coast of the USA. The vessel used a single trawl spread by steel otterboards. The otterboards were attached directly to the wings, using only short chain extensions. The headrope length was 24.7 m, and the footrope was 25.3 m, giving a spread of approximately 20-21 m between wing ends. The net was equipped with rubber rockhopper gear, with discs 35 cm in diameter spaced every 1.2 m, with 12 cm discs between (Figure 17). To avoid damage, the net was also equipped with floats on the ground line and in the belly of the net. The mesh size in the body and wings of the net was 10.2 cm, with 5.1 cm (2") mesh in the cod end. The net was equipped with a bycatch reduction device similar to a “fish eye” consisting of a reinforced opening in the top of the net, the forward end of which was weighted with chain. In the depths of water fished, 450-500m of wire was used.

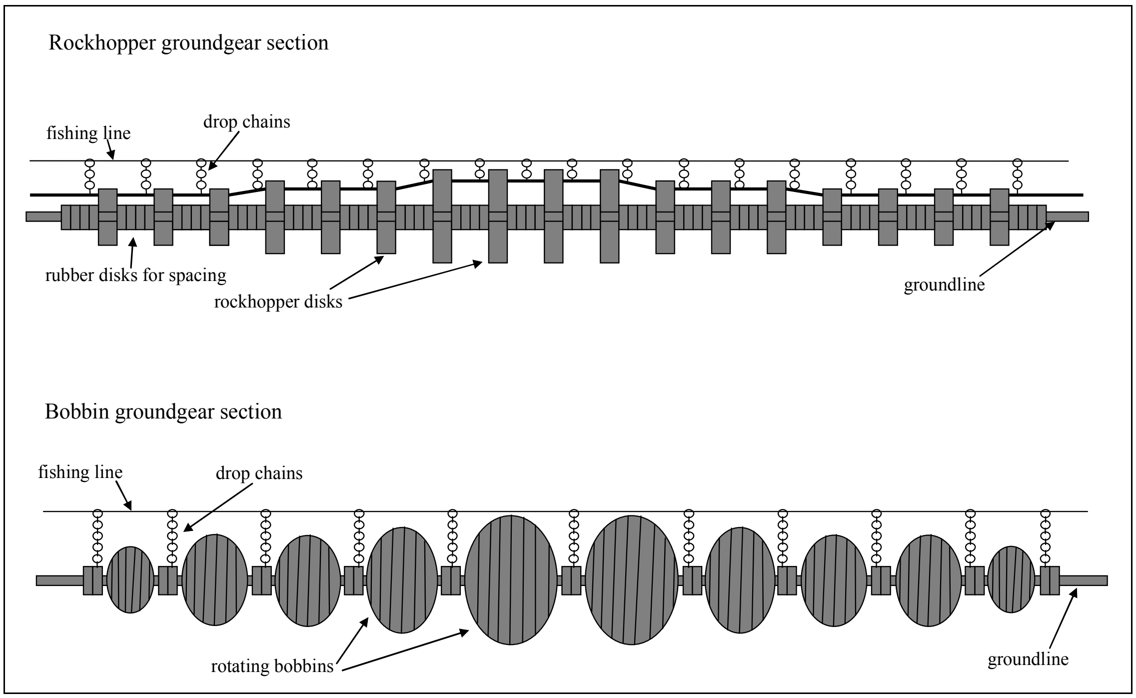


Figure 17: Schematic diagram of trawl ground gear types

Fishing was carried out in an area approximately 30-35 nautical miles to the West of Grays Harbor, in 165 to 275 m depth (Figure 18). Tows generally followed the depth contours and were not straight lines as indicated in the figure. Seven tows were made during the trip. Bycatch was sorted from 5 of these tows. Two tows were not sampled, as they were not considered typical due to gear problems. During the last tow (tow 7) it appeared that one of the otterboards may have flipped for a time. However, there was a substantial catch in this haul and it was sampled and included in the analysis.

The area off Grays Harbor was very heavily fished by trawl gear in the years before this trip. As an example of the fishing pressure, the density of tows made in the area in 1997 is also shown on Figure 18.

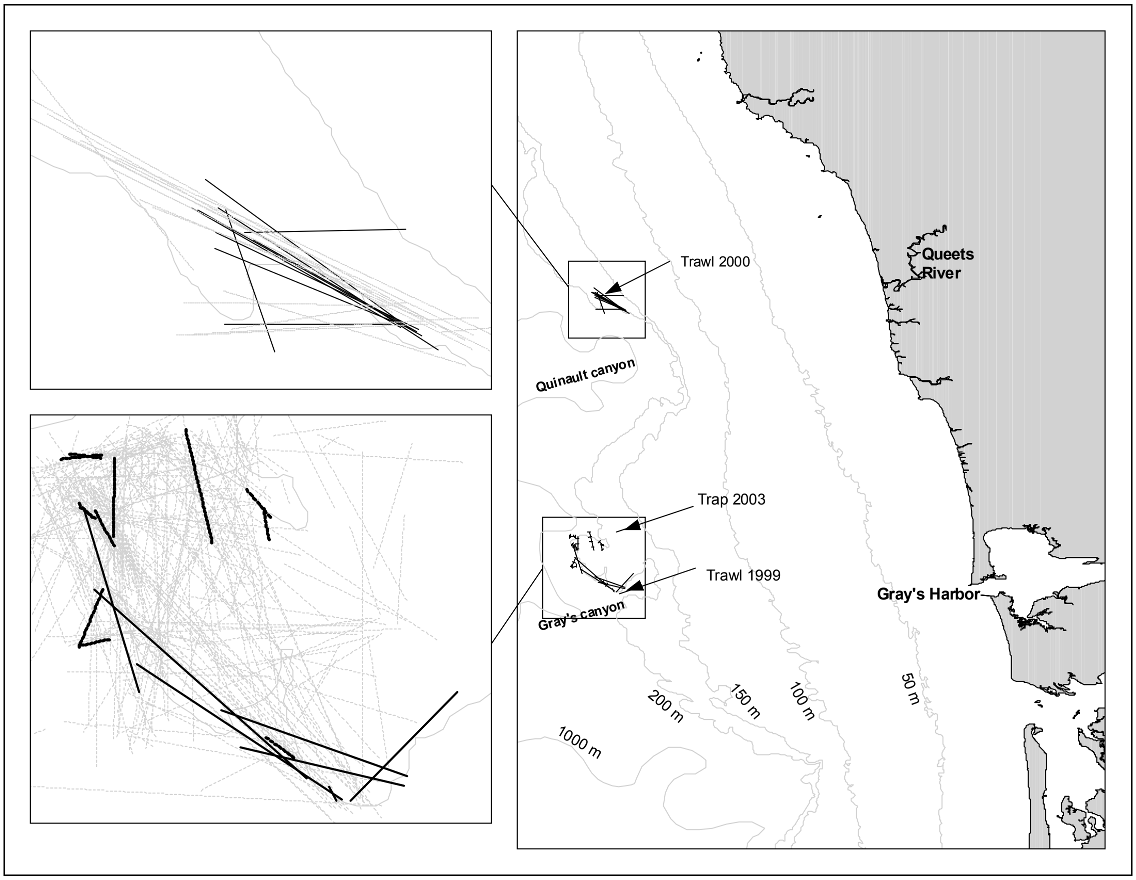


Figure 18: Fishing locations for bycatch observations off Washington. Sampled trawl hauls and pot sets are shown as solid lines. Faint dotted lines on the left hand panels represent trawl tracks for 1997 fishing activity from logbook data.

At the end of each haul the catch was dumped from the cod-end directly onto the deck. The spot prawns were separated from the bycatch, graded, packaged in two-pound boxes and frozen. During 4 hauls a random sample of between 50 and 100 prawns was taken prior to the grading process, and the carapace length (CL) of each was measured. The presence or absence of eggs was also noted. We were unable to identify differences between the two sexes for smaller individuals that were not carrying eggs due to time constraints. The total weight of spot prawns in each haul was estimated from the number of boxes processed by the crew.

The remainder of the bycatch was sorted. Fish were sorted to species, with the exception of Cottids (sculpins), poachers and skates, which were not keyed out. Invertebrates were sorted into categories of sponges, sea urchins, and "others", which consisted mainly of sea stars, sea cucumbers and anenomes. All samples were weighed, and fish numbers counted before discarding. Some length measurements for the major fish species were also made for some hauls.

Results

The five tows observed yielded 79 kg of spot prawns and 558 kg of bycatch. Spot prawn catch rates ranged from 2.3 to 16.3 kg per hour, averaging 7.2 kg per hour.

The lengths of 264 prawns were measured. Of these, 100 were ovigerous. Carapace lengths (CL) ranged from 30 to 55 mm. Almost all of the prawns over 45 mm CL were carrying eggs, with the exception of two large individuals which were soft because they had obviously recently molted. The length distribution is shown in Figure 19. Butler (1964) reported finding a group of male spot prawns in British Columbia averaging 33 mm CL, which changed sex at the start of their third year. Given a similar growth rate and pattern in this area, we would have expected that some of the smallest prawns we observed would have been males. The modes in this distribution probably represent 2.5, 3.5and 4.5 years age (1997, 1996 and 1995 year classes).

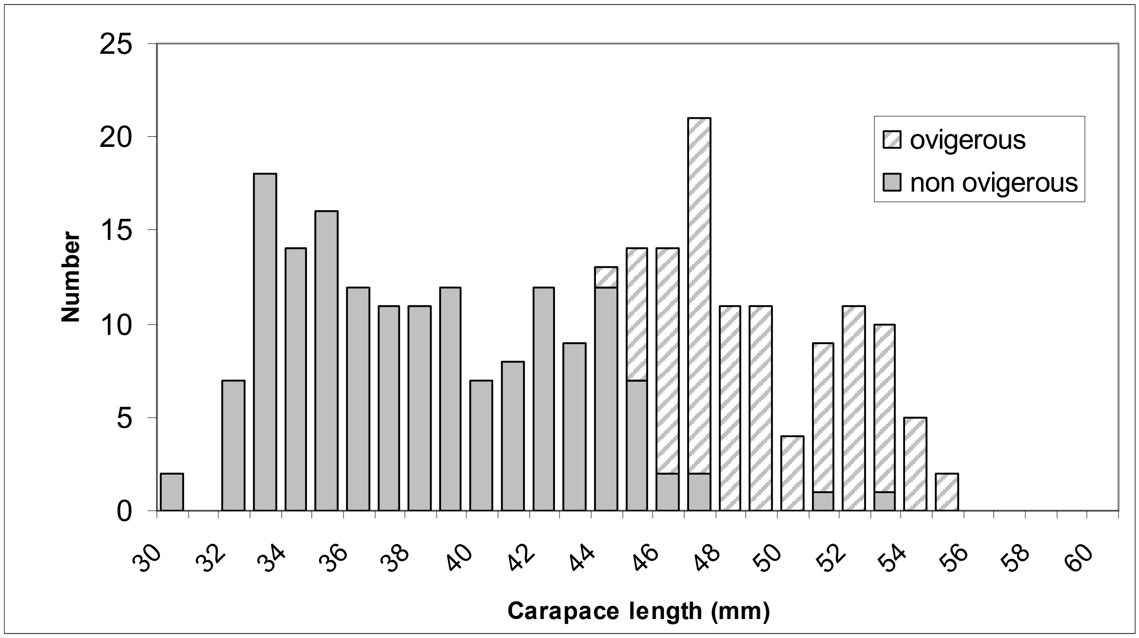


Figure 19: Spot prawn length distribution for trawl bycatch observations off Washington in 1999

The total fish bycatch during the 5 tows was 283 kg. This consisted of 86 kg of rockfish (mainly sharpchin rockfish and shortspine thornyheads), 141 kg of flatfish (mainly Dover sole, rex sole, halibut and arrowtooth flounder) and 56 kg of elasmobranchs (ratfish and skates), Pacific hake and other fish. Full details of catch by weight are given in Table 7.

The sizes of the rockfish caught during haul 6 were measured. Sharpchin rockfish ranged in size from 19 to 35 cm and thornyheads from 11 to 25 cm. The majority of the rex and Dover sole caught were small, below marketable size (approximately 30 cm).

Table 7 Catch and bycatch weights (kg) for trawl bycatch observations off Washington in 1999.

	Haul	1	2	4	6	7	total
	Towing duration (hours)	2.0	2.0	3.17	2.0	1.83	11.0
Shrimps							
spot prawn	*Pandalus platyceros*	32.2	15.4	7.7	18.1	5.9	79.4
Sidestripe shrimp	*Pandalopsis dispar*	0.05	0.2	0.05	0.0	0.05	0.4
yellowleg pandalid	*Pandalus tridens*	0.05	0.05	0.0	0.05	0.05	0.2
Rockfish							
Sharpchin	*Sebastes zacentrus*	3.1	0.6	2.3	23.0	11.1	40.0
Rosethorn	*Sebastes helvomaculatus*	0.1	0.1	0.0	2.7	0.6	3.5
Splitnose	*Sebastes diploproa*	0.7	2.2	0.0	1.5	1.0	5.3
Greenstriped	*Sebastes elongatus*	0.0	0.0	2.0	0.0	0.2	2.3
Widow	*Sebastes entomelas*	0.0	0.0	1.6	0.0	1.5	3.1
Redbanded	*Sebastes babcocki*	0.1	0.0	0.0	0.0	0.1	0.2
Yelloweye	*Sebastes ruberrimus*	0.0	0.0	0.0	0.0	0.0	0.0
shortspine thornyhead	*Sebastolobus alascanus*	10.3	12.9	1.4	6.4	0.2	31.2
Flatfish							
halibut (estimated weight)	*Hippoglossus stenolepis*	18.1	0.0	0.0	0.0	4.5	22.7
rex sole	*Errex zachirus*	11.7	7.0	9.3	11.1	2.5	41.6
Dover sole	*Microstomus pacificus*	9.0	13.6	15.6	10.5	1.1	49.9
slender sole	*Eopsetta exilis*	1.1	3.3	2.4	0.9	0.0	7.7
arrowtooth flounder	*Atheresthes stomias*	4.0	0.9	5.8	1.9	6.2	18.8
English sole	*Pleuronectes vetulus*	0.3	0.0	0.0	0.0	0.0	0.3
longnose skate	*Raja rhina*	9.3	5.0	6.8	6.5	0.0	27.6
electric ray	*Torpedo californica*	0.0	0.0	0.0	0.0	7.0	7.0
Other roundfish							
Pacific hake	*Merluccius productus*	1.4	0.3	3.4	1.0	0.0	6.1
unid. poachers	*(Agonidae)*	0.1	0.9	0.2	0.0	0.0	1.3
unid. sculpins	*(Cottidae)*	0.0	0.1	0.0	0.0	0.0	0.2
Ratfish	*Hydrolagus colliei*	0.5	9.1	1.7	0.0	0.0	11.2
blacktail snailfish	*Careproctus melanurus*	0.0	0.6	0.0	0.0	0.0	0.6
Sablefish	*Anaplopoma fimbria*	0.0	0.0	0.0	2.3	0.0	2.3
invertebrates							
hexactinellid sponge	*Aphrocallistes vastus*	1.7	11.3	0.6	1.8	15.1	30.5
sea urchins	*Allocentrotus fragilis*	44.6	91.2	11.3	67.9	15.1	230.1
starfish, sea cucumbers anenomes etc.		4.5	9.5	0.0	0.0	0.5	14.5
Total							
Fish		69.7	56.7	52.5	67.9	36.2	283.1
invertebrates		50.8	112.0	11.9	69.7	30.6	275.1
total catch		120.5	168.7	64.5	137.7	66.8	558.2
Rockfish		14.3	15.8	7.3	33.6	14.7	85.7
Flatfish		53.5	29.8	39.9	31.0	21.4	175.7
other fish		1.9	11.0	5.4	3.4	0.0	21.7
ratio fish:prawn		2.2	1.7	6.8	3.7	6.1	3.6

The invertebrates were sorted into 3 categories: sponge, sea urchins, and others (consisting of sea stars, sea cucumbers (*Parastichopus californicus*), anemones (*Metridium sp*.), tritons (*Fusitriton oregonensis*) and various species of crabs). The sponges caught were mostly a species of hexactinellid sponge, *Aphrocallistes vastus*, although there may also have been some of a similar species, *Heterochone calyx*. Both these species have a hard silaceous skeleton and for this reason the crews of some fishers refer to it as coral. A large proportion of the sponge caught during the first 4 hauls appeared to be dead. The sponges were broken up into small pieces, and their surface was covered with what appeared to be brown algal growths.

During haul 7, a large quantity of live sponge was caught. Most of this was broken up into pieces less than 15 cm in length, but it included at least one very large (approx. 1m in diameter) *Aphrocallistes vastus* colony. The sponge was pale yellow/cream in color, had no algae covering the surface and appeared to be recently broken. A number of organisms were found inside the main atrial cavities of these sponges, although it is impossible to tell if these were actually resident in the sponges or became lodged in the openings during the towing, hauling and dumping of the cod-end.

Discussion

Catch rates of spot prawns were lower during this trip than had been expected by the captain, and were lower than the average reported for this vessel in logbooks. Given these catch rates, the normal procedure would have been to move to a different area, but this was not done as this was a short trip, and moving would have taken out too much fishing time. The percentage of the catch that is the target species (14.2%) is therefore probably lower than would be expected during a normal trip.

Rates of bycatch were quite high. The ratio of total bycatch to spot prawn catch was 7:1, and the ratio of fish bycatch to spot prawn catch was 3.6:1. The most commonly caught fish species were Dover sole, rex sole and sharpchin rockfish. Of overfished rockfish species, only two widow and one juvenile yelloweye rockfish were caught.

The catch composition during haul 7 was notably different from the others. This haul had the lowest proportion of flatfish to total catch and a high proportion of rockfish. There were also relatively fewer sea urchins. According to the captain, this tow was made in an area that had not previously been heavily fished due to low catch rate of spot prawns. It is not clear if the difference in catch composition was related to the fact that it was a different area, if it was to do with the gear performance during this tow or if it was due to a change in the sea floor habitat and hence associated fish communities caused by frequent trawling and destruction of the sponge communities. I observed a similar pattern during a trip on a spot prawn trawler in California (Section 2.2). A very mixed bag of bycatch was caught along with large amounts of sponges in "new" areas, and less sponge, more flatfish, and more sea urchins in "old" areas.

2.4 Observations of bycatch in commercial spot prawn trawling operations off Washington, July 30 - August 1, 2000.

Research objectives

The objective of this trip was to collect further information on the bycatch in the Washington spot prawn fishery. Secondary objectives were the collection of further data on the size composition of the spot prawn population and samples for genetic analysis.

Methods and equipment

<u>Vessel and study area</u>

The "Wild Mary" is a 23 m, 1150hp, 129 GRT steel shrimp trawler. The vessel participated in the spot prawn trawl fishery off Washington from 1998, and was one of 4 vessels that held an emerging commercial fishery permit to trawl for prawns off Washington in 2000.

The gear used was a single, custom made spot prawn trawl, designed and built by Robert Driscoll Net Service of Warrenton, Oregon. It was made from 4.4 cm (1 ¾ inch) mesh throughout. The headrope and footrope lengths were 26.8 m, overall net length was approximately 22.9 m and wing height was approximately 1.5 m. It was a short bodied, wide net, designed to have a low vertical opening in order to reduce fish bycatch. The ground gear consisted of rubber bobbins (Figure 17) that varied in size from 25 cm in the wings to 61 cm in the center of the net. They were mounted on simple bearings, which allowed them to rotate freely. 20 floats were mounted on the footrope to help reduce ground contact, and floats were used in the belly and cod-end to keep the netting off the bottom. The net was equipped with a pair of steel framed "fish eye" bycatch reduction devices mounted in the cod-end. It was spread by a pair of 2.74 m * 1.8 m steel vee otterboards (Amco) attached directly to the wings. Swept width with this gear was probably 18 – 21 m. Scope used was approximately 1.5:1, and towing speed approximately 1.6 knots.

Fishing was carried out in an area approximately 20 nautical miles off the mouth of the Queets River, in 165 to 275 m depth (Figure 18).

Fourteen tows were made during the trip, and bycatch was sorted from 10 of these. Analysis of commercial logbooks shows that this area had been fished consistently by both trawls and pot vessels since 1996.
At the end of each haul the catch was dumped from the cod-end directly onto the deck. The spot prawns were separated from the bycatch and immediately transferred to refrigerated holding tanks to be maintained alive for live sale. A random sample of prawns was taken during sorting, and the carapace length (CL) of each was measured. The presence or absence of eggs was also noted. The total weight of spot prawns in each haul was estimated from the number of baskets filled by the crew. The remainder of the bycatch was sorted. Fish were sorted to species. Invertebrates were sorted into categories of sponges, sea urchins, sea stars and sea cucumbers. All samples were weighed, and fish numbers counted before discarding.

Results

The 10 tows observed yielded 395 kg of spot prawns and 1391 kg of bycatch. Spot prawn catch rates ranged from 15.4 to 23.1 kg per hour, averaging 20.9 kg per hour. Spot prawns made up 22% of the total catch. Details are given in Table 8.

Table 8: Catch and bycatch weights (kg) for trawl bycatch observations off Washington in 2000.

		Night tows	**Day tows**	**Total**
	Number of hauls	2	8	10
	Total towing duration (hours)	3.9	15.2	19.1
fish		504.2	559.8	1064.0
invertebrates		11.7	221.4	233.2
total		588.7	1196.8	1785.5
spot prawn	*Pandalus platyceros*	72.6	322.1	394.6
pink shrimp	*Pandalus jordani*	0.2	93.1	93.3
yellowleg pandalid	*Pandalus tridens*		0.4	0.4
Rockfish				
Sharpchin	*Sebastes zacentrus*	29.3	47.4	76.7
Rosethorn	*Sebastes helvomaculatus*	20.7	16.1	36.8
Splitnose	*Sebastes diploproa*	0.5	1.5	2.0
greenstriped	*Sebastes elongatus*	40.0	27.6	67.6
Redbanded	*Sebastes babcocki*	1.9	3.9	5.8
darkblotched	*Sebastes crameri*	2.9	19.0	21.9
Pacific Ocean perch	*Sebastes alutus*		2.3	2.3
Canary	*Sebastes pinnniger*		1.2	1.2
stripetail	*Sebastes saxicola*	0.0	0.3	0.4
redstriped	*Sebastes proriger*	4.1	10.3	14.5
yellowtail	*Sebastes flavidus*	3.2		3.2
shortspine thornyhead	*Sebastolobus alascanus*	11.2	13.9	25.1
Flatfish				
halibut (estimated)	*Hippoglossus stenolepis*		5.4	5.4
rex sole	*Errex zachirus*	2.7	1.7	4.4
Dover sole	*Microstomus pacificus*	79.5	53.4	132.9
slender sole	*Eopsetta exilis*	4.4	0.6	5.0
arrowtooth flounder	*Atheresthes stomias*	187.4	274.8	462.2
longnose skate	*Raja rhina*	4.1	22.4	26.5
sandpaper skate	*Bathyraja kinkaidii*	5.2	4.0	9.2
Other fish				
Pacific hake	*Merluccius productus*	6.3	0.5	6.7
Pacific cod	*Gadus macrocephalus*	6.9	1.1	8.0
poachers unid.	*(Agonidae)*	0.8	0.3	1.1
threadfin sculpin	*Icelinus filamentosus*	1.6	1.4	3.0
spotted ratfish	*Hydrolagus colliei*	4.2	2.4	6.5

Table 8 continued

		Night tows	Day tows	Total
blacktail snailfish	*Careproctus melanurus*	0.0		0.0
sablefish	*Anaplopoma fimbria*	15.3	26.4	41.7
Lingcod	*Ophiodon elongatus*	65.7	18.6	84.3
eulachon	*Thaleichthys pacificus*	5.0	2.9	7.9
prickleback unid.	*(Stichaeidae)*	0.0	0.1	0.1
hagfish	*Eptatretus stouti*	0.0	0.3	0.3
combfish	*Zaniolepis sp.*		0.0	0.0
bigfin eelpout	*Aprodon cortezianus*	0.4		0.4
Black dogfish	*Centroscyllium fabricci*	0.6		0.6
invertebrates				
hexactinellid sponge	*Aphrocallistes vastus*		0.2	0.2
other sponge			0.2	0.2
starfish etc.		4.6	21.4	26.0
sea cucumbers		7.2	197.5	204.7
sea whip			0.0	0.0
jellyfish			1.8	1.8
octopus unidentified			0.2	0.2
squid unidentified			0.0	0.0

Carapace lengths (CL) of 413 prawns were measured. These ranged from 25 to 50 mm (Figure 20). 9 prawns between 39 and 45 mm were ovigerous (2.2% of the total). This was unexpected for this time of year, and may indicate that spawning occurs earlier than expected in this population. Recent analysis of spot prawn samples taken from offshore and the Straits of Juan de Fuca have shown that the prawns in Washington waters change sex at 39 – 44 mm CL. Few females were seen during this trip. However, there does seem to be a strong mode in the 32 – 40 mm range. These prawns are probably age 2+ (1998 age class).

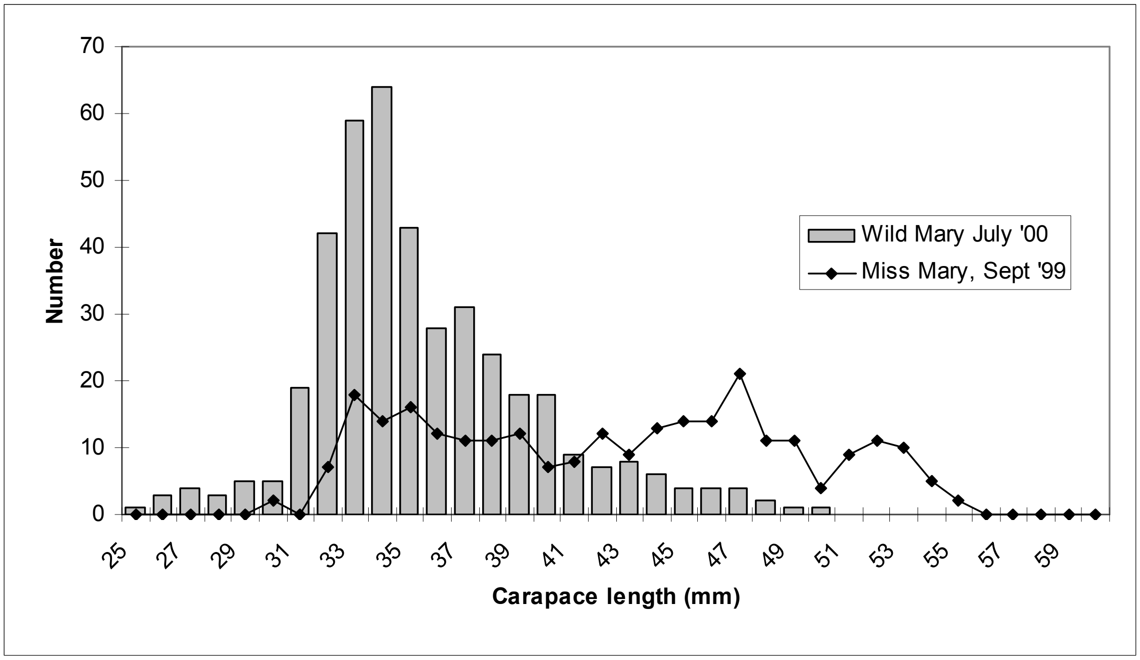


Figure 20: Spot prawn length distribution for trawl bycatch observations off Washington in 1999 and 2000

A total of 33 species of fish were seen in the 1064 kg of fish taken as bycatch during the trip. The overall ratio of fish to spot prawns was 2.7:1. The primary species by weight were arrowtooth flounder, Dover sole, lingcod, sharpchin, greenstriped and rosethorn rockfish. Two hauls were made in the late evening, after dusk. These hauls produced a much higher amount of bycatch than the daytime tows. Full details are given in Table 8, divided into day and night fishing.

The lengths of the fish were not measured. However, it is clear by observation of the average weights that many of the rockfish were of marketable size, as were a substantial proportion of the other fish.

The most common invertebrate species was the California sea cucumber (*Parastichopus californicus*). Large numbers of these were taken almost every haul. Some sea stars of various species were also taken in every haul. Tanner crabs (*Chionoecetes* sp.) and a few sea whips (*Halipteris californica*) were also caught.

Few sponges or sea urchins were seen, which is in marked contrast to the catch observed in 1999 (Section 2.3).

Discussion

The average CPUE for prawns was 20.7 kg per hour. This is a viable commercial catch rate, and similar to the catch rates of other trawl vessels reported in logbooks submitted to WDFW. The observations of bycatch are also considered representative of the usual bycatch levels taken by this vessel. Great efforts had been made by the captain to reduce his bycatch levels via gear modifications such as the use of a low opening net, bobbin ground gear and the fish eye BRD. The success of these efforts is reflected in overall ratio of fish to prawns observed on this trip (2.7:1), which is lower than any other observation of bycatch in spot prawn trawls, with the exception of my study using a Nordmøre grid (Section 2.2)

It is notable that the composition of the bycatch seen in the catches of the Wild Mary was distinctly different from that seen in the catches of the Miss Mary one year previously (Table 9).

Table 9: Comparison of trawl bycatch composition for two studies off Washington.

	Miss Mary 1999		**Wild Mary 2000**	
	Catch (kg)	**%**	**Catch (kg)**	**%**
spot prawn	79.4	12%	394.6	22%
other shrimp	0.5	0%	93.7	5%
rockfish	85.7	13%	257.5	14%
flatfish	175.7	28%	645.7	36%
other roundfish	21.7	3%	160.8	9%
sponge	30.4	5%	0.5	0%
urchin	230.0	36%	0.2	0%
other invertebrates	14.5	2%	232.7	13%
	637.9	100%	1785.8	100%

Two major factors are likely to account for the difference in bycatch between observed trips: species composition in the areas fished, and the effect of the use of different ground gear types. The nets used by the two vessels had similar head and footrope lengths, and therefore were expected to have similar swept width. The major difference was that the Miss Mary used rockhopper gear and the Wild Mary used rolling bobbin gear (Figure 17). The Miss Mary used gear with a maximum diameter of 36 cm and the largest bobbins used by the Wild Mary were 61 cm.

Neither gear type would be expected to be very effective at catching organisms that are on the sea floor, due to the size of the gear. The key difference between the gear types is that rockhopper gear discs have a hole in the outer part of the disc, which has a rope or cable threaded through it, to which the fishing line of the trawl is attached (Engas and Godo 1989). Thus the rockhopper discs do not roll along the sea floor as bobbins do when they are working properly. Rather, rockhopper gear has a skipping, bounding motion as it comes free after sticking on sea floor features. This means that the discs can drag when they contact the sea floor, and hence collect heavier benthic invertebrates like sea urchins and sessile organisms such as sponges, which bobbins would roll over. This is seen in the data. The Miss Mary catches contained three times more benthic invertebrates than those from the Wild Mary. The extent of damage to benthic invertebrates that are rolled over by the bobbins is unknown.

A similar effect would be expected with the catch of flatfish, due to the difference in gear size and type. The Wild Mary’s catch by weight was dominated by arrowtooth flounder, of which few were seen in the Miss Mary’s catch. Arrowtooth are a large active species and are easily caught in trawls. Without these, the rest of the flatfish only make up 10% of the Wild Mary’s total as opposed to 36% for the Miss Mary.

The net used by the Miss Mary was expected to have a much greater headline height, and therefore be more effective at catching rockfish, but this was not seen in the data. It may be that there were simply more rockfish in the area fished by the Wild Mary, especially as this area has been much less heavily fished than the Gray’s canyon area.

Both vessels use bycatch reduction devices of the fish eye type, which would be expected to reduce the fish bycatch somewhat. These BRDs are thought to be effective at releasing both roundfish and flatfish, although not as effective as Nordmøre grids. Both vessels use a cod-end mesh size that would retain a high percentage of the bycatch compared to the larger mesh size used in groundfish trawls.

There was a distinct difference in the size composition of the spot prawns in the catches from the two trips. Figure 20 shows the size composition of both. The smallest prawns previously seen in trawl catches in deep water were about 30 mm carapace length, 2+ year old males. Smaller prawns were presumably either not present in these areas or not available to the gear, possibly in shallow water. In late 1999, we saw relatively few of these small prawns in the catches of the Miss Mary. In 2000 there were few of the next size class, which would have been age 3+ and would have been 30-35 mm one year previously. There were also few of the largest prawns. These results reflect the relatively small size of the 1997 year class, which I estimated as being approximately one third the size of the 1998 year class (see Chapter 4).

2.5 Observations of bycatch in the commercial pot fishery off Washington April – May 2003.

Research objectives

The primary objective of this trip was to describe and quantify the bycatch in the spot prawn pot fishery off the Washington coast. The trawl fishery in this area was closed at the start of 2003, but there was no information on bycatch in the pot fishery which continued to operate and was expected to expand. Secondary objectives were to monitor the size composition of the spot prawn population and to assess the mesh selectivity of the pots used in the fishery by comparing the catch with catch in small-mesh pots.

Methods and equipment

Vessel and study area

Spot prawn pot fishing operations were observed aboard the vessel “Watchman” during a three day trip in April – May 2003. The “Watchman” is an 83 ft, 165 tonne steel vessel, built in 1982 of a design similar to those used for crab fisheries in Alaska.

The pots used were manufactured by Ladner traps, of Delta BC. The regulations for this fishery state that the pot mesh size is required to be over 2.2 cm (7/8 inches, defined such that a 7/8” dowel can freely pass through the mesh). The stretched mesh size to achieve this is 3.8 cm. Pots were fished on longlines with a large anchor at either end of the line. Each pot was baited with approximately 1 pound of ground fish in a bait container. During this trip the bait was mostly hake, although herring or mackerel is preferred. The vessel was fishing 479 pots, configured as four strings of approximately 100 pots and two strings of 50 during this trip. The pot limit for the fishery was 500 pots per vessel.

Twenty experimental small mesh pots were also used. Ten of these were fished alternating with standard pots on the ground line of two strings. The small mesh pots were 1.27 cm mesh, also made by Ladner traps. They were slightly smaller than the commercial pots, but of a similar design. The same amount and type of bait was used in all pots. The aim of using these smaller mesh pots was to attempt to determine the selectivity of the standard pots and to look for the presence of small, immature prawns on these grounds.

The pots were hauled using a large power block. As each pot was brought aboard, it was disconnected from the ground line and the catch was emptied onto a table. Prawns were then sorted out into a water-filled tote, ready to be transferred into live tanks after the string was completed or the tote was full. Samples of prawns were taken for measurement by taking the entire catch from a series of pots until we had a sample of approximately 100 prawns from that string. For the alternating small mesh and standard pots, the catch from each pot was kept separate for measurement.

Bycatch would normally be shoveled straight overboard immediately after the pot was emptied, before the next pot was brought onboard, but for this trip it was shoveled into a basket ready for sorting. The pots were then baited and stacked ready for re-setting the string. Bycatch was sorted to species after the string had been hauled. Most species were counted, and then weights were estimated according to the average size of individuals. For large catches of individual species, the total weight was measured and numbers estimated.

The fishing area for this trip was the north side of Gray's Canyon (Figure 18). Depth was 160 – 250 m. The area overlapped slightly with the area fished during the 1999 trip with the Miss Mary observing trawl bycatch. This area was heavily fished by trawlers whilst that fishery was open.

Results

12 string hauls were observed, totaling 958 individual pots. The gear had been set three days before hauling the first observed hauls, resulting in a 72-hour soak time. These pots were re-baited and re-set, and a second set of hauls was observed after 24 hours.

565 kg of spot prawns were caught in the 958 observed pot hauls. 318 kg were caught on the first day, hauling 479 pots after a 72-hour soak time, and 247 kg the second day hauling 479 pots after a 24-hour soak time.

The length frequency of the prawns caught in pots with a 72-hour soak time (n=566) and 24-hour soak time (n=520) are shown in Figure 21. There is a significant difference between the length frequencies according to soak time (Two-sample Kolmogorov-Smirnov test D = 0.1463, p-value = 3.292e-06). More large and fewer small prawns were caught after the 24-hour soak time than the 72-hour soak time.

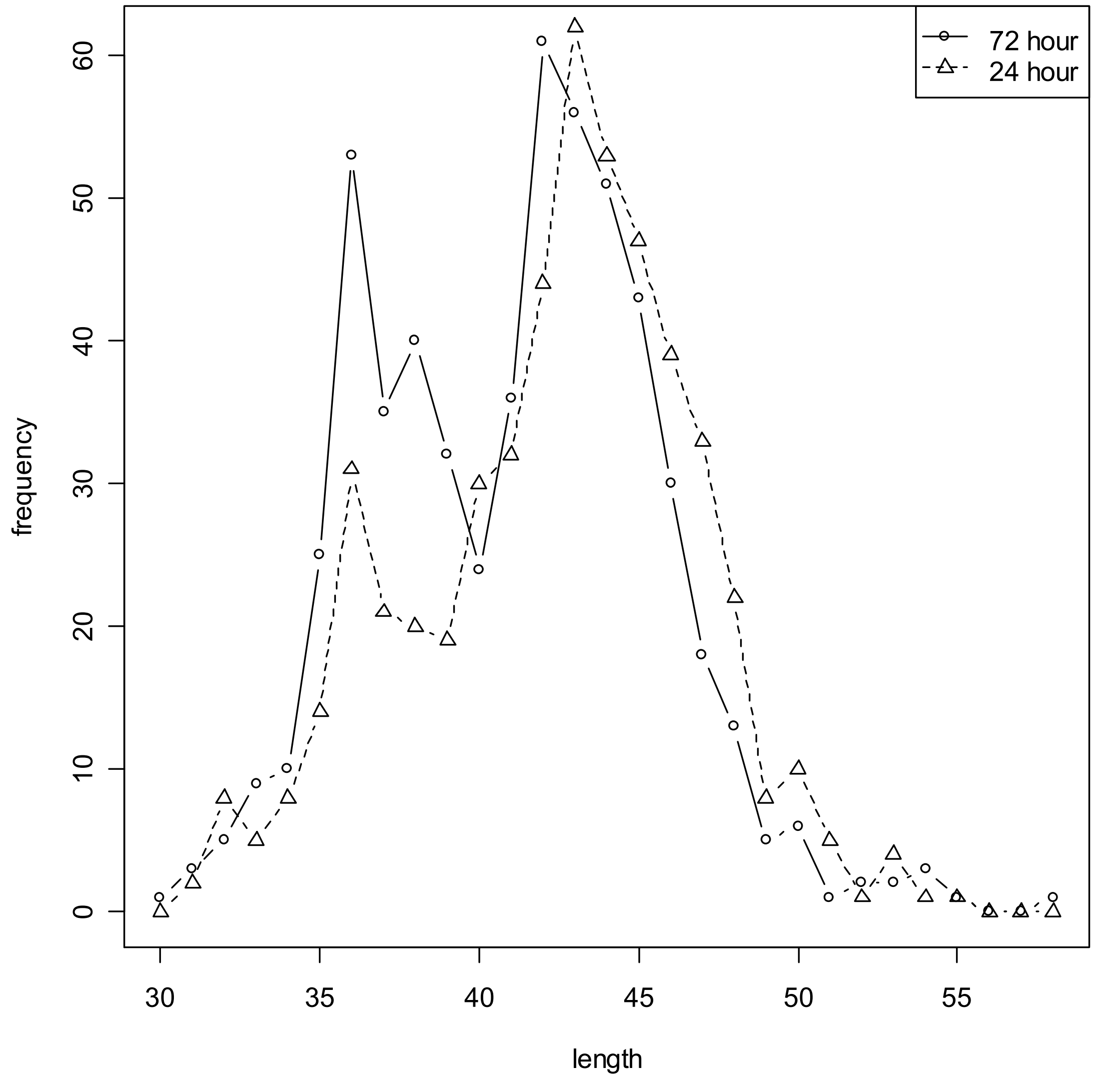


Figure 21: length frequency of prawns caught in pots with a 72 hour soak time (n=566) and 24 hour soak time (n=520)

Length frequency of prawns caught in the alternating small (n=174) and large mesh (n=236) pots are shown in Figure 22, normalized to equal sample size. No difference was noted between the length frequency of the spot prawns caught with the small and large mesh pots (Two-sample Kolmogorov-Smirnov test D = 0.1005, p-value = 0.2641). Slightly more prawns were caught per pot in the standard pots (11.8 prawns / pot) than the small mesh pots (8.7 prawns / pot), but this difference was not significant (Two-sample t-test t=-1.23, p-value = 0.22).

