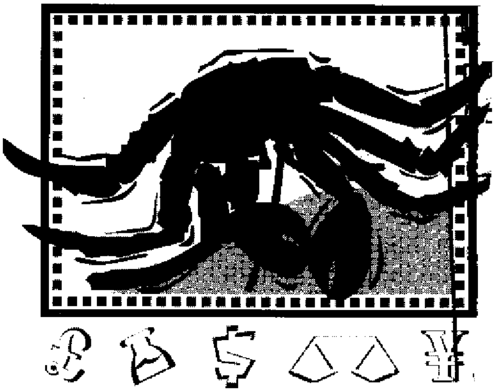
Lowell Wakefield Fisheries Symposium

HIGH LATITUDE CRABS

BIOLOGY, MANAGEMENT, AND ECONOMICS



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Sea Grant is a unique partnership with public and private sectors combining research, education, and technology transfer for public service. This national network of universities meets changing environmental and economic needs of people in our coastal, ocean, and Great Lakes regions.

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About the Lowell Wakefield Symposium Series

The University of Alaska Sea Grant College Program has been sponsoring and coordinating the Lowell Wakefield Fisheries Symposium series since 1982. These meetings are a forum for information exchange in biology, management, economics, and processing of various fish species and complexes as well as an opportunity for scientists from high latitude countries to meet informally and discuss their work.

Lowell Wakefield was the founder of the Alaskan king crab industry. He recognized that the two major ingredients necessary for the king crab fishery to survive were ensuring that a quality product was available to the consumer, and that a viable fishery could only be maintained through sound management practices based on the best scientific data available. Lowell Wakefield and Wakefield Seafoods played important roles in the development and implementation of quality control legislation, in the preparation of fishing regulations for Alaskan waters, and in drafting international agreements for the high seas. Toward the end of his life, Lowell Wakefield joined the faculty of the University of Alaska as an adjunct professor of fisheries, where he influenced the early directions of the university's Sea Grant program. This symposium series honors Lowell Wakefield and his many contributions to Alaska's fisheries.

About This Symposium

The International Symposium on Biology, Management, and Economics of Crabs from High Latitude Habitats is the thirteenth Lowell Wakefield symposium, and is the fifth crab symposium in the series, following Tanner crab (1982), Dungeness crab (1984), king crab (1985), and king and Tanner crab (1989). The program concept was submitted by A.J. Paul in mid-1993, and the meeting was held October 11-13, 1995, in Anchorage, Alaska.

The symposium was organized and coordinated by Brenda Baxter, Alaska Sea Grant College Program, with the assistance of the program committee. Committee members are: William E. Donaldson, Alaska Department of Fish and Game, Kodiak; Robert S. Otto, National Marine Fisheries Service, Kodiak; A.J. Paul, Institute of Marine Science, University of Alaska Fairbanks, Seward; and David B. Witherell, North Pacific Fishery Management Council, Anchorage.

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Attendees at the International Symposium on Biology, Management, and Economics of Crabs from High Latitude Habitats, October 11-13, 1995, Anchorage, Alaska.

High Latitude Crabs: Biology, Management, and Economics
Alaska Sea Grant College Program • AK-SG-96-02, 1996

Symposium Introduction

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In opening the symposium, I'd like to focus on the international aspect of the research being presented here. Eight nations are represented in the program: Argentina, Australia, Canada (both coasts), Chili, Norway, Russia and the United States—that includes both Alaska and, as Alaskans say, "Outside."

Our list of topics includes nearly every aspect of management, economics, and biology of high latitude crabs. Not only are the topics inclusive, but the research deals with an extensive list of species. I have counted 20 species of crabs that are discussed in the collection of abstracts.

In keeping with the international highlighting, the notes I have made on the papers to be presented are purposely limited to research that was conducted at locations off the continent of North America. There is a large body of work being presented from Canada and the United States that I cannot review in the short time that I have. My apologies go to my Canadian and American colleagues. There is one sad note on the subject of internationalism. Our Russian associates from Kamchatka will not be joining us due to problems in getting visas from the United States.

Wyngaard, Bertuche, Iorio, and Fischbach from Argentina will give a paper on Beagle Channel crab fisheries. They will review for us the 60-year-old fishery on southern king crabs and the more recent fishery on the softshell red crabs, and will discuss new management measures that include selective gear.

A number of papers from Japan will be presented. The distribution around the Japanese archipelago of the four species of *Chionoecetes* will be discussed and related to management strategies by Kon. An unusual, unfished stock of *C. opilio* in the Sea of Japan is the subject of a paper by Kon, Ietugu, and Ryoke. The paper shows, among other things, that the breeding area there extends deeper than do breeding areas of other *C. opilio* stocks in the region. A paper by Yosho and Nagasawa centers on the biology of zoea of *C. opilio* and shows that the origin of many zoeae is the western part of the Sado Strait in the Sea of Japan. These larvae are advected to the northeast.

Nagao, Munehara, and Shimazaki show that the maturation cycle of the valuable horsehair crab in southern Hokkaido requires three years for completion from the germinal egg to hatching. With this kind of parental involvement, what must be the energetics cost of reproduction? And what is the adaptive significance? You will hear a paper by Munehara, Nagao, and Maruyama on the design of an artificial reef for the purpose of increasing the stocks of horsehair crabs.

A joint Norwegian-Russian paper by Kuzmin, Olsen, and Gerasimova will give us an update on the transplant of the red king crab during the 1960s from the Kamchatka area to the Barents Sea. A full population age-class structure has now developed, and the species is spreading southward along the Norwegian coast. In another Norwegian paper, Mortensen and Damsgard will discuss the potential for aquaculture of red king crab.

From Australia we will hear two papers on the giant crab, *Pseudocarinus gigas*. Levings and Mitchell will discuss the fishery that ranges from 100 to 400 m, and that has been expanding. Their research indicates that only half of the mature females spawn in any given year. We will then hear a paper by Gardner on a laboratory investigation of behavior of the zoeae of this species.

I want to end my introduction on a slightly less serious note. You will likely guess the source of the following quotation before you finish reading it. I hope you enjoy this early and imaginative ocean biology.

> Fishes got up under our feet like birds in the long grass. The massive rocks were rent with impenetrable fractures, deep grottoes, and unfathomable holes, at the bottom of which formidable creatures might be heard moving. My blood curdled when I saw enormous antennae blocking my road, or some frightful claw closing with a noise in some cavity. Millions of luminous spots shone brightly in the midst of the darkness. They were the eyes of giant crustacea crouched in their holes; giant lobsters setting themselves up like halberdiers and moving their claws with the clicking sound of pinchers; a titanic crab pointed like a gun on its carriage; and frightful looking polyps interweaving their tentacles like a living nest of serpents. (Jules Verne. 1870. *Twenty thousand leagues under the sea*. P.J. Hetzel Publisher, Paris, France.)

High Latitude Crabs: Biology, Management, and Economics
Alaska Sea Grant College Program • AK-SG-96-02, 1996

Overview of Southern King Crab and False King Crab Fisheries in the Magellanic Region

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Abstract

The southern king crab or "centolla" (*Lithodes santolla)* and the false king crab or "centollón" (*Paralomis granulosa*) represent an important mixed fishery in the Magellanic zoogeographic region. The history of both crab fisheries is marked by fluctuating resource abundances and the declines of landings in certain places was accompanied by the development of new areas to replace those that had declined. Magellanes Strait and Tierra del Fuego archipelago are the main capture areas, with recent important landings of centolla near Chiloe Island (X Region, Chile). Argentine captures have been low compared with to those of Chile. No serious studies have been conducted to assess the stocks of both species. The Atlantic Patagonian continental shelf appears to offer commercially exploitable stocks of centolla, but this fishery must be highly seasonal. *P. granulosa*, a lesser size crab, is captured mainly in waters surrounding Tierra del Fuego. With a 10-year generation time, the species appear very sensitive to exploitation.

Introduction

In southern South America, various lithodid species are distributed in the cold-temperate waters of the Magellanic Region. This biogeographical region is characterized by the influence of the Circumpolar Current or West Wind Drift, with water temperatures between 3° and 15°C.

The species of *Lithodes* are the largest of the local representatives of the family. The commercial *L. santolla* has a maximum size and weight of 190 mm carapace length (CL) and 8 kg. On the Atlantic coast of South America, *L. santolla* is distributed south of 34°S latitude, from the Uruguayan coast to Tierra del Fuego (Figure 1). On the Pacific coast, they are distributed south to 40°S latitude. In its southern range, *L. santolla* is distributed from subtidal down to 150-200 m. *Lithodes confundens* is morphologically similar to *L. santolla*, and the two species probably overlap in distribution (Macpherson 1988). Therefore, it is likely that *L. confundens* is landed as *L. santolla* in some places.

In the Magellanic Region, crabs of the genus *Paralomis* are also commercially exploited. *Paralomis granulosa* measures 120 mm CL of maximum size and 1.5 kg of maximum weight. This is the only species of the genus that inhabits shallow coastal waters (Macpherson 1988). This species is distributed in coastal waters of Tierra del Fuego and Islas Malvinas (Falkland Islands), from subtidal down to 70 m depth. *Paralomis spinosissima* is found off South Georgias Islands (55°S latitude). Very recently, this species has attracted commercial attention (G.A. Lovrich pers. comm.).

Other species of the family Lithodidae are in the area. *Lithodes turkayi*, a species closely related to *L. murrayi*, inhabits Atlantic waters off the Falkland Islands and Pacific waters off the coast of Chile, from 70 to 400 m depth (Campodónico and Guzmán 1972). *Neolithodes diomedae* is a deepwater species that lives off the Pacific coast of Chile. So far, no commercial interest has been demonstrated for this species.

Although lithodids are widely distributed, the fishery has mainly developed in coastal waters of the Archipelago of Tierra del Fuego. This is probably because major coastal concentrations occur in the Strait of Magellan and in the Beagle Channel. Since *Lithodes santolla* and *Paralomis granulosa* are sympatric and trapped simultaneously in this area, they constitute a mixed crab fishery. The Chilean fishery for king crabs is centered in Punta Arenas, on the north coast of the Strait of Magellan. So far, the main exploited areas of Chile have been the Strait of Magellan, the Beagle Channel, and the Cape Horn area. More recently, the fishery has developed northward, near Chiloé Island (40°S latitude; Figure 1). The Argentinean fishery is mainly in the Beagle Channel, near the city of Ushuaia. Nevertheless, some catches occur on the Atlantic coast, near Comodoro Rivadavia, and off Mar del Plata and Montevideo.

Brief History of the Fisheries

In the late 1920s, the commercial fisheries of the Strait of Magellan (Chile) and of the Beagle Channel (Argentina) started by fishing *L. santolla* exclusively by means of tangle nets. In Chile, from 1930 to 1960, the fishing season lasted only three months per year. The activities were re-

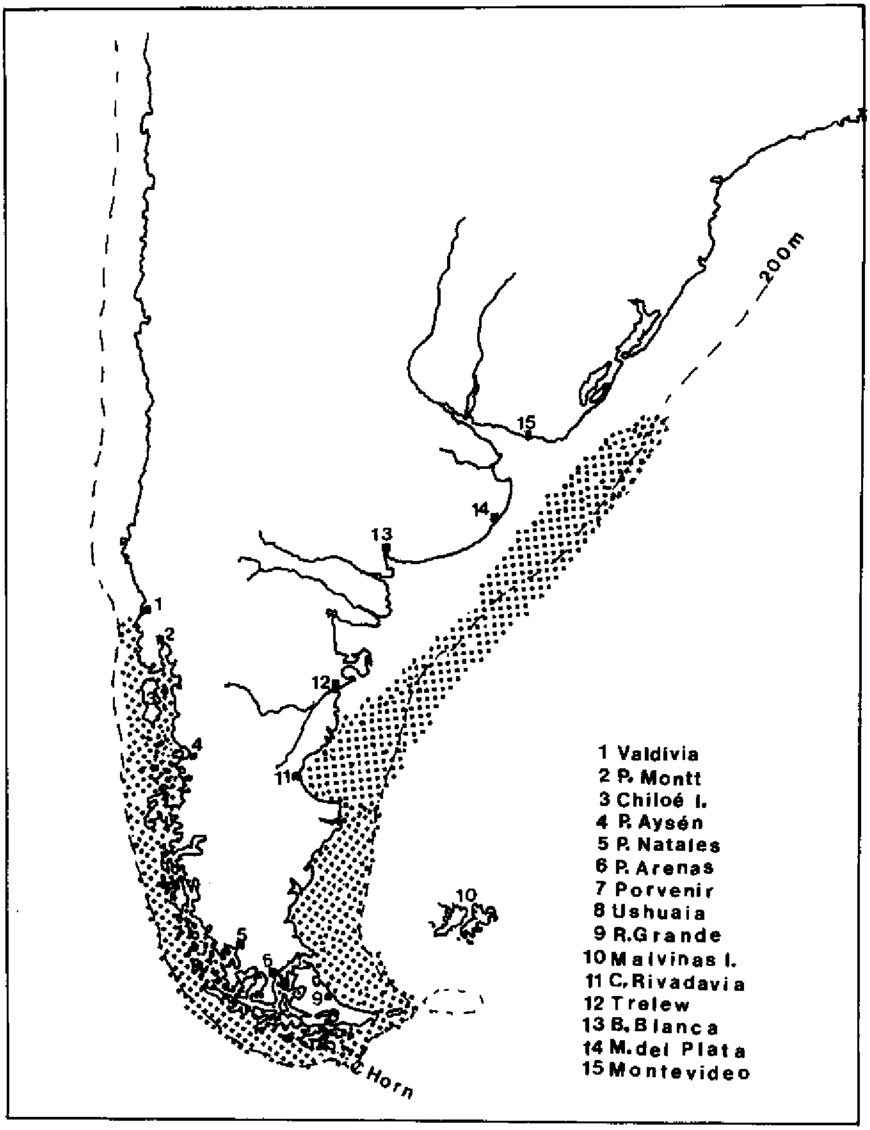

Figure 1. Southern tip of South America, showing landing ports and distribution of L. santolla.

stricted to 75-100 km from Porvenir, mainly in the Strait of Magellan. At that time, landings varied between 50 and 150 mt. In 1934, the first regulations were imposed on the fishery, without supporting biological studies. The first rule was the exclusive landings of males of a minimum size of 120 mm CL. Landing of ovigerous females (those that carry eggs) were explicitly prohibited. A closed season between February and June was also imposed. Some years later the closed season was reduced to two months. These regulations persist today, with the exception of the exclusive use of traps to catch both species. In 1993, for the XII Region, the closed season was extended to seven months between December and June, to protect reproductive and molt periods of both sexes.

In the 1960s, in the XII Region, fishing for *L. santolla* was more intensive than in the past. Landings of *L. santolla* increased steadily to reach 516 mt in 1967 (Table 1). The decrease in catch in some areas was compensated by moving to previously unexploited areas. In the early 1980s, in some areas symptoms of overexploitation appeared. For example, in 1981 Bahía Inútil was closed to fishing for four years. After it was reopened, the catch per unit effort was less than in 1980. Apparently, the number of animals in the population was reduced to a point of non-return: the largest crabs, males and females, were extracted and the reproductive fraction was removed. Evidently, the four-year closure was not enough to allow recuperation. Stock assessments for *L. santolla* are scarce for the Chilean fisheries. Often, crab biomass was monitored by evaluating the changing catch per unit effort.

In Argentina, the main fishery for *L. santolla* and *P. granulosa* has been the Beagle Channel. Until 1975, *L. santolla* was fished only with tangle nets. Traps are now the only gear permitted to fish king crabs. In 1978 additional regulations, similar to Chilean ones, were put in force: a minimum size of 120 mm CL, exclusive male landings, and a maximum of 1,000 traps in an area of the Beagle Channel near Ushuaia. In 1993, a minimum size of 90 mm CL was imposed to land males of *P. granulosa*. Since 1992, fishing effort on lithodids increased slightly. The government of Tierra del Fuego gave new fishing permits to fishers with smaller boats, which formerly had fished mollusks and sea urchins.

Scientific surveys are scarce for *L. santolla* and nonexistent for *P. granulosa*. In 1981-1982, Boschi et al. (1984) calculated the only stock assessment for *L. santolla* in an Argentinean fishery. Consequently, a maximum effort of 1,000 traps was imposed in the area. Surveys of 1988 and 1994 showed a permanent decrease in yields of *L. santolla*, a decrease in the mean size of males and females, and a decrease in the percentage of ovigerous females, down to 30% (Bertuche et al. 1990). These observations indicated symptoms of overexploitation, and in 1994, the area near Ushuaia was closed to fishing.

Landings of *L. santolla* from other sites of the Atlantic coast are from two sources. First, a small fishery has developed in coastal waters

Table 1. Landings of *L. santolla* in diferent areas.