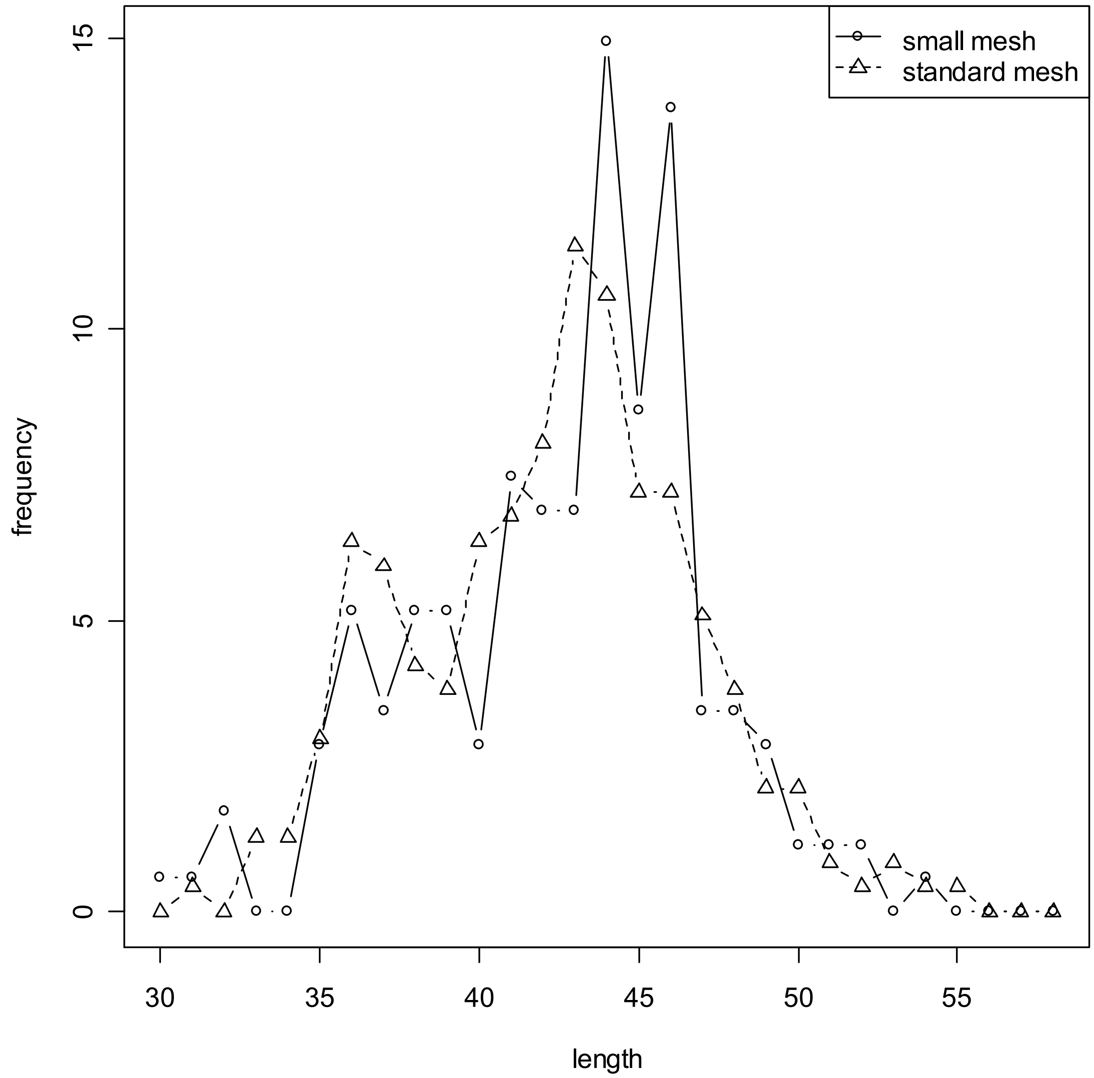


Figure 22: Length frequency of prawns caught in alternating small (n=174) and large mesh (n=236) pots, normalized to equal sample size of 100 for comparison.

A total of approximately 444 kg of bycatch was caught in the 958 pot hauls. Full details of the bycatch are shown in Table 10, with a breakdown by taxonomic groups in Table 11.The largest components of this were 291 kg of sea urchins (*Allocentrotus fragilis*), 52 kg of Oregon tritons (*Fusitriton oregonensis*), and 50 kg of various species of starfish. Very few fish were caught in the pots. The most common fish species was the threadfin sculpin (*Icelinus filamentosus*), of which 31 individuals were caught. Of commercially important fish, 6 sablefish and 2 pacific cod were caught. 10 rosethorn and 5 redbanded and 1 unidentified rockfish were also caught. A very small quantity of dead hexactinellid sponge (probably *Aphrocallistes vastus*) was brought up attached to the outside of the pots. This is expected based on the observation that the sponges are present in the area, as shown during previous trawl bycatch studies (Section 2.3).

Table 10 Bycatch in spot prawn pots by species, and breakdown by soak time.

		Kilograms			**Count**		
	soak time	**72 hour**	**24 hour**	**total**	**72 hour**	**24 hour**	**total**
rosethorn rockfish	*Sebastes helvomaculatus*	0.9		0.9	10		10
redbanded rockfish	*Sebastes babcockii*	0.1	0.1	0.2	3	2	5
unidentified rockfish		0.1		0.1	1		1
sablefish	*Anoplopoma fimbria*	1.4	6.1	7.5	1	5	6
pacific cod	*Gadus macrocephalus*	0.7	0.7	1.4	1	1	2
spotted ratfish	*Hydrolagus colliei*	0.9		0.9	2		2
Threadfin sculpin	*Icelinus filamentosus*	3.9	0.3	4.2	29	2	31
dusky sculpin	*Icelinus burchami*	0.2		0.2	5		5
blackfin sculpin	*malacocottus kincaidi*	0.1		0.1	1		1
blackfin poacher	*Bathyagonus nigripinnis*		0.1	0.1		1	1
hagfish	*Epatatretus stoutii*	0.2	1.9	2.1	4	42	46
red octopus	*Octopus rubescens*	8.2	5.8	13.9	24	17	41
oregon triton	*Fusitriton oregonensis*	45.2	7.3	52.5	399	64	463
smirnia whelk	*Neptunea smirnia*	1.9		1.9	13		13
brown box crab	*Lopholithodes formaminatus*		2.7	2.7		6	6
spiny lithode crab	*Acantholithodes hispidus*	1.6	0.5	2.0	7	2	9
hermit crab	*Pagurus sp.*	1.7	0.8	2.5	38	18	56
yellow leg pandalid	*Pandalus tridens*		0.0	0.0		2	2
sunflower star	*Pycnopodia helianthoides*	5.9	8.8	14.7	9	19	28
vermillion star	*Mediaster aequalis*	8.4	9.4	17.8	93	105	198
blood star	*Henricia leviuscula*	1.5	0.6	2.0	32	12	44
fish eating star	*Stylasterias forreri*	10.0	4.1	14.1	88	36	124
unidentified crinoid			1.0	1.0		11	11
unidentified starfish			0.2	0.2		3	3
sea cucumber	*Parastichopus californicus*		0.1	0.1		1	1
fragile pink sea urchin	*Allocentrotus fragilis*	270	20	291	2456	222	2678
total		367	77	444	3216	588	3804

Table 11 : Bycatch breakdown by taxonomic group, and ratio of bycatch to spot prawn catch.

	Catch (kilograms)			Ratio catch : spot prawn catch		
	72 hour	24 hour	total	72 hour	24 hour	total
spot prawn	317.5	247.2	564.7			
total bycatch	366.6	77.0	443.6	1.15	0.31	0.79
total fish	8.4	9.1	17.6	0.03	0.04	0.03
rockfish	1.1	0.1	1.2	0.003	0.0004	0.002
molluscs	55.4	13.0	68.4	0.17	0.05	0.12
crustaceans	3.3	4.0	7.3	0.01	0.02	0.01
echinoderms	295.9	44.6	340.5	0.93	0.18	0.60

It is notable that the quantity of bycatch caught during the 72 hour soak time was far greater than that caught during the 24 hour soak time. This was especially the case for sea urchins; over 13 times as many were caught during a long soak time than a shorter one. More of almost all species, including rockfish were caught during the longer soak time.

Little difference was seen in the bycatch between the standard and small mesh pots, with the exception that the small mesh pots retained more hagfish than standard mesh pots. The mesh size of the standard pots is such that hagfish can easily escape while the pot is being hauled.

Discussion

The difference observed in the length frequency of prawns caught in identical pots with different soak times is hard to explain. It would be expected that during a 72 hour soak the bait would be consumed and prawns would then attempt to leave the pot, resulting in only larger individuals being retained. Other authors have noted that during very short soak times the proportion of small prawns captured is greater, and hypothesized that territoriality of larger prawns drives these smaller individuals out of the pots (Wright and Panek 2000). However, these observations have only been made comparing soak times of a few hours with up to 24 hours, and over longer periods other factors may apply. A variety of explanations can be offered. Some predation on prawns in the pots was noted in the 72 hour soak; empty carapaces of consumed prawns were found in the pots. This predation was probably by octopus, and they may have been selectively eating larger prawns. The very small size of the holes in the bait containers combined with a relatively large quantity of bait may have enabled the pots to continue fishing effectively for a longer period, and thus catch prawns from a wider area. Smaller prawns may move more slowly and thus arrive after all the large prawns in the area have already been captured. A further possibility is that prawns are actually aggregating in the pot, and small ones are attracted by the presence of large ones.

The lack of a difference between the length frequency of the small and standard mesh pots is an indication that there is little if any sorting of prawns through the meshes as the pots are hauled. The size of the prawns captured supports this assertion, the smallest prawns caught were 30 – 35 mm carapace length (CL), and prawns of this size would have difficulty in escaping through a 7/8" mesh. With the pot design used, the meshes on the bottom of the pots are stretched into a diamond shape and thus have a much smaller opening than those on the sides, which further reduces the chance of small prawns escaping during hauling. The small mesh pots would have been expected to catch prawns as small as 10mm CL, and the lack of any in the pots is an indication that they are not present on these fishing grounds. The location of the nursery areas for immature prawns which supply this fishery is still unknown, but they are most likely to be in shallow inshore areas. Juvenile prawns thus have to undertake a long migration to reach the adult grounds.

The length frequency of the prawns caught during this trip cannot, however be considered representative of the length frequency of the population of prawns present on the grounds. The factors listed above in the discussion of the differences between long and short soak times will all have an effect on the size of prawns encountering and entering the pots. It is likely that the proportion of large prawns caught is higher than that in the general population, and this is supported by the comparison of sizes caught by trawlers (which would be expected to be more representative of the general population) and pot fishers fishing similar areas in previous years (see chapter 1).

The total quantity of bycatch taken during this trip was relatively large, but consisted mostly of sea urchins. The ratio of total bycatch in pots to spot prawn catch (0.79:1) was slightly lower than that reported from an observer program conducted by California Department of Fish and Game (Reilly and Geibel 2002). Ratios of total fish and rockfish bycatch (0.03:1 and 0.002:1 respectively) were also lower than California observations. The only significant catch of a fish of commercial interest was 7.5 kg of sablefish (6 individuals). If it is assumed that the entire 250,000 pound quota is captured with the same ratio of sablefish bycatch, then the expected sablefish catch would be just over 1350 kg. This represents approximately 0.03% of the sablefish quota north of Point Conception. None of the rockfish species captured are considered overfished, or are specifically targets of fisheries in the area.

A larger ratio of bycatch to spot prawn catch was taken during a 72 hour soak time, compared to a 24 hour soak time (1.15:1 and 0.31:1 respectively). The distribution of soak times from logbook data is shown in Figure 23, and further discussed in chapter 4. It is clear from this figure that the majority of pots were hauled after less than 36 hours in the water, and would be expected to have a low bycatch as shown in this study. However, 19% of pots were hauled after more than 36 hours, and one set as long as 33 days. In longer soaks such as this there would be greater mortality of animals in the pots due to predation, starvation and crowding. Predation of fish by amphipods was observed in the Californian observer study (Reilly and Geibel 2002). The dead animals would act as bait to attract further individuals to enter the pot, in the same way as ghost fishing gear continues to fish. The consumption of spot prawns by octopus is a particular concern, as it will contribute to the fishing mortality caused by the spot prawn fishery, but not be accounted for in the catch and thus have the potential to be a cause of overexploitation of the fishery. Fishery managers should address these problems by limiting the maximum soak time that pots are allowed to be fished for. When pots are to be left out on the fishing grounds between trips, as was the case on this trip, then they should be un-baited and left open to allow animals that do enter to escape.

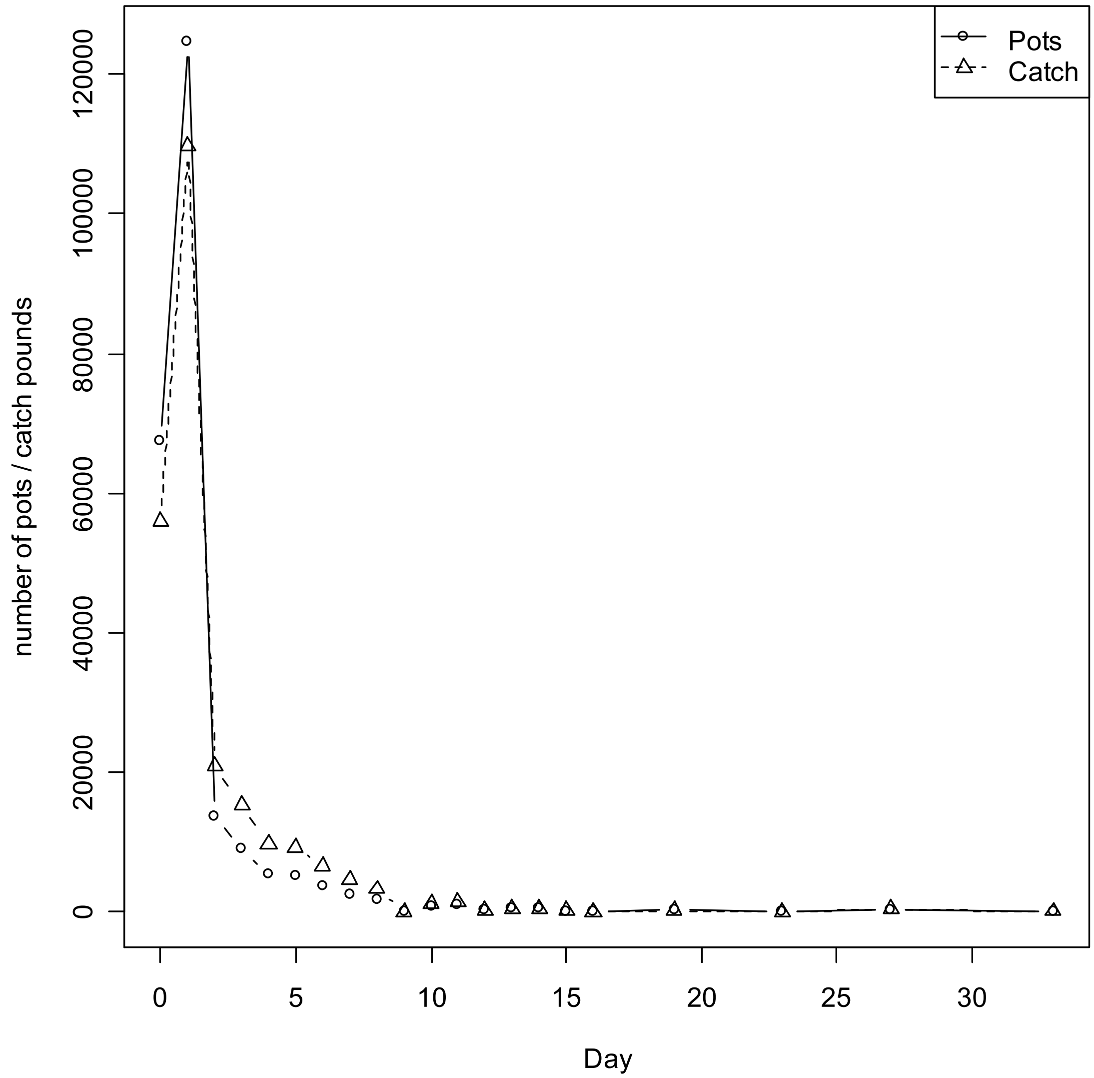


Figure 23 : Distribution of soak time from spot prawn logbook data off Washington 1993-2003. On the X axis, 0 days = 0-12 hours, 1 day = 12-36 hours etc. Only hauls where all necessary data was available are included.

Survival of most discarded bycatch species in this fishery would be expected to be relatively high. The handling practice on board this vessel is typical of the fleet, and bycatch spends very little time on the deck before being sent back overboard. Survival of fish without swimbladders (sablefish, ratfish, sculpins) would be close to 100%, as would survival of mollusks, including octopus. Crustaceans and echinoderms would have high expected survival unless they were crushed or otherwise damaged. High mortality is expected for fish with swimbladders, such as rockfish and Pacific cod as the depth of the fishery is great and the swimbladders of these fish are usually burst by the time the pot is brought on board.

2.6 Discussion

As with many other trawl fisheries for shrimp, my studies showed significant and diverse bycatch of fish and invertebrates. In many areas, large bycatch of slow-growing structure forming invertebrates (corals and sponges) indicated the fishery was damaging benthic habitats which are slow to recover. Although my initial study showed bycatch reduction devices (BRDs) had good potential for reducing bycatch of rockfish and other fish species, the use of BRDs did not appear to reduce bycatch adequately and did nothing to ameliorate the problem of damage to benthic habitats. Fishery regulators in all Pacific states closed all trawling for spot prawns within 6 years of my initial study. A pot fishery for spot prawns has partly replaced the trawl fishery, and my last bycatch study found minimal bycatch of rockfish and other fish species.

The study of bycatch reduction devices presented in Section 1 showed that although the correct use of BRDs in the spot prawn fishery had potential to reduce the amount of bycatch caught in this fishery, the actual bycatch was much more diverse than had been previously thought. This study provided the first reliable snapshot of the bycatch in this fishery. More than four times as much bycatch as spot prawns was caught overall, even with the use of BRDs. The bycatch included at least 35 species of fish, including cowcod and boccacio rockfish, which were listed as overfished species by NMFS. Sponges and other structure forming invertebrates were also caught, showing that the fishery was damaging benthic habitats.

Following the BRD study, my research priorities changed. The second and third studies had the objective of assessing the bycatch in the spot prawn trawl fishery off the Washington coast, which was previously unknown. The species composition in this area is very different to that seen off southern California, but nevertheless, the bycatch rate and diversity was high. In the first study off Washington, the overall ratio of bycatch to spot prawn catch was 7:1. The bycatch had at least 25 species of fish, including 8 species of rockfish. The fishery was clearly causing significant damage to benthic habitats; a large amount of reef building hexactinellid sponge was also caught, along with many other invertebrates. In the second study off Washington, which was in a different area to the first, the ratio of total catch to spot prawns was 3.5:1. The bycatch included at least 33 species of fish, including 12 rockfish species. The overfished species Pacific Ocean perch, canary and darkblotched rockfish were caught. The major invertebrate bycatch species was a sea cucumber, but some sponges and corals were also caught.

The fourth study was an analysis of bycatch in the spot prawn pot fishery that continued off Washington after the trawl fishery was closed at the start of 2003. The overall ratio of bycatch to spot prawns was 0.79:1. The major bycatch species caught were the fragile pink sea urchin (*Allocentrotus fragilis*) and the Oregon triton (*Fusitriton oregonensis*), which constituted 66% and 12% of the bycatch respectively. 11 species of fish were caught in small numbers, including three species of rockfish (16 individual rockfish with a catch of 565 kg of prawns). This is clearly a far lower rate of bycatch than observed in trawls. There was no evidence of habitat damage caused by the pots, and in general, pots are thought to cause much less damage to benthic habitats than trawls (Eno et al. 2001).

Other studies of bycatch in spot prawn fisheries.

Trawl gear

Prior to my study described in Section 1 of this chapter there had been few studies of bycatch in spot prawn fisheries. By the time of writing, four additional studies have been reported on bycatch in the California trawl fishery, and none in other areas. None of these studies are published outside grey literature, so the results are fully summarized here. A comparison of all available studies is given in Table 12.

Table 12: Summary of studies of bycatch in spot prawn fisheries

Trawl fisheries								
Year	**Trawl Tows**	**bycatch:spot prawn ratio**			**BRD used**	**Area**	**Overfished rockfish species caught**	**Reference**
		Fish	**Rock fish**	**Inverte-brates**				
1981	9	20.2	7.4	?	none	Northern California	bocaccio, cowcod	Reilly and Geibel 2002
1982	6	4.4	?	?	none	Northern California	bocaccio, canary, cowcod	Reilly and Geibel 2002
1997	6	26.7	22.3	?	experimental	Northern California	?	pers. comm. 1998
1998	10	2.5	1.8	0.2	Nordmøre	Southern California	none	Section 1
1998	15	3.6	1.6	0.9	none	Southern California	cowcod and bocaccio	Section 1
1998	4	6.6	1.1	3.5	fisheye	Southern California	none	Section 1
1999	6	7.4	0.6	?	fisheye	Northern California	?	Reilly and Geibel 2002
1999	5	3.6	1.1	3.5	fisheye	Washington	widow, yelloweye	Section 2
2000	10	2.7	0.7	2.5	fisheye	Washington	darkblotched, POP, canary	Section 3
2000-2001	71	7.5	2.1	1.3	fisheye	Northern California	bocaccio, cowcod, yelloweye, canary	Reilly and Geibel 2002
2000-2001	15	17.7	1.5	2.9	fisheye	Southern California	bocaccio, cowcod	Reilly and Geibel 2002
mean		9.4	4.0	2.1				
Pot fisheries								
		bycatch:spot prawn ratio						
Year	**Pots**	**Fish**	**Rock fish**	**Inverte-brates**		**Area**	**Overfished rockfish species caught**	**Reference**
2000-2001	1600	0.15	0.04	0.9		Northern California	cowcod, yelloweye	Reilly and Geibel 2002
2000-2001	3000	0.22	0.07	1.8		Southern California	cowcod, bocaccio	Reilly and Geibel 2002
2003	958	0.03	0.002	0.7		Washington	none	Section 4
mean		0.13	0.04	1.13				

Two studies by California Department of Fish and Game (CDFG), off northern California in 1981 and 1982 are described in Reilly and Geibel (2002). The results of these studies had not been previously reported. In the first of these, nine hauls were observed on a chartered trawler, resulting in a fish:spot prawn ratio of 20.2:1. The predominant rockfish in the catch were the small species, stripetail and shortbelly rockfish, but substantial quantities of boccacio rockfish were also caught. In the second, which was a test of a 4.5” cod end mesh, the ratio was 4.4:1 in six hauls. Boccacio, canary and cowcod rockfish were reported. No information on bycatch of invertebrates was reported for either study.

Concern about the bycatch in the California spot prawn fishery was heightened by the results of my BRD study, leading to a further observed trip by CDFG off Monterey in early 1999.Six hauls were observed, resulting in a fish:spot prawn ratio of 7.4:1, with a fairly low catch of rockfish. Again, no information on invertebrates was reported.

A dedicated observer program studied bycatch by spot prawn fishing vessels during the period September 26, 2000 to September 19, 2001 (Reilly and Geibel 2002). Only nine trawl vessels were involved, and a total of 86 hauls were observed. The total catch of prawns during these hauls was 1942 kg, which represents just over 2% of the total prawn catch landed during the observed period. The plan adopted by the Fish and Game Commission aimed to cover 10% of all spot prawn trawl vessel trips, from July 2000 to June 2001. This level was not achieved, in part due to vessel owners refusing access to observers (Reilly and Geibel 2002). More of the sampling took place off northern California than southern California.

The results for northern California (north of Pt. Conception) and southern California were markedly different. For northern California the ratio of fish bycatch to prawn catch was 7.5:1, with the most common species (by weight) being Pacific hake, Dover sole, sablefish, English sole and rex sole. Rockfish were caught at a ratio of 2.1:1 and the most common species were splitnose, shortbelly, stripetail, sharpchin and chillipepper rockfish. Invertebrates other than spot prawns were caught at a ratio of at least 1.3:1 and included sea urchins, squid, sea stars, sea slugs, crabs, sea cucumbers, sponges and anemones.

For southern California, the ratio of fish bycatch to prawn catch was 17.7:1, with the most common species (by weight) being Pacific hake, Pacific sanddab, slender sole Dover sole and sablefish. Rockfish were caught at a ratio of 1.5:1 and the most common species were chillipepper, sharpchin, shortbelly, stripetail and greenspotted rockfish. Invertebrates other than spot prawns were caught at a ratio of 2.9:1 and included sea urchins, squid, crabs, sea stars, sea slugs, pink shrimp, octopus and sea cucumbers. All of the observed hauls were made north of the Santa Barbara Channel Islands, and did not cover the area fished during my BRD study. The differences in bycatch composition that I observed between areas are thus not reflected by the observer study.

Pot gear

Few observations of bycatch in spot prawn pot gear have been reported. One trip in the Gray's canyon area off Washington was observed by WDFW in May 1997 (S. Barry, WDFW pers comm. 1998). In 360 pot hauls, approximately 287 kg of prawns were caught. The bycatch consisted of several box crab, hagfish and octopus, approximately 50 Spiny lithode crab (*Acantholithodes hispidus*), one scaled crab (*Placetron wosnessenski*), 2 green sea urchins and two small red rockfish. These pots were set in the same area as the pots described in Section 4 separated by six years, and the bycatch is markedly different. In my study, the number of spiny lithode crabs was far lower, and the number of pink sea urchins, gastropods and starfish far higher.

The CDF&G observer program (Reilly and Geibel 2002) covered 17 vessels, and a total of 262 pot strings. These strings generally consisted of between 10 and 25 pots. For northern California the most common species were sablefish, rosethorn rockfish, greenblotched or similar species of rockfish, spotted cusk eel and filetail catshark. Invertebrates included various species of sea stars, red rock crabs (*Cancer productus)* sea slugs, galatheid crabs and urchins. Ratios of fish and invertebrates to spot prawns were 0.15:1 and 0.9:1 respectively. Observed strings caught approximately 4.4% of the total spot prawn catch north of Point Conception during the study period.

Off southern California, the most common fish species were lingcod, greenblotched or similar species of rockfish, threadfin sculpin, sablefish and swell shark. The most common invertebrates were sea urchins (fragile pink urchin) decapod crabs, sea slugs and octopus. The prevalence of urchins could have been linked to longer soak times used off southern California. Ratios of fish and invertebrates to spot prawns were 0.22:1 and 1.8:1 respectively. Observed strings caught approximately 2.1% of the total spot prawn catch south of Point Conception during the study period.

Three further observations of bycatch in spot prawn pots are reported in (Reilly and Geibel 2002). Observations in 1996 identified 31 species of fish in pots set in Carmel Canyon, near Monterey. In 1999 and 2000, CDFG conducted studies comparing plastic and wire mesh pots. The bycatch observed in these trials was enumerated, but not weighed. Common species of fish were stripetail and greenblotched rockfish, and the results were not dissimilar to those reported during the bycatch observer study.

There is little comparison of trawl and pot bycatch. Bycatch in pots is far lower in all respects. Fewer fish species are caught and fewer individuals of those species are caught. Lingcod and sablefish are two of the most common species, and these would be expected to survive being caught and discarded. The only concern is the small number of rockfish that are caught, which are unlikely to survive being brought to the surface due to pressure differences causing their swimbladders to burst. There is some scope for development of new pot designs that will reduce the number of rockfish that enter the pots, and the use of shorter soak times may also have an effect on the rate of rockfish bycatch.

Benthic habitat damage caused by spot prawn fisheries

It is unquestioned that some trawl fisheries cause severe damage to benthic habitats, and this damage can reduce biodiversity and alter ecosystem function (Dayton et al. 2002), (Morgan and Chuenpagdee 2003), (Løkkeborg 2005). I found substantial evidence that spot prawn trawl fisheries were causing habitat damage. The majority of spot prawn trawl vessels used rockhopper gear, which is designed to be able to be trawled over hard, rugged seafloors. These hard substrates provide suitable attachment points for long lived, slow growing organisms such as corals and sponges that increase habitat complexity, making it more favorable for fish.

In my BRD study off southern California (Section 1) the most common category of bycatch in some areas was sponge. A large number of different types of sponge were caught in most hauls. Submersible observations have shown that these are some of the most important habitat forming species in the area fished (Tissot et al. 2006). The major observer study carried out by CDFG did not identify invertebrates beyond general types. However, sponges and corals were observed in some hauls (Reilly and Geibel 2002).

In the studies off Washington, large quantities of habitat forming organisms were also caught. Primary amongst these was the reef building hexactinellid sponge *Aphrocallistes vastus.* Anecdotal reports from fishermen also note large catches of this type of sponge as the spot prawn trawl fishery developed off Washington in the early 1990's. Pot fishers who pioneered the fishery petitioned WDFW in 1994 to limit trawling for spot prawns for this reason (S. Barry, pers. comm. 1998). Recent remotely operated vehicle (ROV) work in the Olympic coast National Marine Sanctuary off the northern Washington coast identified the rare stony coral *Lophelia pertusa* and gorgonian (soft) corals. Many of these consisted of "dead and broken skeletal remains" (Hyland et al. 2005). The area studied was close to an area heavily fished by spot prawn trawlers between 1994 and 2003.

The catch of *Aphrocallistes vastus* is particularly interesting. Large reefs formed by this species have been reported from British Columbia waters. These reefs can reach heights of tens of meters above the seafloor and be tens of kilometers in length (Conway et al. 2005). Formations shown on sidescan sonar images from the area of Gray's Canyon are thought to be large hexactinellid sponge reefs up to 25 m high (Paul Johnson, University of Washington, School of Oceanography, 2005). The sidescan sonar images appear almost identical to those of sponge reefs identified off British Columbia. The silica skeletons of the sponges that build the reef are fragile and would be easily damaged or even completely destroyed by the heavy trawl gear used in the spot prawn fishery.
The growth rate of this species is not reported in published work. However, the growth rate reported for *Rhabdocalyptus dawsoni*, another hexactinellid found in British

Colombia, is 1.98 cm per year (Leys and Lauzon 1998). If the growth rate of this species is similar, then large colonies of the sort seen in trawl bycatch may be 50 to 100 years old. Structures of the size of those seen on sidescan sonar may be thousands of years old.

A number of authors have noted the role of hexactinellid sponges in providing structure for benthic communities (Barthel 1992; Bett and Rice 1992; Gerdes et al. 1992; Kunzmann 1996; Barthel 1997) and especially the role of this sponge class in providing habitat for young fish (Konecki and Targett 1989; Barthel 1997), including rockfish (Freese and Wing 2004) and shrimp species (Bruce and Chace 1986; Hayashi and Ogawa 1987; Bruce 1988; Bruce 1991; Goy 1992), many of which are commensal with the sponge. It seems unlikely that there is an obligate functional relationship between the sponges and spot prawns, but it is likely that they use the sponges as cover for protection from predation. The presence of a complex habitat is likely to attract large numbers of fish such as juvenile rockfish and invertebrates, which would use the reef as cover from predators. Live sponge reef habitat has higher taxonomic richness than either dead reef or near off-reef areas (Cook 2005). Damage to these habitats from trawl fisheries may have long lasting effects on the productivity of many fisheries.

Although I found compelling evidence that the spot prawn trawl fishery caused substantial damage to benthic habitats prior to its closure, the total extent and severity of this damage remains unknown. Little information is available on the frequency, intensity and extent of spot prawn trawling operations. Many of the areas fished for spot prawns were also exploited by other trawl fisheries for groundfish which also may have caused damage. Unfortunately, there is no baseline data available to indicate what the benthic environment was like before trawling started.

How these studies affected regulation and development of spot prawn fisheries

Despite the fact that these studies are far from definitive, they had a large influence on the development and regulation of spot prawn fisheries off Washington, Oregon and California. By the end of 2003, all spot prawn trawl fisheries had been closed.

Concern about high bycatch levels in the spot prawn fishery and the potential for benthic habitat damage had been rising in California throughout the late 1990's, based on anecdotal reports. In 1999, environmental groups and pot fishermen brought these concerns to the California Fish and Game Commission (the Commission). The results of the 1999 observed trip described above were presented to the Commission (Reilly and Geibel 2002), but although the environmental groups were aware of them, the results of my BRD study were not presented. Representatives of the environmental groups asked the Commission to phase out spot prawn trawling by 2004, and allow a conversion of trawlers to pot gear. This request was based on concerns about bycatch of overfished groundfish species, especially lingcod, boccacio, and cowcod, and to bycatch rates in general compared to those of the pot fishery. There were also concerns about damage to benthic habitats especially given that the trawl fishery was using larger roller and rockhopper gear and expanding into new areas and impacting areas that had previously acted as de facto reserves. At the time, CDFG thought there was insufficient information available to justify closing the fishery given the economic hardships for the fishers and communities that a closure would create. Concerns were also raised that it would negatively affect the pot fishery, which was considered already fully capitalized, when trawl vessels attempted to convert to pot fishing. The Commission therefore recommended that more information be collected through an on-board observer program. This program was funded by a tiered fee program based on recent landings, and covered both trawl and pot vessels in the spot prawn fleet.

The observer program (described above) ran from July 2000 until March 2001. The results were released in July 2002, and led the California Fish and Game Commission to ban the use of trawls for the directed take of spot prawns on 18 February 2003. The ban went into effect April 1, 2003. The decision of the Commission was unanimous, and was based on the estimated bycatch levels of overfished rockfish (boccacio, cowcod and darkblotched rockfish). The issue of damage to benthic habitats caused by trawling was a factor in the decision, but not listed in the stated reasons for the closure. The fact that ground gear size had not been limited in the spot prawn trawl fishery, despite the fact that the Pacific Fishery Management Council adopted roller-gear and mesh restrictions for directed groundfish fisheries in order to protect severely depleted rockfish species, was also a factor, as was the availability of an alternative technology (pots) which provide a lower bycatch and were likely to cause less habitat damage. The Commission directed CDF&G to develop a conversion program for the trawl fleet to pot fishing.

The results of my two studies of trawl bycatch off Washington were presented to the WDFW Fish and Wildlife Commission in 2001, along with concerns about overexploitation of the spot prawn resource off the Washington coast. A trawler phase-out proposal was placed before the Commission and passed. This allowed existing trawl permit holders to fish either with trawls or pots in 2002, in order to ease the transition between gears. At least two vessels took advantage of this measure in 2002, although only one has successfully made the transition and continued to fish with pots in subsequent years. To further facilitate the transition, former trawl vessels were given exclusive access to a portion of the spot prawn quota through 2006. The passage of these measures was facilitated by the fact that the spot prawn fishery was governed under the Emerging Commercial Fisheries Act (ECFA). The ECFA was designed to prevent habitat damage and conserve marine resources. It also authorizes the WDFW to limit the number of fishery permits issued annually. By 2001, there were only 4 trawl permits remaining in the fishery, so the overall impact was small.

The fishery off Oregon was governed by regulations similar to those in Washington, and by 2003 when the Washington trawl fishery closed, there were only two trawl permits remaining. The Oregon Developmental Fisheries Board elected to bring their fishery into line with the other fisheries on the coast and converted these permits to pot permits on

January 1 2004. One of the main reasons behind this decision was the high levels of bycatch seen off Washington, given the assumption that bycatch would be similar off Oregon.

2.7 Conclusion

Spot prawn trawl fisheries suffered from large quantities of bycatch and probably caused substantial amounts of habitat damage. The mix of fish species encountered in the bycatch varied across the range of the fisheries from southern California to Washington, but large amounts were caught in all areas. My initial study showed bycatch reduction devices (BRDs) had good potential for reducing bycatch of rockfish and other fish species. The lowest ratio of fish to prawns (2.5:1) was achieved with the use of a Nordmøre grid. However, the use of BRDs did nothing to ameliorate the problem of damage to benthic habitats. In many areas large amounts of slow-growing structure forming invertebrates (corals and sponges) were caught, which indicated the fishery was damaging benthic habitats which would be slow to recover.

Fishery regulators in all Pacific states closed all trawling for spot prawns within 6 years of my initial study. A pot fishery for spot prawns has partly replaced the trawl fishery, and my last bycatch study found minimal bycatch of rockfish and other fish species in pots.

Chapter 3. Development of microsatellite markers and investigation of population structure of spot prawns

3.1 Introduction

Understanding the spatial population structure of commercially fished species is necessary for the development of sound, sustainably managed fisheries. Such structure in marine invertebrates usually consists of sub-populations linked by dispersal of planktonic larvae. These spatially structured populations are at risk of serial depletion of population patches if the fishery is managed at an inappropriately large scale (Orensanz and Jamieson 1998). The life history of spot prawns indicates that some form of population structure is likely. The adults are relatively sedentary (Kimker et al. 1996; Schlining 1999), the distribution of the adults is patchy and linked to habitat type, and a planktonic larval stage probably links patches of adults (Butler 1980). Demographic techniques to test for spatial population structure, such as mark-recapture, were developed mainly for terrestrial systems and are difficult and prohibitively expensive to implement for marine invertebrates. However, if the amount of migration between patches is sufficiently low, genetic differences will accumulate over time and can be used to identify spatial population structure. In order to investigate the population structure of spot prawns, I developed microsatellite markers for the species and used these to analyze the genetic relatedness of samples from 10 sites in Washington waters.

For management strategies to be robust and cost-effective, structured populations require management at spatial scales appropriate to the structuring. Ideal schemes manage fisheries at the largest appropriate spatial scale and with the least complexity. Doing so reduces the cost of setting up the system, monitoring, data management and maintenance. Additionally, fishers prefer less regulation and less complexity of regulation. The consequence of managing at too large a spatial scale is the serial depletion of patches (Orensanz et al. 1998). Patches closer to ports are subject to higher and more frequent fishing pressure. Fishers move on to more distant patches when their catch rate is severely reduced in the local patches. The cost of fuel and travel time to fish more distant patches is greater, so this strategy makes sense from an economic point of view. However, conservatism within the fleet and lack of knowledge of distant fishing areas means they tend to move locations later than would be expected from a strictly financial viewpoint (Branch et al. 2006). Additionally, fishing may remain economically viable on a local patch long after it has been fished down to a critical level from which it cannot quickly recover. The result is fishing out of patches one by one. Serial depletion of spot prawn resources in Alaska were documented by Orensanz et al (1998), and was seen off the Washington coast as that fishery developed, leading to the development of quotas on a smaller spatial scale (Chapter 4). The species is vulnerable to recruitment overfishing due to its life history (Chapter 1). Spot prawns first mature as males and then change sex. The fisheries target primarily the large females and so may reduce the supply of larvae into the population. If patches provide a large proportion of their own recruitment, then this problem will be exacerbated and may lead to extinction of patches.

Although the management of both the inshore and offshore spot prawn fisheries in Washington includes some area specific components (Chapter 5), these are not based on knowledge of the genetic stock structure or the locations and relationships between patches. Rather, they have developed in response to the behavior of the fleet moving from area to area as some patches are fished down to low levels. The rate of recruitment to the fishery is not understood. No information exists as to whether there is transport of larvae between areas, or if each area provides its own recruitment.

A number of lines of evidence point towards the existence of several distinct sub-populations of spot prawns in Washington: complex geography and currents in the Puget Sound; complex sea floor topography; short larval planktonic phase; and regional morphological variation. The geography and currents of the Puget Sound region could limit gene flow among populations via larval transport (Ebbesmeyer et al. 1984; Buonaccorsi et al. 2002; Sotka et al. 2005). The Sound is part of a large fjord system, which is divided by numerous peninsulas, passes, islands and underwater sills. Four major areas are easily identified (Figure 24), divided by shallow sills at the Tacoma narrows (depth 50m), the North end of Hood Canal (depth 50m), Deception Pass (depth 20m), Admiralty Inlet (depth 60m) and south Whidbey Island (depth 90m) (Ebbesmeyer et al. 1984). The currents in the area are driven by tides, wind, and water runoff. Basins have fairly long turnover times ranging from about 1 month for the main basin and 1.9 months for the southern basin to 5.4 months for the Whidbey basin and 9.3 months for the Hood Canal basin (Ebbesmeyer, et al. 1984). These dynamics could reduce passive transport of spot prawn larvae. Retention of larvae within the basin where they were hatched and negligible gene flow between basins is possible. The Strait of Juan de Fuca is the main connection of Puget Sound to the Pacific and is also bounded by an outer sill. To the north, the Strait of Georgia has similarly complex bathymetry and hydrography, which may also restrict transport of planktonic larvae between spot prawn patches.

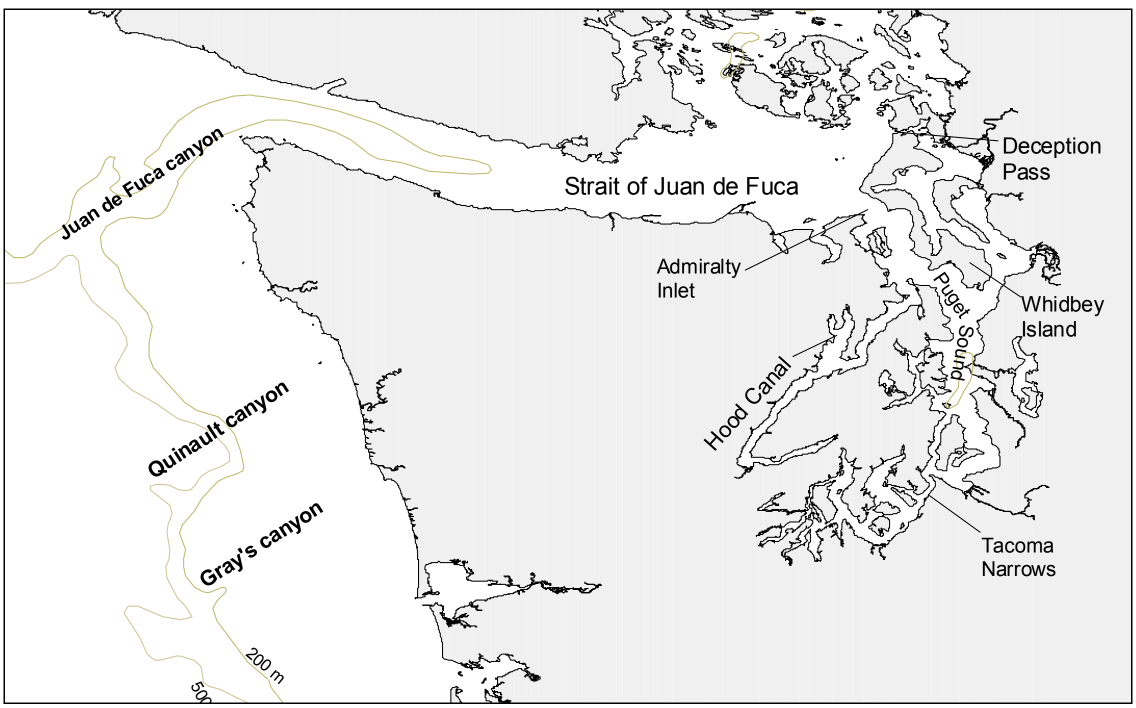


Figure 24: Major features of Puget Sound and the Washington Coast

The sea floor topography at depths inhabited by spot prawns offshore (~200-400 m) is generally complex. In particular, on the Washington coast, the shelf break is indented by a number of submarine canyons (Hickey 1989) (Figure 24), several of which support spot prawn fisheries. Both observations and numerical models demonstrate the tendency for such canyons to contain counterclockwise rotating eddies that could retain larvae within the canyon (Hickey 1995; Hickey 1997; Hickey et al. 2000; Klinck et al. 2000). Moreover, enhanced upwelling from these canyons may lead to enhanced productivity and thus food supply in their vicinity (Klinck 1996). It is possible that this larval retention mechanism may lead to genetically distinct populations in each of the canyons.

Recent work (Dunagan and Lowry in review) showed that the planktonic phase of the spot prawn life cycle is very short in comparison with other Pandalids, and the larvae settle at the third larval stage after less than 15 days in the water column. In inshore areas, larvae settle in shallow water where there is good cover such as seaweed beds, and migrate to adjacent deep water as they mature (Marliave and Roth 1995) (Barr 1973). The locations of such nursery areas is not known for coastal populations, but is presumed to be in similar habitat types, with the young prawns undertaking a longer migration to the adult grounds (see Chapter 1). The availability of suitable nursery areas may be a further factor structuring spot prawn populations. The larvae are very advanced at hatching in comparison with other Pandalids and it is possible that directed migration behavior also contributes to structuring populations.

The morphology and life history of spot prawns shows some variation by area. Prawns in Hood canal are slightly smaller at the same age than those in Puget Sound (Chapter 1), which are in turn smaller than those offshore. The size at which they change sex is correspondingly different, and there may be some behavioral differences as well. However, environments differ in each area, as well as the amount of fishing pressure. Pandalid shrimp have been shown to have plastic life histories in response to fishing pressure and environmental differences, which may explain some of these differences (Charnov and Anderson 1989; Hannah 1993; Hansen and Aschan 2000; Kristjansson 2001; Charnov and Hannah 2002).

The complex oceanography and sea floor topography combined with short larval period could serve to limit the amount of dispersal of planktonic larvae between sub-populations. This limited gene flow could result in measurable genetic differences between sub-populations which could be used to determine spatial population structure. The objective of this study was to use molecular genetic techniques to analyze the population structure of the spot prawn in Washington. To accomplish this objective, I first had to develop microsatellite markers for spot prawns (Section 1), and use these markers on samples of spot prawn DNA collected throughout the study region (Section 3). I also determined heredity of these markers and the likelihood of multiple vs single fathers of spot prawn broods (section 2). The aim was to collect samples from all the major basins in Puget Sound, all three of the canyons with known spot prawn populations off the Washington coast plus outgroups from Alaska and other areas if possible. I hypothesized that I would likely find population differentiation between Puget Sound and coastal populations and would possibly find differences between basins within Puget Sound and between canyons off the Washington coast.

3.2 Isolation and characterization of microsatellite loci for spot prawns.

Introduction

Microsatellites are long sequences of short repeats of base pair motifs (such as CACACA). The number of repeats of the motif can be highly variable within and amongst species. They are neutral markers, co-dominant and not generally affected by selection. They can have a very large number of different alleles due to a high mutation rate. Mutations in microsatellite loci are several times more likely than in normal nonrepetitive DNA (Chistiakov et al. 2006). Models indicate that this high mutation rate is explained by DNA polymerase slippage in replication or unequal recombination (Chistiakov et al. 2006). These processes add or subtract repeat units from the microsatellite sequence. Flanking sequences are not subject to the same mutation processes as the repeating part and are therefore more conserved. These conserved sequences are ideal for the purpose of priming sites for PCR to amplify the microsatellite sequence. The high mutation rate increases the rate of genetic drift within isolated populations, and so makes microsatellites more sensitive than other marker types. Microsatellites also provide relatively more information per locus screened than other marker types (such as allozymes), due to the higher average number of alleles per locus (Chistiakov et al. 2006). This can improve resolution to determine population differentiation at small scales (Shaklee and Bentzen 1998).

There is no published work on genetic population structure of spot prawns. Genetic studies on other pandalid shrimp have concentrated on allozyme electrophoresis (Kartatsev et al. 1993; Oloef et al. 1996; Jonsdottir et al. 1998; Drengstig et al. 2000) or randomly amplified polymorphic DNA (RAPD) analysis Martinez et al. (1997). I chose not to use allozymes because their use is very demanding of sample collection methods and would preclude getting samples from commercial fishers. RAPD analysis is also more demanding of sample quality and DNA extraction methods than microsatellites (Bentzen, Pers Comm., 2000).

A number of studies have identified highly variable microsatellite sequences in Penaeid shrimps (Bagshaw and Buckholt 1997; Ball et al. 1998; Vonau et al. 1999), and identified genetic differences between populations (Garcia et al. 1994; Aubert and Lightner 2000; Xu et al. 2001; Valles-Jimenez et al. 2004; Gusmao et al. 2005). However, Penaeid shrimp are not closely related to spot prawns, so primers developed on Penaeid species are unlikely to be useful in this study due to primer specificity.

The method chosen to isolate microsatellites from spot prawns was based on that used by Hamilton et al (1999). This is described as an “enrichment” procedure, that is, a library of closed DNA fragments is created which has a higher proportion of fragments containing a microsatellite repeat unit than is seen in the genome overall.

Methods

Microsatellite isolation from genomic DNA

Microsatellite loci were isolated from spot prawns using a slightly modified version of the protocol of Hamilton et al. (1999). This procedure was repeated five times with variations in an effort to get larger numbers of loci. Total genomic DNA was extracted from muscle samples using a kit (DNeasy kit, Qiagen, Valencia, CA). The DNA was digested either Rsa I or Hinc III restriction enzymes. The fragmented DNA was then ligated to the SNX linker (Hamilton et al. 1999) using T4 DNA ligase in the presence of the Xmn I restriction enzyme. The second through fifth isolation rounds used a combined digestion/ligation variation in the protocol, where both of the restriction enzymes and the ligase were added to the genomic sample simultaneously. This protocol has been used successfully on a number of fish species (Spies pers. comm. 2000).

Fragments containing suitable repetitive motifs were extracted from the mixture of ligated fragments using biotin labeled tetranucleotide probes ($GACA^4$ or AAG/C^6) and streptavidin coated magnetic beads. The extracted single stranded fragments are then made double stranded and amplified by PCR using the SNX primers.

The selected DNA fragments containing microsatellites were ligated into a plasmid and inserted into chemically competent *E. coli* cells, using a commercially available cloning kit (Topo TA cloning kit, Invitrogen corp. Carlsbad CA). Positive colonies were screened for incorporated DNA fragments150-500 bp by PCR and electrophoresis using primers that were part of the plasmid.

DNA templates for sequencing were prepared using either miniprep kits (Qiagen) or templiphi reactions (Amersham Biosciences). Sequencing was carried out on a Megabace sequencer according to standard protocols. Sequence data was analyzed using programs provided by ABI and Sequencher (Gene Codes Corp. Ann Arbor, MI).

Primers were designed using "Primer-3" software (Rozen and Skaletsky 2000). Primers were designed to be most efficient at 54 - 60 degrees, and were between 18 and 26 bases in length.

Primer pairs were tested using genomic DNA extracted from the prawn which was used in the isolation step as a template. The initial PCR used a gradient program over a range of 50 to 64 degrees. Variations in magnesium chloride concentration and primer concentration were also tested as appropriate. Initial reactions were carried out in 10 µl volumes, containing 1X PCR buffer, 2.5 mM Mg Cl_2, 0.2 mM each dNTP, 0.5 µM each primer, and approximately 100 ng template DNA. The general program was 2 minutes at 94°, followed by 30 cycles of 30 seconds at 94°, 30 seconds at the annealing temperature, and 30 seconds at 72° for extension. The last step was a 10 minute extension step at 72°.

PCR products were run on 6% polyacrylamide gels, stained with SYBR, and scanned on an FMBIO laser scanner (Miraibio, San Fransisco, CA). Allele sizes were estimated by comparison with a size standard (100/20 bp ladder). Loci that produced products of the expected size were optimized and tested for polymorphism with a set of 12 individuals from diverse populations.

Results

Microsatellite isolation

Over 300 clones were produced over the five rounds of isolations (Table 13). Of these, 205 were considered positive, in that they contained an inserted fragment between 150 and 500 base pairs. Many of the inserts that were successfully sequenced were identical. This was expected, as there were several PCR amplification steps in the protocol. In any of these PCRs any single fragment can be replicated numerous times. These served as useful confirmations for some sequences.

Table 13: Results of microsatellite isolations. Positive clones were those with an inserted DNA fragment between 150 and 500 base pairs. Successful sequencing was production of at least one high quality sequence from a clone. Clones with microsatellites were those unique sequences with repetitive regions of at least 3 repeat units, microsatellites with flank were those with at least 18 non-repetitive bases each side of the repetitive region.

Round	Probe motif	Positive clones	Successfully sequenced	Unique sequences	Clones with microsatellites	Microsatellites with flank
P	(GACA)4	>50	20	12	8	2
A	(GACA)4	22	20	13	13	4
B	(AAG/C)6	25	17	9	7	3
C	(GACA)4	85	75	32	30	7
D	(GACA)4	57	50	39	34	16

Most of the clones isolated contained microsatellites. The majority of these matched the probe sequence (CTGT or TTC/G). Some of the microsatellites isolated using the tetranucleotide probe $(GACA)^4$ contained dinucleotide repeats $(CA)^n$ or $(GT)^n$. Two of the clones isolated using the trinucleotide probe (AAG/C) contained GCC repeats. There were many fragments with multiple sets of tandem repeats of the same or different motifs, and some that were generally repetitive. The greatest problem was the lack of flanking sequence which was the case in 48% of the clones.

An unusual problem was noted in the last round of isolations. Some matched through large sections of the fragment, but appeared to contain insertions or deletions, or areas where the match was close, but not exact. This may indicate a problem with the procedure employed to isolate the microsatellites.

<u>Primer design and testing</u>

Thirty two pairs of primers were designed based on the sequences obtained which had sufficient flanking sequence. I was able to get a clean PCR product of approximately the expected size for 13 or these primer pairs. Many of the other primer sets produced nonspecific bands at temperatures that were much lower than the melting temperature (Tm) of the primer, indicating that the primer does not match the genomic DNA sequence.

Of the 13 primer sets that amplified a single product, only five were polymorphic when tested with multiple individuals. The other 8 produced an identical product for all individuals. In some cases this was unsurprising, as the target microsatellite sequences were short, consisting of just a few repeat units. Primer sequences for the polymorphic loci are shown in Table 14, optimum reaction conditions are given in Table 15.

Table 14: Primer sequences, melting temperature [Tm] for the 5 loci that were polymorphic in initial testing.

Locus	Primer 1	Tm	Primer 2	Tm
A14	AGGTCTACCATTTGAAGCTG	58	ATGACACTGTGATGCATGG	56
B3	CTTAATTATCCTTCCCTTTCG	58	GACTGGTTGGCATAAGGC	56
D10	TGCTATGTTGGAGGATTT	53	ATCTTTGACCTTGACCTTT	54
D12	TATAATGCACCGATTGTCTG	56	TTTCCCACCACTCTTTGA	55
P2	ACGAAGTGCGTTGTGTCTACAGA	63	TCGGGATGACTGAAACTGACC	63

Table 15: Optimum reaction conditions for each primer pair

Locus	Microsatellite	Expected Product length (bp)	Optimum reaction conditions		
			°C	Mg (mM)	Primer (uM)
A14	(GTCT)6	127	64	2.5	0.5
B3	(AAC)6,(CAA)4,5,5	302	57	2.5	0.5
D10	(GTCT)6	244	54	4	0.4
D14	(GTCT)4,6	183	58	4	0.4
P2	(CAGA)7	117	57	2.5	0.5

Inheritance of these five microsatellite loci were tested with DNA samples from ovigerous female prawns and the fertilized eggs that they had produced in order to verify Mendelian heritability (for methods see section 3.3). Loci A14, B3, and P2 in all cases showed a distribution of alleles that was consistent with Mendelian inheritance of the microsatellite, i.e. every egg showed at least one allele in common with the mother.

This was not true for the other two loci. Both locus D10 and D14 produced multiple bands, and these were not necessarily the same as those produced from maternal DNA. In the case of locus D14, between one and four bands appeared on each gel. Two different loci appeared to have been amplified. However, neither of these was consistently seen, and it was not possible to isolate one or the other by varying the PCR conditions.

For locus D10, up to four bands were amplified for each individual and these did not appear to always be inherited in a Mendelian fashion, i.e. bands appeared that were not seen in the maternal genotype, and were not at the expected ratios. No other alleles apart from these four were seen in over 100 individual adult prawns that were screened with this locus, which shows a level of diversity that may be too small to be informative in population studies. Due to these problems, neither of these loci was used for further population screening.

Discussion

Despite repeated rounds of microsatellite isolation from enriched libraries and assessment of 32 potential microsatellite primers, I was able to find only 3 reliable microsatellite markers. Getting good results from PCR with samples of shrimp DNA was generally more difficult than with tissues from other animal groups (such as fish). The tendency for shrimp DNA to be difficult to work with has been noted by others (L. Hauser, pers. comm. 2002), and may be due to other compounds (probably polysaccharides) purifying along with the DNA causing inhibition of PCR.

Many of the primer sets generated did not appear to amplify anything when run at their expected annealing temperature, and only produced products at lower temperatures at which there would have been non-specific binding to the template. This indicates that either the primer sequences were incorrect, or they were not annealing to the template DNA at the correct spacing. The sequence data from which these primers were derived was of a very high quality, so incorrect primer sequences are unlikely. A possible conclusion is that many of the clones that were isolated and sequenced contained fragments that were chimeras, i.e. they consisted of multiple fragments of genomic DNA from different sites which had become joined together. Many of the fragments sequenced had multiple repeat regions, which could be an indication of this. The most likely stage at which this could have happened is the digestion + ligation step, which was the first step in the isolation procedure. The relative concentrations of the linker and the genomic DNA in this step are critical to making the reaction work properly. There must be a surplus of the linker fragments compared with genomic fragments. If there is a surplus of blunt ended genomic fragments then the chance of two of these joining is higher than the chance of a genomic fragment joining with a linker fragment. Chimeras may have formed by the ligation of fragments cut by the two restriction enzymes used in the digestion/ligation step (Xmn I and Hinc III). However, the motif created from this is identifiable, and did not occur at a frequency any higher than expected given random distribution of nucleotides. The most likely source of blunt fragments is the original genomic DNA sample. These samples may have contained enough small fragments to bias the ligations towards the formation of chimeras. This is especially true for the later rounds of microsatellite isolation, as the tissue samples from which the DNA was derived had had more time to degrade. This problem can be solved by performing the original digestion separately, followed by gel purification and extraction of a known size range of fragments. The number of available “ends” in this type of sample can be much more accurately estimated, and thus the relative concentrations of linkers and fragments can be more accurately assessed.

The protocol used contains two PCR steps, before and after the hybridization step. Errors could potentially be introduced during these steps if amplification is unreliable. The use of these steps also multiplies the number of copies of each fragment, and thus increases the chance of getting multiple copies of the same clone. The formation of large numbers of similar clones which occurred in the final round of microsatellite isolation may have been an artifact of the repeated PCR steps.

Despite these difficulties, the three loci which were isolated were very robust and worked at a range of PCR conditions and with DNA samples of varying quality. These three loci were used in the following analysis of paternity and population structure.

3.3 Assessment of spot prawn paternity.

Introduction

Multiple mating is common throughout the animal kingdom (Krebs and Davies 1997), and can lead to the situation where broods of eggs that are apparently siblings in fact have multiple different fathers. Multiple mating can affect the effective population size (Martinez et al. 2000) if there is an unequal contribution by one sex. In extreme cases, multiple mating can lead to the evolution of different mating strategies amongst individuals in a population (Neff et al. 2003).

Multiple paternity has been detected using genetic methods in species of burrow dwelling brooding shrimp (Baragona et al. 2000; Bilodeau et al. 2005), and in Dungeness crabs (P.C.Jensen pers comm. 2003). No reports of whether there is singular or multiple paternity of broods in Pandalid shrimp are known (Correa and Thiel 2003) The only known observation of spot prawn mating showed multiple males mating with a single female in captivity (Hoffman 1973), and competition for females in other Pandalid species in captivity has been noted (Bergstroem 2000). However, little is known about mating systems for Pandalid shrimp in the wild. The availability of robust microsatellite loci enabled the paternity of spot prawn broods to be studied and sheds some light on the mating system of the spot prawn.

Methods

I collected samples of ovigerous prawns (i.e., adult females carrying a brood of eggs) from the Gray’s Canyon area off the Washington coast in 2003. I selected females which were carrying eggs near to hatching to ensure the highest DNA concentration. A newly fertilized egg consists mostly of yolk with a very small embryo and has little total DNA. In a near term egg almost all of the yolk has been converted to embryonic cells.

Sixteen eggs were used from each of 14 adult females to determine if there was multiple paternity within a brood of spot prawns. This sample size was estimated using the computer program PrDM (Neff and Pitcher 2002) in order to give a 95% chance of detecting two sires in a brood using the three microsatellites, given the population allele frequency generated by screening all the tested populations combined (see section 3), assuming equal contributions from two fathers and unknown parental genotypes.

Egg DNA was extracted using a chelex resin protocol (Sigma-Aldrich, St. Louis, MO) which has been shown to be effective for fish (Hedgecock pers. comm. 2003.). This extraction method produces fragmented DNA. The sample is also likely to contain other compounds from the egg which may be PCR inhibitors. High concentrations used in PCR reactions produced less product than lower concentrations, hence a low quantity was used as the PCR template. Even with these precautions, the reactions with egg DNA were not very reliable. Extractions from adult DNA using this method were less reliable than those from eggs, so DNA was extracted from the adult using a Qiagen DNeasy kit.

Microsatelllite sizes were assessed using the same technique as used for the rest of the population screening (see section 3). Sizes of egg microsatellites were matched with those from the mothers and size standards.

The number of fathers in the brood can be determined by examining at the distribution of alleles in the offspring. If both parents are heterozygous, we would expect to find no more than two non-maternal alleles (i.e., a total of four alleles in the offspring). If more than two non-maternal alleles are found then there must be two or more fathers. In cases where the mother and father share an allele or alleles, it may be possible to determine the number of sires by analysis of the distribution of alleles. In each offspring there is expected to be one allele from the mother and one from the father; any deviation from this likely indicates more fathers. The count of each allele over the whole brood can also be used to indicate whether there is multiple paternity. Equal numbers of each of the maternal and paternal alleles are expected.

Results

Due to the unreliability of the reactions using the egg DNA, complete genotypes with three microsatellite markers were obtained for only 13 adults and 66 eggs. Partial genotypes were obtained for one further adult and 128 eggs. 30 of the egg samples failed completely. Even though the sample size was not as large as desired, this experiment still had substantial power. As the maternal genotype is known, the power to detect two fathers is over 90% for 10 out of 14 broods (Table 16)

Table 16: Results of genotyping for paternity analysis. Number of offspring genotypes is the number of successful results achieved out of 16 eggs tested at each locus for each brood. Paternal alleles are those alleles which were found in genotypes of the offspring but not the mother, and therefore must have come from the father. Finding three or more paternal alleles at a locus is evidence that there are multiple fathers. PrDM is the probability of detecting multiple fathers in the brood, given the known maternal genotype and the number of offspring genotypes, assuming equal contributions from two fathers (Neff and Pitcher 2002).

	# offspring genotypes per locus			# paternal alleles per locus			
brood	**P2**	**A14**	**B3**	**P2**	**A14**	**B3**	**PrDM**
1	7	15	10	1	1	2	0.926
2	6	14	8	1	0	1	0.914
3	7	15	8	0	0	1	0.922
4	0	15	12		0	1	0.929
5	7	11	8	0	1	1	0.891
6	0	14	11		0	1	0.921
7	3	11	0	0	1		0.459
8	7	14	0	0	1		0.539
9	7	15	7	1	0	1	0.915
10	13	14	14	1	1	1	0.948
11	12	13	13	0	1	0	0.944
12	13	13	11	1	0	2	0.944
13	7	12	5	0	1	1	0.894
14	10	13	7	0	0	1	0.929

As can be seen from Table 16, the maximum number of unique paternal alleles was only 2, which does not show multiple fathers in any case. In 11 of 14 cases, the genotypes of the eggs and allele frequency within each brood were consistent with there being only a single father for each brood. An example of the results achieved is shown in Table 17 and Table 18.

Table 17: Genotypes for an example brood and adult female. Allele sizes are given in base pairs (bp)

Locus	**P2**		**A14**		**B3**	
adult female	**117**	**101**	**135**	**127**	**308**	**299**
egg 1	117	101	127	127	308	299
egg 2	117	101	151	135	308	299
egg 3	117	101	151	135	308	299
egg 4	117	101	135	127	299	299
egg 5	117	101	151	127	299	299
egg 6	117	117	127	127	308	299
egg 7	117	117	127	127	308	299
egg 8			151	127	308	299
egg 9	117	101	135	127	299	299
egg 10	117	117	127	127	299	299
egg 11	101	101	151	135	308	299
egg 12	101	101	151	135		
egg 13	117	101	151	135	299	299
egg 14					299	299

Table 18: Allele frequencies for the brood shown in Table 17

Locus	**P2**		**A14**		**B3**	
Female observed genotype	117	101	135	127	308	299
Male expected genotype	117	101	151	127	299	299
allele counts						
Observed	101	11	151	7	299	19
	117	13	135	7	308	7
			127	12		
Expected	101	12	151	6.5	299	19.5
	117	12	135	6.5	308	6.5
			127	13		

Only three individuals of the 192 eggs tested were exceptions to the pattern, and in all cases this was only one unexpected allele from the three loci that were genotyped. This may indicate multiple paternity with the secondary father only contributing a small amount to the total brood. However, there are other potential explanations which seem more likely. Disregarding the odd individuals, allele counts within each of these broods were consistent with there being only one sire. In two of the cases, the result may have been caused by upper allele dropout: The offspring are expected to be heterozygous with different alleles from each parent, but are homozygous. The missing allele is the larger of the two that were expected and the trace on the gel is faint for the smaller allele. This pattern is consistent with that expected in cases of upper allele dropout. In the third case, the unexpected allele is different from either the maternal or paternal expected alleles. This seems most likely to be due to mutation, contamination of the egg sample, or mis-scoring, given that it is only one allele out of a large number. The other loci for this individual and the other 11 eggs genotyped in this brood do not support there being a second father.

Discussion

It appears from this analysis that for spot prawns multiple paternity is not the norm, and that the earlier observation of multiple males mating with one female in captivity was an anomaly caused by the close confines of the holding tank (Hoffman 1973). These results are in contrast with results for burrowing shrimp species, possibly because mating exposes female spot prawns to substantial risks from predators so they avoid harassment by other males after mating by fleeing or hiding (Bergstroem 2000), whereas mating in burrowing species takes place in the burrows where there are no predators. The large size of the female may be the critical factor in determining which males get to mate, despite the excess of males which would be present in a short lived species exhibiting protandric hermaphroditism. Single paternity of broods can be expected to lead to a lower effective population size and lower overall genetic diversity than would be the case if multiple mating was common in the species.

3.4 Analysis of spot prawn population structure

Introduction

Historically, it was generally assumed that marine animals with planktonic larval stages would exhibit little or no detectable genetic differentiation between sub-populations (Wright 1978). However, an increasing number of studies using genetic techniques have demonstrated pronounced stock differentiation over small distances. For example, (Parsons 1996) demonstrated significant genetic subdivision within sites for a marine snail with a short planktonic larval phase (nine allozyme loci F_{ST}=0.16). This was attributed to localized recruitment caused by complex patterns of water movement in the region. Parker et al. (2003) found significant differences in allele frequencies between areas for the native bivalve *Prototheca staminea* within Puget Sound. A number of studies have shown population differentiation among populations of fish within Puget Sound and between Puget Sound and coastal populations using both microsatellite and allozyme markers (Jagielo et al. 1996; Buonaccorsi et al. 2002; Iwamoto et al. 2004; Small et al. 2005).

No research has been published on population genetics of the spot prawn, but some work has been done on genetic identification of other pandalid shrimp stocks. Most of these studies have been done on *Pandalus borealis* and were based on morphology, allozyme electrophoresis (Kartatsev et al. 1993; Oloef et al. 1996; Jonsdottir et al. 1998; Drengstig et al. 2000), or used randomly amplified polymorphic DNA (RAPD) (Martinez et al. (1997)). These studies have generally concluded that Pandalid shrimp stocks are structured on the scale of individual seas or ocean basins, although Oloef (1996) suggested that *P. borealis* may have separate populations in individual fjords in Iceland. These results are unlikely to be directly comparable with those for spot prawns, as the larval period of *P. borealis* is much longer than that of the spot prawn, and it inhabits a distinctly different habitat type.

More work has been done on other crustaceans, including Penaeid shrimp. Much of this research has been directed by the shrimp aquaculture industry (Benzie 1998), for which Penaeid shrimps are the major species. A number of these studies have identified highly variable microsatellite sequences in these shrimps (Bagshaw and Buckholt 1997; Ball et al. 1998; Vonau et al. 1999), and identified genetic differences between populations (Garcia et al. 1994; Aubert and Lightner 2000; Xu et al. 2001; Valles-Jimenez et al. 2004; Gusmao et al. 2005). However, the life history of Penaeid shrimp is sufficiently different to that of Pandalids for general conclusions to be inapplicable between the genera.

I used the microsatellite primers developed in Section 1 to test for population differentiation in samples of spot prawns collected in 10 areas in Washington and 1 in Southeast Alaska. If prawns from different regions are genetically different, we would expect the variability in the microsatellite alleles to be larger between region than within a region. A metric traditionally used for this comparison is F_{ST} (Weir and Cockerham 1984). which summarizes difference in heterozygosity of sub-populations from expectations for equivalent random mating combined populations.

Methods

Sample collection

I collected samples of spot prawn tissue from 10 sites throughout Washington waters and one site in Southeast Alaska between 1999 and 2002 (Figure 25, Table 19). Muscle tissue was taken from the abdomen of each prawn in the sample and stored in 70% ethanol until DNA was extracted. The majority of the samples were taken from freshly killed prawns. Some of the samples were provided by commercial fishers or other scientists that were monitoring spot prawn populations. These samples were frozen immediately after capture, and supplied to me within a few days. Frozen samples were defrosted as soon as possible and tissue samples stored in ethanol. The only exception to this procedure was the sample from Alaska, which had been stored frozen for approximately six months before I received it.

Figure 25: Sample locations in Washington. Numbers represent ID numbers given in Table 19

Table 19: Sample locations

ID	Region	Location	Latitude	Longitude	Date	N
1	WA coastal	Grays Canyon	46.9320	-124.9145	9/15/1999	48
2	WA coastal	Juan de Fuca Canyon	48.0262	-125.2236	5/21/2000	47
3	WA coastal	Quinault Canyon	47.5302	-124.9405	7/31/2000	48
4	Strait of Juan de Fuca	Eastern Straits	48.1809	-123.2448	5/10/2000	48
5	San Juan Islands	San Juan Channel	48.5667	-123.0333	10/2/2000	48
6	San Juan Islands	Griffin Bay	48.5200	-123.0083	11/2/2000	48
7	San Juan Islands	Griffin Bay	48.5200	-123.0083	11/14/2002	48
8	Puget Sound	Saratoga Passage	48.1833	-122.5500	8/17/2001	48
9	Puget Sound	Elliott Bay	47.6167	-122.3667	8/14/2001	48
10	Hood Canal	Point Whitney	47.7667	-122.8500	4/18/2001	48
11	S.E. Alaska	Ernest Sound	56.1100	-132.0000	10/11/2000	47

Two samples were taken from the same area, Griffin Bay, San Juan Island, in 2000 and 2002. This is a spot prawn nursery area where large numbers of juvenile prawns are found during the autumn and winter, and thus the samples represent single age classes, rather than the mixed age groups found in samples from adult grounds. These samples were collected to test for year to year differences caused by sweepstakes recruitment events (Hedgecock 1994; Flowers et al. 2002), where groups of recruits are more closely related than expected in a fully mixed population, and in some cases can show genetic differentiation between cohorts (Flowers et al. 2002; Selkoe et al. 2006). The sample from the San Juan Channel which was also taken in 2000 consists of older individuals than those found in the nursery area and thus can also be used for this comparison.

DNA was extracted from each sample using a kit (Qiagen, DNeasy kit), following the manufacturers protocol. The quality and quantity of the DNA extracted was tested by running samples on 1% agarose gels. This showed that the majority of samples produced reasonable quantities of large sized pieces of DNA. However, the samples that had been frozen produced more fragmented DNA that appeared as a smear on the gel. This was especially the case for the sample from Southeast Alaska, which had been frozen for some time before DNA extraction, and the sample from Saratoga passage in Puget Sound.

Population screening

Populations were screened using fluorescent labeled primers on large 8% denaturing polyacrylamide gels. The primers for the loci P2, A14 and B3 were labeled with Hex, 6-Fam and Hex dyes respectively (Qiagen-Operon corp, Alameda, CA). Sizes were assessed relative to two size standards. The first was a commercially produced 400 base pair standard, which was run in every 25th lane to give an absolute size reference (et-Rox standard 400 bp). The second was an in-lane standard consisting of microsatellite alleles of known size, which was included in every lane of some gels. This size standard was made by running a PCR with DNA from an individual which was homozygous for a known allele, including labeled dUTP. Gels were scanned on an FMBIO laser scanner (Miraibio, San Fransisco, CA. Analysis and scoring of the loci was achieved using an image analysis program (Image analysis version 3 MiraiBio 2001).

Population analysis used GENEPOP (Raymond and Rousset 1995) to calculate allele frequencies, to test for deviations from Hardy-Weinberg equilibrium and to run tests for pairwise population differentiation. FSTAT (Goudet 1995; Goudet 2001) was used to calculate multi locus F_{ST} of pairs of samples (Weir and Cockerham 1984).

Correction of critical significance values for multiple comparisons used the method of Benjamini and Yekutieli (Narum 2006), which is less conservative than the Bonferroni method, and is more appropriate when the comparisons are not independent, as with these type of comparisons.

Results

A total of 526 individual spot prawns from 11 subpopulations were screened with the three reliable microsatellite markers. Of these, genotypes were obtained for 525 at locus P2, 520 at locus A14 and 498 at locus B3. The amount of variability detected with these three loci was fairly small. Over all the populations, the loci P2, A14 and B3 had 5, 7 and 16 alleles respectively (Table 20). Allele distributions by sample are presented in Tables 21–23. Complete information at all loci was obtained for 494 individuals. The success of screening depended on the quality of the samples collected. Those which were not immediately processed or frozen provided lower quality DNA which gave less reliable results in population screening. The results obtained from the sample from Alaska clearly demonstrate this. It is notable that the 137 bp allele of locus A14 is of the wrong modulus (table 22), i.e. it is only two bases different from the adjacent alleles. This is unexpected with a tetra-nucleotide microsatellite, but was confirmed by repeated reactions.

Table 20: Overview of loci used to test population structure

Locus	repeat	size	N	# alleles	size range
P2	(CAGA)7	117	525	5	101-157
A14	(GTCT)6	127	520	7	127-151
B3	(AAC)6,(CAA)4,5,5	302	498	16	278-395

Table 21: Allele frequency for locus P2

Sub-Pop.	Alleles (size in base pairs)					
	101	**109**	**113**	**117**	**157**	**N**
Gray	0.323	0.000	0.073	0.583	0.021	96
JdFC	0.351	0.011	0.096	0.543	0.000	94
Quinault	0.333	0.000	0.042	0.573	0.052	96
Straits	0.362	0.011	0.053	0.553	0.021	94
SJC	0.406	0.000	0.083	0.500	0.010	96
GB01	0.385	0.000	0.042	0.573	0.000	96
GB02	0.365	0.000	0.073	0.542	0.021	96
Saratoga	0.365	0.000	0.052	0.552	0.031	96
Elliott	0.385	0.000	0.052	0.542	0.021	96
Hood	0.375	0.010	0.052	0.542	0.021	96
Ernest	0.383	0.000	0.074	0.521	0.021	94
Total	0.367	0.003	0.063	0.548	0.020	1050

Table 22: Allele frequency for locus A14

Sub-Pop.	Alleles (size in base pairs)							
	127	**135**	**137**	**139**	**143**	**147**	**151**	**N**
Gray	0.490	0.042	0.021	0.302	0.000	0.010	0.135	96
JdFC	0.533	0.000	0.033	0.304	0.000	0.000	0.130	92
Quinault	0.479	0.063	0.000	0.240	0.000	0.000	0.219	96
Straits	0.500	0.065	0.011	0.196	0.011	0.033	0.185	94
SJC	0.489	0.054	0.000	0.326	0.000	0.000	0.130	92
GB01	0.447	0.011	0.011	0.287	0.000	0.011	0.234	94
GB02	0.427	0.010	0.000	0.344	0.000	0.031	0.188	96
Saratoga	0.426	0.032	0.011	0.309	0.000	0.021	0.202	94
Elliott	0.479	0.031	0.021	0.271	0.000	0.021	0.177	96
Hood	0.385	0.031	0.042	0.271	0.000	0.010	0.260	96
Ernest	0.489	0.043	0.000	0.255	0.000	0.021	0.191	94
Total	0.467	0.035	0.013	0.282	0.001	0.014	0.187	1040

Table 23: Allele frequency for locus B3

Sub-Pop.	Alleles (size in base pairs)								
	278	**287**	**290**	**293**	**296**	**299**	**302**	**305**	
Gray	0.000	0.032	0.149	0.213	0.000	0.160	0.064	0.000	
JdFC	0.000	0.100	0.178	0.144	0.000	0.100	0.089	0.011	
Quinault	0.000	0.042	0.125	0.240	0.021	0.188	0.031	0.000	
Straits	0.000	0.034	0.148	0.159	0.011	0.182	0.136	0.000	
SJC	0.000	0.000	0.111	0.078	0.033	0.222	0.078	0.000	
GB01	0.000	0.045	0.125	0.159	0.023	0.159	0.114	0.000	
GB02	0.000	0.098	0.098	0.110	0.037	0.244	0.134	0.000	
Saratoga	0.011	0.120	0.185	0.087	0.033	0.207	0.043	0.000	
Elliott	0.000	0.022	0.141	0.163	0.043	0.228	0.065	0.000	
Hood	0.000	0.064	0.181	0.181	0.021	0.128	0.074	0.000	
Ernest	0.000	0.089	0.167	0.144	0.033	0.211	0.044	0.000	
Total	0.001	0.058	0.147	0.154	0.023	0.184	0.078	0.001	
	Alleles (size in base pairs)								
	308	**311**	**314**	**317**	**320**	**323**	**332**	**395**	**Total**
Gray	0.096	0.021	0.064	0.149	0.043	0.000	0.000	0.011	94
JdFC	0.122	0.022	0.033	0.144	0.056	0.000	0.000	0.000	90
Quinault	0.083	0.031	0.052	0.125	0.021	0.000	0.000	0.042	96
Straits	0.091	0.034	0.045	0.102	0.057	0.000	0.000	0.000	88
SJC	0.133	0.011	0.078	0.144	0.089	0.000	0.000	0.022	90
GB01	0.057	0.000	0.034	0.193	0.080	0.000	0.000	0.011	88
GB02	0.049	0.049	0.049	0.110	0.012	0.000	0.000	0.012	82
Saratoga	0.065	0.054	0.043	0.141	0.011	0.000	0.000	0.000	92
Elliott	0.087	0.000	0.065	0.109	0.065	0.000	0.011	0.000	92
Hood	0.160	0.000	0.032	0.106	0.032	0.011	0.000	0.011	94
Ernest	0.122	0.000	0.067	0.067	0.056	0.000	0.000	0.000	90
Total	0.097	0.020	0.051	0.127	0.047	0.001	0.001	0.010	996

Details of F_{IS} (inbreeding coefficient: reduction in heterozygosity in individuals in a sub-population relative to an equivalent random mating subpopulation), and observed and expected heterozygosity by population are given in Table 24. This shows that there were few significant deviations from Hardy-Weinberg equilibrium. In most populations there was a slight non-significant excess of homozygotes (positive values of F_{IS}), indicating either that there is some inbreeding in the population or errors in scoring the genotypes (missed alleles, upper allele drop out or null alleles). That the only significant deviations are seen in the samples which were the worst quality (Ernest sound and Saratoga passage), and in the locus which was the most difficult to produce reliable reactions and was the most difficult to score (B3), indicates that scoring errors are the most likely explanation. This is confirmed by the use of the Micro-checker program (Van Oosterhout et al. 2004), which indicated an excess of homozygotes across all allele sizes in four cases (Locus B3 for Ernest Sound, Elliott Bay and Saratoga Passage. Locus A14 for Gray's Harbor). This may have been caused by null alleles or mis-scoring of close heterozygotes as homozygotes.