	Area					
Year	I	II	III	IV	V	VI
1965	no data	no data	23.6*	–	5.2	22.9
1966	10.0	–	442.6	–	32.1	27.7
1967	9.0	–	702.2	0.1	22.0	18.1
1968	7.2	–	655.6	2.2	47.9	0.8
1969	4.6	–	632.8	3.1	25.7	4.0
1970	20.6	0.1	622.9	4.6	7.3	4.6
1971	17.2	–	626.3	3.0	11.4	1.3
1972	26.0	–	616.1	6.2	56.4	0.6
1973	24.4	–	473.3	8.9	12.8	0.9
1974	11.2	–	816.6	–	47.0	0.4
1975	12.5	–	847.0	–	57.5	3.0
1976	14.6	–	1216.9	–	75.6	2.0
1977	26.0	–	647.1	–	90.3	10.5
1978	6.9	–	2149.0	–	56.5	4.0
1979	10.2	–	2410.7	–	36.5	2.1
1980	12.0	–	1487.9	–	38.1	5.0
1981	4.0	1.0	1481.4	3.1	32.9	8.3
1982	30.0	2.0	1663.9	–	no data	1.0
1983	21.0	4.6	2876.9	–	no data	2.7
1984	47.0	17.0	2853.0	–	3.5	2.5
1985	30.0	85.0	2713.0	–	no data	2.9
1986	124.0	83.0	2519.5	–	10.5	4.4
1987	39.0	82.0	2202.1	–	no data	30.3
1988	18.0	20.0	2261.8	–	3.6	2.9
1989	11.0	78.0	2323.4	–	64.6	6.5
1990	343.0	14.0	1573.0	–	29.0	1.0
1991	1515.0	76.0	1838.7	–	51.3	2.3
1992	684.0	45.0	1257.0	–	71.6	1.0
1993	1324.0	26.0	1334.1	3.2	119.0	1.9
1994	1033.0	71.0	1110.0	36.1	236.4	1.5

Note: I: X Region; II: XI Region; III : XII Region and Tierra del Fuego Province; IV: Atlantic coasts of Tierra del Fuego and southern Santa Cruz; V: San Jorge Gulf; VI: Deep waters of Buenos Aires Province.

*: data from Beagle Channel only.

near Comodoro Rivadavia (Figure 1, Table 1). Crabs live here in shallow waters (10-60 m) and are fished by means of beam trawls. Hake, cod, elephant fish, soles, and sharks are also landed as bycatch. Second, *L. santolla* landed in other ports such as Mar del Plata or Montevideo are the bycatch of the vessels that fish the Argentinean hake (*Merluccius hubsii*). Landings are from the winter fishing grounds, at 150-250 m depth, in latitudes between 40 and 34°S.

In our opinion, the main factor that makes the fisheries collapse is the continual violation of regulations that has characterized the Argentinean and Chilean fisheries. Usual transgressions are landings of female and sublegal crabs and their slaughter on board; thus the controls on live crabs that arrive in port are avoided. Moreover, the lack of effective controls has promoted violation of fishing regulations.

Landings of *Lithodes santolla*

In Chile, the fishery located in the XII Region was the most important one and until 1989, responsible for more than 95% of Chilean landings (Table 1). Landings increased and reached a maximum in 1983, and then began to decline. Since 1993 landings in the XII Region have been very limited, because of a shorter fishing season of 3 months instead of the former 10-11 months. Main ports of landings are Punta Arenas, Porvenir, and Puerto Natales. The mean size of landed males was 118 mm CL in 1992, 131 mm CL in 1993, and 128 mm CL in 1994. The sublegal fraction varied between 26% and 30% (Alegría pers. comm.).

An important fishery is now located in the X Region with Puerto Montt and Valdivia as the main landing ports (Figure 1). Since 1991, landings have been 10 times those previously recorded (Table 1). Fishing is by means of small boats (5-8 m length) that can manage a limited number of gears. More than 2,000 boats and 5,000 fishers are registered. Fishing season is ten months, from February to November. In this area, legal size is 100 mm CL.

The XI Region is a less-populated area, and fishers and registered boats are fewer than in other areas. There are 590 boats and 1,100 fishers. The main landing ports are Puerto Chacabuco, Puerto Melinka, and Puerto Aysén.

Argentinean landings of *L. santolla* have been low compared to those of Chile. This is mainly because in Argentina, the Beagle Channel has been regularly exploited. The surface of the fishing area is about 250 km^2, small compared to other fishing areas. The landings record was recorded in 1974, and then they began to decline, reaching a low of 32 mt in 1994. The port of landings has been Ushuaia. Currently, only 10 boats are registered to fish in the area. On the east coast of Tierra del Fuego, commercial exploitation of *L. santolla* started in 1993. In 1994, this fishery recorded 31 mt of landings and is growing very fast.

Table 2. Landings of *P. granulosa* in different areas.

Year	XII Region (Chile)	Beagle Channel	Argentine Sea
1978	637	54	–
1979	952	58	–
1980	429	19	–
1981	310	150	–
1982	309	52	–
1983	831	78	–
1984	851	105	–
1985	266	163	–
1986	993	168	–
1987	1773	150	5
1988	2330	186	–
1989	1953	122	–
1990	1865	160	–
1991	3419	189	–
1992	1326	37	–
1993	955	27	14
1994	2220	151	2

The fishery of Comodoro Rivadavia is variable. Landings have been modest and quite varied (Table 1). In the 1970s, landings were recorded at 90 mt; in the 1980s they fell to practically nil. Since the early 1990s, landings have increased to a record of 226 mt.

Landings of *P. granulosa*

Commercial exploitation of *P. granulosa* is exclusively in coastal waters of Tierra del Fuego, i.e., the XII Region in Chile and the Beagle Channel in Argentina. Fishing for *P. granulosa* began as a reaction to declining catches of the sympatric *L. santolla* (Tables 1 and 2). Since 1977, total landings by Argentina and Chile varied from 300 to 3,600 mt. Of these, Chile has harvested about 95%.

Landings have been variable. A maximum of about 1,000 mt was recorded in 1979, and then landings decreased (Table 2). Between 1982 and 1991, landings increased again and reached a record of 3,400 mt. In the following two years, a strong decrease in landings occurred. These variations are associated with market conditions. The product, canned or frozen, is exported to North American and European markets. When the demand for the product decreases, fishing for *P. granulosa* also decreases.

Comments

Exploitation of stocks of both crabs is intensive in southern Chile (X and XII Region) and Tierra del Fuego Province (Argentina).

Between both Chilean regions, the XI Region, there are thousands of kilometers of rugged coastline, no roads for communications, and few and isolated populations. The area has a history of reduced landings, but it is possible that the size of the resources there warrants some investment in crab fishing. Although some observers believe that Chilean stocks of centolla are not sufficient to support great commercial operations, the XI Region (with near 80,000 square kilometers) and the northern area of the XII Region (Trinidad Channel) are potential capture areas.

On the Pacific side, the resource is thinly distributed, since the limiting factor is the extent of the habitat, a narrow band of continental shelf. Argentine stocks have not been assessed on the Atlantic side, but the Patagonian continental shelf extends for hundred of kilometers (Figure 1) and would appear to offer a broad habitat for centolla. Experimental fishing for crabs, however, has found no commercially exploitable stocks in southern Patagonia and surrounding waters of the Falkland Islands. It is possible that seasonal coast fisheries can develop on some areas, when centolla stocks move into shallow waters for reproduction.

P. granulosa is more broadly distributed than centolla, but the stocks are apparently of lesser size. This species is reported on the Atlantic coast near Santos (Brazil), in southern Patagonia, the Falkland Islands, and near Tierra del Fuego to the north to Paso Tenaún, Chiloé Island. Some biological characteristics of the species mark important differences with *L. santolla*: reduced movements, no apparent reproductive migrations, a biennial reproductive cycle, reduced fecundity, and growth (need near 10 years to attain sexual maturity). Thus heavy fishing rates may result in important changes in a population.

Problems with management of this crab fishery change frequently; as the fishery develops in certain areas, intensive landings occur, stocks decrease, and new fishing grounds appear in other areas. Although the two species present similarities in fishing and processing methods, their life cycles differ and that will be the basis of management, taking into consideration the difficulties of collection of data and stock assessment.

Acknowledgment

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Overview of Tanner Crab Fisheries around the Japanese Archipelago

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Abstract

Four species of the genus *Chionoecetes* are distributed in the waters around the Japanese archipelago, while the crab fisheries are operating for three of those species, *C. opilio*, *C. japonicus*, and *C. bairdi*. The *opilio* fishery is operating in the Sea of Japan (Danish seine), the Sea of Okhotsk (trawl), and partly in the Pacific off northern Honshu (trawl). The *japonicus* fishery is operating in the Sea of Japan (trap). The Pacific *bairdi* fishery is only off Hokkaido (gillnet, trap).

There are strict legal regulations for the *opilio* fishery in the Sea of Japan and the Sea of Okhotsk. Male crabs 90 millimeters or larger in carapace width are permitted to be caught. Adult female crabs are also permitted but only in the western and middle areas of the Sea of Japan. According to the legal regulations for *japonicus* in the Sea of Japan, male crabs over 90 millimeters in carapace width are permitted to be caught. However, there are no legal regulations for the *opilio* fishery and the *bairdi* fishery in the Pacific yet.

In 1993, landings of *C. opilio* were 5,094 tons, *C. japonicus* were 26,769 tons, and *C. bairdi* were 138 tons in the waters around the Japanese archipelago. A decrease in the landings of *C. opilio* and *C. japonicus* around the Japanese archipelago is continuing; in 1993 the landing rates compared with maximum landings per year (*C. opilio*, 1967: 30,384 tons; *C. japonicus*, 1984: 55,043 tons) is 16.8 percent for the former and 48.6 percent for the latter. However, as a result of conservation and propagation efforts in the last 10-15 years in the *opilio* fishery in the southwestern Sea of Japan, recently the landings in some waters are constant or slightly increasing.

Introduction

Landings of Tanner crab in 1963 (17,564 tons) were only 39.8 percent of total crab landings (44,114 tons), including anomura, in the waters around the Japanese archipelago. For two decades after 1973, as the landings of Tanner crab, especially *Chionoecetes japonicus*, increased rapidly, total crab landings rose to 55,811 tons, and the landing rate of Tanner crab was as much as 58.3 percent (Figure 1). Tanner crab fisheries are operating for *C. opilio*, *C. japonicus*, and *C. bairdi*. The *opilio* fishery in the Sea of Japan is the oldest, and has been continuing since 1724. This fishery has also been operating in the Sea of Okhotsk since the 1960s and in the Pacific since the 1970s. The *japonicus* fishery began along the middle coast of the Sea of Japan in the 1940s, and spread immediately all over the Sea of Japan including off Hokkaido. For the *bairdi* fishery, started off Hokkaido in the Pacific in 1986, the landings are small and irregular.

There are legal regulations for the *opilio* fishery in the Sea of Japan and the Sea of Okhotsk and for the *japonicus* fisheries in the Sea of Japan. However, as the landings of *opilio* are decreasing, conservation and propagation have been tried, especially in the southwestern waters of the Sea of Japan, and recently the landings in some areas have been constant or slightly increasing. This paper reviews fishery developments, changes of annual landings, legal regulations, and management of the three species around the Japanese archipelago.

Species around the Japanese Archipelago

Three species (*C. bairdi*, *C. angulatus*, *C. japonicus*) and one subspecies (*C. opilio elongatus*) belonging to genus *Chionoecetes* are distributed around the Japanese archipelago (Figure 2). However, Matsuura (1934) and Kamita (1941) did not recognize the distinct difference of *C. opilio elongatus* in the Sea of Japan from typical *C. opilio* in ratio of length of second merus to its width. So most Japanese fisheries researchers do not use the subspecific name. Only one carapace of *C. angulatus* was collected once in 1977 in the Pacific off northern Honshu (Sakai 1976). The hybrids of *C. opilio* and *C. japonicus* are also caught occasionally in the eastern Sea of Japan (Nishimura and Mizusawa 1969).

The *bairdi* Fishery

The distribution of *C. bairdi*, which is called Ou-zuwai crab (means large zuwai crab) in Japanese, is limited to off Hokkaido in the Sea of Okhotsk (Igarashi 1970) and in the Pacific (Watanabe 1992). Because there are insufficient crabs for a directed fishery in the Sea of Okhotsk, fishing areas are limited to only the Pacific. Many small crabs, which were 30-50 millimeters in carapace width in the spring of 1985 and 70 millimeters

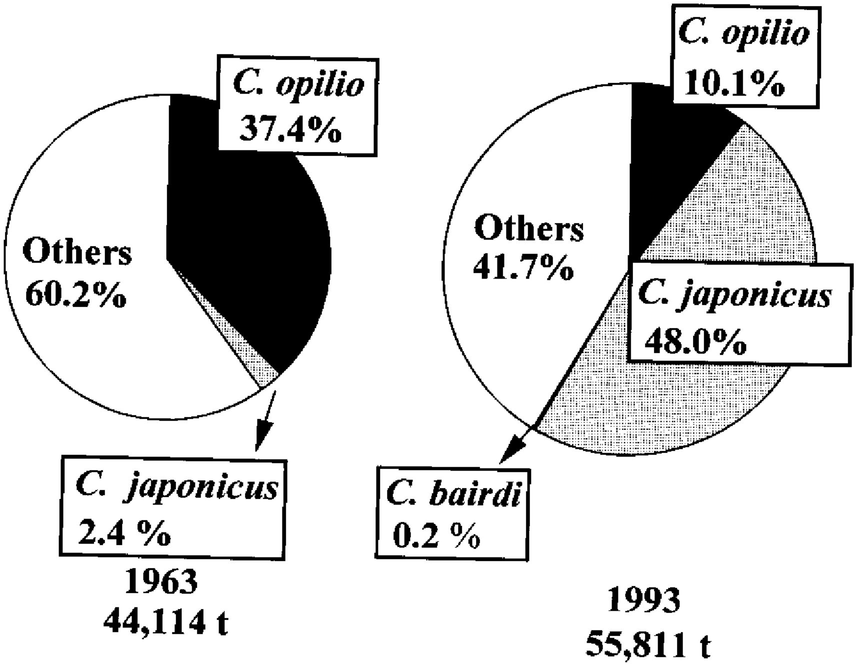

Figure 1. Landings of crabs including anomura in the waters around the Japanese archipelago.

in the autumn, were collected together with *C. opilio* by gillnet for flatfish at less than 80 meters depth off the coast of Hokkaido in the Pacific (Watanabe et al. 1986). As these crabs grew and reached 90 millimeters in 1986, the crab fishery caught 2,301 tons with traps. Around that time the *C. bairdi* fishery started in this area (Figure 3). However, as the population size is not so large and is fluctuating, the catch is not direct but incidental by traps for horsehair crab *(Erimacrus isenbecki)* and by gillnets for flatfish. There are no fishery regulations yet.

The *japonicus* Fishery

Distribution and landings

C. japonicus, which is called Beni-zuwai (means red zuwai crab) in Japanese, is distributed at 500-2,630 meters depth in the Sea of Japan (Yosho and Hayashi 1994), in the Sea of Okhotsk (Watanabe 1991), and in the Pacific off Hokkaido (Nagasawa et al. 1988) and northeastern Honshu to the headland of Inubo (Sakai 1976). In 1941, the fisheries for *C. opilio* using gillnets caught *C. japonicus* at 300-600 meters depth in the

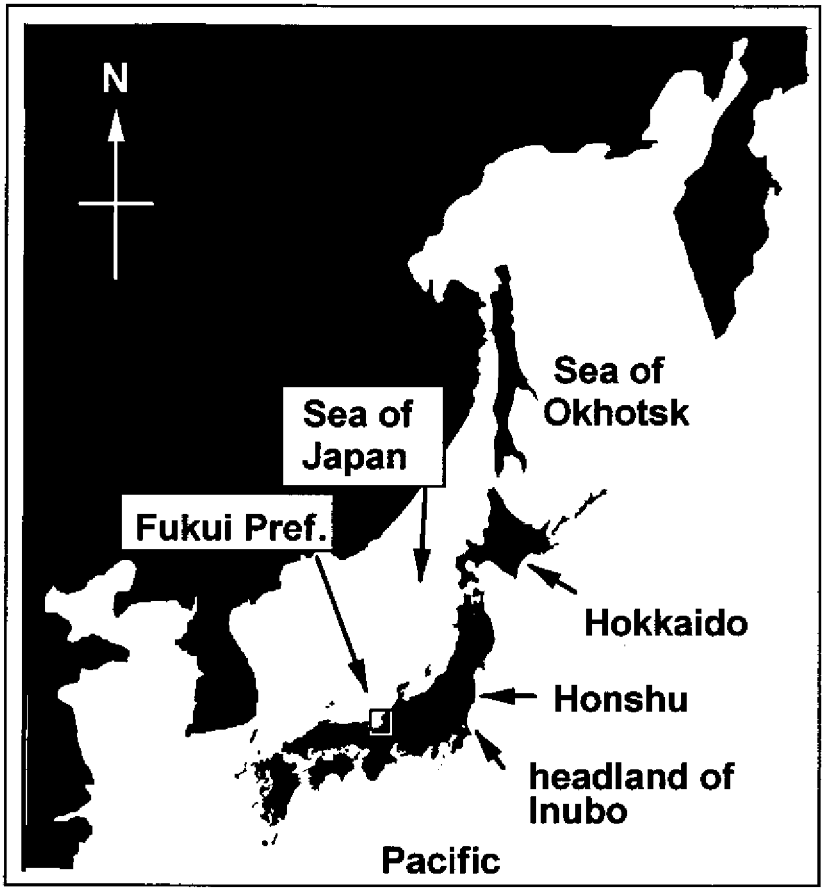

Figure 2. Japanese archipelago and the adjacent sea.

Sea of Japan. Commercial exploitation for *japonicus* using gillnets was developed in the 1950s. Basket traps made from bamboo were devised in 1962, and in 1964 almost all fishing gear changed to basket traps. Fisheries for *C. japonicus* started in the southwestern Sea of Japan in 1967, using basket traps made from iron. New fishing grounds off the west coast of Hokkaido in the Sea of Japan were investigated from the late 1970s to early 1980s, using basket traps, and the commercial catch was started in the 1980s. The annual landings increased rapidly year by year, and the largest landings (53,530 tons) were gained in 1984. After 1985 the annual landings gradually decreased in the Sea of Japan off Honshu, while annual landings off Hokkaido, restricted by quota, have been constant at about 4,000 tons (Figure 4).