Table 24: F_{IS}, observed and expected heterozygosity and probability of deviations from Hardy-Weinberg equilibrium (H-W). Significant deviations from H-W (after Benjamini and Yekutieli (B-Y) correction of significance level (0.0166)) are shown in bold type.

Locus	N2				A14				B3			
	Ho	He	F_{is}	P	Ho	He	F_{is}	P	Ho	He	F_{is}	P
Gray	0.521	0.550	0.063	0.037	0.479	0.648	0.271	0.021	0.830	0.864	0.051	0.296
JdFC	0.532	0.573	0.083	0.642	0.522	0.606	0.149	0.119	0.867	0.879	0.025	0.224
Quinault	0.563	0.556	-0.001	0.977	0.646	0.661	0.034	0.572	0.813	0.860	0.066	0.116
Straits	0.638	0.560	-0.130	0.195	0.660	0.672	0.008	0.390	0.795	0.875	0.102	0.041
SJC	0.583	0.578	0.001	0.906	0.609	0.634	0.052	0.814	0.844	0.872	0.043	0.900
GB01	0.458	0.521	0.131	0.572	0.574	0.663	0.144	0.291	0.795	0.870	0.097	0.178
GB02	0.625	0.568	-0.090	0.149	0.750	0.663	-0.121	0.474	0.854	0.871	0.032	0.057
Saratoga	0.521	0.559	0.078	0.046	0.638	0.681	0.074	0.731	0.674	0.869	0.235	**0.001**
Elliott	0.500	0.555	0.109	0.480	0.604	0.664	0.100	0.612	0.761	0.867	0.133	0.049
Hood	0.583	0.563	-0.026	0.949	0.667	0.707	0.068	0.225	0.851	0.869	0.032	0.544
Ernest	0.532	0.576	0.087	0.503	0.596	0.656	0.103	0.307	0.756	0.869	0.141	**0.005**
Total	0.550	0.561			0.613	0.665			0.803	0.880		

Pairwise F_{ST} values for all pairs of populations are shown in Table 25. Many of the F_{ST} values are negative, which indicates a higher expected level of heterozygosity within sub populations than between them. The largest F_{ST} value is 0.0062, which indicates little genetic differentiation between the populations according to the scale suggested by Wright (1978).

Table 25: Pairwise F_{st}, for all loci combined.

	Grays	Hood	Quina	Strai	Ernes	Ellio	SJC	Sarat	JdFC	GB01	GB02
Grays	-	-0.0015	-0.0062	-0.0042	-0.0037	-0.0066	-0.0008	-0.0021	-0.0064	-0.0050	0.0003
Hood		-	-0.0016	-0.0008	-0.0035	-0.0023	0.0062	-0.0019	0.0010	-0.0033	0.0036
Quina			-	-0.0041	-0.0039	-0.0055	0.0056	-0.0001	0.0028	-0.0026	0.0033
Strai				-	-0.0061	-0.0071	0.0003	-0.0003	-0.0015	-0.0041	0.0006
Ernes					-	-0.0093	-0.0033	-0.0056	-0.0031	-0.0018	-0.0018
Ellio						-	-0.0059	-0.0045	-0.0017	-0.0062	-0.0036
SJC							-	0.0005	0.0006	-0.0001	-0.0003
Sarat								-	-0.0009	-0.0035	-0.0062
JdFC									-	-0.0017	0.0033
GB01										-	-0.0026
GB02											-

Probability values for pairwise tests for population differentiation (Raymond and Rousset 1995) are given in Table 26. The only significant value after correction for multiple tests is between the populations from Juan de Fuca and Quinault Canyons (B-Y correction, critical value for 55 comparisons = 0.01087). Probabilities are low (<0.05) for a number of comparisons with the San Juan Channel sample taken in 2000.

Table 26: P-values for pairwise population differentiation for all loci combined. Significant comparisons, after B-Y correction of 5% significance level for multiple tests (0.01087) are indicated with an asterisk. P values under 0.05 are shown in bold type

	Grays	Hood	Quina	Strai	Ernes	Ellio	SJC	Sarat	JdFC	GB01	GB02
Grays											
Hood	0.7159										
Quina	0.7133	0.3761									
Strai	0.9152	0.5683	0.5402								
Ernes	0.7095	0.7218	0.4626	0.8166							
Ellio	0.9565	0.8256	0.5345	0.9620	0.9878						
SJC	0.4948	**0.0255**	**0.0438**	0.2679	0.2905	0.7664					
Sarat	0.3507	0.3698	0.3481	0.4113	0.6876	0.3342	**0.0154**				
JdFC	0.6745	0.2604	**0.0033***	0.1005	0.1346	0.1393	**0.0158**	0.1106			
GB01	0.5846	0.7100	0.1190	0.5431	0.3111	0.8946	0.1620	0.1707	0.3093		
GB02	0.2420	0.0982	0.0909	0.3667	0.3636	0.3972	**0.0456**	0.9687	0.0668	0.4585	

The data were grouped by region (shown in Table 19) for re-analysis, in an attempt to increase power. The results of this analysis were inconclusive (Table 27). The highest value for F_{ST} (0.0062) is between samples from the San Juan Islands and Hood Canal. Pairwise tests for population differentiation (Raymond and Rousset 1995) show no significant population differentiation between any pairs after correction for multiple tests.

Table 27: Pairwise Fst and pairwise population differentiation probabilities for all loci combined by region. Fst values are above the diagonal and population differentiation probabilities below.

	Coast	Strait	SJI	PS	HC	AK
WA Coast		-0.0024	0.0028	0.0011	0.0004	-0.0023
Strait of Juan de Fuca	0.7233		0.0003	-0.0013	-0.0008	-0.0061
San Juan Islands	0.0800	0.2967		<0.0001	0.0062	-0.0033
Puget Sound	0.1033	0.5933	0.0833		0.0005	-0.0028
Hood Canal	0.7300	0.6933	0.0267	0.2167		-0.0035
Southeast Alaska	0.5167	0.7833	0.2200	0.7567	0.7633	

Discussion

I obtained genotypic data from 525 individuals from 10 samples in Washington and one in Alaska using 3 microsatellite loci. This data showed few genetic differences between samples. The only pair of samples that was shown to be genetically differentiated were those caught in Juan de Fuca Canyon and Quinault Canyon off the Washington Coast in 2000. This is surprising as these were two of the closest spaced samples, separated by approximately 40 miles. The values of pairwise F_{ST} obtained showed a generally low degree of genetic differentiation between putative populations in this region.

The power of this study to detect differences between populations was compromised to a certain extent by the small number of microsatellite loci available for population screening, and the relatively small number of alleles present at each of these loci. The original experimental plan was to isolate a much higher number of loci, as this has been shown via simulation to be the best way to increase power to resolve differences between closely related populations (Ferguson and Danzmann 1998). The importance of having a large number of alleles per locus has also been shown (Kalinowski 2002), and it is unfortunate that two of the loci isolated had few alleles. The two loci with 5 and 7 alleles are less informative than the one with 16 alleles in this study. There was also high variability within populations, which further reduces the power of test to detect genetic differences between populations. Isolation of more microsatellite loci would give greater power to discern differences, especially if these loci had a higher number of alleles.

Given that the duration of the pelagic larval phase of the spot prawn lifespan is rather short, the finding of a lack of differentiation between any of the Washington samples and the outgroup from Southeast Alaska is surprising, and is possibly a reflection of the low power of the set of microsatellite loci mentioned above. Also, the sample from Southeast Alaska was of low quality, which led to problems in achieving reliable results during genotyping. It is possible that this problem may have masked any potential differentiation between this sample and the rest.

Values for pairwise F_{ST} (inbreeding in subpopulations relative to combined population, hence population differentiation) were small, indicating little genetic differentiation between populations. The highest F_{ST} between a pair of samples was 0.0062. In 43 of 55 cases, Fst values calculated in this study for direct comparisons of samples were negative, indicating higher diversity within samples than expected in the total. This scenario is common in studies using microsatellites to determine genetic differentiation of populations, and can lead to underestimation of differences between populations with low gene flow (Hedrick 1999; Balloux et al. 2000).

The F_{ST} values I found for spot prawns are similar to those recorded for Geoducks across a similar area (Vadopalas et al. 2004). These F_{ST} values are in contrast to a number of studies on fish which show higher values for F_{ST} and significant population differentiation between Puget sound and coastal populations (F_{ST} =0.087 for copper rockfish (Buonaccorsi et al. 2002), F_{ST} =0.016 for Pacific Herring (Small et al. 2005) F_{ST}=0.02 for Pacific Hake (Iwamoto et al. 2004)). There has been no work published on population genetics of any shrimp species in the Puget Sound area with which my results can be compared.

A significant genetic difference was found between Juan de Fuca Canyon and Quinault Canyon samples. Both of these were collected in 2000, and represent a similar range of age classes. F_{ST} between these samples is 0.0028, which represents a very low degree of genetic differentiation between the populations. As noted above, counterclockwise gyres form above both of these canyons in spring, which may act as a larval retention mechanism.

Although few significant genetic differences between putative populations were shown, there are suggestions of greater structure in the data. Probability values for genetic differentiation between the San Juan Channel sample and Quinault Canyon, Juan de Fuca canyon, Hood Canal and Saratoga passage samples were all less than 0.05. The finding of little consistent genetic differentiation between populations does not mean that there is no population structure in this area. The number of migrants per generation necessary to mask any genetic differences is far smaller than a level which would be of ecological significance. Furthermore, this study may have lacked sufficient power to detect genetic differences, since only 3 microsatellite loci were isolated and 2 of these had relatively few alleles.

The findings from this study are not strong enough to outweigh the strong possibility of existing population structure in spot prawns based on their life history and habitat: sedentary adults, larvae with a short planktonic phase, and found in a region with complex geography, currents, and underwater topography. In the absence of conclusive proof of the presence or lack of stock structure, management strategies for spot prawns should be conservative and assume such structure exists.

Chapter 4: Analysis of the Washington coastal spot prawn fishery

4.1 Introduction

The Washington coastal spot prawn fishery operates near three submarine canyons (Figure 26). These patches are areas of fairly steep, rocky ground in depths between 150 and 250 m. The bulk of the current pot fishery takes place an average of 30-70 km offshore.

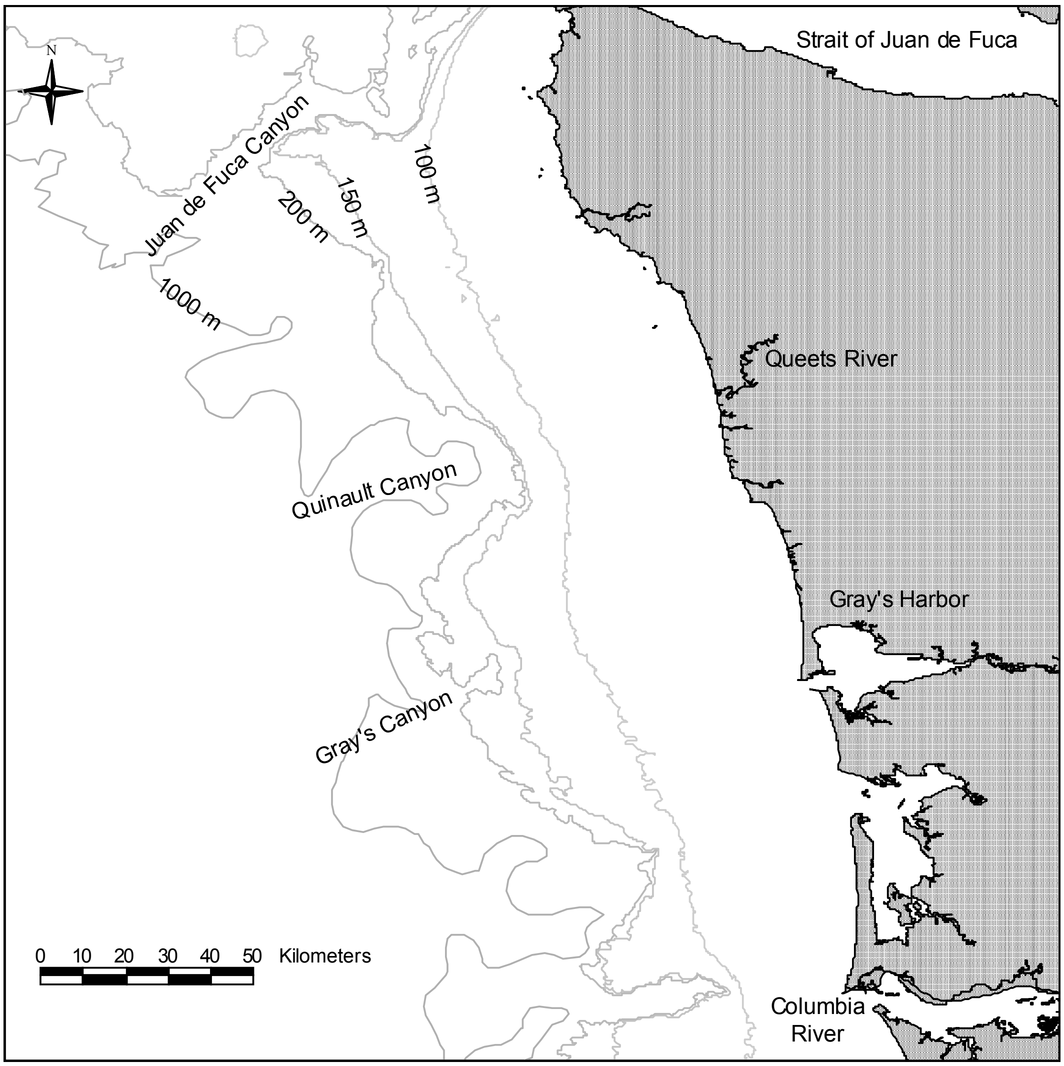


Figure 26: Submarine canyons fished by the coastal Washington spot prawn fishery.

This fishery developed fairly rapidly, with two competing gear types and a lack of informed management. In recent years the exploitation pattern has changed dramatically, due to the mandated switch from mainly trawl to entirely pot gear beginning in 2003.

In this Chapter, I analyze the available fishery data and other supporting information in order to aid development of a management plan based on the best available science. Current management is based on limited entry and a precautionary catch limit which is fairly arbitrary, based on the maximum catch taken in a year. The spot prawn fishery is too new to have a history of consistent catch data which could be used to validate this catch limit. Management and analysis of this fishery will probably always be constrained by lack of key data, as the availability of resources for management and data collection are severely limited. The coastal spot prawn fishery is too small to fund an extensive survey to determine the size of the spot prawn stock. Nor will the fishery be able to support complex in-season management such as is used to manage the British Columbia fishery. Thus this effort attempts to create management guidelines that give a reasonable level of caution in the face of uncertainty, given the existing data gaps.

In this Chapter I present 1) a history of the Washington coastal fishery, 2) summary of available data on the fishery, 3) Estimation of pot gear selectivity, 4) Analysis of yield per recruit, 5) population model using stock synthesis, including population projections and estimation of sustainable catch levels, and 6) Recommendations for future management of this fishery.

4.2 History and management of the fishery

The history of this fishery includes the stages of development typical of most fisheries: discovery, bandwagon growth, fallback, and evolutionary development (Walters 1986).

The offshore directed fishery for spot prawns began in 1992, when two boats based in Westport, Washington actively targeted spot prawns with pot gear, and landed 903 kg from the Grays Canyon area off Westport (Table 28). Prior to this time, spot prawns were an occasional bycatch species in the ocean pink shrimp and groundfish trawl fisheries. An Oregon-based trawler entered the fishery in 1994 and harvested approximately two-thirds of the catch of 25,430 kg in that year. No landings were recorded in 1995. The WDFW believes fishers pursued more lucrative opportunities, particularly for albacore (S. Barry WDFW, pers comm.1999).

The offshore fishery changed dramatically in 1997, when five trawl boats entered the fishery and landed 51,038 kg of spot prawns, approximately 84% of the total offshore catch (Table 1). WDFW and others were concerned about the dramatic increase in fishing effort seen in the 1997 and 1998 seasons (Table 1), especially in the light of significant reductions in groundfish quotas and below-average catches of other important fisheries, such as pink shrimp (*Pandalus jordani*), which made the spot prawn fishery seem more attractive than in previous years. These management concerns and limited knowledge about the distribution, abundance, and sustainability of the resource led WDFW to recommend that the provisions of the Emerging Commercial Fisheries Act (ECFA) be applied to the coastal spot prawn fishery. The Washington State Fish and Wildlife Commission approved this recommendation in November 1997.

An Industry Advisory Board was appointed in 1998 according to ECFA guidelines. The Board's mandate was to recommend to the WDFW the number of permits issued and the type of permit qualification requirements. This advice was incorporated into "a comprehensive regulatory package" that was approved by the Commission in December 1998, along with two fishery management policy statements. Limited entry went into effect in January 1999. Five trawl gear and ten pot gear permits were issued based on historical participation prior to March 1998. Later in 1999, one of these trawl permits was converted to pot at the request of the fisher. These permits are not transferable and not inheritable.

An overall catch quota of 250,000 pounds (113,400 kg) was established and equally allocated to the two gear types. A trawl season of May 1 through November 30 was instituted, and pot vessels were limited to 500 pots per vessel. Pot mesh size is required to be over 7/8" (2.22 cm)(mesh size for this fishery is defined such that a 7/8" dowel can freely pass through the mesh). Due to the fact that trawl gear is "widely reputed to cause inordinate adverse habitat impacts," trawl gear was legally defined so as to prevent the use of "mud and tire and rockhopper gear". To avoid inter-jurisdictional conflict, WDFW and the Oregon Department of Fish and Wildlife (ODFW) outlined an agreement restricting fishers to their State's waters unless they possessed a fishing permit in the other State.

Under this new management regime, effort and catch both declined in 1999. 45,913 kg were landed, 95% of which was landed by three trawl vessels. A substantial proportion of the catch off Washington was landed into Oregon ports (primarily Astoria) until 2003, when the States enacted complementary regulations requiring that prawns caught in each State's waters be landed in that state in order to prevent evasion of new state fishing regulations.

Table 28: Washington offshore spot prawn fishery catches (kg) 1992-2005.

Year	Catch (kg)			Price	Value ($)*	Number of vessels	
	Pot	Trawl	Total	($/kg)		Pot	Trawl
1992	903		903	-	-	2	0
1993	6,794		6,794	9.50	64,567	4	0
1994	10,194	15,236	25,430	10.80	274,695	5	2
1995			0	-	-	0	0
1996	10,774	59	10,833	8.82	95,566	5	0
1997	9,922	51,038	60,960	8.12	494,877	4	6
1998	20,356	93,891	114,247	10.45	1,193,884	10	8
1999	2,333	43,580	45,913	12.58	577,766	5	3
2000	5,373	66,980	72,353	14.45	1,045,786	6	4
2001	10,692	77,407	88,100	14.17	1,248,194	9	3
2002	25,108	54,992	80,100	13.88	1,111,948	6	3
2003	52,138		52,138	13.88	723,776	9	0
2004	62,444		62,444	13.60	848,984	8	0
2005	29,126		29,126	11.88	346,016	5	0

* The values reported to WDFW in recent years may not reflect the actual value of the fishery. Some of the fishers have been reporting extremely low prices when marketing the catch themselves (L Wargo, WDFW pers. comm. 2006). The values reported here are only for landings made in Washington, and have anomalously low values removed. Total fishery value is based on total catch using this price per kg and not the reported figures.

Regulations were modified in 2000 to address concerns about the status of the stock in Grays Canyon, which was being heavily fished. The overall 2000 quota (250,000 lbs. / 113,400 kg) was divided between the southern (100,000 lbs. / 45,360 kg) and northern (150,000 lbs. / 68,040 kg) portions of the Coast. In addition, the opening date for the Grays Canyon fishery was set back until July 1 to reduce the length of the trawling season in this area.

The appropriateness of trawl gear in spot prawn habitat was an issue which had been raised as early as 1994. In that year vessels fishing pots first reported conflicts with trawlers and expressed concerns about habitat damage (S. Barry WDFW, pers. comm. 1999). According to WDFW, there was a lot of discussion about converting the trawl fleet to pots from then on, but no action was taken due to lack of data. I found substantial bycatch in the trawl fishery in 1999 and 2000 (see Chapter 2). Based on this data, along with concerns about overexploitation of the spot prawn resource off the Washington coast, a trawler phase-out proposal was placed before the WDFW Fish and Wildlife Commission and passed in 2001. This allowed existing trawl permit holders to fish either with trawls or pots in 2002, in order to ease the transition between gears. At least two vessels took advantage of this measure in 2002, although only one has successfully made the transition and continued to fish with pots in subsequent years. It was clear to many in the industry that change was on the horizon before the passage of the trawl closure, and some coastal trawlers had experimented with pot conversions prior to 2002. To further facilitate the transition, former trawl vessels were given exclusive access to a portion of the quota through 2006. Management concerns about bycatch in the trawl fishery and the effect of trawl gear on benthic habitat in the Washington coastal fishery are detailed in Chapter 2. As of 2003, there is no longer any directed trawl fishing for spot prawns in Washington. However, the fear remains that the extensive trawl fishing effort in the years 1994-2002 did severe and lasting damage to habitat in the areas inhabited by spot prawns.

After the trawl closure, pot fishing effort increased slightly. Most of the effort increase was in the Grays Canyon area, raising some concern about the sustainability of the fishery in that area under the 100,000 pound (45,360 kg) area specific quota. This quota was slightly exceeded in each year from 2000 to 2003, followed by a drop to 22,600 kg in 2004 and 8,165 kg in 2005.

The permit conditions established under the ECFA state that to retain a permit, each permit holder must land at least 1000 pounds of spot prawns every two years (10,000 pounds for trawl vessels when the trawl fishery was open). A number of permit holders have landed just enough every other year to retain their permit. This may be due to the availability of other more lucrative opportunities, or the potential for a windfall profit if the fishery becomes limited entry and the permits transferable. In recent years, some of these permit holders have failed to achieve this and the total number of permits in the fishery had dropped to 11 as of the start of 2006.

The regulations imposed on the fishery by the ECFA were renewed in 2004 at the request of industry representatives. This indefinitely extends the window to be used to gather information and develop management recommendations for the Commission and legislature.

The current overall level of catch and fishing effort does not seem to warrant great concern; only 29,000 kg of prawns were taken in 2005, which is far less than the maximum catch of 114,000 kg. However, there were reports of low CPUE in the Gray's Canyon area in 2004 and 2005. It is not clear if this was due to inexperience on the part of the people fishing (some are alternate operators who have not previously fished for spot prawns) or a real drop in abundance on the grounds.

Some concerns have been expressed by managers about the year long open season in the offshore fishery. Some fishing occurs during the fall and winter when prawns are ovigerous, and they are thought to be vulnerable at this time. A closed season running from September through March has been proposed, and the majority of permit holders appear to be supportive of a closed season (L. Wargo, WDFW pers. comm. 2006).

The fishery's long-term future licensing scheme needs to be decided. This is likely to remain a limited access fishery, but the number of licenses has to be set, and whether the allowable catch is set for the fishery as a whole or for individual vessels also needs to be determined. Catch limits need to be refined to appropriately reflect the size and productivity of the stock, and remain conservative enough to account for the uncertainty in knowledge of the stock size.

4.3 Biological considerations for this stock

Biology of this stock is covered thoroughly in Chapters 1, 2, and 3. An unresolved issue is the relationship between stock and recruitment. The prawns mate in late summer/early autumn and the eggs are carried by females until late March / early April, when they are released and larvae hatch. The fate of larvae is not conclusively known, but it is likely that they are carried into shallow water via upwelling mediated advection, and that they settle in shallow subtidal areas where they can find ample cover. Recruits are not found on the fishing grounds until late in their 2nd year or early in their third year of life, when they are at least 30 mm carapace length. Only 0.5% of the total prawns measured from trawl samples were less than 30 mm CL.

Recruitment is an unknown but important factor influencing the dynamics of the stock. A weak stock-recruitment relationship was shown by Boutillier and Bond (2000), but this was for a stock within a partially enclosed fjord system, where the larvae would settle in areas very close to those used by the adults, and the juveniles would have a short migration to the adult grounds from nursery areas. For the coastal stock, the adults are found 30 – 70 km from the likely nursery areas, and the juveniles have to undertake large migrations. These factors may lead to weaker links between the size of the local spawning stock in a given year and the number of subsequent recruits.

4.4 Data availability for the fishery

Landings

Landings data for catches landed into Washington ports were available from the landings record database ("fish tickets") maintained by WDFW. This only covered a portion of the total landings, as a number of vessels landed the majority of their catch into Oregon ports. The landings data for Oregon was obtained through WDFW. Catches that were taken in Oregon waters were eliminated using data from the fish tickets and corresponding logbooks. Total landings by gear type are given in Table 28 above.

Logbooks

Although there were few regulations covering the fishery in its early stages when it was open access, one of them was the mandatory keeping of logbooks and submission of them to WDFW at the end of the season. Some vessels that were based out of Oregon submitted their logs to ODFW, but I also obtained these and created a fairly complete database of log data covering the period 1993 – 2003.

The proportion of the catch covered by this database varies by year (Figure 27). In general, vessels that had a longer history in the fishery provided more comprehensive logs. Many vessels that only participated in the fishery for one season or part of a season did not keep or submit logs. This is especially apparent in 1998, where the coverage is only 70%.

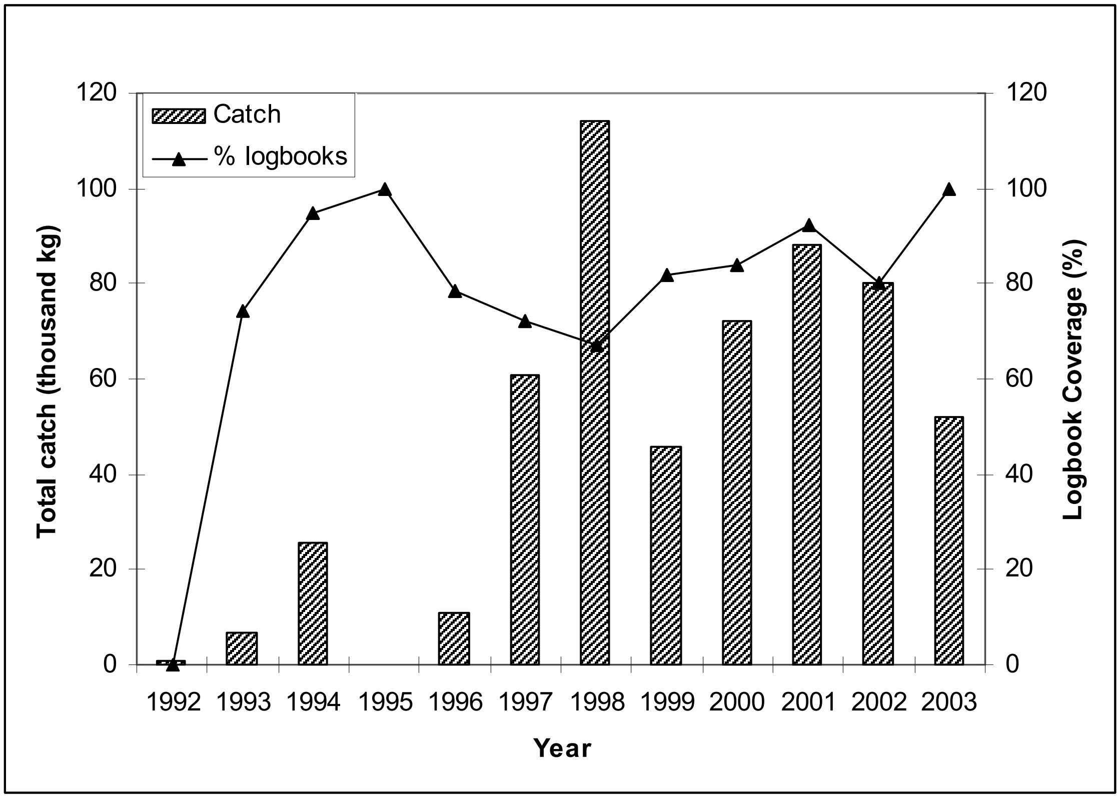


Figure 27: Coastal Washington spot prawn fishery. Total catch and logbook coverage expressed as % of catch represented in logbooks.

I carefully evaluated the logbook data for accuracy. Catches from each trip were compared with the corresponding landing tickets, and generally agreed very closely. Position data for each trawl haul or pot string was mapped and verified with a geographical information system (Arcview GIS). Depth data were compared with bathymetry, and outliers were corrected where possible, or removed from the dataset.

Seasonal distribution of catch and effort

Figure 28 shows the catch by month for years 1993 – 2003. This shows that this fishery is primarily a summer fishery. The majority of the annual catch and effort (over 80%) was in May – September. The exceptions to this are 1998 and 2003, when there was substantial fishing earlier in the season, and 1997 when the season continued until October. These years were unusual in that 1998 was the last year before effort limitation and 2003 was the first year after cessation of trawling. 1997 was a year with a strong El-

Nino, and weather conditions remained fair long after bad weather would have normally been expected to curtail fishing. There are only slight differences between gear types in effort distribution, pot fishers tended to fish more at the start of the season, whereas trawlers worked more throughout the whole summer. Catch per unit effort shows no clear annual pattern. Variation between years is greater than within year variation.

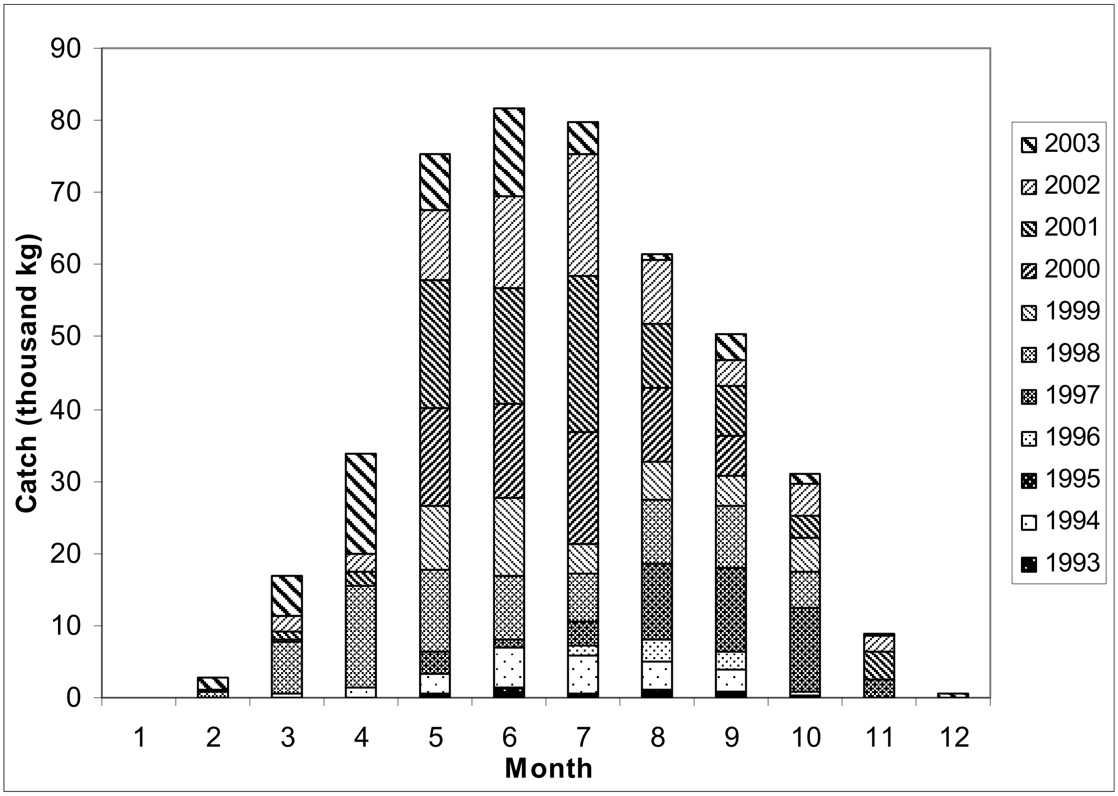


Figure 28: Catch (kg) by month and year for the coastal Washington spot prawn fishery

Spatial and temporal distribution of catch and effort

The spatial distribution of catches by year and gear type is shown in Figure 29a-q. The initial fishing effort was in the Gray's canyon area in 1992, and the fishery expanded from there in 1993, including some exploratory fishing in and to the west of Juan de Fuca Canyon. The area fished by the pot fleet expanded in 1994 to include an area further to the northwest. The trawl fishery in 1994 explored all the areas used by the pot fleet, plus areas further south towards Gray's Canyon. Most of the productive spot prawn grounds were discovered by 1994, although their full extent was not fished. There was no directed fishing for spot prawns in 1995, and no trawling in 1996, but pot fishing resumed. However, the majority of the catch was taken by one vessel which had not previously participated in the fishery, and fished slightly different areas to the others in previous years. The major growth years in 1997 and 1998 were characterized by an expansion of the areas fished by the trawl fleet. Although no new areas were discovered, the full extent of each patch was fished, with the exception of the southern side of Gray's Canyon. The area fished by the pot fleet did not expand greatly in these years, partly due to gear conflicts in which the pot vessels were unable to set gear on the primary trawling grounds due to the risk of trawlers catching the gear.

The management changes beginning in 1999, coupled with lower CPUE in that year severely reduced effort, but the extent of the grounds fished by the trawl fleet remained similar in 1999, followed by a gradual contraction to a few core areas until the trawl fishery was closed in 2002. The pot fishery contracted to core areas in 1999 and gradually expanded through 2002. In 2003, without the risk of gear conflicts, and with the presence of some larger vessels in the pot fleet, the areas fished by pots expanded dramatically, covering the entire core trawling grounds north of Gray's Canyon. This trend continued after 2003, and by 2004 the pot fleet exploited all the grounds that had previously been trawled (J. Oakes, commercial spot prawn fisher, pers. comm. 2004).

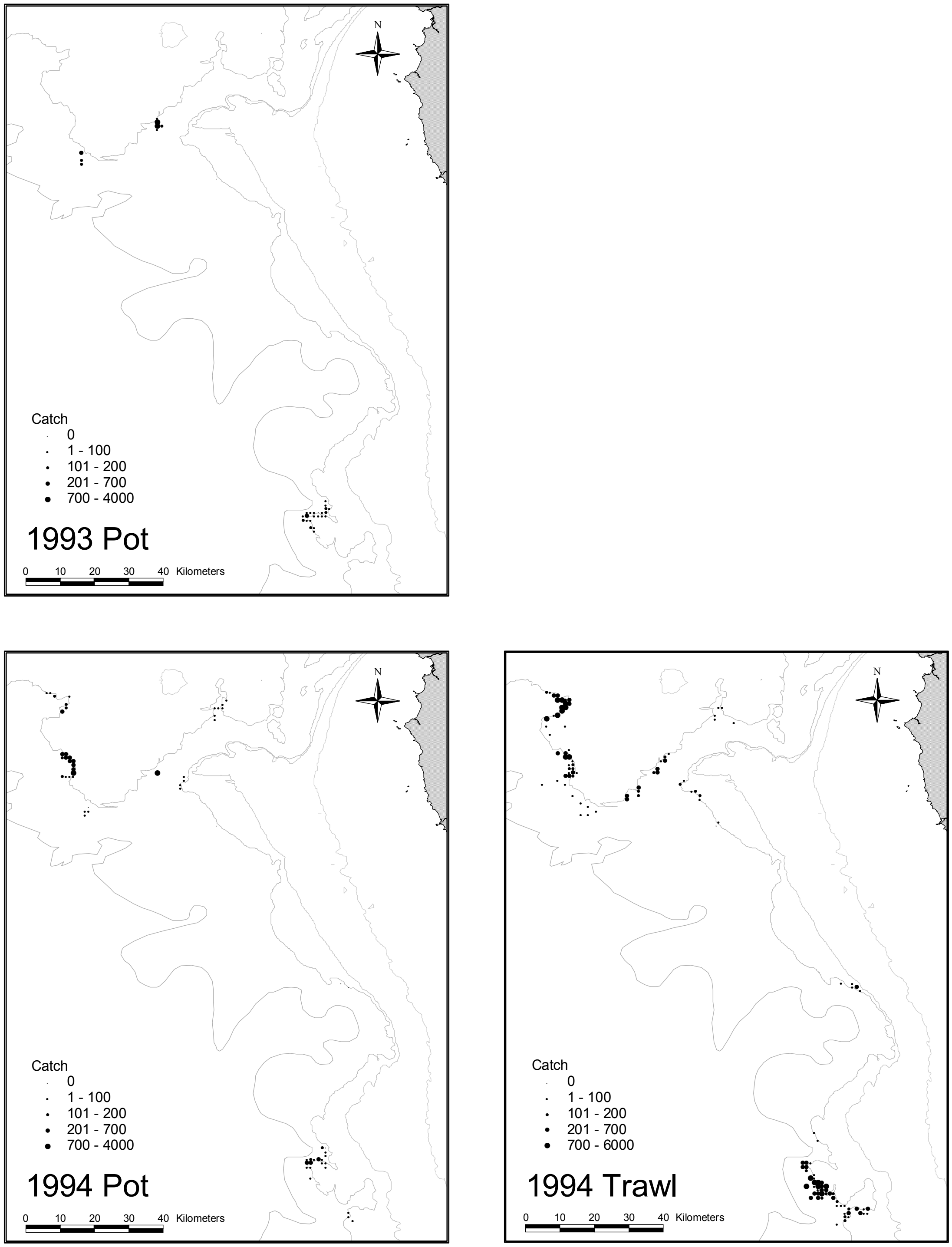


Figure 29 a-c: Catch locations for the coastal Washington spot prawn fishery. Total catch (pounds) by 0.01 degree blocks by year is shown. Symbols are proportional to catch size. Depth contours shown are 50, 100, 200 and 1000 meters.

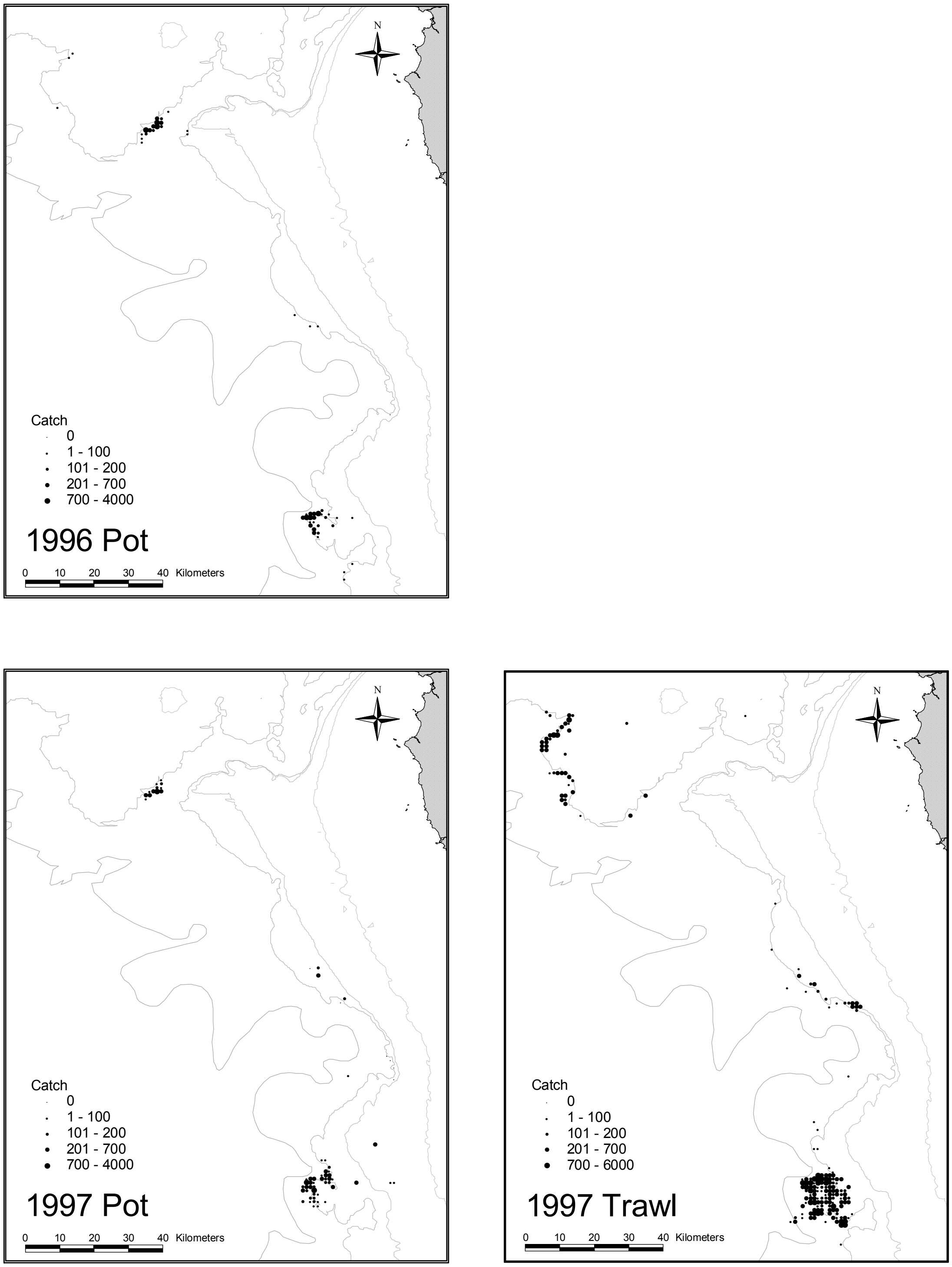


Figure 29 d-f: Catch locations for the coastal Washington spot prawn fishery. Total catch (pounds) by 0.01 degree blocks by year is shown. Symbols are proportional to catch size. Depth contours shown are 50, 100, 200 and 1000 meters.

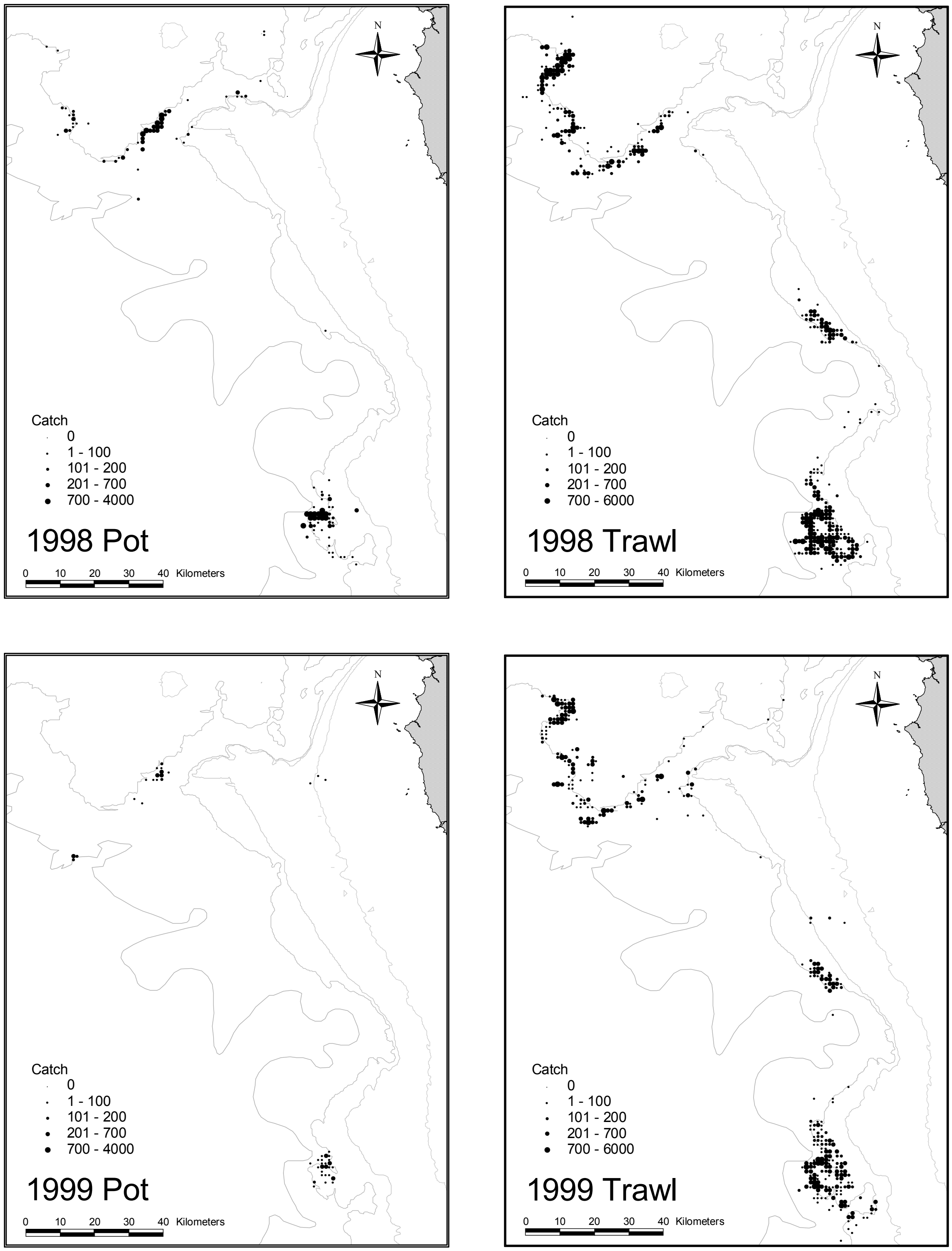


Figure 29 g-j: Catch locations for the coastal Washington spot prawn fishery. Total catch (pounds) by 0.01 degree blocks by year is shown. Symbols are proportional to catch size. Depth contours shown are 50, 100, 200 and 1000 meters.

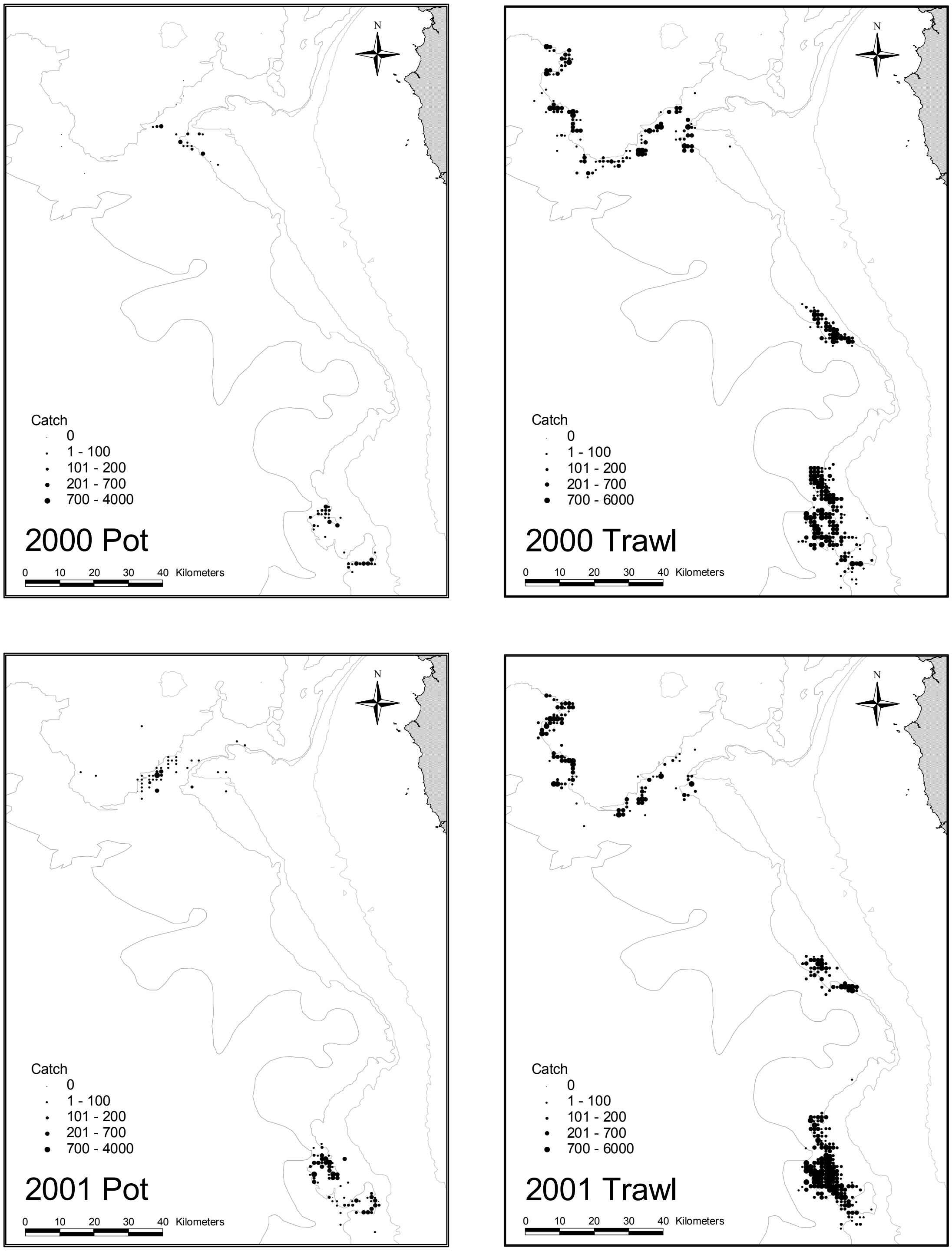
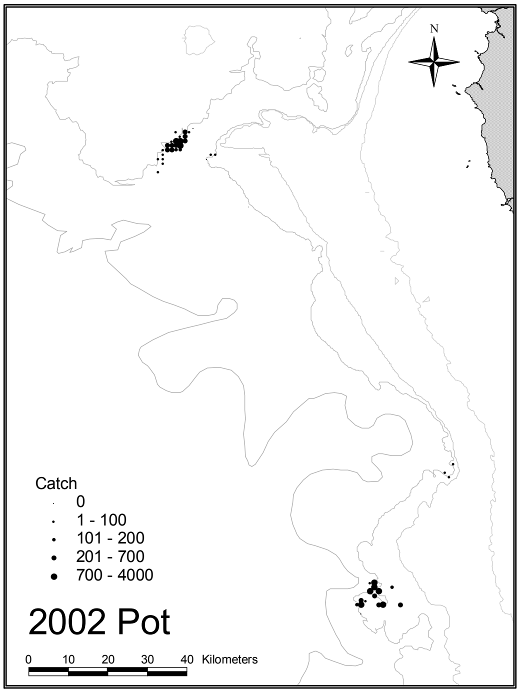
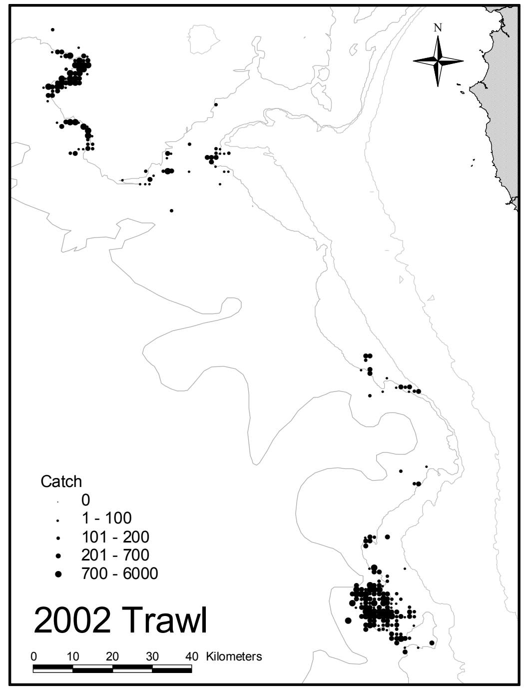


Figure 29 k-n: Catch locations for the coastal Washington spot prawn fishery. Total catch (pounds) by 0.01 degree blocks by year is shown. Symbols are proportional to catch size. Depth contours shown are 50, 100, 200 and 1000 meters.





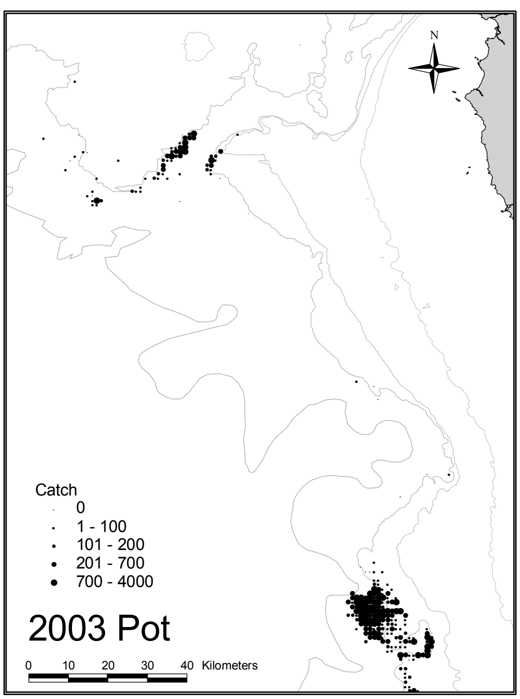


Figure29 o-q: Catch locations for the coastal Washington spot prawn fishery. Total catch (pounds) by 0.01 degree blocks by year is shown. Symbols are proportional to catch size. Depth contours shown are 50, 100, 200 and 1000 meters.

Catch and catch per unit effort series divided into three areas are shown in Figure 30 to Figure 32. The three areas represent Gray's Canyon, Quinault Canyon and the Juan de Fuca Canyon areas respectively. Latitude divisions for these areas are 46.5°– 47.31°, 47.31°-47.675°, and 47.675°-48.5° respectively.

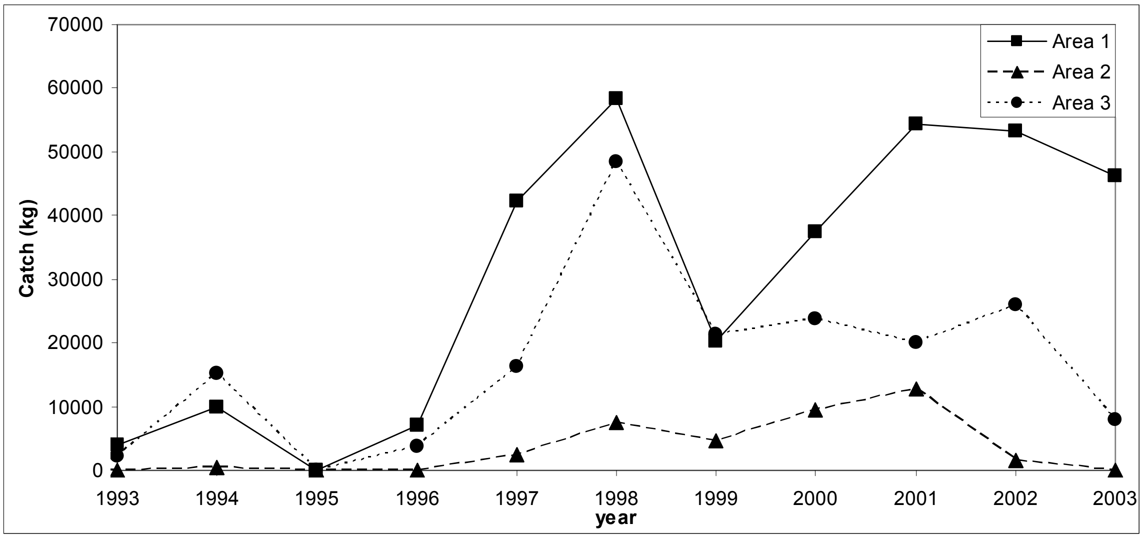


Figure 30: Catch (kg) by area. Areas 1-3 represent Gray's Canyon, Quinault Canyon and the Juan de Fuca Canyon areas respectively.

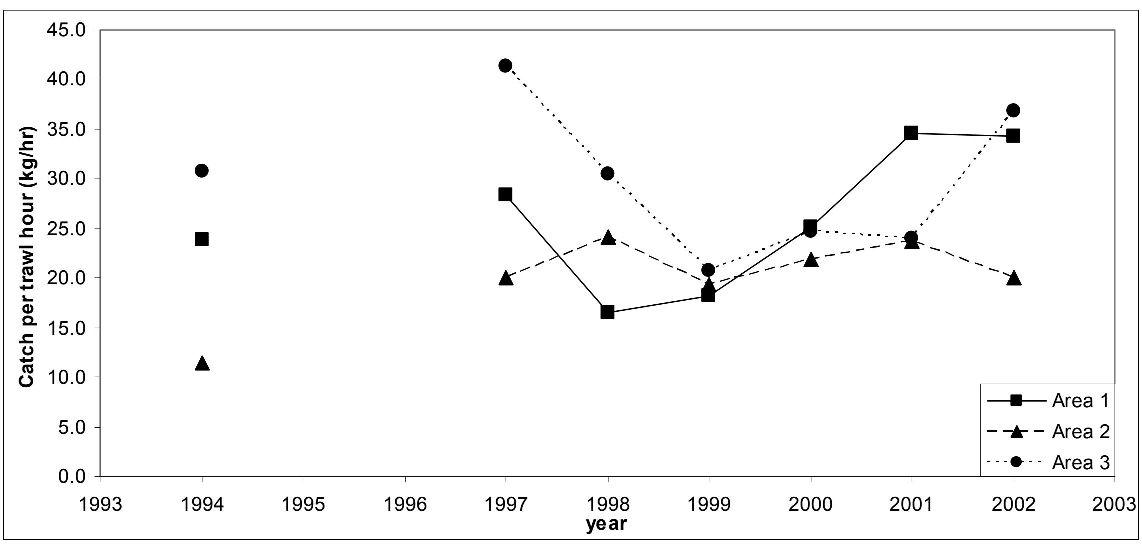


Figure 31: Trawl catch per unit effort (kg per trawl hour) by area

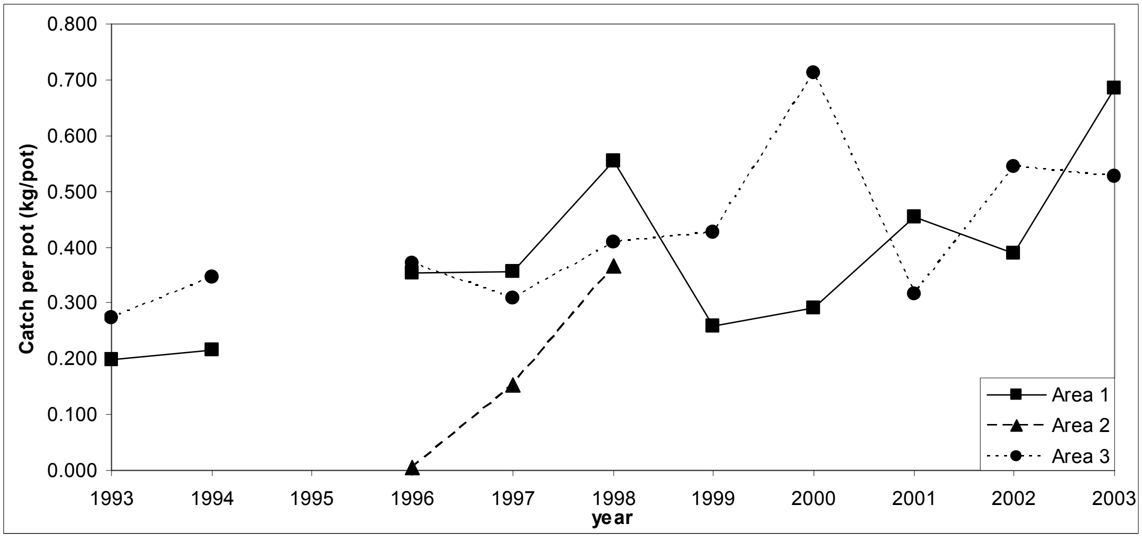


Figure 32: Pot catch per unit effort (kg/pot set) by area.

Following high catch years in 1997 and 1998, trawl CPUE declined markedly. However, this same pattern was not seen in the pot fishery. Overall, the data show CPUE generally increasing, especially in the pot fishery. This may be the effect of technological improvements and increase of experience on catch efficiency. An increasing CPUE is not unexpected for a recently established fishery. Fishermen involved in the fishery estimated that these improvements in efficiency increased catch rates by at least 5-10% per year over the first few years of the fishery. Detailed studies of spot prawn pots in British Columbia concluded that there were large increases in efficiency due to pot design and changes from natural to manufactured baits (Boutillier and Sloan 1987; Rutherford et al. 2004).

The catch by the trawl fishery was dominated by four vessels, which took approximately 90% of the trawl catch from the start of the trawl fishery in 1994 until its end in 2002. Close examination of time series of CPUE by vessel show a very similar pattern for all vessels Figure 33. Systematic differences between vessels are also apparent, as would be expected given differences in gear type used; two of the vessels used twin trawls, two single, and ground gear varied widely (see Chapter 2). The amount of variation in gear between vessels frustrated attempts to standardize the data using variables based on vessel characteristics and gear type.

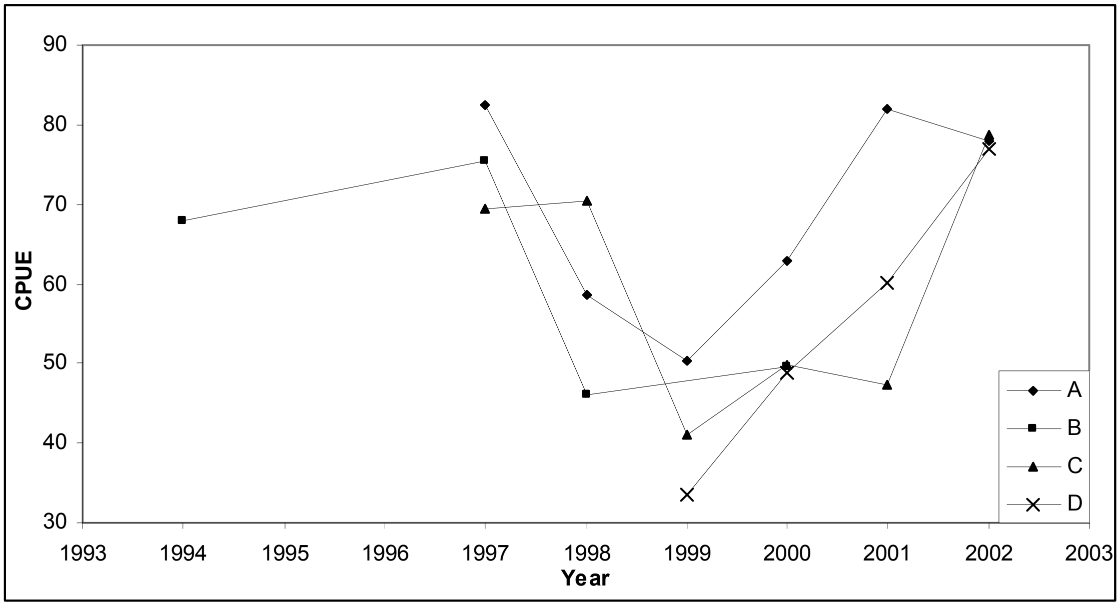


Figure 33: Catch per unit effort series by vessel, trawlers

Catch was not as asymmetric within the pot fleet, with the top 5 vessels accounting for only 63% of the total catch from 1992-2003. There were a large number of vessels that only participated in the fishery for a few years, and only 4 for which logbook data was available for five or more years. CPUE series for these four vessels are shown in Figure 34. These series show the same increase in CPUE from 1999 onwards, but the early years are less consistent. The data from 1993-4 is based on small catches and relatively few pot lifts, so may not be reliable.

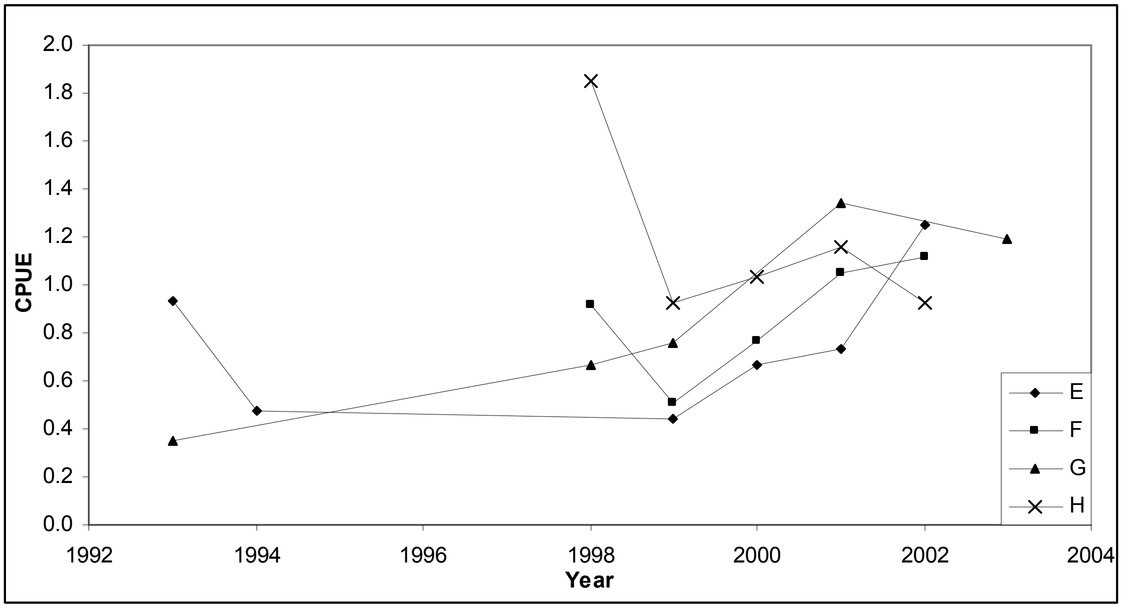


Figure 34: Catch per unit effort series by vessel, pot vessels

Overall, the available CPUE series are short, and show relatively little variation. However, the series from individual vessels appear more consistent than aggregated series, have lower variance within years, and avoid problems which could be caused by including vessels that only fished in one season and have anomalously low or high CPUE. These individual vessel series were therefore used in model fitting. This has the added advantage of avoiding the need to standardize CPUE between vessels, which proved problematic with this dataset.

Diurnal variation in CPUE

Most of the trawl effort was made during day time. Approximately 80 % of hauls were set between 5 am and 8 pm, which are daylight hours during the main fishing season. However, there is no evidence that there was any effect of daylight on the catch rate for trawls (Figure 35). CPUE remains relatively constant across start hours in each year. The same analysis cannot be performed for pot gear, as the majority of the pots are set for more than 24 hours.

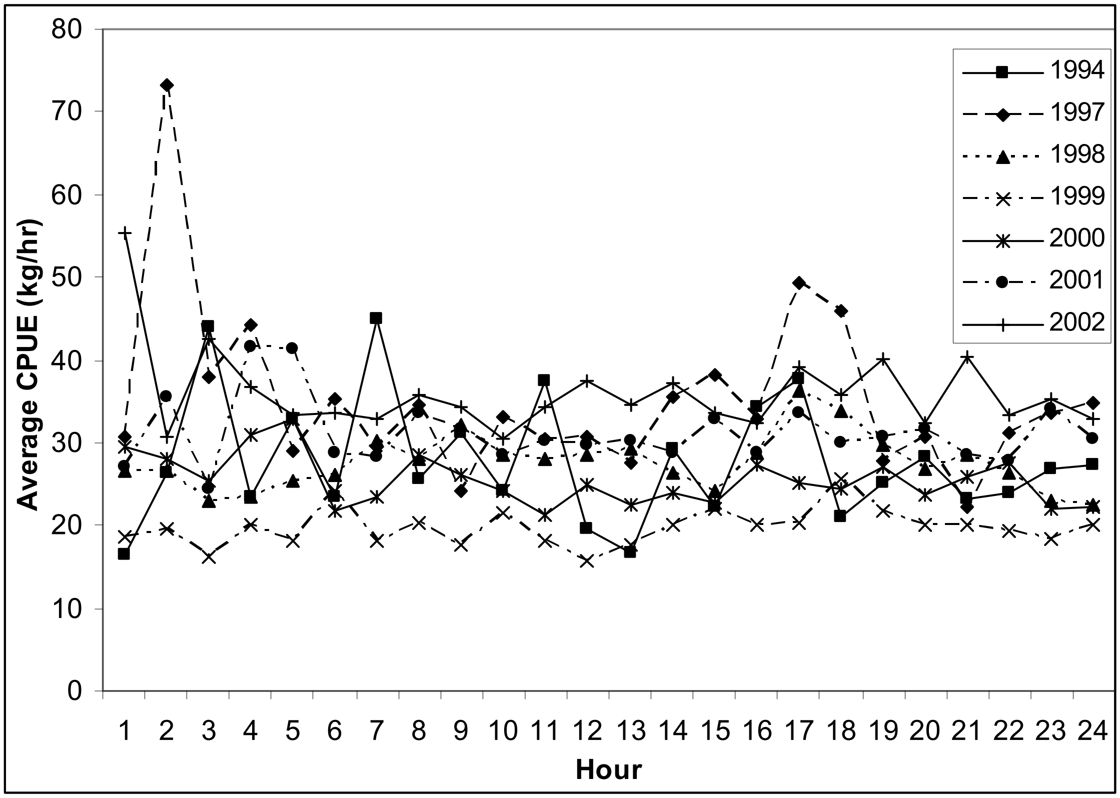


Figure 35: Average catch rate by year and time of day.

Length frequency data

A very limited amount of size data is available for this fishery. No biological sampling was done until 1997, when a WDFW biologist participated in a trip on a pot vessel and obtained some length frequency data. One length frequency sample was also taken in 1998, from a pot vessel landing. I collected prawn length frequency and sex data on trips observing bycatch in 1999 and 2000 (see Chapter 2), and sampling of landings was carried out by WDFW in 2000 (3 samples), 2001 (3 samples) and 2002 (21 samples). Nevertheless, the lack of any size data from the first five years of the fishery is a large data gap. The fact that many of the samples were also taken from pot gear catches adds an extra complication, as pot gear is highly size selective for large spot prawns. Most samples came from the Gray’s Canyon area. One sample from Quinault canyon was taken in 2000, and three from Juan de Fuca Canyon in 2002.

Length frequencies from each year by month are shown in Figure 36 for trawl gear and Figure 37 for pot gear. The trawl samples are presumed to be representative of the length frequency present in the population on the grounds, as the gear is not selective for those sizes. The 2001 and 2002 samples clearly have a greater proportion of prawns less than about 35 mm carapace length. These represent mostly 2+ male prawns, which are expected to be mostly between 31 and 39 mm, with the peak size being 35mm CL in late June. 1999 and 2002 show a different pattern with a lower proportion of age 2+ prawns, and relatively more large sizes. This may indicate that recruitment of age 2 prawns was better in 2000 and 2001. Average CPUE was also lower in 1999 than 2000 and 2001, although CPUE in 2002 was higher.

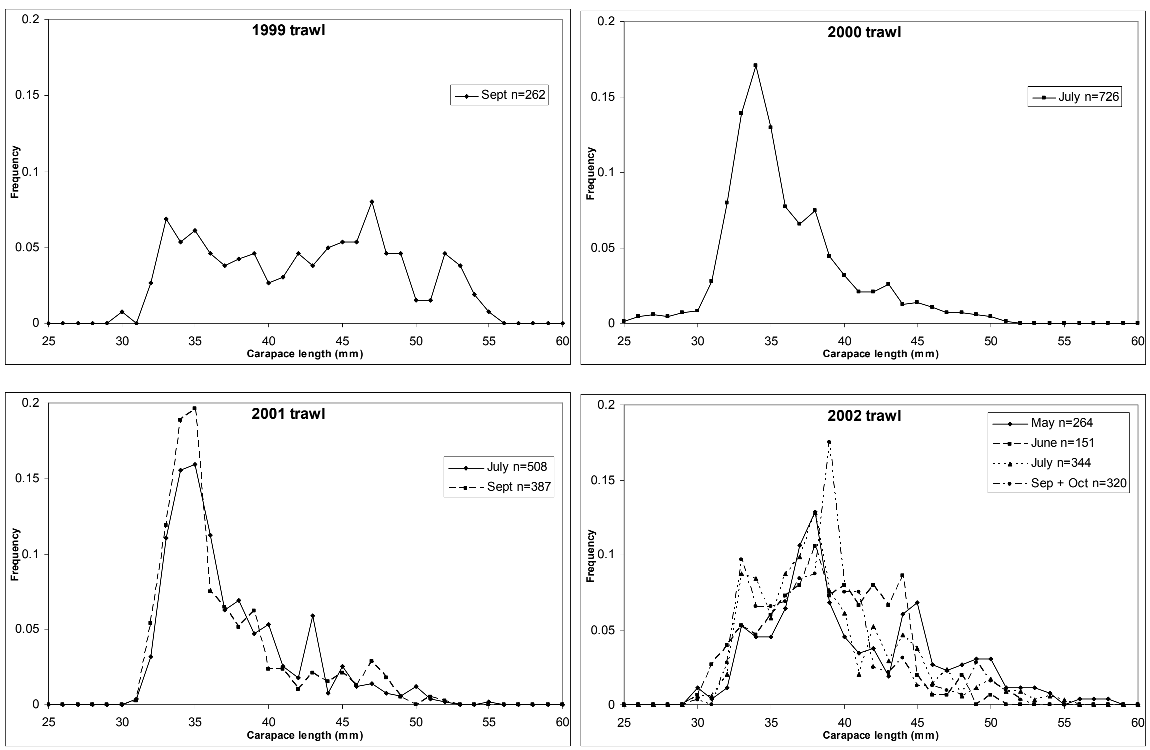


Figure 36: Length frequencies by year for trawl gear samples

The pot fishing samples shown in Figure 37 are more complicated to interpret due to the selectivity of the pot gear. There are peaks in the distribution near 35mm in both 2000 and 2001, which are not present in the 1997 and 1998 samples which may be an indication of higher recruitment in those years.

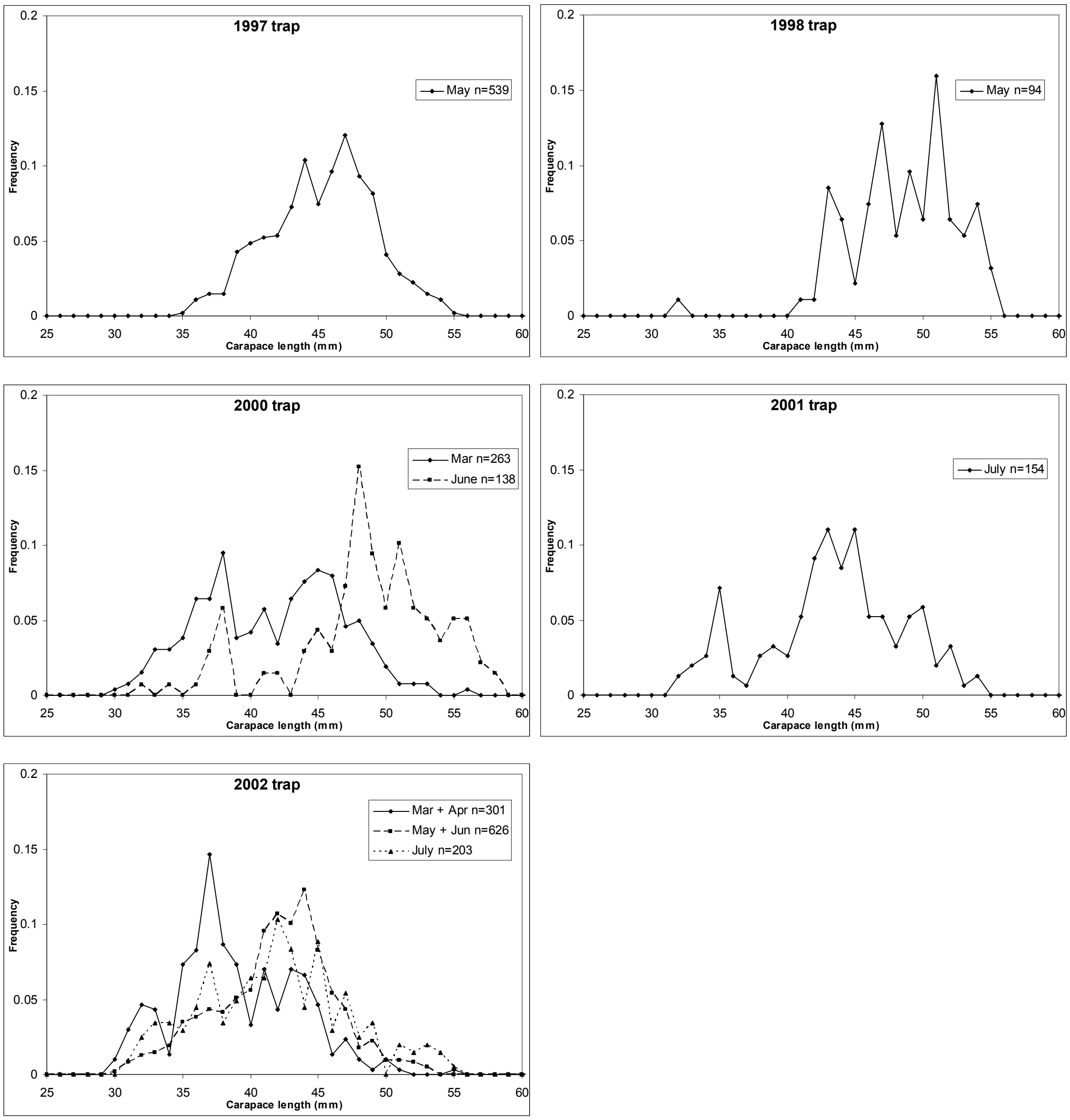


Figure 37: length frequencies by year for pot gear samples

4.5 Estimation of selectivity of pot gear

Pot gear and trawl gear used in the coastal Washington spot prawn fishery catch very different size compositions, as can be seen in Figure 36 and Figure 37. The change from primarily trawling to entirely pots which went into effect at the start of 2003 led to a great change in the selectivity of the fishery. Estimation of the relative selectivity of the two gear types is important in order to model the effect of this change in gear type.