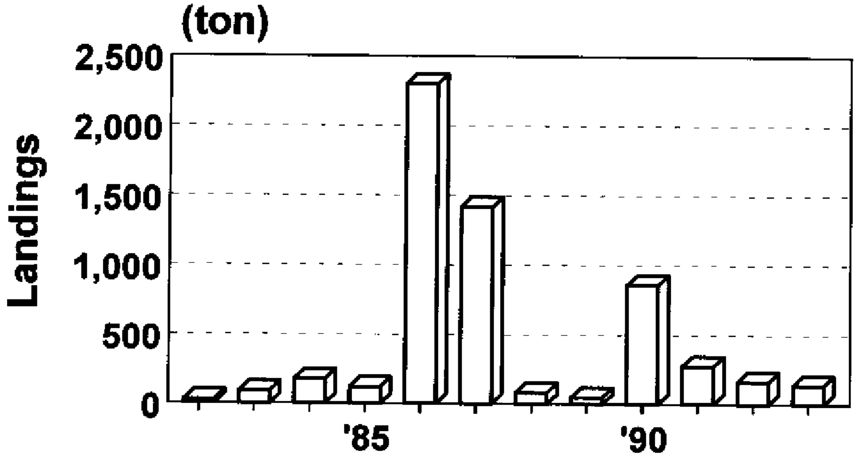

Figure 3. Landings of C. bairdi in the Pacific off Hokkaido, Japan.

Legal regulation

The *japonicus* fishery in the Sea of Japan had been permitted by local governments (prefecture) until 1989 under each prefectural fishery regulation. In 1990 the national government laid down regulations for the *japonicus* fishery in the central and western Sea of Japan; areas permitted by local governments are limited to coastal waters. The regulations laid down by national and local governments are almost all as follows. A fisherman who operates in the central and western areas of the Sea of Japan has to have a permit from the national government, and a fisherman who operates in the coastal areas of the Sea of Japan has to have a permit from each local government. Male crabs 90 millimeters or smaller in carapace width and female crabs should not be taken, possessed, sold, or processed. Fishing season is from September 1 through June 30. Only basket traps have been used.

The *opilio* Fishery

Distribution and fishing ground

C. opilio, which is called Zuwai crab in Japanese, is widely distributed in the coastal zone of the Sea of Japan, the Sea of Okhotsk, and the northern Pacific (from the headland of Inubo). This species is found at depths ranging from 200 to 450 meters in the Sea of Japan, and from 150 to 300 meters in the Sea of Okhotsk (Rathbun 1924, 1925; Yokoya 1933; Matsuura 1934; Kamita 1941; Sakai 1976; Kobayashi and Yamaguchi 1978; Kanno 1972).

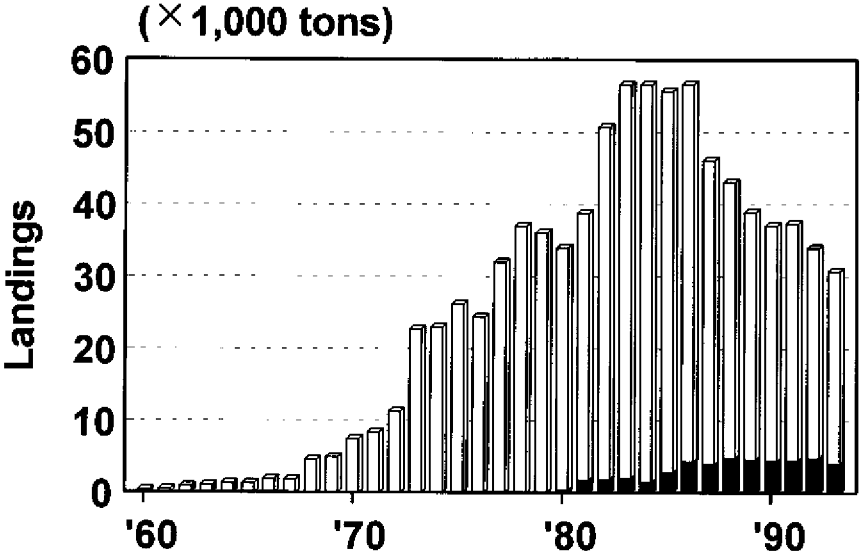

Figure 4. Landings of C. japonicus in the Sea of Japan (☐ = off Honshu, ■ = off Hokkaido).

It is presumed that the *opilio* fishery started first in the southwestern Sea of Japan. It was reported in 1724 that *C. opilio* had been used for food in the locality of Fukui prefecture. In the northwestern Sea of Japan off Hokkaido, fishing grounds for *C. opilio* were investigated starting in 1919 and commercial catches using basket traps started in 1930. As the catch volumes of horsehair crab and king crab *(Paralithodes camtschaticus)* had decreased, the new crab resource, *C. opilio*, was exploited in the Sea of Okhotsk. Investigations of fishing grounds were done using basket traps in 1963, but now the *opilio* fisheries in these waters are operated by trawl. After catch volumes of *C. opilio* decreased and prices increased in the Sea of Japan in the early 1970s, the otter trawl fishery started to catch *C. opilio* in the Pacific off northern Honshu in the late 1970s.

Fishery regulations

There are regulations for the *opilio* fisheries in the Sea of Japan, which is divided into three areas (A-C area), and in the Sea of Okhotsk (D area) (Figure 5). Male crabs smaller than 90 millimeters should not be taken, possessed, sold, or processed in all waters; however, the terms for fishing season and the conditions for adult female crabs are different in each area. In the Sea of Japan *C. opilio* is caught by Danish seine except in most western waters where basket traps are used.

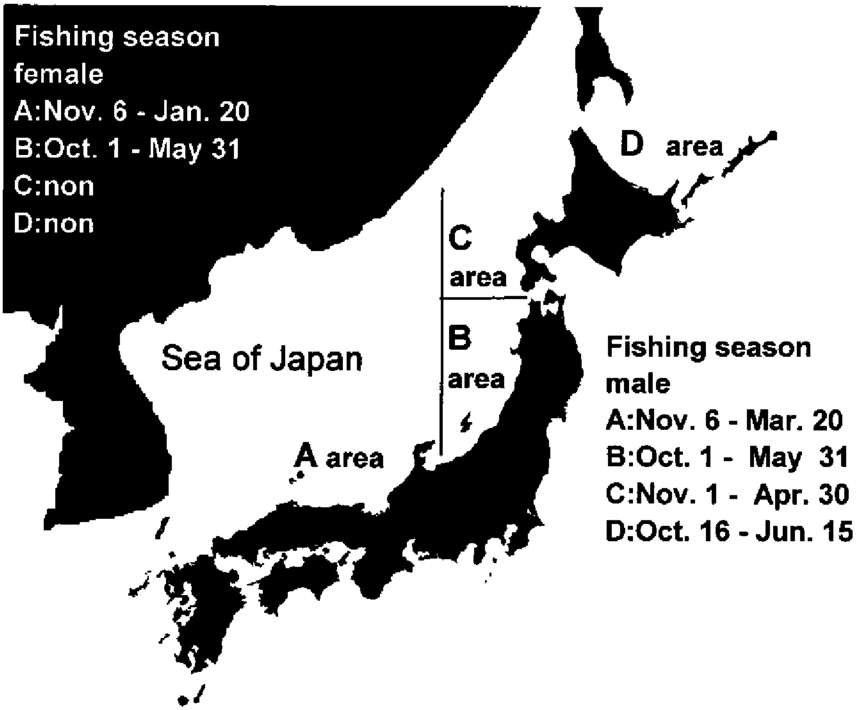

Figure 5. Fishing areas and fishing seasons for C. opilio in Japan.

Landings

In the Sea of Japan the maximum catch volume (15,822 tons) was recorded in 1970. Since then the catch volume has been decreasing, and in 1993 was about 2,000 tons. In the Sea of Okhotsk the maximum catch volume (18,505 tons) was recorded in 1967; however, recent catch volumes are 2,000-4,000 tons. In the Pacific off Hokkaido and northern Honshu, catch volumes are small and fluctuating, with recent catch volumes less than 1,000 tons. Total catch volumes around the Japanese archipelago recorded a maximum (30,384 tons) in 1967; however, these are continuing to decrease, and only 5,149 tons were caught in 1993 (Table 1).

Conservation and Propagation in the Southwestern Sea of Japan

In the southwestern Sea of Japan, Danish seines catch many species besides *C. opilio*, such as flatfishes, shrimps, and snails. The crab season

Table 1. Landings of *C. opilio* around the Japanese archipelago.

Year	Sea of Japan	Sea of Okhotsk	Pacific	Total
1952	5,860			5,860
1953	7,505			7,505
1954	8,974		15	8,989
1955	8,839		2	8,841
1956	8,107		23	8,130
1957	9,608		15	9,623
1958	10,994		67	11,061
1959	10,860		39	10,899
1960	13,281		130	13,411
1961	13,014		27	13,041
1962	14,850		67	14,917
1963	15,603	659	243	16,505
1964	15,534	4,200	400	20,134
1965	11,061	4,030	875	15,966
1966	10,459	8,115	922	19,496
1967	10,554	18,505	1,325	30,384
1968	12,633	15,306	1,147	29,086
1969	12,762	13,364	100	26,226
1970	15,822	13,062	657	29,541
1971	13,008	9,974	737	23,719
1972	12,876	9,480	1,025	23,381
1973	9,022	8,699	242	17,963
1974	8,097	6,522	118	14,737
1975	5,463	6,694	463	12,620
1976	5,073	5,686	202	10,961
1977	6,212	3,311	501	10,024
1978	5,951	3,215	672	9,838
1979	6,564	3,017	708	10,289
1980	6,668	3,808	1,116	11,592
1981	4,827	3,870	706	9,403
1982	4,207	4,632	948	9,787
1983	4,767	2,660	929	8,366
1984	3,665	2,596	639	6,900
1985	3,576	5,311	493	9,380
1986	3,194	6,540	2,513	12,247
1987	2,608	4,614	1,495	8,717
1988	2,452	3,192	478	6,122
1989	2,274	3,553	211	6,038
1990	2,136	1,634	1,029	4,799
1991	2,560	4,681	418	7,659
1992	1,975	4,125	230	6,330
1993	2,298	2,273	578	5,149

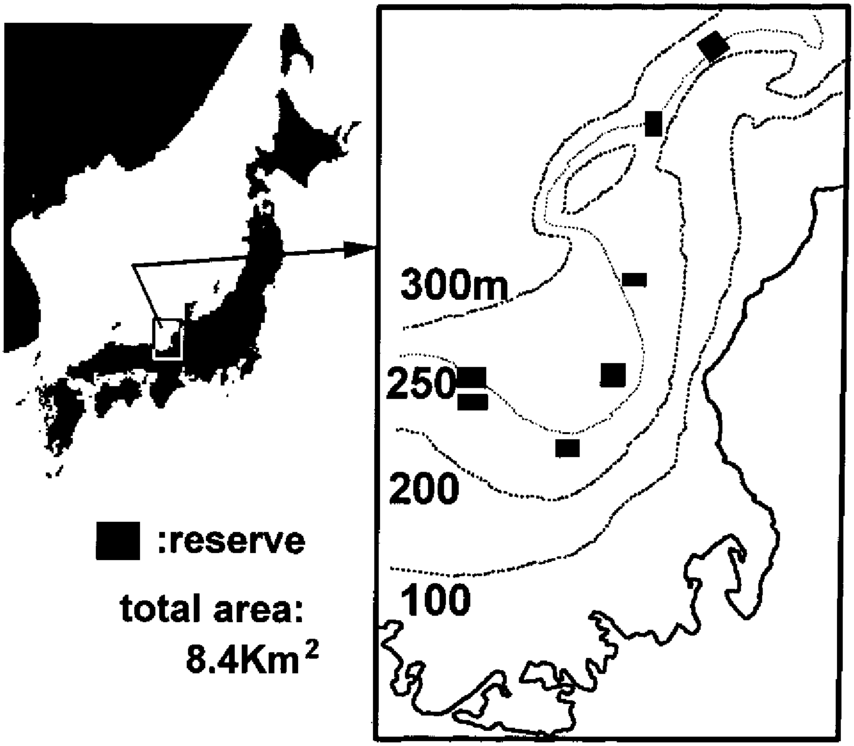

Figure 6. Artificial reserves for snow crab off Fukui prefecture in the Sea of Japan.

(Nov.-Mar.) takes place during the Danish seine season (Sep.-Jun.). Crabs make up 5 percent of the volume of the total Danish seine catch, but they make up 25 percent of the total value. So crabs are the most important species in the Danish seine fishery. Studies on the ecology and life cycle of the crab have been conducted over the last 30 years. In 1988-1992, studies on the conservation and propagation of the stock were done, and researchers proposed several management methods such as reduction of number of boats as a fishery policy, shortening of the fishing season, enlargement of prohibited areas and so on. One suggestion is to construct artificial reserves that protect adult female crabs from high exploitation by Danish seine. The prefectural government of Fukui constructed seven artificial reserves off Fukui prefecture (Figure 6). Each reserve has 5-13 square kilometers and is surrounded by about 60 concrete blocks (3.25 meters cubed and 13 tons weight) which are separated by 250 meters distance. On the inside of these blocks, another 33

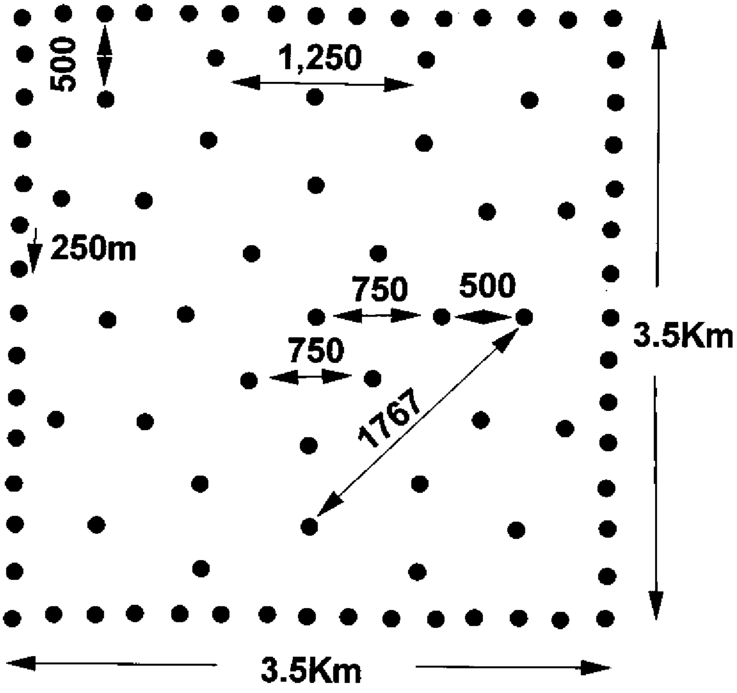

Figure 7. One sample of an artificial reserve for C. opilio constructed off Fukui prefecture in the Sea of Japan (● = concrete block; N = 89).

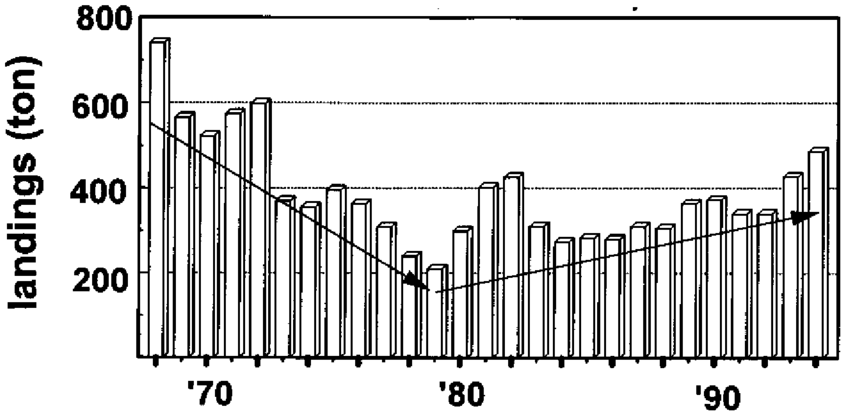

Figure 8. Landings of C. opilio in each fishing season (Nov. - Mar.), Fukui prefecture in Japan.

concrete blocks were set on the seabed (Figure 7). This makes it impossible to operate a Danish seine in this area. As a result of this conservation and propagation, the landings on Fukui prefecture have been increasing gradually, and in the fishing season starting in 1994 the landings recorded 502 tons. This is more than double the lowest volumes (230 tons) in 1980, and is the largest since 1974 (Figure 8).

Acknowledgments

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Status of the Southern King Crab *(Lithodes santolla)* Fishery of the Beagle Channel, Argentina

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Abstract

The present status of southern king crab *(Lithodes santolla)* stock in its traditional fishing grounds of the Beagle Channel (Argentina) is briefly described, and a comparative analysis between present and historical available data is also performed, in order to learn about the temporal evolution of the stock in the area. Results indicate that a sharp decline in stock abundance has occurred through the years, and that a structural break in length composition in compared areas has happened. The deterioration of the reproductive potential of the stock is found to be the most dramatic feature of stock damage: global proportion of ovigerous females were sharply under minimum estimates of previous years, and the estimated size at which 50% of females were carrying embryos has increased markedly with regard to historical records. These factors, combined with decrease in absolute female abundance, will have strong detrimental consequences over future recruitments. General recommendations for the managerial authorities are also discussed.

Introduction

Crab fisheries for the southern king crab (*Lithodes santolla)* and the false southern king crab (*Paralomis granulosa)* in the Argentine jurisdiction of the Beagle Channel (Province of Tierra del Fuego, Antártida, e Islas del Atlántico Sur) extend back to 1930, although commercial efforts were not undertaken until the late 1960s. Historically, the target species in this fishery has been the southern king crab, for its much higher price and constant market demand, factors which have conditioned the false southern king crab (or soft shell red crab) harvest.

These fisheries have great economic importance at a regional level. In the 1970s and early 1980s, when the southern king crab fishery made its best performance, three shore-based processing plants and a small fleet of artisanal and semi-artisanal vessels were settled in Ushuaia, the southernmost city of Argentina. Since then, sustained declining landings for this species occurred. Until 1992, these losses were partially offset by redirecting efforts over the *P. granulosa* stock, favored by the availability of markets for this product. The false southern king crab is the only alternative resource upon which fishermen have relied for their livelihood. Actually, there exist in the Beagle Channel a variety of unexploited commercial species (like mussels, king clip, Malvinas herring, hake, octopus), although local fishermen never diversified for their capture.

In 1992-1993, the lack of suitable markets curtailed the *P. granulosa* harvest, and the dramatic low abundance of the southern king crab was put in evidence, alarming the industrial segment as well as local authorities, concerned for the socioeconomic consequences of a fishery closure. Managerial authorities of Prov. of Tierra del Fuego, Antártida, e Is. Atlántico Sur, implemented a six-month closure in the traditional fishing grounds, and requested the INIDEP assistance for technical support.

The Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), is the only research institution of the National Government to advise on management of fishing resources of the Argentine Sea. It had conducted previous surveys in the area (1975-1976, 1978-1982, and 1987-1989), setting forth the basis of the legislation in force in the Beagle Channel. Current regulations limit the harvest to males above a minimum legal size (110 mm), establish a fishing season in order to protect stock during molting-mating (January/October), limit the effort to be applied in the area to a maximum number of pots (1,000), and permit fishing by gear trap only.

A cooperative plan between scientists, managers, and industry was developed, setting research priorities in order to optimize efforts and costs, in the framework of restricted funding. The basic goals of this plan have been: (1) to advise on the present state of the southern king crab and false southern king crab stocks in the area; (2) to develop a selective fishing gear, aiming to favor the southern king crab avoidance; (3) to develop the fishery of unexploited commercial local resources; and (4) to set a choice of alternative management measures to protect fishing resources in the area, maximizing global production, and minimizing the socioeconomic consequences of possible restrictions to the *L. santolla* fishery.

Several surveys were conducted in the Beagle Channel during 1994. Major research effort was directed toward the preserved zone, to give prompt advice on the southern king crab stock status in order to assess on closure renewing. To know about the temporal evolution of the stock in the area, and its perspectives, a comparative analysis between present and historical data was undertaken; regional crab landings for the period 1972-1995 were also analyzed. Results of this initial study

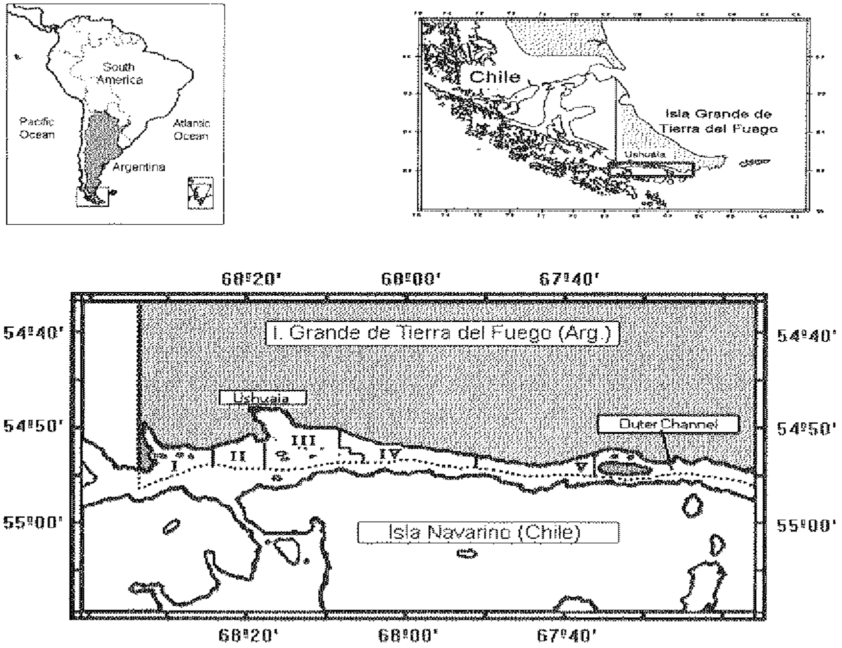


Figure 1. Beagle Channel, Province of Tierra del Fuego, Antártida, e Islas del Atlántico Sur, Argentina. Location of survey areas (I to V).

are presented in this paper, and the general recommendations produced for the managerial authorities are also discussed.

Materials and Methods

The Beagle Channel is shown in Figure 1; following previous surveys (Boschi et al. 1984), the inner channel was subdivided into 5 areas. The preventive 1993 southern king crab fishery closure comprised areas II and III, the traditional fishing grounds which have historically supported the most intense exploitation.

Pot surveys were initiated in April 1994, on a bimonthly basis; surveys were conducted in Areas I, II, and III, and the outer channel was preliminarily prospected. Research was carried out onboard standard operating commercial vessels, with 10 on-line pots, fishing for 48 hours. Iron frame gear pots (measuring 1.50 m in the base and 0.80 m height) are commercially used in this fishery. Collected crabs were measured (carapace length, CL), sexed, and ovigerous females recorded.

Concerning the population structure, size class distributions of the recruited fractions of males and females (5 mm intervals), proportion of males in the catches, percentage of legal size males from total males, and proportions of ovigerous females in each length class, were estimated from pooled data (April through October) for Areas I, II, III.

In order to learn about the temporal evolution of the southern king crab stock in the area, a comparative analysis between present and historical data was also undertaken. Information concerning the population structure and abundance, collected in previous surveys (1975-1976, 1978-1982, 1987-1989) had been gathered and analyzed by Bertuche et al. (1990). These authors chose a three-month period June-July-August (JJA) from years 1975, 1981, 1988, and 1989 for comparative purposes, thus avoiding bias in the population structure caused by critical periods, like maximum probability of molting of males (March-April), or hatching and molting-mating of females (September/December) (Boschi et al. 1984, Vinuesa 1984, Bertuche et al. 1985). On its basis, the 1994 June and August surveys were pooled, and a new set of data was obtained; a complete temporal series (1975-1994) was only available for Area III.

Series of male and female carapace length distributions, from different areas and years, were compared using a Kolmogorov-Smirnov nonparametric test (INIDEP, PRG: KS1, Aubone 1994). A logistic function was fit to the proportion of ovigerous females in each length class interval for the same 3-month period from years 1981, 1989, and 1994, in order to characterize the size at which 50% of the females would be expected to carry embryos as computed by fitted lines. Curves were fit using nonlinear least squares (Microsoft Excel 5.0, Newton algorithm).

Catch per unit effort (CPUE) refers to number of crabs per pot lift, and was estimated in the commercial grounds. Landing statistics were provided by the Dir. General de Recursos Naturales, Prov. Tierra del Fuego, Antártida e Islas del Atlántico Sur.

Results

Annual crab landings for the period 1972 to 1994, and the 1995 June preliminary values, are represented in Figure 2. Southern king crab landings peaked at a record of 381 tons in 1974, and a sustained declining trend was observed since. In 1993, when the preventive closure was implemented, regional landings accounted for 42 tons. Although catch and effort statistics were not available prior to 1989, it may be assumed that effort has remained relatively constant through the years (with exceptions for 1979 and 1980, when the inner channel was closed); in this sense, southern king crab annual landings are grossly reflecting stock abundance. With regard to the false southern king crab, directed harvests were initiated in the 1980s; drastic declines registered in 1992 and 1993 are related to the unavailability of trading markets, rather than to

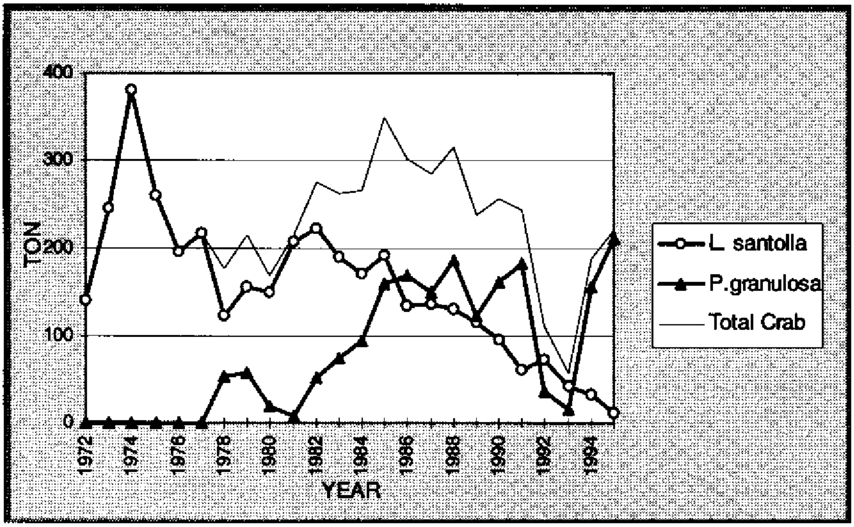


Figure 2. Annual regional landings of Lithodes santolla and Paralomis granulosa from 1972 to 1995. Source: D.G. Recursos Naturales, Prov. Tierra del Fuego, Antártida, e Is. del Atlántico Sur (1995, June preliminary landings).

variations in stock abundance. Partial June 1995 landings for this species (210 tons), have already surpassed historical records. The global output of this fisheries for the period 1972-1994 averages 230 tons.

Estimated 1994 mean CPUEs for Areas I, II, and III were 1.58, 2.80, and 1.57 crabs/pot, respectively, with a mean global CPUE for the whole area of 1.98 crabs/pot of which 0.12 corresponded to commercial males. A preliminary estimate for the outer channel (May) was 0.6 crabs/pot. Mean 1994 JJA-CPUE, estimated in the preserved area (Areas II and III) for comparative purposes, was 1.45 crabs/pot. This estimate represents 12.6%, 15.6%, and 27.9% of estimated mean CPUEs from years 1975 (11.5 c./p.), 1981 (9.26 c./p.), and 1989 (5.20 c./p.), for the same period and area. These estimates and southern king crab annual landings are plotted in Figure 3; a good correlation was obtained (R = 0.99) among series of data.

Regarding the 1994 population structure, mean carapace length and percentages of ovigerous females, males from total catch, and legal size males estimated for Areas I, II, III, are presented in Table 1. Male and female length structure for these areas are plotted in Figure 4. Results of comparisons among sets of male and female length frequencies (Kolmogorov-Smirnov test) from Areas I to III indicate that highly significant differences ($P < 0.01$) exist among distributions tested for males, as well

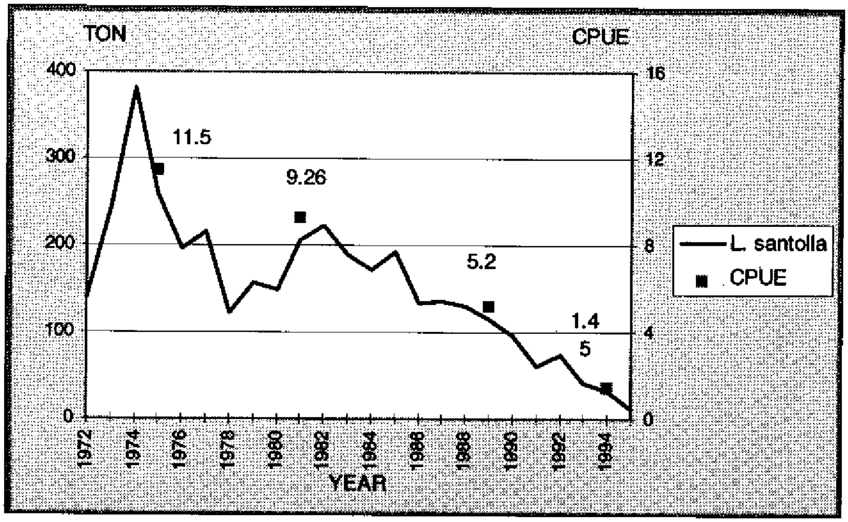


Figure 3. Southern king crab annual landings and mean CPUEs estimated for Areas II and III in 1975, 1981,* 1989,* and 1994 (*Bertuche et al. 1990).*

as for females with the exception of Areas I and III, where significant differences ($P < 0.05$) were detected. It can be observed that smaller size individuals are aggregated in Area II, and have little incidence in the remaining areas; this is also noticed in the varying proportions of legal size males. The global proportion of ovigerous females from total female catch in each area were 44.5%, 11.2%, and 49.6% for areas I to III respectively; these estimates are sharply below historical records.

Structural variations in the size structure of males and females from years 1975, 1981, 1989, and 1994, in the period June-July-August for Area III, were also analyzed (Figure 5). Results of the Kolmogorov-Smirnov test indicate that highly significant differences ($P < 0.01$) exist among series of male length distributions through the years; similar results were obtained for females. It can be noticed that 1994 distributions are strongly distorted with respect to curves observed in previous years. Mean carapace length and percentages of males, legal size males and ovigerous females for the same period and area, are presented in Table 2. A significant decrease in mean carapace length of both sexes was observed by Bertuche et al. (1990) from 1975 to 1989; in 1994, increased mean sizes are registered. The proportion of males in the catches in 1994 has remained in the range of previous years; a relative increment of legal size males from total male catch and a sharp decline in the percentage of ovigerous females are also observed.

Table 1. *Lithodes santolla* pooled data (April-October 1994), for Areas I, II, and III, Beagle Channel.

Area	CLM	SD	N	CLF	SD	N	%M	%LSM	%OF	CPUE	POT
I	111.2	22.73	139	102.2	14.35	113	55.2	56.0	44.1	1.58	160
II	90.7	12.19	457	85.2	9.84	519	46.6	8.1	11.4	2.80	349
III	104.3	16.35	432	98.0	14.05	439	49.4	41.3	49.6	1.57	550

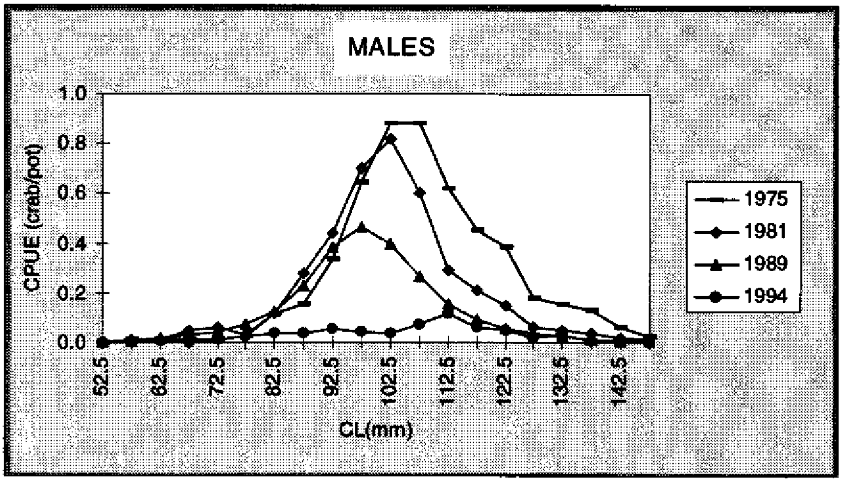
Male (CLM) and female (CLF) mean carapace length, standard deviation (SD), sample size (N), percentage of males from total catch (%M), percentage of ovigerous females (%OF), percentage of legal size males (%LSM), mean CPUEs, and number of pot lifts (POT).

For another perspective to analyze the observed distortions in the structural composition of the southern king crab stock in 1994, the CPUE size class distribution from years under comparison were plotted (Figure 6). Male CPUEs for Area III (JJA) 1975, 1981, 1989, and 1994 were 6.37, 5.28, 2.74, and 0.82 crabs/pot, respectively; female estimates were 5.20, 3.98, 2.46, and 0.63 crabs/pot. A more realistic approach to analyze the temporal variations of the population structure is obtained: a progressive decrease in abundance of modal classes and larger size individuals, for both sexes, is observed through the years. In 1994, male and female distributions are drastically flattened, and the low incidence of the smaller size individuals is causing the observed increments in mean sizes and percentages of legal size males.

The global proportion of ovigerous females in 1994 for the period and area under comparison (JJA-Area III), is well below historical data (Table 2). Distribution of percentages of ovigerous females in each length class is represented in Figure 7. A logistic function was fit to each series, in order to estimate the size at which 50% of the females would be expected to carry embryos; these estimates were 71.1 mm, 73.9 mm, and 102.6 mm CL for 1981, 1989, and 1994, respectively.

Discussion

Crab fisheries of the Beagle Channel historically accounted for most of the total output of Argentina. Major interest in this fishery was always centered on the southern king crab harvest, for its much higher price and constant market demand, factors which have conditioned the *P. granulosa* harvest. The outlook was promising in the 1970s, but since then, a sustained downward trend was observed. By 1986, southern king crab landings were no longer dominant, and the harvest of the false southern king crab helped to sustain the local industry. In 1993, the critical level of southern king crab stock abundance precipitated fishery closure in its traditional fishing grounds, and research was initiated in 1994 in order to advise on its present state and future.