Pot regulations in this fishery include the use of 7/8" (22.2 mm) mesh (i.e. a 7/8" dowel can freely pass through the mesh). Almost without exception, the pot design used is a "cone-stackable" pot of the type sold by Ladner traps[2]. As noted in chapter 2, this mesh size and pot design ensures that most prawns over 30mm CL (the smallest size consistently found on the coastal fishing grounds) encountering the pots are retained. However, other factors also affect pot selectivity regardless of mesh size. These include encounter rate; larger individuals are capable of faster movement that smaller ones, and in searching for food are therefore more likely to encounter a pot and be captured by it. Competition and dominance relationships between individuals may also play a part. Individuals compete for food sources and larger ones usually win. The larger individuals in a pot will attempt to drive the smaller ones out, possibly in order to monopolize the food source (bait) (Potter et al. 1991; Gobert 1998). This effect has been noted in spot prawn pots, in that short soak times lead to a larger proportion of small than large prawns being captured (G. Bishop ADF&G, M. Kattilakoski DFO Canada, pers. comm. 2005).

Trawl regulations in the fishery required the use of at least 43mm (1 ¾") mesh in the cod-end. The majority of operators used either this size or 50mm (2") mesh in a relatively thick (3-5 mm) twine size. The cod-ends used were also rather wide (over 200 meshes round) (pers. obs 1999 -2002). Thicker twines have been shown to reduce selectivity of cod-ends (Lowry and Robertson 1996), as has the use of wide cod-ends where catches are small (Reeves et al. 1992). The combination of the two would effectively reduce selectivity such that very few if any prawns over 30 mm would escape. Given that there

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[2] Ladner Traps. 3593 River Road West, Delta, B. C., Canada.

are few prawns under this size on the grounds, the trawl gear used can be considered unselective for all available size classes. Selectivity studies on similar size ranges of pandalid shrimps with similar mesh sizes give a selection factor (L_{50}/mesh size) of approximately 0.4 (Fonseca et al. 2007). This translates to L_{50} of 18 – 20 mm for the spot prawn fishery. The result is that the trawls would be expected to retain virtually all of the prawns that enter under normal fishing conditions.

As the trawl gear is considered unselective, overall selectivity of the pot gear can be estimated by comparing the size frequency of the pot catches relative to that of the trawls. The approach taken was to use length frequencies collected by WDFW from pot and trawl vessels in 2000 - 2002 (L. Wargo WDFW pers comm). These samples were mostly collected from commercial catches at landing by WDFW personnel. A random sample was taken of the total catch and the carapace length of each prawn measured to the nearest mm. Comparison between samples was limited to those samples that were caught in the same area within one month of each other in order to avoid complications due to growth between sampling times. This provided 7 pairs of samples that could be used for this analysis (Table 29)

Table 29: Data used for selectivity estimation.

	Trawl sample		Pot sample		
Sample #	date	N	date	N	Area
1	7/6/2000	314	6/9/2000	98	Gray's Canyon
2	7/27/2001	507	7/20/2001	154	Gray's Canyon
3	5/17/2002	251	5/25/2002	204	Juan de Fuca Canyon
4	7/18/2002	106	7/14/2002	94	Gray's Canyon
5	7/23/2002	238	7/22/2002	90	Gray's Canyon
6	10/6/2002	101	10/21/2002	108	Gray's Canyon
7	9/20/2002	219	9/27/2002	103	Gray's Canyon

Two selectivity models were fitted to each pair of samples in this data set to model the selectivity of the gear. The first was a standard logistic selection curve

$$r(l) = \frac{\exp(a + bl)}{(1 + \exp(a + bl)}$$

Secondly, a Richards curve was tested.

$$r(l) = \left(\frac{\exp(a + bl)}{(1 + \exp(a + bl)} \right)^{1/\delta}$$

In both cases the parameters *a* and *b* determine the shape of the selectivity curve at each length *l*. In the second case, δ determines the asymmetry of the curve. If δ=1 then this is the same as the logistic curve. Asymmetric Richards curves have in some cases been shown to fit pot selectivity for crustaceans significantly better than symmetric logistic curves (Treble et al. 1998). Models were compared using the Akaike Information Criterion (AIC), which takes into account the number of parameters in the models. The parameters in the model are related to L_{50} (length at which equal numbers of prawns would be expected in both gear types) and selection range (SR, the difference between 25% and 75% selectivity points) by the relationships

$$L_{50} = \frac{-a}{b} \quad \text{and} \quad SR = \frac{2\ln(3)}{b}$$

For the standard curve and

$$L_{50} = \frac{\mathrm{logit}(0.5)^{\delta} - a}{b} \quad \text{and} \quad SR = \frac{\mathrm{logit}(0.75)^{\delta} - \mathrm{logit}(0.25)^{\delta}}{b}$$

For the Richards curve.

The models were fitted to each pair of samples using the SELECT (Share Each Length class Catch Totals) method described by Millar and Walsh (1992). This method incorporates an encounter parameter (*p*). The encounter parameter estimates the chance that a prawn encounters a particular gear type, and thus takes account of the fact that the two gear types are fished at different effort levels.

$$\phi(l) = \frac{pr(l)}{pr(l) + (1 - p)}$$

The model was fitted to each set by maximizing the log-likelihood function (Millar and Walsh 1992)

$$\sum_{l}(N_{lpot}\log\phi(l) + N_{ltrawl}\log(1-\phi(l)))$$

Where N_{lpot} and N_{ltrawl} are the numbers of prawns in each length class in the pot and trawl samples respectively.

Selectivity results

Results are shown in Table 30. Of seven pairs of samples, a good fit to the model (R^2 greater than 0.5) was achieved in four. Two sets showed similar length frequency at all but the smallest lengths, and thus the model estimated knife edge selectivity at close to the smallest length in the sample. In all four cases where the fit to the data was good, the asymmetric curve fitted better than the symmetric logistic curve (lower AIC). In all these cases, this was due to there being a long tail on the left side of the curve, caused by some small prawns being caught. An example data set with fitted model is shown in Figure 38.

Table 30: Selectivity model fits to 7 pairs of length frequency samples. a, b and δ are parameters of the models used, L50 is the length at which 50% of prawns are retained by the gear, SR is the difference between 25% and 75% selectivity points, AIC is Akaike's information criterion. The best fit model selected via lower AIC is shown in bold for each sample set.

Sample	model	Parameters				L50	SR	-log likelihood	AIC	R^2
		a	*b*	*p*	*δ*					
1	Logistic	-19.98	0.43	0.79		46.3	5.1	-118.9	243.7	0.883
	Richard's	**-2125.84**	**44.30**	**0.79**	**120.03**	**46.1**	**3.0**	**-115.9**	**239.8**	**0.908**
2	Logistic	-14.95	0.32	0.74		46.2	6.8	-275.8	557.7	0.896
	Richard's	**-72.48**	**1.60**	**0.63**	**5.29**	**43.1**	**3.8**	**-274.2**	**556.4**	**0.913**
3	Logistic	-14.62	0.38	0.59		38.4	5.8	-296.4	598.8	0.424
	Richard's	**-94.16**	**2.29**	**0.56**	**8.77**	**38.5**	**4.2**	**-291.5**	**591.0**	**0.508**
4	**Logistic**	**-643.49**	**19.48**	**0.49**		**33.0**	**0.1**	**-136.2**	**278.4**	**0.140**
	Richard's	-643.49	19.45	0.49	2.01	33.0	0.2	-136.2	280.4	0.140
5	Logistic	-14.09	0.33	0.57		42.6	6.6	-165.2	336.4	0.724
	Richard's	**-2124.44**	**47.20**	**0.54**	**200.49**	**42.1**	**4.7**	**-164.1**	**336.2**	**0.752**
6	**Logistic**	**-477.77**	**14.51**	**0.53**		**32.9**	**0.2**	**-141.8**	**289.6**	**0.148**
	Richard's	-477.77	14.51	0.53	0.97	32.9	0.2	-141.8	291.6	0.148
7	**Logistic**	**-4.89**	**0.14**	**0.44**		**35.4**	**15.9**	**-200.1**	**406.1**	**0.172**
	Richard's	-559.51	12.32	0.42	178.79	35.4	15.9	-199.1	406.2	0.214

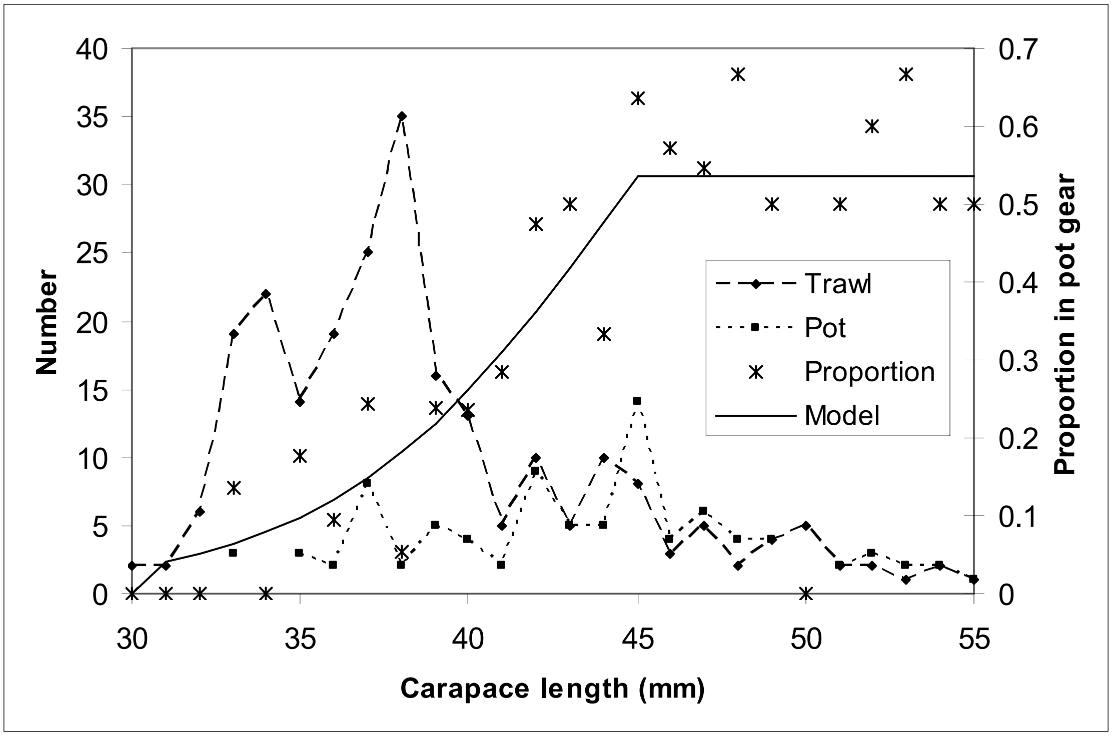

Figure 38: Length frequency and selectivity model fit for sample set 5 (7/23/2002 / 7/22/2002 samples). Model parameters are L50 = 42.1, SR = 4.7, p=0.54.

An average selectivity was estimated by fitting *a*, *b* and δ parameters to all data sets simultaneously using the split values (*p*) from the individual fits above. The likelihood function was maximized over all lengths within all samples. This resulted in parameter estimates a = -486.50 b= 11.06 δ=44.17 (L50=41.21, SR=4.38).

4.6 Yield per recruit model

Yield per recruit analysis is useful to help determine the effect on a stock of changes in exploitation pattern in situations where there is some biological data available, but total biomass is not known, or recruitment variation dominates the dynamics of the stock. Both of these cases apply to this fishery.

An equilibrium yield per recruit (YPR) model was initially used to examine the effect of changing gear types from predominantly trawl to exclusively pot on yield per recruit and egg production per recruit (EPR). The model structure is as follows:

$$N_{a+1} = N_a e^{-(F_a S_a + M_a)}$$

$$C_a = \frac{F_a}{F_a + M_a}(1 - e^{-(F_a + M_a)})N_a$$

$$YPR = \frac{1}{N_1}\sum_a C_a W_a$$

$$EPR = \sum_a N_a E_a$$

Where N_a = number at age *a*, F_a= fishing mortality rate at age *a*, M_a= natural mortality rate at age *a*, C_a= catch of age group *a*, S_a= selectivity for age *a*, W_a= weight (g) of a prawn of age *a*, E_a= number of eggs produced by a prawn of age *a*.

This model used the growth rate, fecundity and weight at length relationships detailed in Chapter 1. For growth rate, the parameters estimated for the Straits of Juan de Fuca were used (L_a= 51.50(1-$e^{(0.478\ (a+0.15)}$)), as this sample was the closest large sample to the coastal fishery area. For fecundity and weight at length the relationships calculated from all areas in Washington were used, E_L=0.000909 $L^{3.9204}$, and W_L= 0.00097 $L^{2.86593}$. The population was modeled as a single sex. This makes the assumption that the reproductive potential of the population is limited by the number and size of females, and that there is always an excess of males to mate with these females and fertilize the eggs. For a protandric sex changing population, this seems a reasonable assumption. The sex ratio is biased in favor of males in all but very exceptional circumstances such as total recruitment failure or extremely heavy fishing on smaller individuals

In order to model the fishery before the trawl closure, fishing mortality needs to be partitioned into fishing by the two fleets with different selectivities. Following (Sun et al. 2002), age specific fishing mortality rates for pot and trawl fleets were modeled relative to an age group that is fully selected by both gear types (age 6 in this case)

$F_{pot,\,a} = S_{pot,\,a} * F_{pot,\,a=6}$

$F_{trawl,\,a} = S_{trawl,\,a} * F_{trawl,\,a=6}$

And $F_a = F_{pot,\,a} + F_{trawl,\,a}$

Where $S_{pot,a}$ = Selectivity of pot gear at age a, $S_{trawl,a}$ = Selectivity of trawl gear at age a, $F_{pot,a}$= fishing mortality in pot gear at age a, $F_{trawl,a}$= fishing mortality in trawl gear at age a, and F_a= total fishing mortality at age a.

The selectivity estimated for pot gear detailed in this chapter was used. For trawl gear it was assumed that all prawns over age 2 (average approximately 33 mm) were fully selected.

A range of natural mortality levels was investigated, from 0.50 to 0.90, covering the range of published and estimated natural mortalities detailed in chapter 1.

Yield per recruit results

Between 1997 and 2002, the trawl fleet took 85% of the catch of the fishery, and the pot fleet the rest. This 85:15 split can be achieved by a variety of different combinations of fishing mortality applied by each fleet (Figure 39). Generally, as the fishing mortality applied by the trawl fleet increases, the pot fishing mortality must increase by a greater amount to maintain the same proportion of the catch.

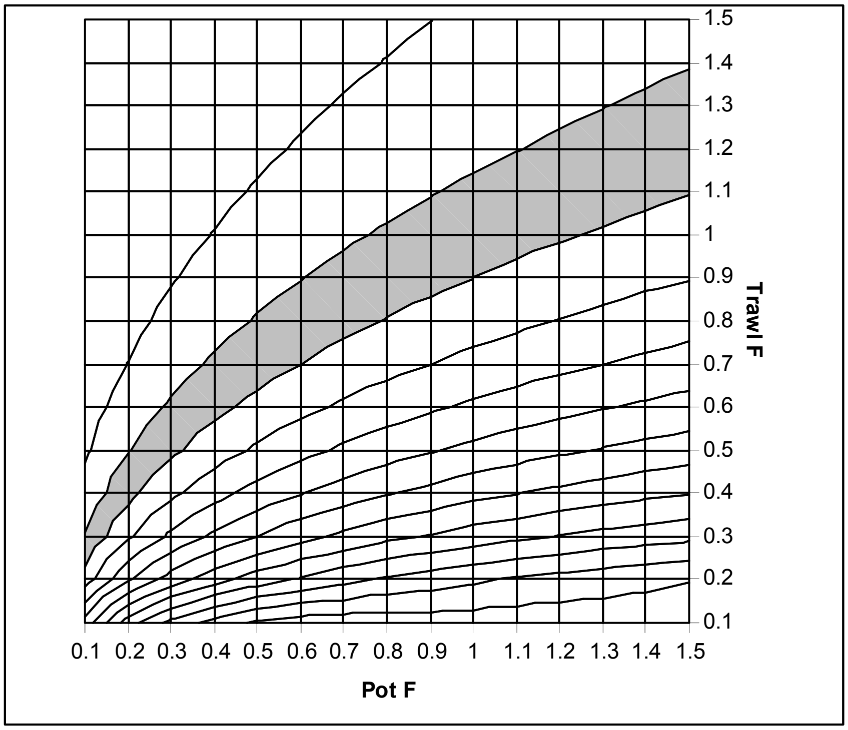

Figure 39: Ratio of pot catch to total catch at different levels of fishing mortality applied by the two fleets. The shaded area represents combinations of fishing mortality that give between 12.5 and 17.5% of the catch to the pot fleet.

As the trawl fleet dominates the catch from the fishery, the base case is modeled as different levels of trawl fishing mortality, with the level of pot fishing mortality varied appropriately to give a catch which is 15% of the total. Results of this across a range natural mortality values are given in Table 31. The values of fishing mortality for the pot fleet at each combination of F_{trawl} and natural mortality is given in Table 32. From this it can be seen that very high levels of fishing mortality for the pot fleet are required in order to catch 15% of the total as trawl fishing mortality increases. Egg production per recruit declines rapidly with increasing fishing mortality, and is less than 10% of the unexploited EPR at all $F_{trawl} > 0.7$, even at the lowest considered value of M. The inclusion of both fleets does not greatly affect the results in comparison with the trawl fleet only, due to the small proportion caught by the pot fleet.

Table 31: Yield and egg production per recruit for the spot prawn fishery, assuming 85% of the total catch is taken by trawling

		Natural mortality									
		0.5	**0.6**	**0.7**	**0.8**	**0.9**	**0.5**	**0.6**	**0.7**	**0.8**	**0.9**
		Yield per recruit (g)					Egg production per recruit				
F_{trawl}	**0**	0.0	0.0	0.0	0.0	0.0	1544	1032	696	475	326
	0.1	4.1	3.0	2.3	1.8	1.4	1091	735	501	344	238
	0.2	6.5	5.0	3.9	3.1	2.4	776	528	362	250	174
	0.3	8.1	6.3	5.0	4.0	3.2	556	381	263	182	127
	0.4	9.1	7.2	5.8	4.7	3.8	400	275	191	133	93
	0.5	9.7	7.8	6.3	5.2	4.3	289	200	139	97	68
	0.6	10.2	8.3	6.8	5.6	4.6	209	145	101	71	50
	0.7	10.5	8.6	7.1	5.9	5.0	151	105	74	52	37
	0.8	10.7	8.8	7.4	6.2	5.2	109	76	54	38	27
	0.9	10.9	9.1	7.6	6.4	5.4	79	55	39	27	19
	1	11.0	9.2	7.8	6.6	5.6	57	40	28	20	14
	1.1	11.1	9.3	7.9	6.7	5.8	41	29	20	14	10
	1.2	11.1	9.5	8.1	6.9	5.9	30	21	15	10	7
	1.3	11.2	9.6	8.2	7.0	6.0	21	15	10	7	5
	1.4	11.3	9.6	8.3	7.1	6.1	15	11	7	5	4
	1.5	11.3	9.7	8.4	7.2	6.3	11	8	5	4	3

Table 32: Values of pot fishing mortality for combinations of F_{trawl} and natural mortality given in Table 31.

		Natural Mortality				
		0.5	**0.6**	**0.7**	**0.8**	**0.9**
F_{trawl}	**0**	0	0	0	0	0
	0.1	0.03	0.03	0.04	0.04	0.05
	0.2	0.07	0.08	0.09	0.10	0.11
	0.3	0.12	0.13	0.15	0.17	0.18
	0.4	0.18	0.20	0.23	0.25	0.28
	0.5	0.26	0.29	0.32	0.36	0.39
	0.6	0.36	0.40	0.44	0.48	0.53
	0.7	0.48	0.53	0.58	0.64	0.69
	0.8	0.62	0.68	0.75	0.81	0.88
	0.9	0.79	0.86	0.94	1.01	1.09
	1	0.99	1.07	1.15	1.24	1.32
	1.1	1.21	1.30	1.39	1.48	1.57
	1.2	1.45	1.55	1.65	1.75	1.84
	1.3	1.72	1.82	1.93	2.03	2.13
	1.4	2.00	2.11	2.22	2.32	2.42
	1.5	2.30	2.42	2.53	2.63	2.73

Yield and egg production per recruit for pot fishing only is given in Table 33. The comparison of the base case and the pot only case shows that much higher values of F are required to achieve the same YPR than is the case with the trawl fleet. This is to be expected, as the pot fleet exploits far fewer of the 2 and 3 age groups, which are fully selected by trawlers. Egg production per recruit is slightly higher at the same level of YPR than with the trawl fleet. The model using pot selectivity is, however, more sensitive to variation in M than the model using both fleets. The ratio of YPR at M=0.9 : M=0.5 ranges from 0.23 to 0.34 for the pot model, compared with 0.35 to 0.55 for the trawl plus pot model. This is again an effect of the trawl fleet exploiting a greater age range.

Table 33: Yield and egg production per recruit for the spot prawn fishery, with all effort applied by the pot fleet.

	Natural mortality									
	0.5	**0.6**	**0.7**	**0.8**	**0.9**	**0.5**	**0.6**	**0.7**	**0.8**	**0.9**
F	Yield per recruit (g)					Egg production per recruit				
0	0.0	0.0	0.0	0.0	0.0	1544	1032	696	475	326
0.1	2.3	1.6	1.1	0.8	0.5	1332	899	613	422	292
0.2	4.1	2.8	1.9	1.4	1.0	1162	792	544	377	264
0.3	5.3	3.7	2.6	1.9	1.3	1023	703	488	340	239
0.4	6.3	4.4	3.2	2.3	1.7	908	630	440	309	218
0.5	7.0	5.0	3.6	2.6	1.9	813	568	399	282	201
0.6	7.6	5.5	4.0	2.9	2.1	734	516	365	259	185
0.7	8.1	5.9	4.3	3.2	2.3	666	471	335	239	171
0.8	8.5	6.2	4.5	3.4	2.5	608	432	309	221	159
0.9	8.8	6.5	4.8	3.6	2.7	558	399	286	206	148
1	9.1	6.7	5.0	3.7	2.8	515	369	265	192	139
1.1	9.3	6.9	5.2	3.9	3.0	477	343	248	179	130
1.2	9.5	7.1	5.3	4.0	3.1	443	320	231	168	122
1.3	9.6	7.2	5.5	4.2	3.2	413	299	217	158	115
1.4	9.8	7.4	5.6	4.3	3.3	386	280	204	148	108
1.5	9.9	7.5	5.7	4.4	3.4	362	263	192	140	102

The higher egg production per recruit seen with the fishery being exploited only by pot fishers should ensure that the population is more robust to exploitation than if trawlers were also involved, i.e. recruitment overfishing is less likely. The flip side of this is that the fishery is more likely to be subject to fluctuations in catch caused by variability in recruitment. Exploiting more age classes would smooth out this variability.

Maintaining spawning biomass per recruit at about 35% of virgin levels has been suggested as a safe target management objective to reduce the risk of recruitment overfishing ($F_{35\%}$) (Clark 1993). Clark considered spawning stock biomass to be a suitable proxy for egg production. In this case, the availability of fecundity estimates allowed me to use egg production directly. At M=0.6, egg production is reduced to 35% at F=1.0 for the pot fishery, with a yield per recruit of 6.7 g. In contrast, with 15% of the catch taken by the pot fishery, F_{trawl} =0.3, F_{pot}=0.13, and YPR=6.3. The values for trawl fishery only are F=0.35, YPR=6.2.

A fishing mortality rate of 1.0 is rather high, equivalent to catching over half of the prawns of selected size every year. It is not clear whether the pot fishery off the Washington coast is efficient enough to catch this high a proportion of the stock or not, given the small number of vessels involved. In order for the pot fishery to be commercially viable, the stock may need to be maintained at a relatively high level. As noted in Chapter 2, (Section 4) selectivity of the pots used by most of the fleet does not appear to be greatly influenced by mesh size. Reduction of pot mesh size to exert a lower F over a larger age range is therefore not a viable option.

4.7 Stock Synthesis model

In order to estimate the biomass and potential yield of the coastal Washington spot prawn fishery, I used a size/age structured dynamic population model. Initial parameter estimates were based on life history data from my own work, and the model was fitted to commercial logbook data, commercial catch records and length frequency data collected by me and by WDFW employees. The use of a dynamic model of this type allowed me to reconstruct the exploitation history of the stock from the beginning of the fishery to near the present day. In contrast to the yield per recruit model discussed above, the use of the logbook and catch data allowed me to estimate the total size of the stock, and the level of recruitment for each year rather than just the yield for an average recruit under equilibrium conditions. I used the model to estimate the size of the spot prawn stock off the Washington coast, and the level of depletion of this stock through 2003. I used projections of future stock dynamics and recruitment to estimate sustainable catch levels for this fishery.

Model structure

I modeled the population using the Stock Synthesis program (Version 2.00c) (Methot 2007). Stock Synthesis is a very flexible size/age structured fish stock assessment modeling program which has been extensively used for assessing fish stocks on the US West Coast. The program can fit to a wide variety of data types and can take account of a range of assumptions about the dynamics of the populations and fisheries. This is the first application of this model for a shrimp or prawn species.

I treated the stock as a single population, rather than as three distinct areas (Gray's Harbor, etc). Although from a biological standpoint it makes sense to differentiate the areas, in practice the paucity of data (especially size data) made it impossible to achieve acceptable model fits. Migration of adult individuals between areas is unlikely, and thus the assumption of there being a single, well mixed population is violated. However, given that the population is dominated by recruitment variation, a single population model should give a reasonable idea of the dynamics as long as recruitment to all areas is broadly similar, and the level of fishing mortality is similar in all areas. Only a limited amount of data is available to test this assertion, but it does support the hypothesis. In 2000 and 2002 length frequency samples from trawl vessels were taken from different areas. In both cases, the length frequency is similar across areas. The samples from 2000 are dominated by one age class of 2 year olds (recruits), whereas those from 2002 show a lower proportion of 2 year olds and a higher proportion of older individuals.

The general structure of the stock synthesis model is based on three components (Methot 2005). The first is a population model which projects the size and age structure of the actual population based on growth, mortality and abundance functions. Secondly, an observation model is used to derive expected values for the data using selectivity and catchability functions. The final component is a statistical model which uses a maximum likelihood approach to find the parameter sets that provide the best fit for the model to the data.

Full details of the model structure are given in Methot (2005) and are not repeated here. The population model is based on an age structured model, but includes size information in order to allow fitting to size data.

Model Parameters

Biological parameters: Fecundity, growth and mortality parameters estimated in Chapter 1 were used in this model Table 34.

Fecundity was converted from number of eggs per unit of length to eggs per unit of weight as required by Stock Synthesis. Fecundity in this application is represented only as the number of eggs produced by females, making the assumption that the population has sufficient males to fertilize these eggs. All prawns age 4 and older were assumed to be mature females. Egg production is a function of weight, where the number of eggs produced is

$\varphi = a + bW_l$

Where a and b are constants, and W_l is weight at length, calculated from $W_l = cL^d$

Growth was re-parameterized to the equation used by Stock Synthesis, and adjusted to a year beginning January 1 rather than April 1. Growth (mean size at age) is modeled as:

$L_a = L_\infty + (L_1 - L_\infty)e^{-K(a-a_3)}$

Where:

L_∞ is mean asymptotic size, which is calculated from $L_\infty = L_1 + \dfrac{L_2 - L_1}{1 - e^{-K(a_4 - a_3)}}$

L_1 is the mean size at age a_3 (a=0)

L_2 is the mean size at age a_4 (a=5)

K is a growth coefficient

Growth parameters and CV were fitted in the base case model, but in all cases the final values were very close to the starting points. Natural mortality (M) was fixed at 0.6 for all ages (the average of the estimates from unfished areas in the Strait of Juan de Fuca and northern Puget Sound). The effect of different values of M and of values of M that vary with age was examined as a sensitivity analysis.

Table 34: Biological parameters used in the stock synthesis model.

Parameter	Value
Natural mortality	0.6
Length at age 0	-2.486
Length at age 5	46.5555
K	0.478966
growth C.V.	0.057
Weight at length scale	0.00097
Weight at length exponent	2.86593
Fecundity intercept	-1151.85
Fecundity scale	91.5003

Selectivity: Size selectivity for pot gear used the average value estimated previously (Table 30). Trawlers were assumed to catch all prawns over 30 mm. This was modeled as a logistic function to allow testing of this assumption by allowing the model to estimate trawl selectivity parameters

Data inputs and settings

Catch data and indices: Catch data was taken from total landed catch from 1992 through 2003 (Table 28). CPUE for the four main trawl vessels and the four pot vessels with the longest time series of logbook data were used as indices (Figure 33 and 34). Because of the unreliability of the earliest years in the time series, and the fact that length data were only available for 1997 - 2002, the base case model only used CPUE data from 1997 onwards. The effect of using the full 1992-2003 CPUE series and using aggregated CPUE series were examined as part of the sensitivity analysis of the model.

Size data: Length frequency data shown in Figure 36 and Figure 37 for years 1997 – 2002 was used. Samples taken outside the summer months were excluded from the analysis to match the assumption of the catch being taken in the middle of the year. Effective sample sizes for each length composition were estimated by iterative re-weighting with a maximum value of 200.

Fishery timing: Timing for the fishery was assumed to be in the middle of the year for the purpose of the model. This corresponds fairly well with the actual peak of fishing (Figure 28).

Sex: The population was modeled as a single sex. This makes the assumption that the reproductive potential of the population is limited by the number and size of females, and that there is always an excess of males to mate with these female and fertilize the eggs. For a protandric sex changing population, this seems a reasonable assumption. The sex ratio is biased in favor of males in all but very exceptional circumstances such as total recruitment failure or extremely heavy fishing on smaller individuals

Stock and recruitment: There is no information about stock-recruitment relationships for prawns in this environment, and from examination of the length frequency data, recruitment is expected to be highly variable. Because of this the model was used to estimate recruitment for each year unconstrained by stock size.

Stock synthesis model results

The model achieved good fit to both length composition and CPUE index data sets. Fitted parameter values were similar to the externally estimated values used as starting points in the estimation phase. Likelihood components associated with each data source are given in Table 35, and key parameter values in Table 36. Parameters for the growth function were estimated inside the model as the length compositions provide a reasonable amount of data which is specific to this fishery, and the actual values of growth parameters are quite variable from area to area (see Chapter 1).

Table 35: Likelihood components.

Log likelihood components		
Total		90.601
Length compositions	pot	61.9544
	trawl	53.2036
Indices	trawl 1	-3.36664
	trawl 2	-1.45588
	trawl 3	-4.75623
	trawl 4	-3.0572
	pot 1	-1.6334
	pot 2	-2.49817
	pot 3	-0.6963
	pot 4	-3.20434
Recruitment		-1.80939

Table 36: Parameter values.

Parameter	**Value**	**estimated**	**Starting value**
Natural mortality		n	0.6
Length at age 0		n	-2.486
Length at age 5	47.3206	y	46.5555
K	0.457242	y	0.478966
growth C.V. 1	0.069525	y	0.057
growth C.V. 2	0.058314	y	0.057
Weight at length scale		n	0.00097
Weight at length exponent		n	2.86593
Fecundity intercept		n	-1151.85
Fecundity scale		n	91.5003
Equilibrium recruitment	3.18863	y	3

The model fit to size composition data is good in most years for both gear types (Figures 40 and 41). An exception is the pot data from 2000; however this is based on a small sample and has a relatively low weight in the model. The fits show large peaks at around

35mm in years 2000 – 2002 indicating strong recruitment in these years. The greater selectivity of the pot gear leads to a distinct difference between the estimated length composition for the two gear types, but there is a secondary peak which shows up in 2001 – 2002 showing the recruitment signal.

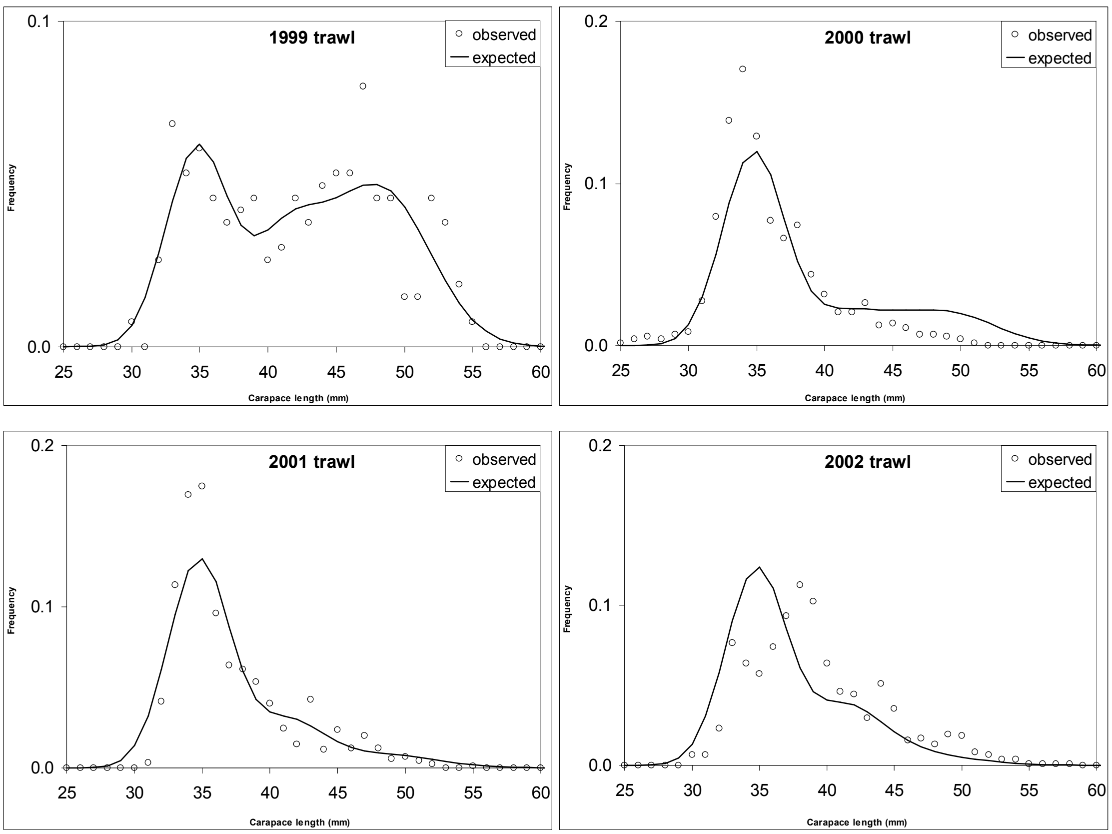

Figure 40: Observed and expected length frequency, trawl fleet.

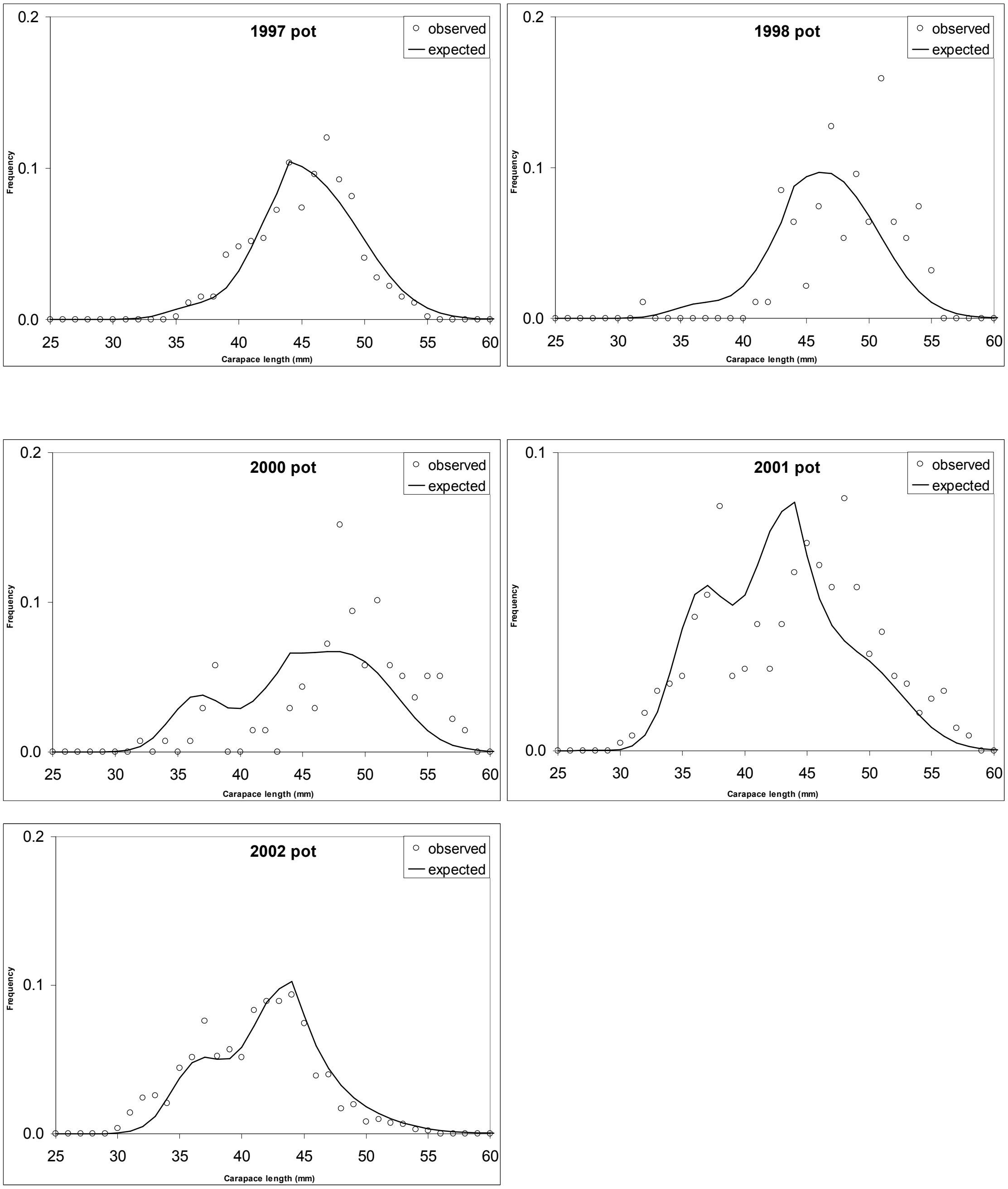

Figure 41: Observed and expected length frequency, pot fleet.