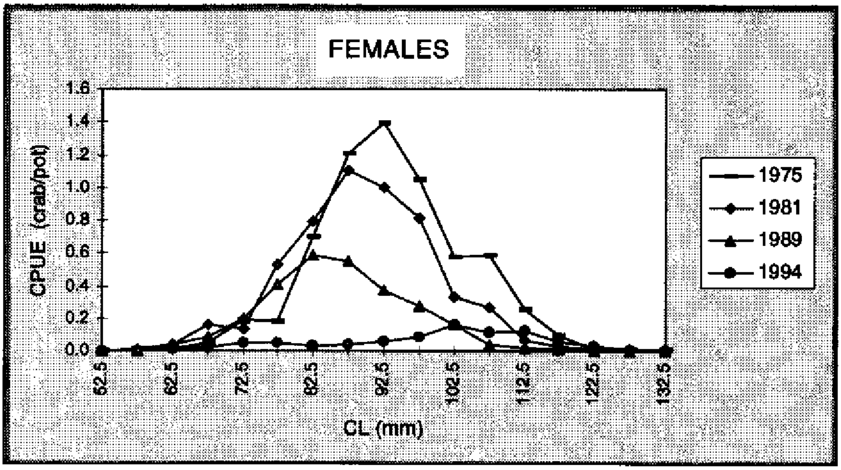


Figure 4. Male and female carapace length frequency distributions, from pooled data (April-October) 1994, for Areas I, II, and III, Beagle Channel.

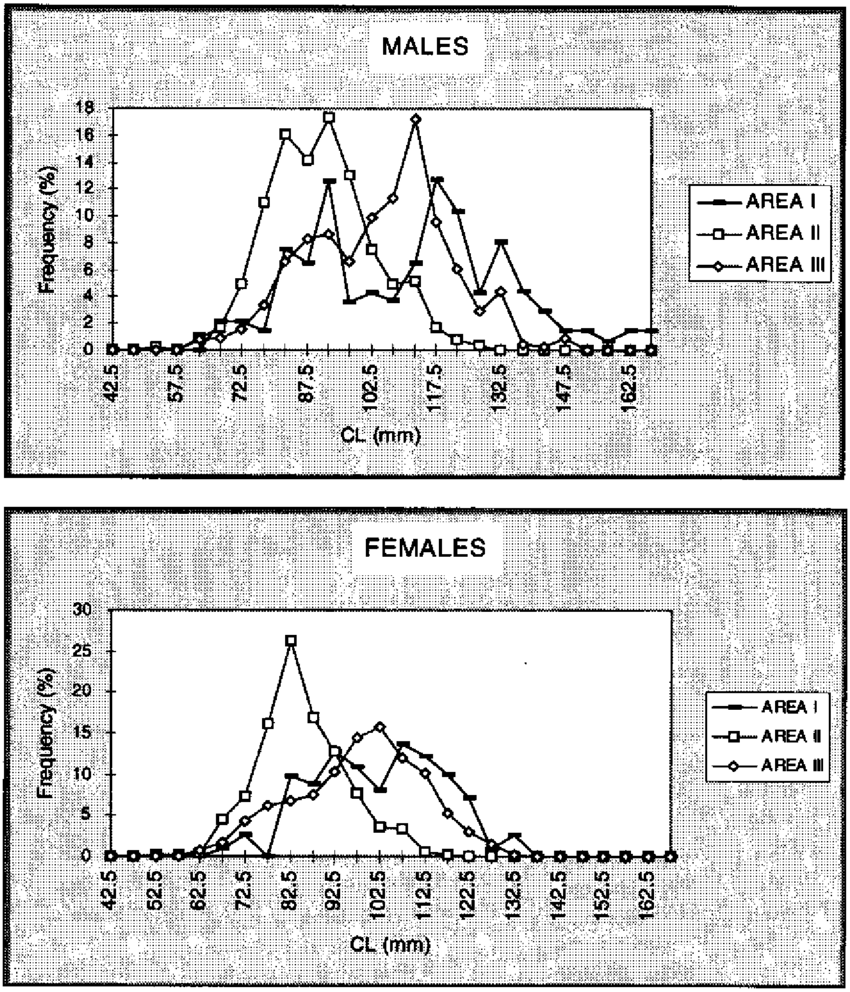


Figure 5. Male and female carapace length frequencies of Lithodes santolla, from pooled data collected in a 3-month period (June-July-August), Area III, 1975, 1981,* 1989,* and 1994 (*Bertuche et al. 1990).*

Table 2. *Lithodes santolla* data for Area III, Beagle Channel, 1975,* 1981,* 1989,* and 1994.

Year	CLM	SD	N	CLF	SD	N	%M	%OF	%LSM
1975	108.2	13.71	2146	93.5	10.28	2652	45.0	—	46.6
1981	102.7	13.09	1228	89.7	10.31	1520	43.3	85.2	26.5
1989	98.6	13.45	762	86.1	10.02	912	47.6	81.2	13.3
1994	105.5	16.92	253	97.3	16.61	283	47.2	27.9	47.2

Male (CLM) and female (CLF) mean carapace length (mm), standard deviation (SD), sample size (N), percentage of males from total catch (%M), percentage of legal size males from total male catch (%LSM), and global percentage of ovigerous females from total female catch (%OF). (*Bertuche et al. 1990.)

Results of research carried out in the area, and evidence brought by the comparative analyses between present and available historical data (Bertuche et al. 1990), have provided some simple but conclusive elements to describe the deterioration of the stock in the area. Regarding stock abundance, a sustained decrease through the years has occurred, being particularly sharp in the past 5. When the temporal variations in CPUEs are analyzed, the 1994 CPUE estimate indicates that stock has declined by 87%, 84%, and 72% with regard to reference years (1975, 1981, 1989). The good correlation obtained among annual landings and CPUEs for Areas II and III leads us to infer that these areas have been closely reflecting regional resource productivity, and thus will provide a helpful index to monitor the evolution of the stock in future years. The state of the resource out of the preserved area seems not to be better; similar yields were obtained in Area I, and regarding Areas IV, V, and outer channel (of open access to fishing), insufficient data was currently collected, although southern king crab landings registered in 1994 and 1995 were negligible.

The sharp decline in stock abundance has produced noticeable distortions in the population structure. The length composition of Areas II and III in 1994 is radically different, a feature not observed prior to 1989 (Bertuche et al. 1990). Smaller size individuals are currently aggregated in Area II, and concerning Area III, the notorious lack of recruitments has produced an aging of the population, determining the observed increments of mean sizes. When the temporal variations in CPUE size class distributions is analyzed (Figure 6), a more realistic approach is obtained: the modal classes have suffered a progressive decline through years, and are absent in 1994. Considering that male legal size is 110 mm CL, it is evident that fishing has been centered in this time lag, in the harvest of females and illegal males.

The most dramatic feature of stock damage is the deterioration of its reproductive potential. Apart from decrease in abundance, the global proportion of ovigerous females in 1994 has been sharply under mini-

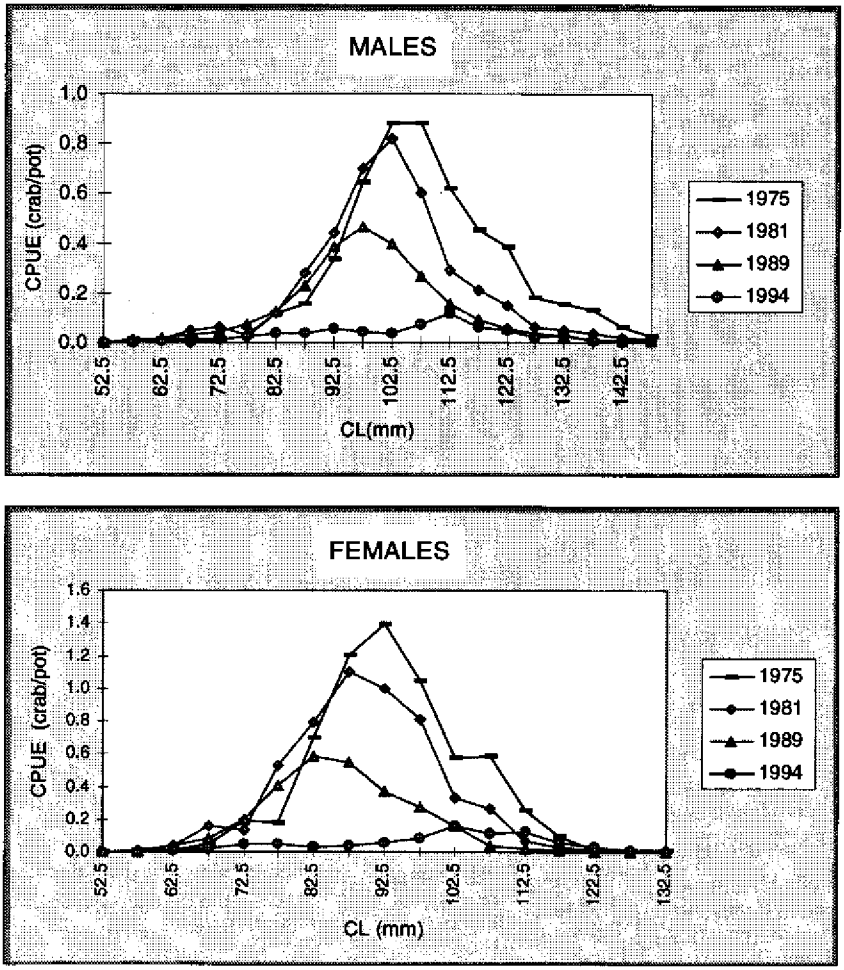


Figure 6. CPUE size class distribution of males and females from years 1975, 1981,* 1989,* and 1994, Area III, Beagle Channel (*Bertuche et al. 1990).*

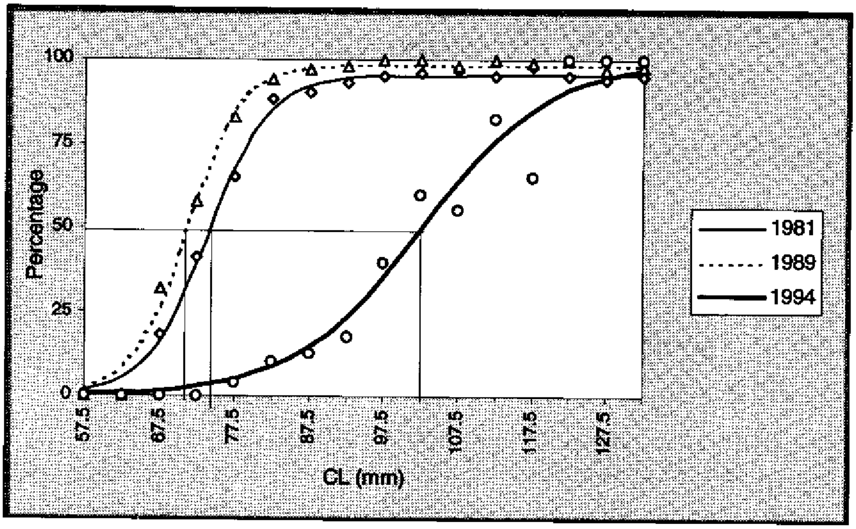


Figure 7. Fitted logistic curves to the percentage of ovigerous females in each length class, from years 1981, 1989,* and 1994, Area III (*Bertuche et al. 1990).*

mum estimates of previous years. Another alarming symptom is the size at which 50% of the females were carrying embryos in the current study period (102.6 mm CL); it has increased markedly with regard to estimates for 1981 (71.1 mm), 1989 (73.9 mm) (Figure 7), and size at maturity (75 mm) mentioned by Vinuesa and Lovrich (1992). These factors are clearly indicating that the reproductive capability of the stock is seriously affected, and this will have strong detrimental consequences over future recruitments.

Undoubtedly, the harvest of females and sublegal males has been a common practice in this fishery, probably the main cause of fishing mortality, the major determinant of the drastic decline in southern king crab stock abundance. Apart from fishing, other sources of crab mortality have not been clearly identified, although a number of factors should be considered: environmental changes, diseases, and the impact of the Chilean fishery in the area. No abnormal incidence of diseases or parasites were macroscopically detected in the current study period. The negative effect of urban waste over the fishing grounds, caused by the dramatic unplanned expansion of Ushuaia city in the past 15 years, cannot be rejected; but if this factor is detrimental, it has acted selectively on the southern king crab stock, as the *P. granulosa* population structure and reproductive potential seem not to be affected. The impact of the Chilean fishery upon the Argentine jurisdiction resource is unknown, and should not be discarded, considering the location of the fishing grounds. Regulatory measures implemented in Chile are similar to those that rule the Argentine fishery, although Chilean researchers (Hernández and Díaz 1986, Díaz 1987) have reported that landings of females and illegal size males have been usual.

Despite reasons for stock decline, it is clear that the state of the southern king crab stock in its traditional fishing grounds is critical, and that stringent management measures, including long-term closures, should be implemented in order to protect and help rebuild the stock. However, perspectives for stock recovery are uncertain, considering that future recruitments will be seriously affected by the currently low reproductive capability.

It is evident that in future years, the Beagle Channel fishery will depend on the *P. granulosa* harvest; trends show that landings will be increased if its commercialization is stabilized. Fishermen have noticed an increase in stock abundance in recent years; a competitive relationship among species, which has favored the false southern king crab expansion in response to southern king crab stock decline, may be posed. Díaz (1987) has made similar observations in Chilean fishing grounds: highest CPUEs were found in areas where the southern king crab became scarce. The outlook for the false southern king crab fishery is good, but stock assessment should be promptly done in order to set adequate harvest levels to preserve its reproductive potential, lowering the risk of recruitment overfishing. The latter is the most serious menace for this 2-year breeding species, which attains sexual maturity after 10 years (Lovrich and Vinuesa 1992, 1993).

Replacement of the southern king crab in this fishery will have important economic consequences for the local industry, taking into account that the false southern king crab is smaller, has a lower meat recovery rate, its international price is one half that of *L. santolla* products, and it has an unstable market demand. The development of unexploited alternative resources of the area could enhance, through diversification, the economic possibilities of fishermen. In addition it will lower the fishing pressure over crab resources.

A complementary training program for the artisanal segment is at present being conducted by the INIDEP research group on fishing gears. Ongoing activities comprise the design of fishing gears adapted to local conditions (50 HP vessels), and training for mid-water pair trawling and coastal longline fishing (Jorge Ercoli, INIDEP, Argentina, pers. comm.). These researchers are also conducting experiments on the selectivity of pot gears, to avoid southern king crab. These studies have been focused in the shortening of the entry tunnel of the pot, and preliminary results obtained with one half cones are encouraging (Jorge Ercoli, INIDEP, Argentina, pers. comm.). If an effective selective pot could be developed, fishing for the false-king crab could be permitted in closed areas, a fact of particular importance for the artisanal fleet, whose search radius is almost limited to the currently preserved zone.

Taking into account the above-mentioned results, the following recommendations were produced for the managerial authorities of Province of Tierra del Fuego, Antártida, e Is. Atlántico Sur:

(a) Not to increase fishing effort in the area.

(b) To implement a long-term closure in the surveyed areas I, II, and III, including the false southern king crab into fishing prohibition.

(c) To continue research on areas IV, V, and outer channel, to determine the present status of stocks in these areas; to monitor periodically closed areas.

(d) Stock assessment for *Paralomis granulosa* in the area, to determine adequate levels of exploitation.

(e) To encourage development of fisheries for new alternative resources.

(f) To continue experiments on selectivity of gear pots, to avoid southern king crab.

(g) To favor the interchange of biological information and fishery statistics with Chile, in order to implement coordinated managerial regulations.

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Evaluation of Alternative Management Measures to Reduce the Impacts of Trawling and Dredging on Bering Sea Crab Stocks

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Abstract

The North Pacific Fishery Management Council is looking for ways to rebuild red king, Tanner, and snow crab stocks in the Bering Sea. The council has delegated authority over crab management to the state of Alaska and is thus constrained to modifying its management strategies for groundfish and scallop fisheries as a means to reduce the impacts on crab populations. We examined several alternative management measures that the council has proposed to reduce impacts of trawling and dredging on crab stocks. These measures include time/area closures, bycatch limits, and market solutions. Our analysis suggested that a comprehensive trawl/dredge closure area in the nearshore waters of Bristol Bay may allow increased red king crab recruitment by protecting juvenile crab and their habitat. Bycatch limits previously established for trawl and dredge fisheries could be reduced to conserve some crabs, but would have little benefit to crab stocks. Similarly, bycatch management through individual vessel bycatch accountability may allow slightly larger harvests of crab predators and competitors such as yellowfin sole and Pacific cod, but the impact on crab rebuilding would be minor.

Introduction

Bering Sea crab stocks are currently at relatively low levels based on the 1994 National Marine Fisheries Service (NMFS) bottom trawl survey data, which indicated that exploitable biomass of Bristol Bay red king crab (*Paralithodes camtschaticus*), and Bering Sea Tanner crab (*Chionoecetes bairdi*) and snow crab (*Chionoecetes opilio*) stocks are about one-fifth record levels (Stevens et al. 1994). Red king crab stocks are at their lowest level since the fishery was closed after the first stock collapse in 1983. In 1994, Bristol Bay was closed to red king crab fishing because the annual trawl survey indicated little prospect for increased recruitment of mature males or females, and low female spawning biomass. Although the Tanner crab fishery in the Bering Sea opened as scheduled, the guideline harvest level was reduced to only 7.5 million pounds. In addition, the area east of 163°W was closed to Tanner crab fishing to minimize the bycatch of female red king crabs. The 1995 snow crab harvest was less than one-fourth of the record 1991 harvest (73.6 million pounds in 1995, 325 million pounds in 1991).

This situation has prompted the North Pacific Fishery Management Council to examine ways to rebuild red king, Tanner, and snow crab stocks in the Bering Sea. In January 1995, the council formed a committee to develop a rebuilding plan for Bering Sea crab stocks. The committee synthesized available information on sources and magnitude of crab mortality and identified alternative management strategies the council might use to enhance the survival of crab stocks and thus promote rebuilding (Witherell 1995b). In addition to establishing the rebuilding committee, the council initiated several analyses to examine impacts of proposals to control crab bycatch in the groundfish fisheries. The first analysis examines the effects of instituting a trawl closure area in the northeast section of Bristol Bay (north of 58°N and east of 162°W) to protect juvenile crabs, seabirds, marine mammals, and spawning herring stocks. A second analysis examines the impacts of reducing the existing crab bycatch limits for groundfish trawl fisheries. In addition, the council initiated an analysis of an individual vessel bycatch accounting program for all Bering Sea trawl fisheries, with the exception of the pelagic trawl pollock fishery.