Fits to the general trends in the CPUE index series are also acceptable (Figure 42, Figure 43). The precision of the observed values is poor, as shown by the size of the error bars, but the fitted points are close to the point estimate in most cases. CPUE declines in the trawl fishery during 1997 -1999 and increases again from 2000 onwards. The pattern is similar for the pot fishery, except that the decrease continues through 2000 and the increase starts later. This reflects the different exploitation patterns by the two gear types, due to selectivity differences.

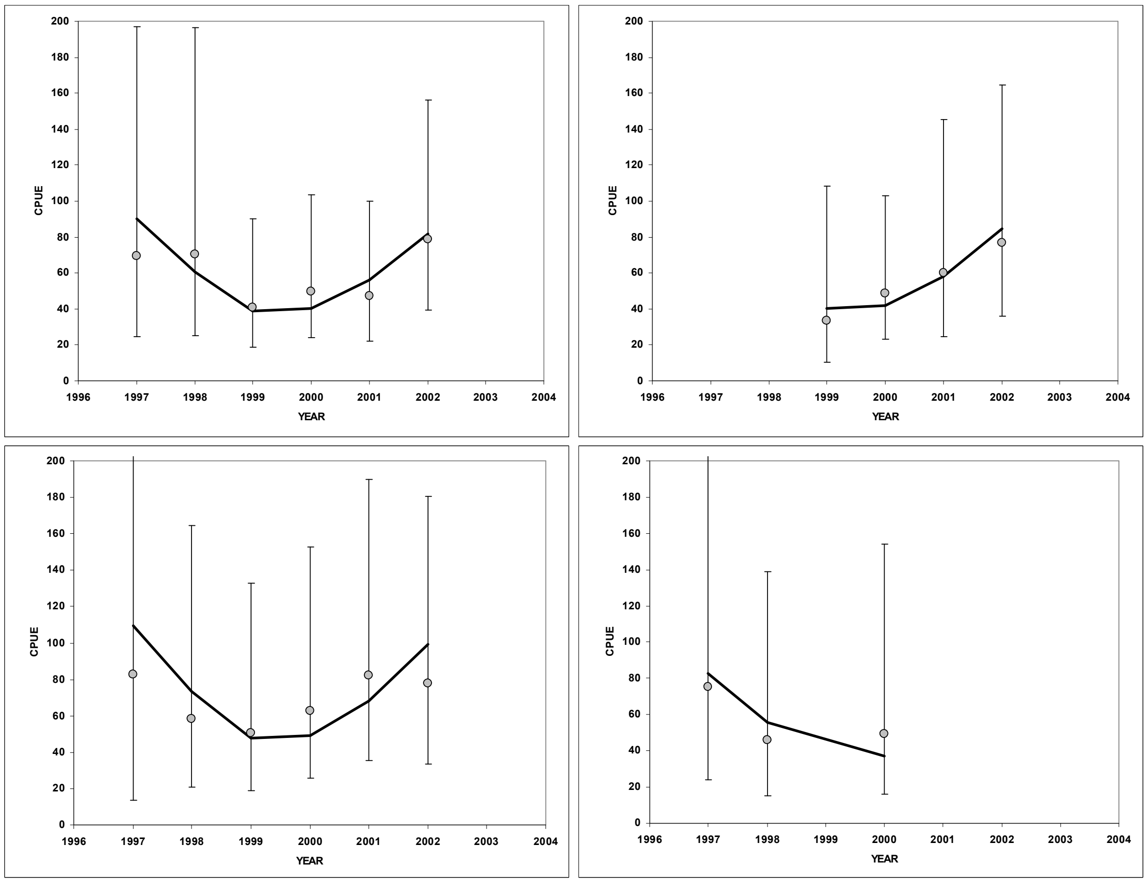

Figure 42: Observed and expected CPUE index, trawl vessels. Error bars represent asymptotic 95% confidence intervals around observed index.

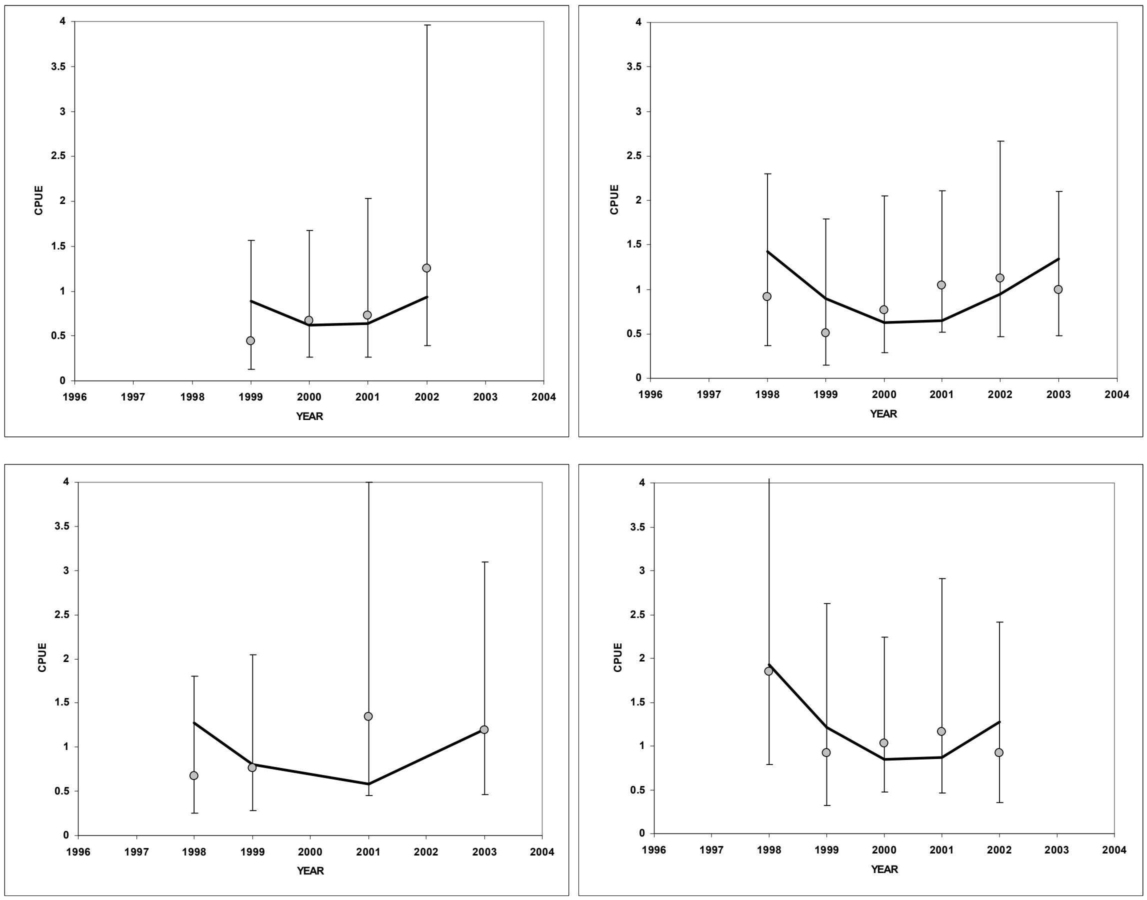

Figure 43: Observed and expected CPUE index, pot vessels. Error bars represent asymptotic 95% confidence intervals around observed index.

Estimated biomass for prawns age 2 and older is shown in Figure 44. Recruitment (of age 2 prawns) varied by more than a factor of 5 over the study period (Figure 45). The model predicts good recruitment in the initial years, declining to a low point in 1999. This is followed by higher recruitment through 2002 (there is no information to estimate recruitment for 2003, so this point is equal to the expected equilibrium recruitment). The biomass series mirrors recruitment to a great extent, with high biomass reducing under relatively heavy fishing pressure (F=0.28 in 1998) and poor recruitment in 1997-1999, followed by some recovery.

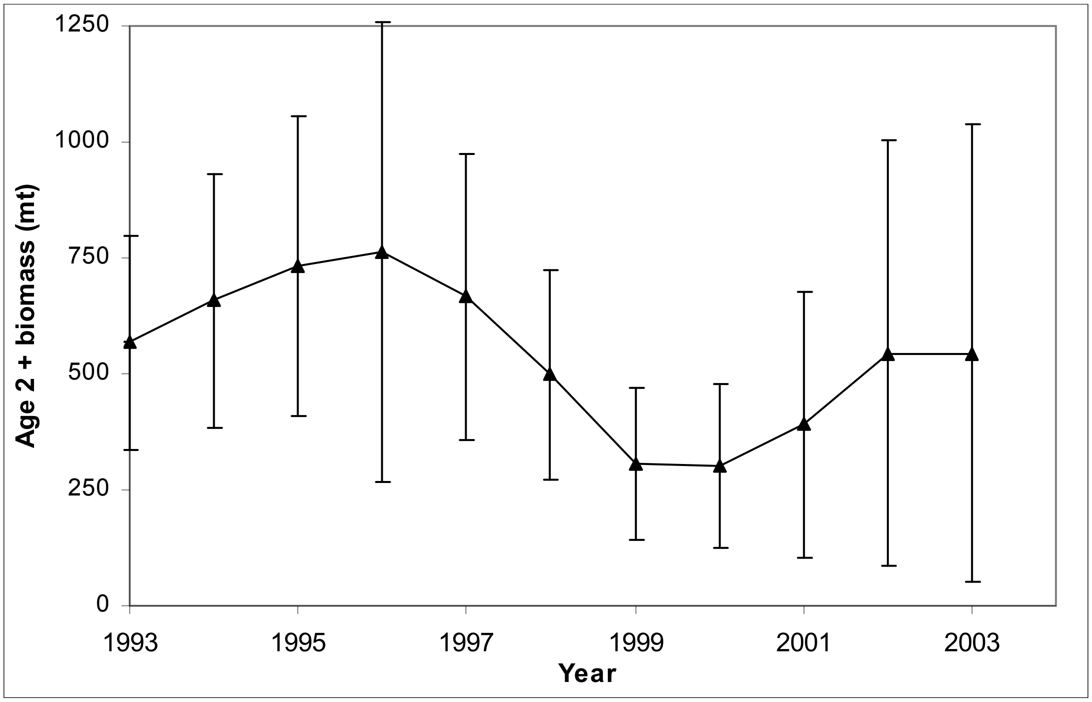

Figure 44: Biomass of age 2+ prawns. Error bars represent 95% confidence intervals.

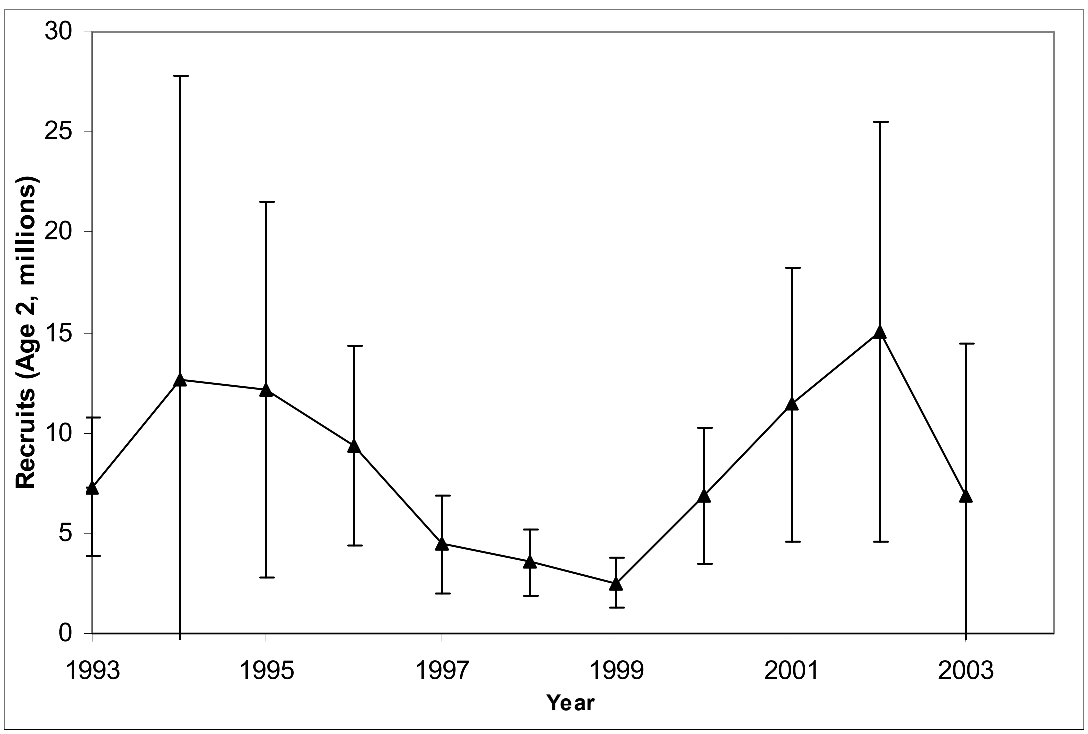

Figure 45: Recruitment. Error bars represent 95% confidence intervals.

Egg production by year (i.e. reproductive potential) is shown in Figure 46 (spawning stock biomass is often used as a proxy in fisheries models, but egg production is a better measure given that the number of eggs, and hence potential number of offspring produced by a population of a particular biomass is dependent on the size of individuals in that population). This shows that egg production was reduced to less than 35% of the virgin level in 2001 and 2002, but that there was some recovery after this time due to high recruitments in those years. Egg production in 2003 was 48% of the virgin level, but could be expected to reach approximately 75% by 2004, based on the large year 2000 cohort reaching maturity. The model does not include a stock – recruitment relationship, and so there is no functional link between egg production and recruitment in this model. It is worth noting that some of the years with the highest estimated egg production (1996 and 1997) resulted in the lowest recruitments to the fishery two years later (1998 and 1999 recruitments).

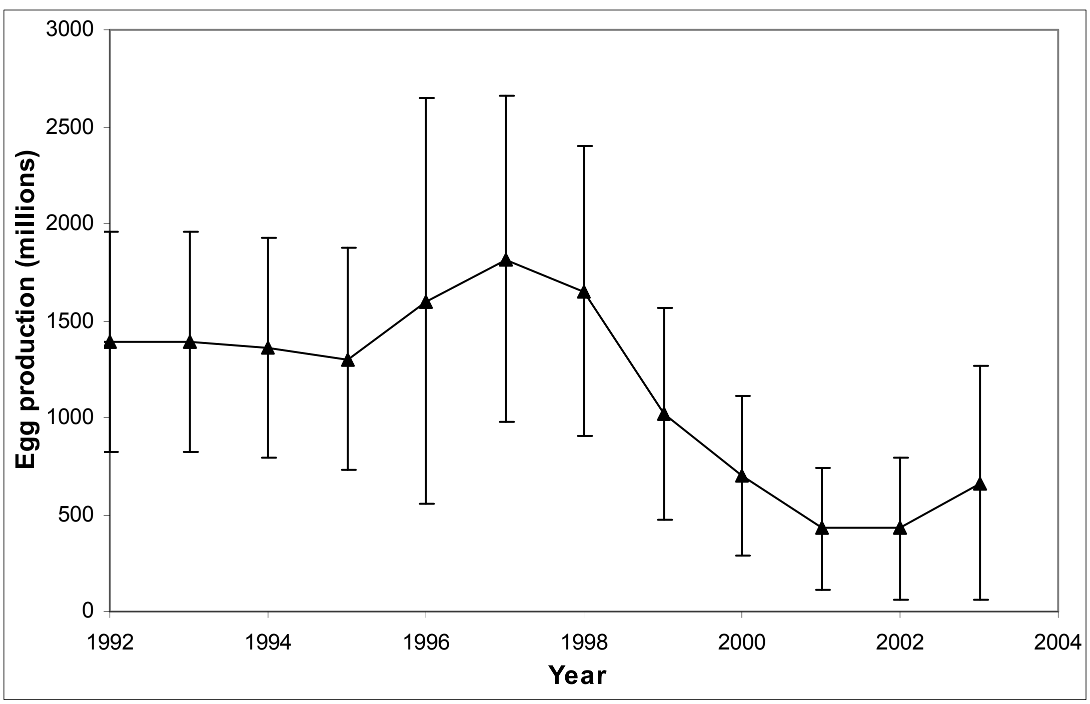

Figure 46: Egg production. Error bars represent 95% confidence intervals.

Stock status

At the model end year (2003) the biomass of prawns aged 2 and older was estimated as 544 mt. This represents 96% of the unfished equilibrium estimate, but was dominated by prawns from the large year 2000 cohort, which were immature. Due to this change in population age composition, egg production was estimated to be 48% of the virgin level in 2003 (Figure 46), but was expected to increase in subsequent years as the 2000 cohort matured. However, these estimates are based on a small amount of data which is of fairly low quality. Thus the precision of the estimates is low. The 95% confidence interval for age 2+ biomass in 2003 ranges from 50 to 1039 mt, and that for egg production ranges from 4% to 91% of the unfished level.

Biological reference points.

Key biological reference points are given in Table 37. The model was unable to estimate maximum sustainable yield (MSY) where recruitment was a free parameter, so a stock-recruitment relationship was assumed such that the steepness of the modified Beverton-Holt spawner recruit curve used by stock synthesis was 0.75. This had the effect of causing average recruitments to begin to decline steeply when the egg production dropped below approximately 35% of the virgin level. Using this S-R relationship had almost no effect on the results of the model compared with the version in which recruitment was a free parameter as used above, as the estimated spawning potential remains above 35% in almost all years.

Table 37: Biological reference points.

Unfished biomass (age 2 +)	mt	663.4
Unfished recruitment (age 2)	thousands	8.57
Unfished egg production	millions	1606
MSY	mt	88.9
BMSY	mt	349.8

MSY estimated with this model was 88.9 mt (95% confidence limits 47.2 – 131.1 mt). This estimate is far lower than the current catch quota of 113.4 mt. However, the average catch level over the last few years of the fishery was substantially less than MSY. The estimated biomass level at MSY (BMSY) is 349.8 mt, which is lower than the estimated biomass in 2003 (544.0 mt). Harvest rate at MSY is rather high, at over 50% of the available prawns (i.e. those that are sufficiently large to be selected by the gear). Given that the highest harvest rate by pot gear achieved over the modeled time series was 18%, it may not be possible for this gear type to fish at MSY at current effort levels. This was also noted in the yield per recruit analysis.

Sensitivity analyses

Natural mortality

The value of natural mortality (M) is a key model parameter. To examine the sensitivity of this model to the value of M, I tested three alternatives to the base case where M=0.6. Low (M=0.4) and high (M=0.8) values and the effect of allowing the model to estimate age-varying M were tested.

Natural mortality is variable with age according to the equation:

$$M_a = \begin{Bmatrix} M_1 & -for \quad a < a1 \\ M_1 + \dfrac{(a-a_1)(M_2 - M_1)}{a_2 - a_1} & -for \quad a_1 < a < a_2 \\ M_2 & -for \quad a \geq a_2 \end{Bmatrix}$$

Where:

M_1 is the natural mortality for age 0

M_2 is the natural mortality for age a

a_1 is the last age for natural mortality equal to M_1 set as a=3 for this application

a_2 is the last age for natural mortality equal to M_2 set as a=5 for this application

The resulting biomass trajectories are shown in Figure 47. As the value of M is increased, both the magnitude and volatility of biomass, recruitment and egg production increase. Allowing the model to estimate M gives values of 0.94 for M for young prawns (<age 3), and 0.29 for old prawns (> age 5). Intermediate values of M are 0.77, 0.61 and 0.45. This scenario results in biomass, recruitment and egg production levels that are similar to the base (M=0.6) case model. Depletion with this scenario is somewhat more than the base case, 30% in 2002, and recovery is slower, with egg production only 37% of the base case in 2006. Likelihood values for each scenario are given in Table 38. The best fit is with the age-varying M, followed by the M=0.6 case.

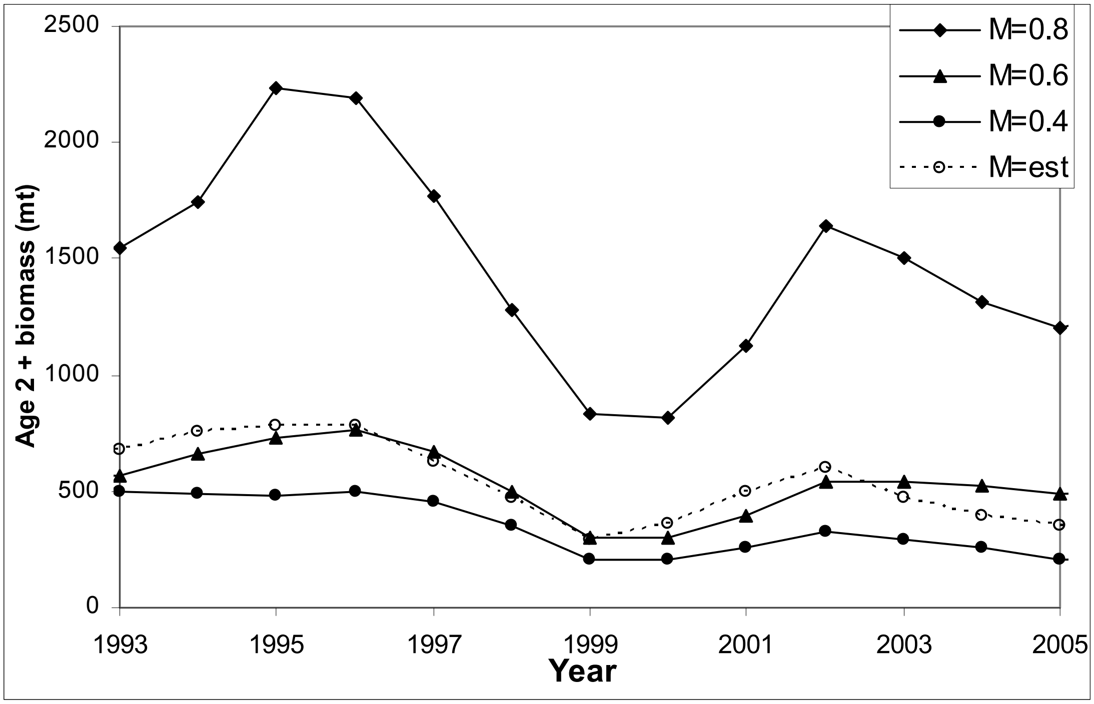

Figure 47: Predicted effect of natural mortality on biomass. As M increases, both the total biomass and the variability in biomass increase. Allowing the model to estimate M gives a result similar to the base case with M=0.6

Table 38: Log likelihood and natural mortality values for 4 scenarios used in testing model sensitivity.

Scenario	M=0.8	M=0.6	M=0.4	M=estimated
Total likelihood	92.6561	90.601	95.1735	88.3129
M at age				
<3	0.8	0.6	0.4	0.94
3	0.8	0.6	0.4	0.77
4	0.8	0.6	0.4	0.61
5	0.8	0.6	0.4	0.45
>5	0.8	0.6	0.4	0.29

CPUE index data series

The base case model uses CPUE index data from 4 trawl and 4 pot vessels starting from 1997, when the volume of the fishery more than doubled from the previous maximum catch taken in 1994. Only three of these 8 vessels fished before 1997, one trawl vessel in 1994, one pot vessel in 1993 and another pot vessel in both 1993 and 1994. CV for these data points are fairly high, ranging from 0.40 to 0.78. However, the addition of these points has a great effect on the final values estimated. Biomass is estimated at approximately 65% higher at all years from 1993 to 2003 using this scenario. As noted above, these data points are not reliable for use as index values because the fishermen involved had not fished for prawns prior to 1993, did not know which areas were the most productive, and the efficiency of the gear improved markedly during the first few years of the fishery.

The use of aggregated CPUE indices rather than individual vessel indices has little effect on the point estimates of the model (Figure 48). However, the confidence intervals are much larger with the aggregated indices, due to there being fewer data points with greater associated uncertainty with those points.

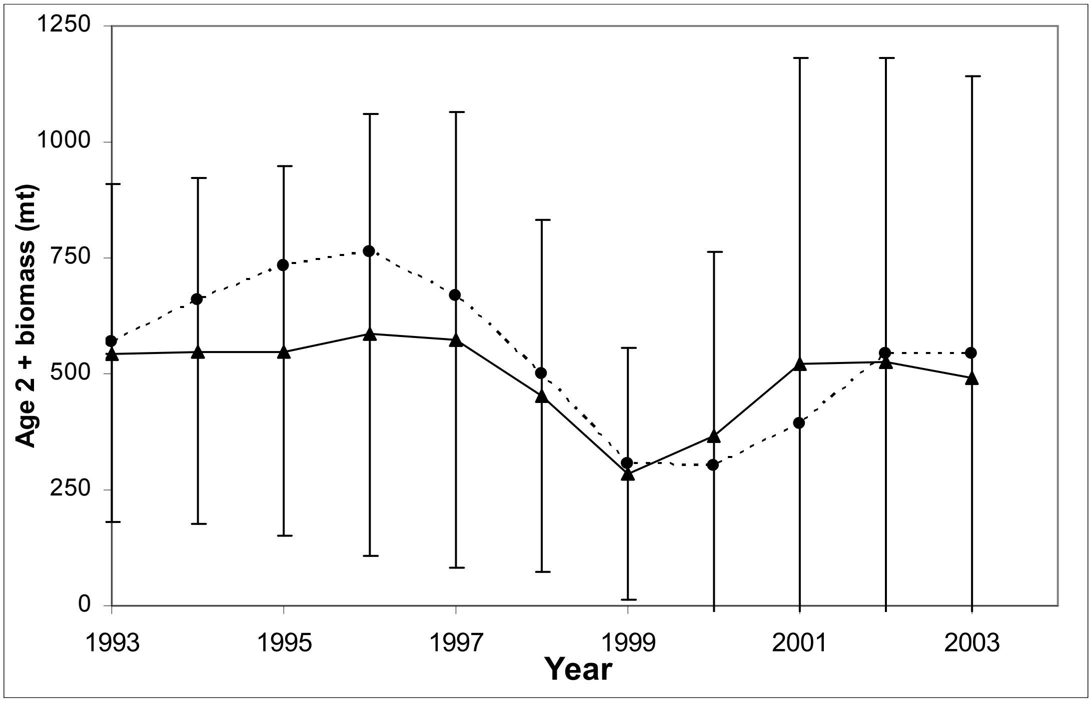

Figure 48: Biomass fits using aggregated CPUE indices (solid line) and individual vessel indices (dotted line). Error bars represent 95% confidence intervals around the aggregated index fit.

Forecasts

I used stock synthesis to explore the possible future state of the stock, based on known catches in 2004-5 and possible future catches in subsequent years. Forecasts were made for 20 years following the last model year (2003). Forecasts were made with the version of the model incorporating a Beverton-Holt stock-recruitment curve with steepness = 0.75.

Forecasts of the effect of various constant catch levels on biomass, assuming average recruitment are shown graphically in Figure 49. This shows a marked decline in biomass if the current catch quota (113.4 mt) is taken each year. The estimated harvest rates are extremely high in this scenario, reaching almost 100% of the vulnerable prawns by 2015. In the final few years of this scenario it is no longer possible to take the full quota amount with the fishery selectivity used for the model as the number of prawns available is too small.

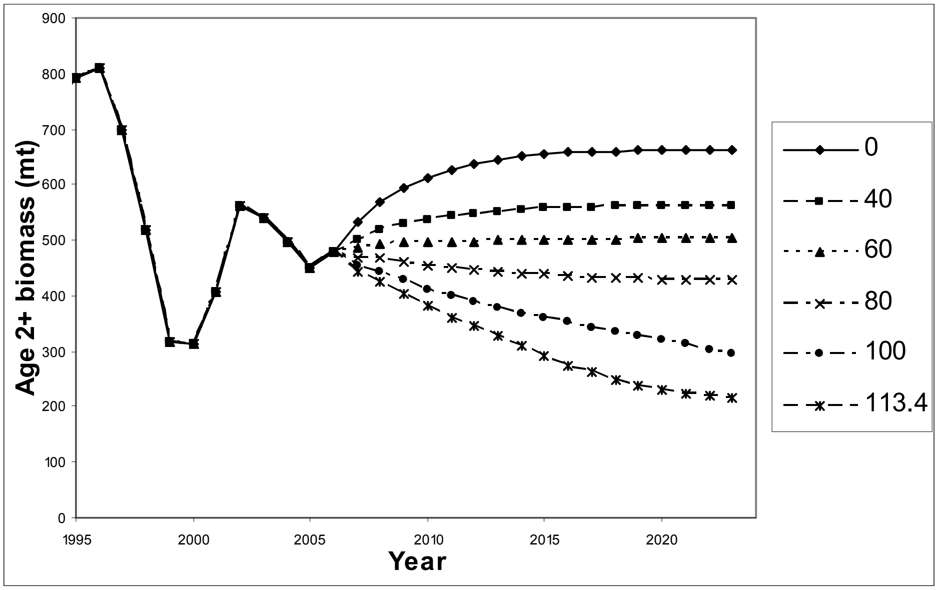

Figure 49: Forecast biomass assuming different levels of catch in the years 2006 – 2024. Catch levels are given in metric tons from 0 to 113.4. 113.4 Is the current precautionary quota level for the Washington coastal spot prawn fishery.

For annual catches of 80 mt and below the forecast biomass and harvest rates reached in 2023 (Table 39) are close to equilibrium with the annual recruitment. The harvest rate needed to catch the maximum sustainable yield is 50% of the available population when selectivity is taken into account. As noted above, the highest harvest rate achieved with pot gear during the modeled time series was 18% in 2003. A constant catch level of 50 mt over 20 years results in a stable harvest rate of 18% in the final year, with biomass of 534 mt. The differences in the biomass under these scenarios would result in a range of catch rates (CPUE). This fishery appears to be only marginally viable commercially for many vessels, in that they only participate when other opportunities are not available. The consequence of allowing the stock to be reduced to close to BMSY may be that CPUE declines to the point where profitability is such that the effort level also declines.

Table 39: Forecast harvest rate and biomass in 2023, given constant recruitment and constant catch from 2006 to 2023.

Constant catch 2006 -2023 (mt)	Harvest rate	Biomass (age 2+) (mt)
88.9 (MSY)	0.50	381
80	0.39	427
70	0.29	468
60	0.23	503
50	0.18	534
40	0.13	563
30	0.09	589
20	0.06	615
10	0.03	639
0	0	663

The uncertainty in these forecasts is extremely high, due to the high degree of variability in recruitment level, and the uncertainty in the model results. Figure 50 shows the biomass forecast assuming that the entire quota catch is taken through 2015. 95% confidence levels in 2015 range from 0 to 1721 mt. Forecasts such as these which take all sources of uncertainty into account are of limited use more than a year or two into the future, unless recruitment is known or estimated with some accuracy.

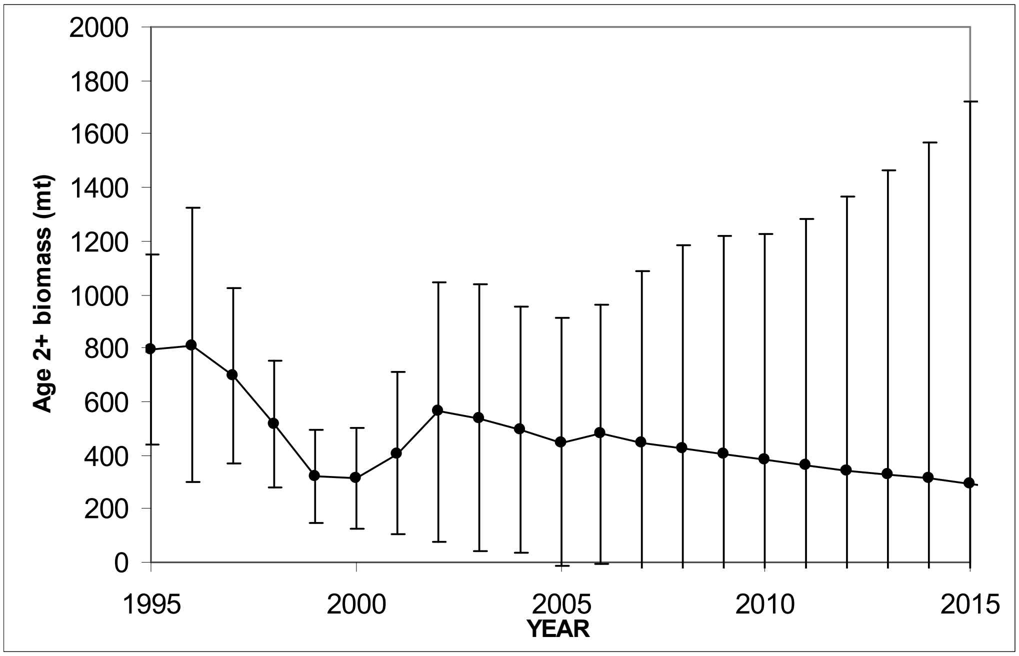

Figure 50: Forecast biomass assuming that the entire quota if 113.4 mt is caught in all years from 2007 to 2015. Error bars represent 95% confidence limits.

4.8 Discussion and Implications for Management

The Washington coastal spot prawn fishery has a relatively short history, with two very different gear types and an inconsistent catch history. Trawling was permitted from the start of the fishery in 1992 until 2003, when this gear type was phased out due to concerns about bycatch and habitat damage. Current management is based on effort limitation (limited entry) and a precautionary quota which is equal to the highest catch ever taken from the fishery.

The available data on this fishery is limited to commercial fishing logbooks, landings data, and a limited number of size frequency samples from some years. The lack of data has presented difficulties in determining a management regime for the fishery.

I used length data to estimate the selectivity of pot gear in this fishery by assuming that the trawl gear was unselective for the sizes of prawns that are available on the fishing grounds. This estimate, along with biological parameter estimates, enabled me to use two mathematical models to explore the effect of the gear type change and estimate the size and status of the stock which the fishery exploits.

Yield per recruit analysis showed that the switch from trawling to pot fishing as the primary method is likely to make the stock more robust to exploitation as the selectivity of pots means that the reproductive output is somewhat protected. However, the more selective pot gear exploits a smaller age range of prawns and means that the annual catch will be more volatile in response to variations in recruitment.

I used the stock synthesis program to model the population and estimate the biomass and potential yield of the stock. The results show that the dynamics of the coastal Washington spot prawn are driven mainly by recruitment variability. Estimated recruitment varied by a factor of 5 over the modeled time series. Heavy fishing in 1997 to 2002 combined with low recruitment in 1997 to 1999 reduced the stock to less than 50% of its virgin level. However, the stock appeared to be reasonably healthy at the end of the modeled time series, due to fairly large recruitments of 2 year old prawns to the fishery in 2001 and 2002 combined with reduced catch associated with the closing of the trawl fishery.

The small amount and low quality of the data used to fit the model, combined with uncertainties in the parameters, led to low precision in the estimated quantities, which needs to be considered in using these results for management purposes. The lack of precision in current estimates is compounded by the unknown degree of variation in future recruitment, and so long term forecasts are of little value in this case.

Equilibrium maximum sustainable yield estimated by the model (88.9 mt) is substantially less than the current quota (113.4 mt), which should be re-examined in the light of the drastically different selectivity of the pot fleet in comparison with trawls. An extremely high harvest rate would be needed in order to harvest at the MSY level. This is probably not feasible from an economic standpoint, in that the fishery would not be economically viable at the low CPUE that would result from the stock being reduced towards BMSY.

An annual catch of approximately 50 mt under equilibrium conditions would maintain the stock at a high enough level that the harvest rate could be under 20%, which was the highest rate estimated to have been taken in prior years by the model.

However, the fact that recruitment variability is the driver of the dynamics of the stock means that a regime where the fishery is managed via a constant annual catch is not optimal. Constant catch levels are not conservative in situations where recruitment is highly variable, in that if there is a consistent series of low recruitment events then stock collapse is inevitable no matter how conservative the catch level is. The recruitment levels seen in 1997 to 1999 (age classes spawned in 1995, 1996 and 1997) are too low to support a catch of 50 mt without causing a reduction in the stock and consequent egg production, potentially leading to further low recruitments.

In other spot prawn stocks which are similarly recruitment driven, pre-season (Hood Canal fishery) or in-season (BC fishery) surveys have been used to set catch targets or closing times which are specific to the strength of the stock in that year, and thus take account of recruitment variation. For the Washington Coastal fishery, an annual survey would be a useful management tool. A trawl survey could be used to assess the size of the recruiting (age 2) year class and the current total stock, whereas a pot based survey would not be as useful regardless of whether small or large mesh pots were used, as the pot fishery is unselective for age 2 prawns and so could only assess the current stock level. A strong argument against conducting a trawl survey is that it would have a large associated bycatch of fish, and there would be damage to habitat which is currently protected from trawling by ground gear size regulations and rockfish closures, so it is probably not a viable option. Resources for such surveys are unlikely to be available for management of such a small fishery as this one in any case. A cooperative effort between commercial fishers and agencies may be possible, with the costs offset by the sale of the catch, but even this limited effort is unlikely to be viable on a sufficient scale to be useful.

The available data is therefore likely to be limited to total catch, catch per unit effort, and some length frequency data from commercial pot catches. These length compositions carry only a limited amount of information about the recruiting year class, and perhaps can only be used to indicate whether there is a large or small recruitment. However, even this limited amount of information, when coupled with the use of a model such as the stock synthesis model presented here could be used to set a conservative catch level on an annual basis. This would be a better approach than setting a constant annual catch limit given the variation in recruitment seen over the study period.

Conclusions and recommendations

Here I present a brief review of the main findings in each chapter, highlight future research possibilities, and discuss implications for management of spot prawn fisheries.

1. Spot prawn biology

In Chapter 1 I summarized the current state of knowledge of the biology of the spot prawn. This chapter clarified several issues, including the range of the species and the length of the planktonic phase of the life cycle. I also improved estimates of the fecundity, growth rate, survivorship and longevity of this species, with reference to stocks in Washington.

However, some knowledge gaps still exist, especially regarding nursery areas, factors controlling recruitment, and effects of trawling on adult habitat and predators. The locations of nursery areas are still undefined for stocks where the adults are found in deep water off the Pacific coast. Research should be conducted to locate these areas and to protect them if necessary. Adult populations are likely limited by suitable habitat and predation, both of which were strongly impacted by heavy trawling in the 1990's. Trawling effects on habitat structures such as hexactinellid sponge reefs could reduce the carrying capacity of an area for spot prawns (and other species), and may take decades to recover. Overfishing has also severely reduced populations of rockfish, likely a major predator of the spot prawn. As rockfish stocks rebuild, they could have substantial impacts on spot prawn fisheries.

2. Bycatch in spot prawn fisheries

In this chapter I described experiments to test bycatch reduction devices in trawl gear off Southern California and observations of bycatch in commercial fishing operations off Washington. The results of the bycatch reduction experiments were generally positive, showing that Nordmøre grid type devices had the potential to reduce bycatch by a significant amount. However, the main conclusion was that the quantity of bycatch was far greater than had been previously thought. The ratio of total bycatch to spot prawn catch was 4.3:1, even with BRD's in use. The bycatch included overfished rockfish species, and a significant amount of structure-forming invertebrates. The fishery likely caused damage to benthic ecosystems by removing these invertebrates.

The first two studies off Washington showed that the bycatch in the trawl fishery in this area was also significant, with the ratio of total bycatch to spot prawns being 7:1 and 3.5:1 respectively. The bycatch included overfished species of rockfish and in one haul a large amount of reef-forming hexactinellid sponge. In contrast, the corresponding bycatch ratio in the pot fishery was 0.8:1, and consisted to a large extent of sea urchins and whelks. Only 16 rockfish were caught in 958 pots.

As a result of these and other studies of bycatch in spot prawn fisheries, all trawl fisheries were closed by 2003. Bycatch of fish was clearly excessive in trawl fisheries, and although the evidence for significant habitat damage was less conclusive, it was compelling enough for action to be taken in all areas.

Pot fisheries have replaced trawl fisheries in some areas of California and Washington. Although my study and a few other studies of bycatch have shown that it is generally low in spot prawn pot fisheries, the effect of these fisheries on benthic ecosystems is not fully understood. Strings of pots joined together could be dragged over the sea floor during hauling operations, and cause damage to benthic structures. Research into these effects is needed. I noted that some sets off Washington were left to fish for long periods. These pots had higher bycatch and evidence that some animals that had entered the pots had been consumed by predators. Management of spot prawn pot fisheries should be refined to avoid these issues, possibly by using maximum limits on soak time or by requiring that pots which are to be left unattended for long periods are unbaited and open so that anything entering can exit again.

3. Development of microsatellite markers and investigation of population structure of spot prawns

In Chapter 3 I developed three reliable microsatellite markers and showed that these were polymorphic within the species. However, I was unable to show the expected pattern of population structure, probably due to a lack of power caused by the small number of loci and the low level of polymorphism within the samples that I analyzed. I did use the markers successfully to analyze the parentage of samples from 14 broods of eggs taken from wild ovigerous females. This showed no evidence for multiple mating in this species, in contrast to other species of shrimp. Single paternity of broods can be expected to lead to a lower effective population size and lower overall genetic diversity than would be the case if multiple mating was common in the species. If other markers can be added to the set of markers that I developed, further studies would have greater power to resolve genetic differences between spot prawn populations.

4. Analysis of the Washington coastal spot prawn fishery and management of spot prawn fisheries

In Chapter 4 I investigated the coastal Washington spot prawn fishery, which exploits habitat patches found at the heads of submarine canyons. I estimated the selectivity of the pot fishery relative to the concurrent trawl fishery. I analyzed a dataset consisting of commercial logbooks to create a set of indices based on individual vessel catch per unit effort. I combined these CPUE estimates with length frequency data and parameter estimates based on data compiled in Chapter 1 to fit a population model. The resulting estimates of stock size and yield showed that variability in recruitment from year to year was a major factor determining the size of the stock exploited by this fishery. As yet we do not know what factors (e.g. density dependence, physical forcing, or climate change) control this variability. Establishing predictive links would greatly facilitate fisheries management, but requires a much longer data series on recruitment. I predicted that the current precautionary quota is probably too high given the exploitation pattern of the pot fishery. I recommended that the fishery not be managed in future via a constant annual quota, but rather by a method that takes into account the potential for higher or lower yields due to variation in recruitment.

This is the first time that a complex stock assessment model has been applied to spot prawns. Models such as this should have applicability in other spot prawn fisheries that are currently managed by other methods, but for which substantial amounts of data have been accumulated. Models could be used to reconstruct the history of the stock and its response to exploitation. Some fisheries have longer time series which may allow some inferences to be made into the factors that affect recruitment.

In order to ensure the sustainability of the spot prawn fishery in the long term, a wider view needs to be taken. Experience of fishery collapses has shown that managing at a single species level can cause unforeseen effects on the ecosystem of which the species is a part. The biggest challenge facing spot prawn stakeholders is to place the management of the spot prawn fishery in its ecological context, and ensure the sustainability of the entire ecosystem, rather than just one small component. Understanding the relationships between species in marine ecosystems is one part of this; the second part is understanding the effect of environmental variation on the components of the ecosystem, and how this affects the relationships. In the case of the spot prawn we have just begun to scratch the surface of these issues. Study of marine ecosystems and ecosystem management is a priority in many institutions, and the results of these studies will ultimately benefit spot prawn management.

In the short term, most spot prawn fisheries appear to be relatively well managed and sustainable. Current management schemes have some capacity to limit effort and to manage on a relatively small spatial scale. Some areas also have catch limits set by area. Even with catch limits in place, the scale of management may need to be refined to prevent depletion of local patches. The genetic structure and dynamics of larval dispersal of spot prawns is unknown, so management needs to be very precautionary with respect to local depletion.

In most jurisdictions, there are areas which are known to or probably contain spot prawns which are currently either not fished or very lightly fished. These areas may act as de-facto refuges for spot prawns which provide a supply of larvae to fished areas. This type of scenario has been implicated in the long term sustainability of other fisheries, regardless of the management or regulatory system applied. Consideration should be given to formalizing the refuge status of some spot prawn habitat in each jurisdiction, either by the establishment of a network of marine protected areas (MPAs) or by designating specific spot prawn fishing areas in known productive areas. MPAs have been shown to have positive effects for spot prawns (Schlining 1999), and have significant benefits beyond the single species.

References

Anderson, P. J. and J. F. Piatt (1999). Community reorganization in the Gulf of Alaska following ocean climate regime shift. Marine Ecology-Progress Series **189**: 117-123.

Anon (2001). 2001 Prawn and shrimp by trap integrated fisheries management plan - Internet information supplement. Department of Fisheries and Oceans, Canada. Pacific Region., Nanaimo, B.C.

Aubert, H. and D. V. Lightner (2000). Identification of genetic populations of the Pacific blue shrimp *Penaeus stylirostris* of the Gulf of California, Mexico. Marine Biology **137**: 875-885.

Bagshaw, J. C. and M. A. Buckholt (1997). A novel satellite/microsatellite combination in the genome of the marine shrimp, *Penaeus vannamei*. Gene **184**(2): 211-214.

Baldwin, J. D., A. L. Bass, B. W. Bowen and W. H. Clark (1998). Molecular phylogeny and biogeography of the marine shrimp Penaeus. Molecular Phylogenetics and Evolution **10**(3): 399-407.

Ball, A. O., S. Leonard and R. W. Chapman (1998). Characterization of (GT)n microsatellites from native white shrimp (*Penaeus setiferus*). Molecular Ecology **7**(9): 1251-1253.

Balloux, F., H. Brunner, N. Lugon-Moulin, J. Hausser and J. Goudet (2000). Microsatellites Can Be Misleading: An Empirical and Simulation Study. Evolution **54**(4): 1414-1422.

Baragona, M. A., L. A. Haig-Ladewig and S. Y. Wang (2000). Multiple paternity in the grass shrimp *Palaemonetes pugio*. American Zoologist **40**(6): 935-935.

Barr, L. (1973). Studies of spot shrimp, *Pandalus platyceros*, at Little Port Walter, Alaska. Marine Fisheries Review **35**(3-4): 65-66.

Barthel, D. (1992). Do hexactinellids structure Antarctic sponge associations? Ophelia **36**(2): 111-118.

Barthel, D. (1997). Fish eggs and pentacrinoids in Weddell Sea hexactinellids: Further examples for the structuring role of sponges in Antarctic benthic ecosystems. Polar Biology **17**(1): 91-94.

Benzie, J. A. H. (1998). Penaeid genetics and biotechnology. Aquaculture **164**(1-4): 23-47.

Bergstroem, B. I. (2000). The Biology of Pandalus. Advances in Marine Biology **38**: 55-245.

Berkeley, A. A. (1931). The post embryonic development of the common pandalids of British Columbia. Contributions to Canadian biology and fisheries **6**(1-26): 80-163.

Bett, B. J. and A. L. Rice (1992). The influence of hexactinellid sponge (*Pheronema carpenteri*) spicules on the patchy distribution of macrobenthos in the Porcupine Seabight (bathyal NE Atlantic). Ophelia **36**(3): 217-226.

Bilodeau, A. L., D. L. Felder and J. E. Neigel (2005). Multiple paternity in the thalassinidean ghost shrimp, *Callichirus islagrande* (Crustacea : Decapoda : Callianassidae). Marine Biology **146**(2): 381-385.

Botsford, L. W. (2001). Physical influences on recruitment of California Current invertebrate populations on multiple scales. ICES Journal Of Marine Science **58**: 1081-1091.

Boutillier, J. A. and J. A. Bond (1999). A progress report on the control of growth and recruitment overfishing in the shrimp trap fishery in British Columbia., Northwest Atlantic Fisheries Organization., Dartmouth, NS (Canada).

Boutillier, J. A. and J. A. Bond (2000). Using a fixed escapement strategy to control recruitment overfishing in the shrimp trap fishery in British Columbia. Journal of Northwest Atlantic fishery science **27**: 261-271.

Boutillier, J. A. and N. A. Sloan (1987). Effect of trap design and soak time on catches of the British Columbia prawn (*Pandalus platyceros*). Fisheries Research **6**(1): 69-79.

Bower, S. M. and J. Boutillier (1990). Sylon (*Crustacea: Rhizocephala*) infections on the shrimp in British Columbia. *in* Pathology in Marine Science. S. O. Perkins and T. C. Cheng (Eds.), Academic Press.

Bower, S. M., G. R. Meyer and J. A. Boutillier (1996). Stained prawn disease (SPD) of *Pandalus platyceros* in British Columbia, Canada, caused by a rickettsial infection. Diseases Of Aquatic Organisms **24**(1): 41-54.

Branch, T. A., R. Hilborn, A. C. Haynie, G. Fay, L. Flynn, J. Griffiths, K. N. Marshall, J. K. Randall, J. M. Scheuerell, E. J. Ward and M. Young (2006). Fleet dynamics and fishermen behavior: lessons for fisheries managers. Canadian Journal of Fisheries and Aquatic Sciences **63**(7): 1647-1668.

Brewer, D., D. Heales, D. Milton, Q. Dell, G. Fry, B. Venables and P. Jones (2006). The impact of turtle excluder devices and bycatch reduction devices on diverse tropical marine communities in Australia's northern prawn trawl fishery. Fisheries Research **81**: 176-188.

Briggs, J. C. (1974). Marine Biogeography. McGraw-Hill, New York.

Broadhurst, M. K. (2000). Modifications to reduce bycatch in prawn trawls: A review and framework for development. Reviews in Fish Biology and Fisheries **10**: 27-60.

Bruce, A. J. (1988). *Bannereus anomalus*, new genus, new species, a deep-sea alpheid shrimp from the Coral Sea. Pacific Science **42**(3-4): 139-149.

Bruce, A. J. (1991). Crustacea Decapoda: Further deep-sea Palaemonoid shrimps from New Caledonian waters. (RESULTS OF MUSORSTOM CRUISES: VOL. 9). MEM. MUS. NATL. HIST. NAT. (FRANCE) (A ZOOL.). **152**: 299-411.

Bruce, A. J. and F. A. Chace, Jr. (1986). *Paralebbeus zotheculatus*, n.gen., n.sp., a new hippolytid shrimp from the Australian Northwest Shelf. Proceedings of the Biological Society of Washington **99**(2): 237-247.

Buonaccorsi, V. P., C. A. Kimbrell, E. A. Lynn and R. D. Vetter (2002). Population structure of copper rockfish (*Sebastes caurinus*) reflects postglacial colonization and contemporary patterns of larval dispersal. Canadian Journal of Fisheries and Aquatic Sciences **59**(8): 1374-1384.

Butler, T. H. (1964). Growth, reproduction and Distribution of pandalid shrimps in British Columbia. Journal Of The Fisheries Research Board Of Canada **21**(6): 1403-1452.

Butler, T. H. (1970). Synopsis of biological data on the prawn *Pandalus platyceros* Brandt, 1851. FAO fisheries report **57**(4): 1289-1316.

Butler, T. H. (1980). Shrimps of the Pacific coast of Canada. Canadian bulletin of fisheries and aquatic sciences **202**: 280 p.

Campbell, C. (1999). Cultivated spot prawns offer promise in British Columbia. Shellfish World **1**(2): 14-15.

Charnov, E. L. (1979). Natural selection and sex change in pandalid shrimp test of a life-history theory. American Naturalist **113**(5): 715-734.

Charnov, E. L. (1981). Sex reversal in *Pandalus borealis*: effect of a shrimp fishery? Marine Biology **2**: 53-57.

Charnov, E. L. and P. J. Anderson (1989). Sex change and population fluctuations in pandalid shrimp. American Naturalist **134**(5): 824-827.

Charnov, E. L. and R. W. Hannah (2002). Shrimp adjust their sex ratio to fluctuating age distributions. Evolutionary Ecology Research **4**: 239-246.

Charnov, E. L. and U. Skuladottir (2000). Dimensionless invariants for the optimal size (age) of sex change. Evolutionary Ecology Research **2**(8): 1067-1071.

Chew, K. K., D. Holland, J. W. Wells, D. H. McKenzie and C. K. Harris (1974). Depth distribution and size of spot shrimp, *Pandalus platyceros*, trawled in Dabob Bay of Hood Canal, Washington from 1966 to 1971. Proceedings of the National Shellfisheries Association **64**: 28-32.

Childers, R. K., R. A. Elston and J. Winston (2004). Fouling organism (*Triticella* sp.) of the spot shrimp Pandalus platyceros. Journal of Shellfish Research **23**(2): 652.

Chistiakov, D. A., B. Hellemans and F. A. M. Volckaert (2006). Microsatellites and their genomic distribution, evolution, function and applications: A review with special reference to fish genetics. Aquaculture **255**: 1-29.

Clark, W. G. (1993). The effect of recruitment variability on the choice of a target level of spawning biomass per recruit. *in* Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations. G. Kruse, D. M. Eggers, R. J. Marasco, C. Pautzke and T. J. Quinn (Eds.). Fairbanks, Alaska., Alaska Sea Grant College Program, University of Alaska. **93-02:** 233–246.

Conway, K., M. Krautter, J. V. Barrie, F. Whitney, R. E. Thomson, H. Reiswig, H. Lehnert, G. Mongov and M. Bertram (2005). Sponge reefs in the Queen Charlotte Basin, Canada: controls on distribution, growth and development. *in* Cold-water Corals and Ecosystems. A. Freiwald and J. M. Roberts (Eds.). Berlin Heidelberg, Springer-Verlag**:** Pages 601-617.

Cook, S. E. (2005). Ecology of the Hexactinellid Sponge Reefs on the Western Canadian Continental Shelf. Dept of Biology. Victoria, BC, University of Victoria. **MS**.

Correa, C. and M. Thiel (2003). Mating systems in caridean shrimp (Decapoda: Caridea) and their evolutionary consequences for sexual dimorphism and reproductive biology. Revista Chilena de Historia Natural **76**: 187-203.

Dahlstrom, W. A. (1970). Synopsis of biological data on the ocean shrimp *Pandalus jordani* Rathburn, 1902. FAO fisheries report **57**(4).

Dautov, S. S., L. I. Popova and A. I. Begalov (2004). Fecundity of the Grass Shrimp, *Pandalus kessleri* (Decapoda: Pandalidae), near the Southern Kuril Islands. Russian Journal of Marine Biology **V30**(3): 199-203.

Dayton, P. K., S. Thrush and F. C. Coleman (2002). Ecological effects of fishing in marine ecosystems of the United States. Pew Oceans Commission, Arlington, VA.

Drengstig, A., S. E. Fevolden, P. E. Galand and M. M. Aschan (2000). Population structure of the deep-sea shrimp (*Pandalus borealis*) in the north-east Atlantic based on allozyme variation. Aquatic Living Resources **13**(2): 121-128.

Dunagan, C. and N. Lowry (in review). Settlement and Habitat Preference in Larval Spot Prawns (*Pandalus platyceros*) Journal of Shellfish Research.

Eayrs, S. (2005). A Guide to Bycatch Reduction in Tropical Shrimp-Trawl Fisheries. Food and Agricultural Organization (FAO) of the United Nations Rome, Italy.

Ebbesmeyer, C. C., G. A. Cannon and C. A. Barnes (1984). Synthesis of current measurements in Puget Sound, Washington. Volume 3. Circulation in Puget Sound: An interpretation based on historical records of currents. NOAA Tech Memo **1984**: 88 pp.

Engas, A. and O. R. Godo (1989). Escape of Fish under the Fishing Line of a Norwegian Sampling Trawl and Its Influence on Survey Results. Journal Du Conseil **45**(3): 269-276.

Eno, N. C., D. S. MacDonald, J. A. M. Kinnear, S. C. Amos, C. J. Chapman, R. A. Clark, F. Bunker and C. Munro (2001). Effects of crustacean traps on benthic fauna. ICES Journal of Marine Science **58**(1): 11-20.

Ferguson, M. M. and R. G. Danzmann (1998). Role of genetic markers in fisheries and aquaculture: useful tools or stamp collecting? Canadian Journal of Fisheries and Aquatic Sciences **55**(7): 1553-1563.

Field, J. C., R. C. Francis and K. Aydin (2006). Top-down modeling and bottom-up dynamics: Linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current. Progress in Oceanography **68**: 238-270.

Flowers, J. M., S. C. Schroeter and R. S. Burton (2002). The recruitment sweepstakes has many winners: Genetic evidence from the sea urchin *Strongylocentrotus purpuratus*. Evolution **56**(7): 1445-1453.

Fonseca, P., A. Campos and R. B. Millar (2007). Codend selection in the deep-water crustacean trawl fishery in Portuguese southern waters. Fisheries Research **85**(1-2): 49-60.

Freese, J. L. and B. L. Wing (2004). Juvenile red rockfish, *Sebastes* sp. associations with sponges in the Gulf of Alaska. Marine Fisheries Review **65**(3): 38-42.

Garcia, D. K., M. A. Faggart, L. Rhoades, A. A. Alcivar-Warren, J. A. Wyban, W. H. Carr, J. N. Sweeney and K. M. Ebert (1994). Genetic diversity of cultured *Penaeus vannamei* shrimp using three molecular genetic techniques. Molecular Marine Biology and Biotechnology **3**(5): 270-280.

Gerdes, D., M. Klages, W. E. Arntz, R. L. Herman, J. Galeron and S. Hain (1992). Quantitative investigations on macrobenthos communities of the southeastern Weddell Sea shelf based on multibox corer samples. Polar Biology **12**(2): 291-391.

Gobert, B. (1998). Density-dependent size selectivity in Antillean fish traps. Fisheries Research **38**(2): 159-167.

Goudet, J. (1995). FSTAT (Version 1.2) A computer program to calculate F statistics. Journal of Heredity **86**: 485-486.

Goudet, J. (2001). "FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3). Available from http://www.unil.ch/izea/softwares/fstat.html. ."

Goy, J. W. (1992). Systematics and zoogeography of eastern Pacific stenopodidean shrimps (Crustacea: Decapoda). Proceedings of the San Diego Society of Natural History.(22): 7 pp.

Gusmao, J., C. Lazoski and A. M. Sole-Cava (2005). Population genetic structure of Brazilian shrimp species (*Farfantepenaeus* sp., *F. brasiliensis, F. paulensis* and *Litopenaeus schmitti*: Decapoda : Penaeidae). Genetics and Molecular Biology **28**(1): 165-171.

Hamilton, M. B., E. L. Pincus, A. Di Fiore and R. C. Fleischer (1999). Universal linker and ligation procedures for construction of genomic DNA libraries enriched for microsatellites. Biotechniques **27**(3): 500-+.

Hannah, R. W. (1993). Influence of environmental variation and spawning stock levels on recruitment of ocean shrimp (*Pandalus jordani*). Canadian Journal Of Fisheries And Aquatic Sciences **50**: 612 - 622.

Hannah, R. W. (1995). Variation in Geographic Stock Area, Catchability, and Natural Mortality of Ocean Shrimp (*Pandalus Jordani*) - Some New Evidence for a Trophic Interaction with Pacific Hake (*Merluccius Productus*). Canadian Journal of Fisheries and Aquatic Sciences **52**(5): 1018-1029.

Hannah, R. W. (1999). A new method for indexing spawning stock and recruitment in ocean shrimp, *Pandalus jordani,* and preliminary evidence for a stock-recruitment relationship. Fishery Bulletin **97**(3): 482-494.

Hannah, R. W. and S. A. Jones (1991). Fishery-Induced Changes in the Population-Structure of Pink Shrimp *Pandalus Jordani*. Fishery Bulletin **89**(1): 41-51.

Hansen, H. O. and M. Aschan (2000). Growth performance, size and age at maturity of shrimp *Pandalus borealis* in the Svalbard area related to environmental parameters. Journal of Shellfish Research **19**(1): 551.

Harrington, J. M., R. A. Myers and A. A. Rosenberg (2005). Wasted fishery resources: discarded by-catch in the USA. Fish and Fisheries **6**(December 2005): 350-361.

Hayashi, K. I. and Y. Ogawa (1987). *Spongicola levigata* sp. nov., a new shrimp associated with a hexactinellid sponge from the East China Sea (Decapoda, Stenopodidae). Zoological Science **4**(2): 367-373.

Hedgecock, D. (1994). Does variance in reproductive success limit effective population size of marine organisms? *in* Genetics and evolution of aquatic organisms. A. Beaumont (Ed.). London, Chapman and Hall**:** 122-134.

Hedrick, P. W. (1999). Perspective: Highly Variable Loci and Their Interpretation in Evolution and Conservation. Evolution **53**(2): 313-318.

Hickey, B. M. (1979). The California Current System- hypotheses and facts. Progress in Oceanography **8**: 191-279.

Hickey, B. M. (1989). Patterns and processes of circulation over the Washington continental shelf and slope. *in* Coastal Oceanography of Washington and Oregon. M. Landry and B. M. Hickey (Eds.). Amsterdam, Elsevier Science**:** 41-115.

Hickey, B. M. (1995). Coastal submarine canyons. *in* Proceedings of the University of Hawaii 'Aha Huliko'a Workshop on Flow Topography Interactions. P. Mueller and D. Henderson (Eds.). Honolulu, Hawaii., SOEST Special Pub.**:** 265 pp.

Hickey, B. M. (1997). Response of a narrow submarine canyon to strong wind forcing. Journal of Physical Oceanography **27**(5): 697-726.

Hickey, B. M., J. M. Klinck, M. Dinneman and S. Allen (2000). Comparison of modeled and observed circulation in Astoria submarine canyon. Journal of Geophysical Research.

Hoffman, D. L. (1973). Observed acts of copulation in the protandric shrimp, *Pandalus platyceros* Brandt (Decapoda, Pandalidae). Crustaceana **24**(2): 242-244.

Hyland, J., C. Cooksey, E. Bowlby, B. M.S. and I. S. (2005). A Pilot Survey of Deepwater Coral/Sponge Assemblages and their Susceptibility to Fishing/Harvest Impacts at the Olympic Coast National Marine Sanctuary (OCNMS). Cruise Report for NOAA Ship McARTHUR II Cruise AR-04-04: Leg 2. NOAA Technical Memorandum NOS NCCOS 15. Charleston, SC., NOAA/NOS Center for Coastal Environmental Health and Biomolecular Research**:** 13 pp.

Isaksen, B., J. W. Valdemarsen, R. B. Larsen and L. Karlsen (1992). Reduction of Fish by-Catch in a Shrimp Trawl Using a Rigid Separator Grid in the Aft Belly. Fisheries Research **13**(3): 335-352.

Iwamoto, E., M. J. Ford and R. G. Gustafson (2004). Genetic population structure of Pacific hake, *Merluccius productus*, in the Pacific Northwest. Environmental Biology of Fishes **69**(1-4): 187-199.

Jagielo, T. H., L. L. LeClair and B. A. Vorderstrasse (1996). Genetic variation and population structure of lingcod. Transactions of the American Fisheries Society **125**(3): 372-386.

Jensen, G. C. (1995). Pacific coast crabs and shrimps. Sea Challengers, Monterey, California.

Jonsdottir, O. D. B., A. K. Imsland and G. Naevdal (1998). Population genetic studies of northern shrimp, *Pandalus borealis*, in Icelandic waters and the Denmark Strait. Canadian Journal of Fisheries and Aquatic Sciences **55**(3): 770-780.

Kalinowski, S. T. (2002). How many alleles per locus should be used to estimate genetic distances? Heredity **88**: 62-65.

Kartatsev, Y., K. A. Zgurovskii and Z. Fedina (1993). Morphological variability of pink shrimp *Pandalus borealis* in Far Eastern seas and its association with the species' population structurization. Russ. J. Mar. Biol.; Biol. Morya/Mar. Biol. **18**(3-4): 100-106; vol. 18.

Kelleher, K. (2005). Discards in the world's marine fisheries: an update. FAO Fisheries Technical Paper(No. 470): 131 pp.

Kimker, A., W. Donaldson and W. R. Bechtol (1996). Spot shrimp growth in Unakwik Inlet, Prince William Sound, Alaska. Alaska Fishery Research Bulletin **3**(1): 1-8.

Klinck, J. M. (1996). Circulation near submarine canyons: a modeling study. Journal of Geophysical Research **101**(C1): 1211-1223.

Klinck, J. M., J. She and B. M. Hickey (2000). Circulation near submarine canyons: transient wind forcing. Journal of Geophysical Research.

Koeller, P. A. (2000). Relative importance of abiotic and biotic factors to the management of the northern shrimp (*Pandalus borealis*) fishery on the Scotian Shelf. Journal of Northwest Atlantic fishery science **27**: 21-33.

Koeller, P. A. (2006). Inferring shrimp (*Pandalus borealis*) growth characteristics from life history stage structure analysis. Journal of Shellfish Research **25**(2): 595-608.

Koeller, P. A., R. Mohn and M. Etter (2000). Density dependant sex change in northern shrimp, *Pandalus borealis*, on the Scotian Shelf. Journal of Northwest Atlantic fishery science **27**: 107-118.

Komai, T. (1999). A revision of the genus *Pandalus* (Crustacea: Decapoda: Caridea: Pandalidae). Journal of Natural History **33**(9): 1265-1372.

Konecki, J. T. and T. E. Targett (1989). Eggs and larvae of *Nototheniops larseni* from the spongocoel of a hexactinellid sponge near Hugo Island, Antarctic Peninsula. Polar Biology **10**: 197-198.

Krebs, J. R. and N. B. Davies (1997). Behavioural Ecology: An Evolutionary Approach. Blackwell Science., Oxford.

Kristjansson, J. (2001). Changes in population structure of the shrimp (*Pandalus borealis*) stock at Flemish Cap, 1995-2000, Northwest Atlantic Fisheries Organization, Dartmouth, NS (Canada).

Kunzmann, K. (1996). Associated fauna of selected sponges (Hexactinellida and Demospongiae) from the Weddell Sea, Antarctica. Berichte zur Polarforschung/Reports on polar research.(210): 93 pp.

Larson, M. (2001). Spot Prawn. *in* California's living marine resources: A status report, California Department of Fish and Game**:** 121-123.

Leys, S. P. and N. R. J. Lauzon (1998). Hexactinellid sponge ecology: growth rates and seasonality in deep water sponges. Journal of experimental marine biology and ecology **230**: 111-129.

Løkkeborg, S. (2005). Impacts of trawling and scallop dredging on benthic habitats and communities. FAO Fisheries Technical Paper(472).

Love, D. C. and G. Bishop (2005). Pot shrimp stock assessment survey results from 1996-2003 in districts 3,7,12 and 13 of Southeastern Alaska. Fishery Data Series No. 05-32, Alaska Department of Fish and Game, Divisions of Sport fish and Commercial Fisheries**:** 57 pp.

Lowry, N. and J. H. B. Robertson (1996). The effect of twine thickness on cod-end selectivity of trawls for haddock in the North Sea. Fisheries Research **26**: 353-363.

Marliave, J. B. and M. Roth (1995). Agarum kelp beds as nursery habitat of spot prawns, *Pandalus platyceros* Brandt, 1851 (Decapoda, Caridea). Crustaceana **68**(1): 27-37.

Martinez, I., T. Skjerdal, B. Dreyer and S. M. Aljanabi (1997). Genetic structuring of *Pandalus borealis* in the North Atlantic. 2. RAPD analysis. ICES Council Meeting Papers, ICES, Copenhagen (Denmark) **ICES-CM-1997/T:24**: 12 pp.

Martinez, J. L., P. Moran, J. Perez, B. de Gaudemar, E. Beall and E. Garcia-Vazquez (2000). Multiple paternity increases effective population size of southern Atlantic salmon populations. Molecular Ecology **9**: 293-298.

McCrary, J. A. (1971). Sternal Spines as a Characteristic for Differentiating between Females of Some Pandalidae. Journal of the Fisheries Research Board of Canada **28**(1): 98-102.

Methot, R. D. (2005). Technical Description of the Stock Synthesis II Assessment Program. Seattle, WA, NOAA Fisheries**:** 54 pp.

Methot, R. D. (2007). Stock Synthesis 2, using Otter Research AD model builder 7.0.1. 03/26/2007. Seattle, WA, NOAA fisheries.

Millar, R. B. and S. J. Walsh (1992). Analysis of trawl selectivity studies with an application to trouser trawls. Fisheries Research **13**: 205-220.

Morgan, L. and R. Chuenpagdee (2003). Shifting Gears: Addressing the Collateral Impacts of Fishing Methods in U.S. Waters. The Pew Charitable Trusts, Washington, D.C.

Narum, S. R. (2006). Beyond Bonferroni: Less conservative analyses for conservation genetics. Conservation Genetics **7**: 783-787.

Neff, B. D., P. Fu and M. R. Gross (2003). Sperm investment and alternative mating tactics in bluegill sunfish (*Lepomis macrochirus*). . Behavioral Ecology **14**: 634-641.

Neff, B. D. and T. E. Pitcher (2002). Assessing the statistical power of genetic analyses to detect multiple mating in fishes. Journal of Fish Biology **61**(3): 739-750.

Oloef, D., O. D. B. Jonsdottir and A. K. Imsland (1996). Population genetic studies of northern shrimp (*Pandalus borealis* Kroeyer) in Icelandic waters and Denmark strait. ICES Council Meeting Papers, ICES, Copenhagen (Denmark) **ICES-CM-1996/K:9**: 18 pp.

Opresko, D. M. (2005). A new species of antipatharian coral (Cnidaria: Anthozoa: Antipatharia) from the southern California Bight. Zootaxa **852**: 1-10.

Orensanz, J. M., J. Armstrong, D. A. Armstrong and R. Hilborn (1998). Crustacean resources are vulnerable to serial depletion - The multifaceted decline of crab and shrimp fisheries in the Greater Gulf of Alaska. Reviews in fish biology and fisheries **8**: 1-60.

Orensanz, J. M. and G. S. Jamieson (1998). The assessment and management of spatially structured stocks: An overview of the North Pacific Symposium of Invertebrate Stock Assessment and management. North Pacific Symposium of Invertebrate Stock Assessment and management, Can. Spec. Publ. Fish Aquat. Sci.

Parker, M. S., P. A. Jumars and L. LeClair (2003). Population genetics of two bivalve species (*Prototheca staminea* and *Macoma balthica*) in Puget Sound, Washington. J. Shellfish Res. **22**: 681-688.

Parsons, D. G., V. L. Mercer and P. J. Veitch (1989). Comparison of the growth of northern shrimp (*Pandalus borealis*) from four regions of the Northwest Atlantic. Journal of Northwest Atlantic fishery science **9**(2): 123-131.

Parsons, K. E. (1996). The genetic effects of larval dispersal depend on spatial scale and habitat characteristics. Marine Biology **126**: 403-414.

Potter, I. C., P. J. Chrystal and N. R. Loneragan (1991). Movement, fishing sector impact, and factors affecting the recapture rate of tagged sand crabs, *Portunus pelagicus* (L.), in Moreton Bay, Queensland. Australian Journal of Marine and Freshwater Research **42**: 751-760.

Price, V. A. and K. K. Chew (1972). Laboratory rearing of spot shrimp larvae (*Pandalus platyceros*) and descriptions of stages. Journal Of The Fisheries Research Board Of Canada **29**(4): 413-422.

Raymond, M. and F. Rousset (1995). GENEPOP (Version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity **86**: 248-249.

Reeves, S. A., D. W. Armstrong, R. J. Fryer and K. A. Coull (1992). The effects of mesh size, cod-end extension length and cod-end diameter on the selectivity of Scottish trawls and seines. ICES Journal of Marine Science **49**: 279-288.

Reilly, P. N. and J. Geibel (2002). Results of California Department of Fish and Game spot prawn trawl and trap fisheries bycatch observer program 2000-2001, California fish and game commission**:** 23 pp.

Rensel, J. E. and E. F. Prentice (1977). First record of a second mating and spawning of the spot prawn, *Pandulus platyceros*, in captivity. Fishery Bulletin **75(3)**: 648-649.

Roberts, S. and M. Hirshfield (2004). Deep-sea corals: out of sight, but no longer out of mind. Frontiers in Ecology and The Environment **2**(3): 123-130.

Rozen, S. and H. Skaletsky (2000). Primer3 on the WWW for general users and for biologist programmers. . *in* Bioinformatics Methods and Protocols: Methods in Molecular Biology. . M. S. Krawetz S (Ed.). Totowa, NJ, Humana Press**:** pp 365-386.

Rutherford, D. T., H. Nguyen and G. E. Gillespie (2004). Update on effort standardization for the in-season monitoring of the prawn by trap fishery. Canadian Science Advisory Secretariat, Research Document 2004/015. Nanaimo. BC, Fisheries and Oceans Canada, Science Branch.**:** 13 pp.

Schlining, K. L. (1999). The spot prawn (*Pandalus platyceros* Brandt 1851) resource in Carmel submarine canyon, California: Aspects of fisheries and habitat associations. Moss Landing Marine Laboratories. Stanislaus, California State University. **M.Sc.:** 54 pp.

Schlining, K. L. and J. D. Spratt (2000). Assessment of the Carmel Bay spot prawn, *Pandalus platyceros*, resource and trap fishery adjacent to an ecological reserve in central California. Crustacean issues **12**: 751-762.

Selkoe, K. A., S. D. Gaines, J. E. Caselle and R. R. Warner (2006). Current shifts and kin aggregation explain genetic patchiness in fish recruits. Ecology **87**(12): 3082-3094.

Shaklee, J. B. and P. Bentzen (1998). Genetic identification of stocks of marine fish and shellfish. Bulletin Of Marine Science **62**(2): 589-621.

Shumway, S. E., H. C. Perkins and D. F. Schick (1985). Synopsis of biological data on the pink shrimp (*Pandalus borealis*) Kroyer 1838. FAO fisheries synopsis **144**: 57.

Simpson, A. C., B. R. Howell and P. J. Warren (1970). Synopsis of biological data on the shrimp *Pandalus montagui* Leach, 1814. FAO fisheries report **57**(4).

Small, M. P., J. L. Loxterman, A. E. Frye, J. F. Von Bargen, C. Bowman and S. F. Young (2005). Temporal and spatial genetic structure among some Pacific herring populations in Puget Sound and the southern Strait of Georgia. Transactions of the American Fisheries Society **134**(5): 1329-1341.

Sotka, E. E., J. A. Hempelmann and C. H. Biermann (2005). Genetic evidence of postglacial population expansion in Puget Sound rockfish (*Sebastes emphaeus*). Marine Biotechnology **7**(3): 223-230.

Sun, C.-L., N. M. Ehrhardt, C. E. Porch and S.-Z. Yeh (2002). Analyses of yield and spawning stock biomass per recruit for the South Atlantic albacore (*Thunnus alalunga*). Fisheries Research **56**(2): 193-204.

Sunada, J. S. (1984). Spot prawn (*Pandalus platyceros*) and ridgeback prawn (*Sicyonia ingentis*) fisheries in the Santa Barbara Channel. Reports of California Cooperative Oceanic Fisheries Investigations **25**: 100-104.

Sunada, J. S. (1986). Growth and reproduction of spot prawns in the Santa Barbara channel. California Fish and Game **72**(2): 83-93.

Terry, A., G. Bucciarelli and G. Bernardi (2000). Restricted gene flow and incipient speciation in a disjunct Pacific Ocean and Sea of Cortez populations of a reef fish species (*Girella nigricans*). Evolution **54**(2): 652-659.

Tissot, B. N., M. M. Yoklavich, M. S. Love, K. York and M. Amend (2006). Benthic invertebrates that form habitat on deep banks off southern California, with special reference to deep sea coral. Fishery Bulletin **104**: 167-181.

Treble, R. J., R. B. Millar and T. I. Walker (1998). Size-selectivity of lobster pots with escape-gaps: application of the SELECT method to the southern rock lobster (*Jasus edwardsii*) fishery in Victoria, Australia. Fisheries Research **34**: 289-305.

Vadopalas, B., L. L. Leclair and P. Bentzen (2004). Microsatellite and allozyme analyses reveal few genetic differences among spatially distinct aggregations of geoduck clams (*Panopea abrupta*, Conrad 1849). Journal of Shellfish Research **23**(3): 693-706.

Valles-Jimenez, R., P. Cruz and R. Perez-Enriquez (2004). Population genetic structure of pacific white shrimp (*Litopenaeus vannamei)* from Mexico to Panama: Microsatellite DNA variation. Marine Biotechnology **6**(5): 475-484.

Van Oosterhout, C., W. F. Hutchinson, D. P. M. Wills and P. Shipley (2004). MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Molecular Ecology Notes **4**: 535-538.

Vonau, V., M. Ohresser, N. Bierne, C. Delsert, I. Beuzart, E. Bedier and F. Bonhomme (1999). Three polymorphic microsatellites in the shrimp *Penaeus stylirostris*. Animal Genetics **30**(3): 234-235.

Walters, C. J. (1986). Adaptive management of renewable resources. . MacMillan Publishing Company, New York.

Wardle, C. S. (1993). Fish behaviour and fishing gear. *in* Behaviour of teleost fishes. T. J. Pitcher (Ed.). London., Chapman & Hall.

Watson, J., I. Workman, D. Foster, C. Taylor, A. Shah, J. Barbour and D. Hantaway (1993). Status report on the potential of gear modifications to reduce fin fish bycatch in shrimp trawls in the southeastern United States 1990–1992. NOAA Tech. Memo.(NMFS-SEFSC-327): 131 p.

Watson, L. J. (1994). Shrimp. ADFG Wildlife Notebook Series. Anchorage, AK, Alaska Department of Fish and Game.

Weir, B. S. and C. C. Cockerham (1984). Estimation of F statistics for the analysis of population structure. Evolution **38**: 1358-1370.

Wieland, K. (2004). Length at sex transition in northern shrimp (*Pandalus borealis*) off West Greenland in relation to changes in temperature and stock size. Fisheries Research **69**(1): 49-56.

Wright, C. S. and P. Panek (2000). Effect of Trap Soak-Time on the Trap-Selectivity Profile and By-Kill in Prawn-Trap Fisheries. International institute of fisheries economics and trade conference 2000, Corvallis, Oregon USA.

Wright, S. (1978). Evolution and the genetics of populations. Volume 4. Variability within and among natural populations. University of Chicago Press, Chicago.

Xu, Z., J. H. Primavera, L. D. de la Pena, P. Pettit, J. Belak and A. Alcivar-Warren (2001). Genetic diversity of wild and cultured Black Tiger Shrimp (*Penaeus monodon*) in the Philippines using microsatellites. Aquaculture **199**(1-2): 13-40.

Zetterstrom, T. (2003). The European Union's consumption of tropical prawns. *in* The blues of a revolution, the damaging impacts of shrimp farming. I. de la Torre and D. Barnhizer (Eds.). Seattle, Industrial shrimp action network**:** 311-349.

Vita

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