The focus of this paper is what the council can do to lessen the impacts of trawling and dredging as an aid to rebuilding crab stocks. Three primary alternatives (time/area closures, bycatch limits, and vessel bycatch accounts), which have been proposed by the council as potential measures to reduce the impact of groundfish fishing on crab resources, were examined from a rebuilding perspective.

Alternatives and Options

A rebuilding plan for crab stocks would be based on changing management strategies for crab, scallop, and groundfish fisheries to maintain adequate crab spawning stock and provide suitable habitat. In addition to natural mortality, the magnitude of these fisheries determines the survival of juvenile crabs after settlement.

Crab fisheries appear to be the largest source of mortality, and therefore changes to management of these fisheries may have significant impacts on crab rebuilding. Mortality attributable to the crab fishery includes harvest of large males, handling mortality of females and sublegal males, and ghost fishing by lost pots. In 1993, approximately 2 million red king crabs, 7 million Tanner crabs, and 228 million snow crabs were harvested. An additional 6 million red king crabs, 30 million Tanner crabs, and 6 million snow crabs were taken as bycatch (Tracy 1994). Although handling mortality of king and Tanner crab has generally been found to be low in laboratory experiments (MacIntosh et al. 1996, Zhou and Shirley 1995), examination of historical abundance data suggested that handling may result in relatively high mortality of red king crab (Zheng et al. 1995a). Mortality caused by ghost fishing of lost crab pots and groundfish pots remains unquantified, but escape mechanisms have been required to reduce potential impacts (Kruse and Kimker 1993).

Under the terms of the king and Tanner crab fishery management plan for the Bering Sea and Aleutian Islands area, conservation of crab is mainly at the state's discretion. The state is in the process of developing a crab rebuilding plan based on limiting crab harvest (Zheng et al. 1995a). Recently, the state has focused research efforts on crab stock dynamics (Zheng et al. 1994, Zheng et al. 1995b, Tyler and Kruse 1995), and evaluating changes to crab fishery management (Kruse 1993, Schmidt and Pengilly 1993, Murphy et al. 1994, Kruse 1995, Zhou and Shirley 1995). Modifications to crab harvesting strategies (based on size limits, sex restrictions, and seasons) and gear design that would reduce bycatch and handling mortality are also being evaluated (Kruse 1995).

Although the council delegates management authority of the crab fishery to the state, the council does have direct control over the groundfish and scallop fisheries in federal waters. In harvesting groundfish and scallops, mobile gear fisheries take crab as bycatch and possibly damage crab habitat. Among the objectives of the Bering Sea and Aleutian Islands groundfish fishery management plan is minimizing the impact of groundfish fisheries on crab and other prohibited species, while providing for rational and optimal use of the region's fishery re-

Table 1. Crab bycatch in the 1993 Bering Sea and Aleutian Islands groundfish and scallop fisheries, by gear type.

	Red king	Tanner	Snow
Trawl	248,121	3,412,342	14,631,617
Hook and line	417	7,949	127,966
Groundfish pot	11	1,535	1,138
Scallop dredge	6	276,000	15,000

sources. All gear types used to catch groundfish have some potential to catch crab incidentally and impact habitat, but fishery managers and crab industry representatives have been primarily concerned with reducing the impacts of dredge and trawl fisheries (NPFMC 1986, Thomson 1990, NPFMC 1995).

Trawling and dredging can have direct and indirect effects on crab survival. Direct mortality can be estimated from observer bycatch data. In 1993, trawl and dredge fisheries caught about 248,500 red king crabs, 3,700,000 Tanner crabs, and 14,800,000 snow crabs, and some additional crabs taken by other gear types (Table 1). This bycatch equates to about 0.6% of the red king crab stock, 1.2% of the Tanner crab stock, and 0.1% of the snow crab stock in the Bering Sea as indexed by NMFS bottom trawl surveys. Because not all these crabs die, the direct mortality due to groundfish fisheries may be lower than suggested by bycatch numbers alone. Stevens (1990) found that 21% of the king crabs and 22% of the Tanner crabs captured incidentally in trawl fisheries survived at least 2 days following capture. Observations of the 1993 Bering Sea scallop fishery indicated immediate survival of bycaught crabs was about 80-90% (Urban et al. 1994). Indirect mortality of crabs that come into contact with trawl and dredge gear yet are not captured may be an additional source of mortality. In an experiment using tethered red king crabs, Donaldson (1990) found that only 2.6% of the crabs in a trawl's path (but not captured by the trawl) were injured. Indirect mortality associated with trawling has proven difficult to quantify because the impacts occur on the ocean floor and cannot be directly observed.

Trawling and dredging may also negatively impact crab habitat. Studies have shown that trawling and dredging impacts the seabed through scraping and ploughing, sediment re-suspension, and physical destruction, removal, or scattering of non-target benthos (Messieh et al. 1991, Jones 1992). Trawling and dredging can destroy or eliminate epifaunal communities (Hutchings 1990). Because juvenile red king crabs in the Bering Sea depend on both physical substrate and biotic assem-

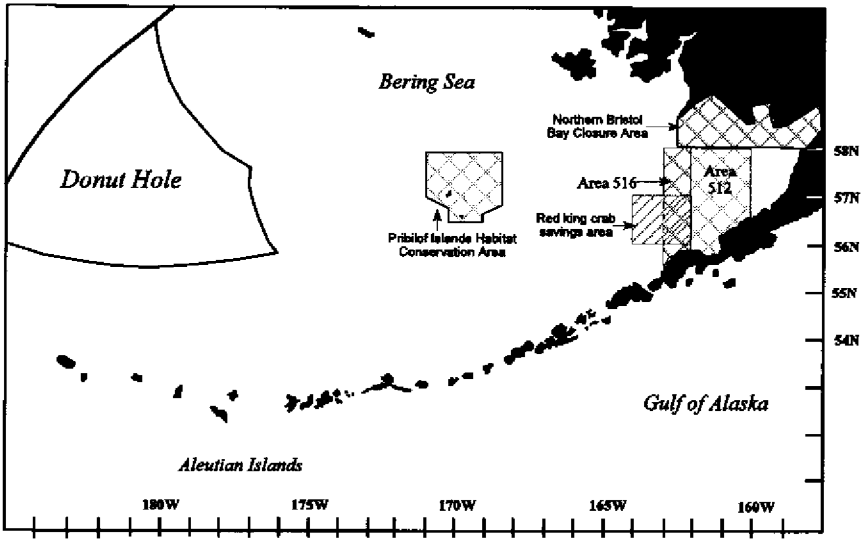

Figure 1. Areas closed to trawling in the Bering Sea to protect king crab. The international waters of the central Bering Sea have been termed the Donut Hole.

blages for settlement, food, and protection from predators (McMurray et al. 1984, Stevens et al. 1992), impacts of trawling and dredging could have long-term negative impacts. Both the physical substrate (cobble, shell) and biotic assemblages (such as ascidians and tube-building polychaete worms) are vulnerable to trawling. If habitat is impacted by trawling and dredging, then settlement and survival of crabs could be reduced, resulting in lower recruitment and spawning biomass.

Time/area closures

Large portions of the Bering Sea have been closed to trawling to protect adult king crabs and crab habitat (Figure 1). Crab protection areas were implemented in 1987 to prevent the incidental catch of adult male and female red king crabs in the domestic trawl fisheries. Protection Area 512 is closed to trawling year-round, and Protection Area 516 extends the closure west to 163°W from March 15 to June 15. The Pribilof Islands Habitat Conservation Area was implemented in 1995 to protect blue king crabs and their habitat by prohibiting trawling year-round. The Red King Crab Savings Area was implemented as a seasonal closure beginning in 1995 to reduce bycatch of adult red king crabs in Bristol Bay.

Closure areas have also been proposed to protect juvenile crabs and their habitat from negative impacts associated with bottom trawling.

Armstrong et al. (1993) suggested that nearshore areas from Unimak Island to east of Port Moller be closed to trawling to protect these important breeding, hatching, and settlement areas. In January 1995, the council initiated an analysis of a trawl area closure in northern Bristol Bay east of 162°W longitude and north of 58°N latitude. One objective of the proposed year-round closure is to increase crab recruitment into the adult populations, rebuilding the population of red king crab to their relative historical level. This area, as well as other nearshore (< 50 m) areas in Bristol Bay, is known to contain juvenile red king crab habitat. In addition to protecting red king crabs, the northern Bristol Bay closure was proposed as a protection measure for migrating herring, seabirds, and marine mammals. Portions of the northern area are already closed to protect walrus. Since 1992, the areas within a 12-mile radius of Round Island, the Twins, and Cape Pierce have been closed to all fishing from April 1 through September 30.

The effectiveness of any trawl/dredge closure designed to protect juvenile red king crabs hinges on our understanding of recruitment dynamics and the distribution of juveniles and their habitat. It has been hypothesized that red king crab encounter a critical intersection at the settlement and juvenile stage, when the availability of appropriate habitat constrains the abundance of juveniles, in turn affecting the year-class strength and recruitment (Cassano et al. 1995, Tyler and Kruse 1995). Larval crabs drift with the current before they settle on the sea floor. Larval settlement and survival patterns vary according to ocean currents and availability of appropriate substrate. If the current transports the larvae to an area without suitable habitat, the chances of survival are slim (McMurray et al. 1984, Jewett and Onuf 1988). Larval crabs settle in late July and August in areas with biotic assemblages and rocky substrate, where they stay as juvenile crabs for the first two years before they move to deeper waters. Juvenile red king crabs are solitary and cannibalistic, and require habitat that provides protection. Therefore, during this time they are mainly found among biotic assemblages, such as tube building polychaete worms, erect bryozoans, mussels, kelp, and ascidians (McMurray et al. 1984, Stevens et al. 1992, Armstrong et al. 1993). If no epifaunal community exists, juveniles can be found on rocky or gravel substrate (McMurray et al. 1984).

In the Bering Sea, juvenile red king crabs inhabit depths less than 50 m, and have been found along the Alaska Peninsula and around Kvichak and Togiak bays. Within this area juveniles live among epifaunal communities, which are associated with gravel/cobble substrate. Juvenile distribution in Bristol Bay can be interpreted from the distribution of gravel/cobble substrate (Hood and Calder 1981, McMurray et al. 1984) and areas sampled for young crabs (McMurray et al. 1984, Stevens et al. 1992, Armstrong et al. 1993). Suitable juvenile habitat is "extremely patchy" in Bristol Bay (McMurray et al. 1984, Jewett and Onuf 1988). Areas shown by surveys to contain age 0-2 juvenile crabs likely underes-

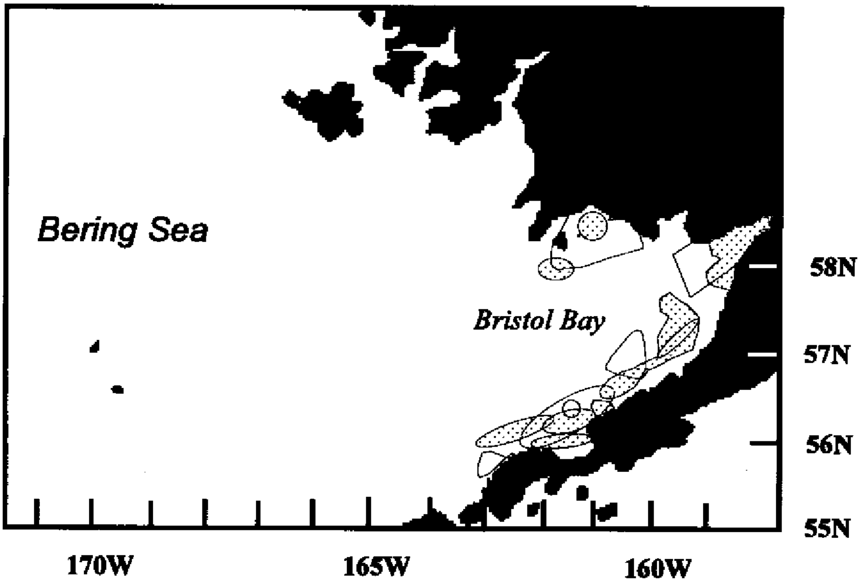

Figure 2. Generalized distribution of age 0-2 red king crab (stippled areas), and gravel sediments (open areas) in Bristol Bay, Alaska. Source: Hood and Calder 1981, McMurray et al. 1984, Stevens et al. 1991.

timate their actual distribution because the entire area has not been sampled, and young crabs are difficult to catch with sampling gear, particularly in cobble habitats (Stevens et al. 1992). Furthermore, distribution of juvenile red king crab may be affected by year-class strength. Juvenile surveys were conducted in years of low stock abundance, 1984 and 1991. The abundance and distribution of juveniles might have been more encompassing and conclusive had the surveys occurred in the early 1970s. Sample areas with low abundance could be viable habitat in times of high abundance. From the existing survey data it is not possible to determine the exact distribution of juveniles in any given year. However, by combining the survey data of where juveniles have been sampled with substrate information, a general map of juvenile red king crab habitat can be constructed (Figure 2).

Although the proposed closure area in northern Bristol Bay would protect some juvenile red king crab habitat, more comprehensive nearshore area closures may be considered. Due to the depressed state of the stock and the existing knowledge that trawling may potentially damage juvenile habitat, a modified trawl closure might be warranted. Both Armstrong et al. (1993) and Cassano et al. (1995) proposed more extensive trawl closures to protect both spawning females and juvenile habitat from impacts of trawling. The lack of suitable habitat could be a population constraint, and habitat protection should be considered as a means to increase red king crab populations (Armstrong 1993, Cassano et al. 1995). Since there is uncertainty about the exact interactions between trawling and juvenile crab and its habitat, the ultimate trawl closure system would allow research trawling in designated areas to study the interactions between trawling, juveniles, and their habitat. As the effects of trawling and the juvenile habitat are better understood, modifications and adjustments could be made to evaluate existing management measures.

Another factor to consider when developing appropriate refugia for juvenile red king crabs is their migration into deeper water as they get older. Cassano et al. (1995) proposed closing migration corridors for juvenile crabs between the ages of 2-4 as they migrate into deeper waters and into the adult protection zone. After the age of 2 juvenile crabs begin podding, forming into large clusters of crabs, for protection from predators as they move into deeper waters (> 50 m) (Jewett and Onuf 1988, Dew 1990, Stone et al. 1993). These pods are vulnerable to trawling, which could cause direct mortality or break up pods and expose crabs to predation. Migration corridors may allow the juveniles to move safely from nearshore nursery areas into the existing adult protection areas.

Analysis of area closures should take into account costs to the affected fisheries, benefits to future crab fisheries and effects of the displaced trawl effort on other areas (Sumerton and June 1984). To date, relatively little domestic trawling has occurred in the nearshore areas of Bristol Bay, so costs to affected fisheries may be minimal. However, combined with the closure of the Pribilof Islands Area to trawling, additional closures in Bristol Bay to bottom trawling could potentially shift trawling to areas containing Tanner and snow crab habitat. Potential benefits of a nearshore closure to future crab fisheries are difficult to quantify. However, if environmental conditions for spawning, settlement, and survival are favorable such that stocks rebuild to historic levels, benefits to crab fishermen would be substantial.

Bycatch limits

Another management measure that has been proposed to rebuild crab is a reduction of the existing prohibited species catch (PSC) limits for king crab and Tanner crab, and implementation of a new PSC limit for snow crab. Prohibited species bycatch limits and zones were designed to control the number of adult red king crabs and Tanner crabs taken as bycatch in trawl fisheries. Current crab PSC limits, which were negotiated by crab and groundfish industry representatives, are 1,000,000 Tanner crab and 200,000 red king crab in Zone 1 and 3,000,000 Tanner crab in Zone 2 (Figure 3). To allocate total groundfish harvest under established PSC limits, PSC is apportioned among trawl fisheries during the annual

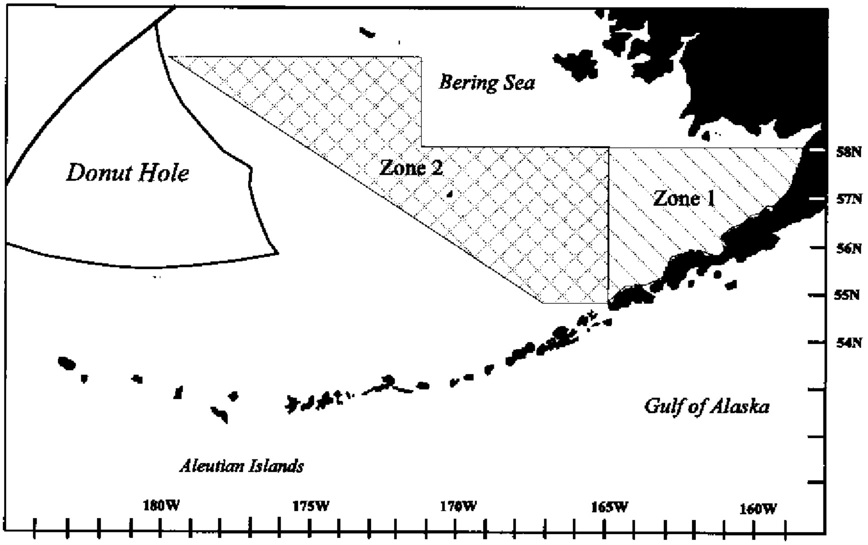

Figure 3. Prohibited species bycatch limitation zones for U.S. groundfish fisheries in the Bering Sea.

specification process. When a target fishery attains a PSC apportionment or seasonal allocation specified in regulations, the bycatch zone to which the allocation applies closes to that target fishery for the remainder of the season.

Bycatch management in the Bering Sea has become increasingly complex over the past ten years, as the groundfish fishery management plan was amended to meet changing management needs. Bycatch limits for domestic fisheries were first adopted in 1986 under Plan Amendment 10, which specified red king crab and Tanner crab PSC limits for the yellowfin sole/other flatfish fishery only. PSC limits of 135,000 red king crab and 80,000 Tanner crab in Zone 1, and 326,000 Tanner crab in Zone 2, were negotiated between representatives of crab and groundfish fishermen. In 1989, Amendment 12a extended crab PSC limits to the remaining trawl fisheries and increased crab PSC limits to the current levels. Amendment 16, adopted in 1990, authorized seasonal apportionment of PSC limits, and apportioned the trawl PSC limits for 1991 into allowances for domestic turbot, rock sole, yellowfin sole/other flatfish, other domestic groundfish, and joint-venture flatfish fisheries. More recently, PSC limits for crab have been apportioned among the following trawl fisheries: yellowfin sole, rock sole/other flatfish, turbot/sablefish/arrowtooth, rockfish, Pacific cod, and pollock/Atka mackerel/other species. Crab PSC limits for the scallop fishery were implemented

Table 2. **Crab bycatch in Bering Sea trawl fisheries, 1992-1994, by zone.**

	Red king (Zone 1)	Tanner (Zone 1)	Tanner (Zone 2)
1992	110,520	853,269	2,326,578
1993	183,713	1,031,985	2,337,884
1994	244,634	752,886	1,692,628
Average	179,622	879,380	2,119,030
PSC limit	200,000	1,000,000	3,000,000

by the state in 1993, and were adopted by the council as part of a federal scallop fishery management plan amendment in June 1995.

By design, crab bycatch limits have constrained the scallop fishery in the Bering Sea. There have been no scallop TACs set for the Bering Sea; consequently, the fishing season ends once a bycatch limit is reached. The state set crab bycatch limits in the Bering Sea based on an acceptable bycatch rate, extrapolated to a limit based on the projected number of vessels participating and limited season length. For 1994, PSC limits were set at 260,000 Tanner crab and 17,000 red king crab. The season closed when 261,365 Tanner crab were taken.

Crab PSC limits have not constrained most groundfish trawl fisheries. Rather, these fisheries close either upon reaching groundfish TACs or attainment of halibut PSC limits. The one notable exception is the rock sole and other flatfish trawl fishery, which was limited in 1993 and 1994 despite relatively high levels of crab PSC apportioned to that fishery. For example, in 1994 Zone 1 was closed on February 28 due to attainment of red king crab PSC limit (110,000 crabs) and Zone 2 closed on May 7 due to the Tanner crab PSC limit (260,000 crabs). In 1995, the red king crab PSC was not reached, in part due to emergency implementation of the red king crab savings area (NPFMC 1995).

Crab PSC limits could be reduced from existing levels, and not impact groundfish fisheries if available PSC is optimally allocated among target fisheries and seasons. As shown by Table 2, the average bycatch taken each year has been less than the PSC limit. Hence, based on average bycatch needs, PSC limits could be reduced by about 20,000 red king crab and 1,000,000 Tanner crab (Zones 1 and 2 combined). Optimal allocation will be difficult to achieve because these apportionments are made pre-season. However, the council is in the process of considering a FMP amendment that would allow additional flexibility for in-season allocation of Tanner crab PSC among the bycatch limitation zones. More flexibility could be achieved with market solutions to bycatch, as discussed later in this paper.

Crab PSC limits serve as an allocative measure, not a conservation measure. Reducing the PSC limits will not do much to rebuild crab stocks. There are several reasons for this, including: (1) bycatch appears to be a relatively minor source of crab mortality, (2) fleet-wide PSC limits provide vessels with no incentive to reduce bycatch rates, (3) halibut PSC limits already constrain most fisheries. Current bycatch limits amount to 0.7% of the red king crab and 2.0% of the eastern Bering Sea Tanner crab stocks based on NMFS survey index of abundance. It has been estimated that approximately 0.75% to 1.5% of the total mature red king crab stock in Bristol Bay is impacted by trawling each year (NPFMC 1995). For comparison, natural mortality annually removes about 20% to 25% of the red king crab stock (NPFMC 1990), and the crab pot fishery harvests 20% of the mature males. The crab fishery has generally incurred a high bycatch of juvenile and female crabs (Tracy 1994), which may suffer mortality due to handling. Because bycatch mortality caused by trawl/dredge fisheries is probably very small relative to other sources of removals due to natural and fishing mortality, reductions in bycatch limits will not result in measurable improvements to crab stock abundance. Potential "savings" of crab through PSC reduction identified in this paper (20,000 red king crabs and 1,000,000 Tanner crabs) are not really savings because they would not be bycaught under the existing constraints of halibut PSC limits anyway. Also, reducing the existing crab PSC caps may cause lower groundfish harvests unless the limits are optimally allocated among target fisheries and seasons (Smith 1993). This may be impossible to achieve, and consequently, groundfish trawl fisheries may be negatively impacted. From a crab rebuilding perspective, a lower bycatch limit may result in fewer crab predators and competitors harvested, thus increasing natural mortality on juvenile crabs.

Market solutions

Individual bycatch quotas, also called individual bycatch accounts, or vessel bycatch accounts (VBAs), have been proposed by the council's Bycatch Team and fishing industry representatives as a means to reduce bycatch rates of halibut and crabs in trawl and scallop fisheries. In June 1995, the council adopted for analysis a VBA program for trawl fisheries as part of a proposed individual transferable quota program for the pollock fishery. Options for a VBA program analysis were proposed in August 1995 by the United Catcher Boats, a groundfish and crab industry group. Analysis of a VBA or other individual vessel bycatch program will require substantial time and consideration.

In theory, a VBA system would provide an incentive for each vessel to reduce its bycatch rate to maximize its catch of groundfish. Fishermen with high bycatch rates would be penalized by having to purchase additional bycatch allowances or by catching less groundfish. Fishermen with low bycatch rates would benefit by being able to catch additional groundfish without being shut down by vessels with higher bycatch rates, as they are under the current PSC system. In the current open access system, individual fishermen have no incentive to avoid bycatch; in fact just the opposite is true, because an individual fishermen who adopts bycatch reducing tactics will probably catch less target species (Huppert et al. 1992).

History has shown that individual vessels can reduce their bycatch with individual vessel incentives. In 1983, Amendment 3 to the groundfish fishery management plan mandated a substantial reduction in foreign bycatch rates of halibut and crab, and total bycatch of salmon over a 5-year period. Foreign fleets successfully accomplished this goal. The Japanese fleet accomplished this by allocating its PSC share among participating vessels based on historical performance. If a vessel allocation was exceeded for any one species, that vessel had to stop fishing unless it purchased unused bycatch shares from other vessels. The result was an accumulated bycatch savings by the entire fleet (Hastings 1991).

One benefit of implementing a VBA program is that it would make reductions in crab PSC limits more acceptable to trawl fishermen. Even under an overall reduced PSC limit, trawl fishermen could potentially increase their groundfish catch under a VBA program. This would be especially true if VBAs were fully transferable among target fisheries and seasons. As previously stated, however, reductions in crab bycatch will not have much impact on crab rebuilding.

From a crab rebuilding perspective, a VBA program could benefit crab stocks by allowing increased harvests of crab predators and competitors, which have increased in recent years. Biomass of crab competitors (inshore benthic infauna consumers such as starfish and flatfish) has increased about 40% from 1979-1993 (Livingston et al. 1993). Most of this increase is attributable to a growing rock sole biomass, and to a lesser extent starfish and flathead sole biomass. Of the crab species, only snow crab comprises a substantial portion of the infauna consumer guild (species that eat clams, polychaetes, etc.). Yellowfin sole had dramatically increased in abundance in the early 1980s to become the largest component of this guild until the early 1990s, when rock sole became co-dominant. Mean size at age has declined for yellowfin sole and rock sole, indicating stress caused by competition, and to a lesser extent a decrease in average bottom temperature (P. Livingston, NMFS, 1995, pers. comm.).

Predation by groundfish may be another factor affecting the recovery of crab stocks. For snow crabs, estimates of annual consumption by groundfish from May through September ranged from 9 billion to 31 billion crabs (Livingston et al. 1993). Snow crabs consumed were primarily age 1, and to a lesser extent age 2 and 3 crabs. Pacific cod is a primary predator of snow crab, particularly softshell female and juvenile crab

(McLellan and Leong 1981, Livingston 1989, Livingston et al. 1991). Flathead sole, yellowfin sole, and rock sole have been found to prey on young snow crabs (Haflinger and McRoy 1983, Livingston et al. 1993). Annual consumption of Tanner crabs by groundfish ranged from 10 billion to 153 billion crabs, consisting primarily of age 0 and age 1 crabs (Livingston et al. 1993). Yellowfin sole and flathead sole were found to be the primary consumers of small Tanner crabs, whereas Pacific cod preyed on the larger juveniles. Although yellowfin sole and Pacific cod are known predators of juvenile and molting red king crab (Haflinger and McRoy 1983, Livingston et al. 1991), data suggest that mortality caused by groundfish predators on adult red king crab may be low during summer months.

It should be noted that even under a VBA program, fisheries will be unable to harvest crab competitors and predators to the point where these groundfish stocks stabilize in abundance. Total annual groundfish harvest in the Bering Sea and Aleutian Islands area is limited by an optimum yield cap of two million metric tons. This cap generally results in TAC allocations to higher valued groundfish species and fisheries with lower halibut bycatch than flatfish fisheries (Witherell 1995a). It is unlikely that pollock TAC would be reduced by 580,000 mt in order to harvest yellowfin sole, rock sole, flathead sole, and other flatfish to biologically acceptable harvest levels.

One potential limitation of a VBA system is that there may still be a race for fish TAC. Unless an individual fishing quota system were implemented in concert with a VBA system, fishermen may harvest fish as early in the season as possible, so as to catch some fish before TACs are reached by the fleet. Additionally, fishermen will tend to race for and use their VBA shares for higher valued species (such as Pacific cod and rock sole), potentially leaving less valuable species unharvested (such as flathead sole). From a crab rebuilding perspective, this may have positive or negative consequences depending on what species are harvested and where and when fishing occurs.

Other options

Penalties and fees have been proposed as a disincentive for individual fishermen to catch bycatch. An evaluation by Marasco and Terry (1982) suggested that economic disincentives would be preferable to PSC limits, time/area closures, gear restrictions, and reduced groundfish quotas as a way to minimize the impact and control costs of incidental catch. Amendment 16 originally contained a "penalty box" system that would temporarily remove vessels with high PSC bycatch rates from the fishery on a real time basis. This system was disapproved by the Secretary of Commerce. In its place, the council adopted a vessel incentive program and gear restrictions. The intended effect of the vessel incentive program is to increase the opportunity to harvest groundfish TACs before established PSC limits are reached. This program is based on specification of bycatch rate standards that, when exceeded, constitute a violation of regulations, and monetary penalties are assessed. In 1994, bycatch rate standards were 2.5 red king crabs per ton of groundfish in the yellowfin sole and non-pollock trawl fisheries in Zone 1. Analysis indicates that the vessel incentive program may have helped reduce crab bycatch rates in the yellowfin sole fishery, but not in the rock sole fishery. Bycatch rates of red king crab in the at-sea processing yellowfin sole fishery were reduced from 0.31 in 1992 and 0.14 in 1993, to only 0.08 crab per metric ton of groundfish in 1994. Bycatch rates in the rock sole fishery increased from 1.12 in 1992 to 2.03 in 1993, and up to 2.77 crab per metric ton of groundfish in 1994 (NMFS 1994). Unfortunately, because the vessel incentive program is based on rates of PSC per metric ton of groundfish, fishermen that use selective gear to reduce juvenile groundfish bycatch may actually be penalized. In addition, due to its cumbersome legal nature, very few cases have been prosecuted.

Gear restrictions have been used to reduce bycatch and ghost fishing. To reduce the potential for ghost fishing by lost pots, pots used in the groundfish fishery require a biodegradable panel constructed of cotton thread. For trawl fisheries, minimum mesh size regulations were recently adopted by the council to reduce the bycatch of juvenile fish. Mesh regulations may also reduce the bycatch of small crabs. At the rebuilding committee meeting, one industry representative suggested that trawls fitted with bigger discs with wide spacing on the footrope would catch less crabs. Season adjustments could possibly be designed to structure the fishing season to avoid times and areas of high crab bycatch; however, they have not been explored at this time.

Discussion

The council has initiated analysis of several proposed measures to reduce potential negative impacts of groundfish fishing on crab stocks. Of all the measures examined, the proposed closure of northern Bristol Bay to protect juvenile habitat appears to offer the most conservation benefit to crab stocks. However, data on habitat and juvenile red king crab distribution suggest that a more comprehensive trawl/dredge closure area in the nearshore waters of Bristol Bay should be considered. Analysis also suggests that bycatch limits previously established for trawl and dredge fisheries could be reduced, but that conservation benefits to crab stocks would be negligible. Bycatch management through individual vessel bycatch accountability provides a means, within existing bycatch limits, to somewhat increase the removal of crab predators and competitors such as yellowfin sole and Pacific cod. However, these measures alone will not rebuild crab stocks.

Crab stocks will rebuild only when recruitment increases. Crab year-class strength depends both on the number of spawners and on environmental condition such as temperature and currents (Tyler and Kruse

1995). Managers can affect recruitment by ensuring there are adequate numbers of spawners, providing adequate habitat available for settlement, and reducing fishing mortality on juvenile crabs. Conservation of spawning stocks can be accomplished by the state through adjustments to GHLs in crab fisheries. Adjustments to existing bycatch limits in other fisheries will have only a very small impact on increasing adult stocks sizes or reducing juvenile mortality. To reduce juvenile mortality by limiting bycatch of non-target crabs in crab fisheries, the council or state could consider implementing measures such as bycatch limits or a VBA program for crab fisheries.

Once these actions have been taken, then crab stocks will be in the best possible position to recover if environmental and other ecological factors create a suitable situation for stocks to flourish. This may take years. For example, although large areas in the Gulf of Alaska have been closed to crab fishing, trawling, and dredging since the early 1980s, stocks of red king crab in that area have not recovered to levels which can support a crab fishery. In cases such as these, there is little more managers can do but wait.

This paper highlights the need for continuing research. Improved knowledge of crab recruitment, life history, habitat needs, the effects of trawling on habitat, as well as a review of crab management strategies around the world would aid in effective management of crab stocks. Some of this work is under way (e.g., Kruse 1995, Tyler and Kruse 1995), and we would encourage government agencies and universities to continue this research.

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Life History Strategies, Recruitment Fluctuations, and Management of the Bonne Bay Fjord Atlantic Snow Crab *(Chionoecetes opilio)*

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Abstract

Commercially harvested stocks of *Chionoecetes* spp. have been observed to fluctuate greatly over the past 20 years. The opinion that these fluctuations are fisheries driven and that a practical management goal should be a sustainable yield, is contrasted with a 10-year series of observations on the recruitment and life history of a little harvested stock

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of *C. opilio* (snow crab) isolated at benthic stages in the fjord of Bonne Bay (Newfoundland).

The stock was thoroughly monitored from egg production to death of adults by senility. The sampling techniques ranged from underwater television, scuba diving, and mini-submarines to plankton nets for the larvae, trawls, dredges, collectors, traps, tangle nets for the benthic stages. Movements were monitored by acoustic tags. Seasonality and annual variations of environmental parameters such as winter ice coverage, prevailing winds generating Ekman transport, stratification and movements of water masses, and timing of phytoplankton blooms, were recorded and compared with recruitment fluctuations.

It is concluded that strong natural fluctuations of recruitment prevail in the Bonne Bay snow crab stock in the absence of any important fishing activity. Series of 3 to 4 successive years of good recruitment are followed by series of 5 to 6 years of poor recruitment.

None of the environmental factors monitored appeared to be directly correlated with these fluctuations; rather, a life history regulation factor could be in many cases identified as a mechanism dampening the environmental effects. For instance, the precise occurrence of the spring phytoplankton bloom was efficiently detected by the crabs and triggered hatching of their eggs and release of their larvae in the plankton at the most opportune time of the year, thereafter negating the possibility that match/mismatch deregulated recruitment. We do not exclude, however, the possibility that the life history regulating responses observed be at times overwhelmed by particularly unusual environmental conditions.

It appears that most of the recruitment variability observed for the Bonne Bay stock results from intra-population effects involving selective cannibalism by predation of older males on early benthic recruits and molting individuals. This "missing cohort dynamics" appears to exist over most harvested stocks of Atlantic snow crab. Further, the success/failure of cohorts appears to be more or less synchronous in all known locations.

In the Gulf of St. Lawrence fishery, there is so far no evidence that setting quotas on the landings has had any effect in regulating recruitment success, as good recruitment years do not correspond with high parental stock. We suggest the existence of natural intra-population effects, based on cannibalism, generating an alternation of good and poor recruitment years, and synchronization between geographic sub-stocks by a superimposed widely distributed environmental factor occurring many years apart, such as the depth oscillations of the shallow and deep thermoclines limiting the depth distribution of *Chionoecetes opilio.*

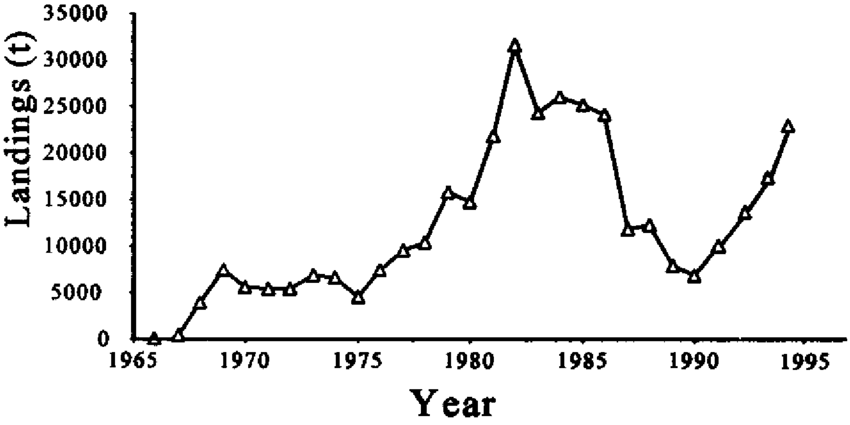


Figure 1. Commercial landings in metric tons of snow crab harvested in the Gulf of St. Lawrence. The variability has been threefold from 1970 to 1995.

Introduction

Snow crab (*Chionoecetes opilio*) is a major commercial species in Eastern Canada. Landings are in the order of 25,000 tons per year, for a value of Can. $100,000,000. A full-scale commercial fishery developed only over the past 15 years during a decline of Alaskan king crab resources. Research emphasis has been set only recently on the understanding of the life history of the species.

In the Southwestern Gulf of St. Lawrence, from 1966 to 1990, the landings first rose with fishing effort from an average of 7,000 tons (1969-1977) to 33,000 tons in 1982. The landings then dropped abruptly to 7,000 tons in 1990 (Figure 1) and have recently risen again to 25,000 tons in 1994.

Such strong harvestable stock fluctuations could not be explained by the prevailing interpretation of the life history of snow crab. Up to 1986, recruitment was believed to be fully protected by a legal minimal harvesting size of 95 mm carapace width. It was generally accepted at that time that all males matured and had the opportunity to mate several times before reaching this legal minimal size. It was believed that females were fully protected from fishing throughout their life span since they achieved a terminal molt at onset of maturity at sizes much smaller than the legal minimal size. The females would mate only once in their life, shortly after the terminal molt, thereafter depending on sperm stored in their spermatheca for further broods. Based on laboratory observations, it was thought that one male would naturally serve several females during the same mating season.

It was also believed that adult males were much larger than females because they kept on growing after reaching maturity. As males used little energy for reproduction, they were expected to have an asymptotic growth curve based on increasing time intervals between successive molts, as it is known for lobsters, and eventually reduced increments in size at molt. Females stopped growing at onset of maturity, because they always carried eggs throughout the year and never had the chance to molt, therefore diverting all their energy to reproduction rather than growth.

Under this interpretation of the snow crab life cycle, it seemed that a yield per recruit model would have ideally served the purpose of managing a snow crab fishery, which benefited from an almost unlimited natural protection of recruitment from fisheries effects. The direct implication would have been to set a very high fishing effort allowing to crop down male snow crab cohorts as soon as they reached a legal minimal size set (1) above the size at which all males reach first maturity, and (2) at the size at which the male component of a cohort reached its maximal weight prior to the age at which individual growth slows down and no longer compensates for biomass decrease by natural mortality. This would have allowed all males to successfully mate, and would have maximized yield.

In practice, the two major elements required for yield calculations: (1) the growth curve of males, through increments in size at molt and reduced frequencies of molting with size, and (2) the natural mortality, were not sufficiently well known. The fishery was therefore preemptively managed by setting a maximum "exploitation rate" (catch/standing harvestable biomass) which would have allowed about 40% of harvestable males to survive the annual fishing season.

The method for calculating annual standing fishable biomass was retrospective and based on the fit of an anticipated linear relationship between the catch over equal successive time intervals during a fishing season and the catch cumulated up to each of these interval. The technique was referred to as "Leslie analysis" (Mohn and Elner 1987 for review) and had underlying assumptions of no recruitment to the fishery, negligible natural mortality, and constant catchability throughout the fishing season. It neglected the dynamic changes affecting the spatial distributions of effort and resource abundance during a fishing season.

Under these simple life history and management assumptions, recruitment was thought to be fully protected, and catch had first been thought to be almost inexhaustible. A close inspection of the sequence of landing statistics (Figure 1), and of the data on catch and effort (Figure 2) reveals, however, that the 1986 sharp drop in landings was most likely due to a failure in recruitment. The catch per unit of effort values

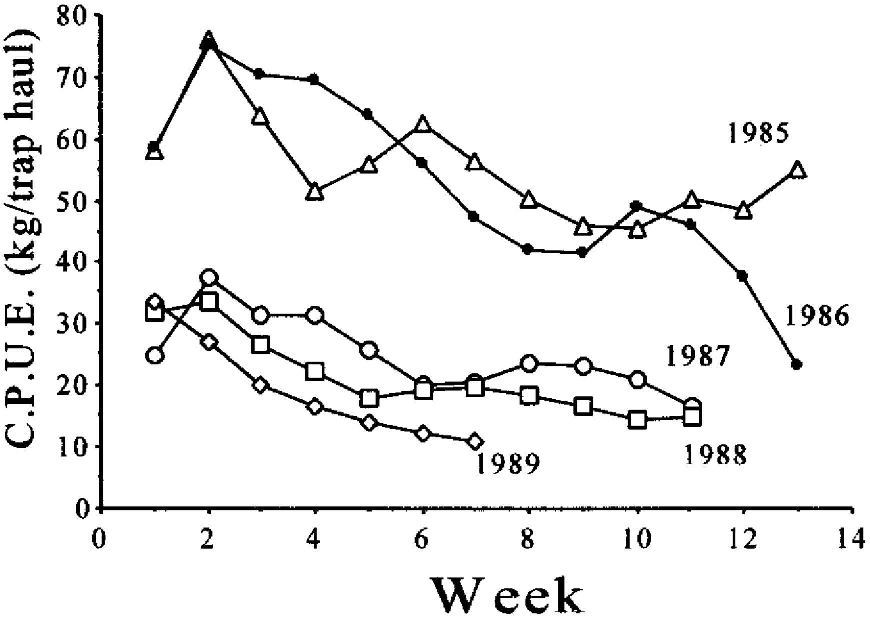


Figure 2. Changes in catch per unit of effort (CPUE), for snow crab harvested in the Gulf of St. Lawrence, and weekly averages over the annual fishing seasons from 1985 to 1989. In most areas the fishing season starts at ice break and extends until either an annual quota is reached, a proportion of white (recently molted) crabs higher than 20 percent is reached, or after 15 weeks of fishing. The drop in landings from 1986 to 1987 was consistent throughout the fishing season and is attributed to a sudden drop in year class strength. Starting in 1989 annual maps of snow crab abundance were prepared by geostatistical analysis from experimental trawl surveys and distributed to fishermen before the opening of the fishing season. The effect was immediate: CPUEs were at their maximum immediately in the first week instead of increasing during an initial costly search period. The trawl surveys are now financed by the fishermen.

were low right at the start of the 1987 fishing season and remained as such until 1989. Simultaneously, landings of large amounts of "white," low commercial quality, and apparently recently molted crabs were reported by the fishermen.

Such failures in recruitment and fluctuations in quality of catch did not match the idealistic initial views. It logically entailed that initials concepts on life history needed to be reassessed, and that it was of paramount importance to identify whether the fluctuations in recruitment were natural or fishery induced. The temptation to apply standard population dynamics models (Mohn 1988) had grown too fast prior to basic knowledge of the life history of the species.

At the request of the fishermen's organizations, and with the backup of fisheries biologists, management reacted to the fluctuations in catch by tightening standard measures such as setting quotas on catch, limiting effort in number of traps per boat and number of fishing licenses, and closing the fishing season when too many "white crabs" appeared in the catch. Prior to the drop in landings, the fishable biomass was retrocalculated after the end of the fishing season from the cumulated catch in season, with no possibility to forecast, "preemptive quotas" were defined on the basis of the catch in the previous year, and always turned out higher than the actual catch. For the first time, quotas were now adjusted annually on the basis of reliable direct fishable biomass estimates made prior to the fishing season from trawl survey data designed and processed by geostatistical techniques (Conan et al. 1988c, Conan et al. 1994). No rational basis existed, however, for defining the ratio of the annual quota to the now available fishable biomass predictions; the ratio was arbitrarily defined as a "target exploitation rate" preset for management purposes.

Starting in 1990 the landings increased quite steadily and management measures were taken optimistically (Loch et al. 1995). However, a cursory analysis of the catch and some understanding of snow crab growth shows that the new waves of enhanced recruitment were not generated by the parental size classes "protected" by the newly introduced fishing restrictions. The actual effect of these intuitive management measures on the snow crab stock is at the least uncertain or null.

We did not attempt to justify the standard management measures which had been intuitively set for regulating recruitment fluctuations. We advocated a systematic analytical approach to understanding and regulating these recruitment fluctuations. We held that the determinism of success for a year class from egg to adult could be understood and managed only after the interactions between the life history of the species and the ambient environmental factors were sufficiently well known. We proposed that the respective influence of natural versus fisheries induced effects on the recruitment could be contrasted by moni-

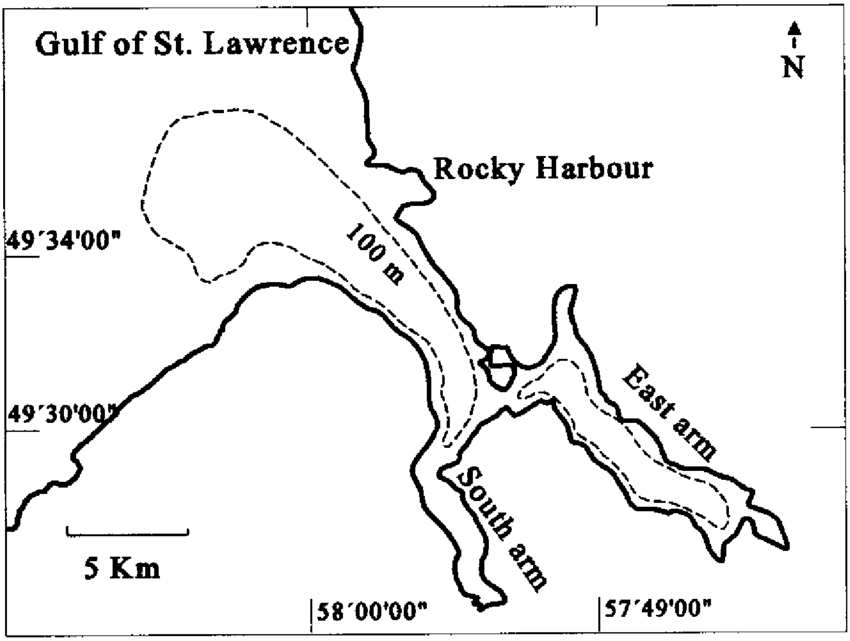


Figure 3. Geographic location and simplified depth structure of the Bonne Bay fjord (Western Newfoundland). Snow crab are found in intermediate −1° to +1°C, 33‰ winter formed water which remains trapped all year in two basins exceeding 100 m depths.

toring an unharvested snow crab stock. Only then could targeted efficient management methods be designed.

After reviewing basic biology and fisheries literature on other majid species (Conan et al. 1990a), we contributed to the quest for new information and novel management methodologies by setting up a long-term pilot monitoring experiment on a small snow crab stock. The stock selected is isolated at benthic stages inside a fjord. A shallow sill at the entrance of the fjord of Bonne Bay, Newfoundland (Figure 3), retains year-round deep (100-200 m) and cold (−1° to +1°C) winter formed water (Comeau et al. 1991, Gilbert and Pettigrew 1993) suitable for sustaining the crab stock. By studying this microcosm we avoided the difficulty of extracting more complex information from multiple geographic population sub-components intermixing over a whole commercially harvested stock.

Material and Methods

Site selection

In the Gulf of St. Lawrence, the commercial fishing grounds are located at up to 8 steaming hours from harbor. Year-round biological monitoring of the stock would require considerable investments and would not be possible during winter months under thick but unstable ice cover. Local geographic differences exist in the seasonality of the environment and the life history events, and complicate the interpretation of the evolution of the stock as a whole.

Bonne Bay (49°30′N, 57°55′W) is used as a microcosm model for the Gulf of St. Lawrence. Bonne Bay is a double fjord system separated from the Gulf of St. Lawrence by a shallow 50 m sill. A main 130 m deep basin branches laterally into a 200 m deep East Arm, from which it is separated by a second 15 m sill. The seasonal environment and the biological events, although not perfectly synchronized within the whole fjord, are amenable to global monitoring. The Bonne Bay snow crab stock is encountered in the two arms, close to shore, down to depths of 100 to 200 m (Figure 3). The stock can therefore be sampled at close range from shore throughout the year, including in winter by trapping and setting gillnets, plankton nets, and probes through thick and stable sea ice.

Sampling techniques

The preferred sampling gear for benthic stages is a *Nephrops* Bay of Biscay "Bigouden" otter trawl. A small shrimp "Devismes" otter trawl has been used for catching the very first benthic stages. These trawls are less differentially selective for different biological categories of crab than traps. With the combined use of precise satellite locating gear (GPS) and acoustic measurements of on bottom gear aperture (SCANMAR), these trawls (Conan et al. 1994) can provide accurate measures of resource abundance suitable for global estimates and mapping.

The most important events in the life history of crustaceans, molting and reproduction, are followed when possible throughout the year by direct observations while scuba diving, by Remotely Operated Vehicles (ROV) and from mini-submarines, or by determining molting and reproductive stages in the catch. In order to define the timing and success of the mating season, mating couples are searched for, by diving down to 55 m, and over the whole depth range, down to 150 m, using tangle nets. Couples will remain together in tangle nets, but will separate when caught in traps or trawls. ROV and mini-submarine in situ observations provide information down to the maximum depths of the fjord. The mini-submarines PICES and SDL are operated by the Canadian Navy from the HMCS *Cormorant*.

The relative importance of initial changes in larval stage abundance on the determinism of recruitment is assessed. The seasonal successions in the occurrence of planktonic snow crab larval stages and their food are monitored from vertical hauls of a one meter diameter hoop net. The density and spatial distribution of larvae are assessed using oblique hauls of a 1 m^2 Tucker net. The vertical profile of the larval distribution is sampled using a 0.5 m bongo sampler fitted with remotely operated opening and closing devices. All samplers are equipped with General Oceanic flow-meters and their track recorded from a VEMCO acoustic depth transmitter system.

The effects of oceanic environmental factors on the survival of larvae and on the phasing of life events of benthic stages are assessed. Seasonal and year to year changes in the water column, temperature, salinity, and fluorescence profiles are recorded using a Seabird electronic probe coupled with a fluorometer. The 1% light-penetration limit of the euphotic zone is estimated from Secchi disk measurements. During the summer of 1991, 11 current-meters were deployed at 4 mooring sites for assessing passive drift and possible flushing of larvae in and out of the fjord. Oxygen content of water column was estimated from samples taken in a bottle sampler and measured with a hand-held probe.

The effects of sea-air interface factors such as wind-driven currents and sea ice cover are also assessed. Wind-driven water circulation is a possible cause of advection from suitable habitats for crustacean larvae and a possible source of mortality. Wind conditions prevailing around Bonne Bay are provided by the data sets of the Atmospheric Environment Service (AES) at Daniel's Harbour, 80 km northeast of Bonne Bay. High ice cover may reduce the amount of solar flux into the water column, delaying and reducing the spring and summer and delaying the onset of the spring plankton bloom. Data on ice cover is available from the composite charts of aerial, ship, and satellite observations assembled by AES and sampled weekly.

Biomass and production of phytoplankton are measured from chlorophyll *a* in the water column, (1) for checking possible food limitation effects on the survival the pelagic larval stages and (2) for checking possible phasing effects of organic carbon rain on the seasonal life events of the benthic stages. Sinking fluxes of organic matter through the water column to the benthos bottom is estimated from deployments of sediment traps set at different depths. The settled particles are collected for the determination of organic carbon and nitrogen concentrations by CHN analyzer and for algal pigments. Detailed procedures are provided in Starr et al. (1994).

Biological material

Snow crab go through different life stages during their benthic life span (Conan and Comeau 1986, Conan et al. 1988b, Comeau and Conan 1992). Molting and reproduction are the main physiological factors determining these biological stages. The life stages behave differently and are likely to contribute differently to the success of recruitment processes, they must therefore be identified and monitored separately.

Molting stages are defined as described by Drach (1939) for decapod crustaceans in general, and as first applied to *Chionoecetes opilio* by Moriyasu and Mallet (1986). Time elapsed since molting is evaluated using a technique of radioisotope dating at "Centre des Faibles Radioactivités CNRS/CEA" (Gif sur Yvette, France) as described by Le Foll et al. (1988), and Conan et al. (1990b).

The presence, number, and stage (color) of the eggs under the abdomen of the females are recorded. The presence and aspect of the spermatophores in the seminal tract of the males is noted as described by Comeau and Conan (1992). The morphometry of the claw of the males and size of the carapace of the males in relationship with maturity is recorded as described by Conan and Comeau (1986) following Teissier (1933, 1935).

Statistical analysis

The morphometry of male snow crab was analyzed as described by Conan and Comeau (1986), as it is usually done for allometric relationships, after log transformation of the measurements (Teissier 1948). A modified discriminant analysis (Conan 1989) allows to dissociate allometric groups sharing similar slopes but different elevations of allometric regression lines. Angular points formed by two intersecting allometric lines are detected by Gaertner and Laloé's method (1986).

The techniques used for analysis and mapping of spatial distributions (Conan et al. 1988c) are derived from the kriging methodology (Matheron 1971). The spatial associations between biological subgroups are analyzed by correspondence analysis, and the principal factors are mapped on a geographic scale (Allard and Conan 1988).

Results and Discussion

The success of recruitment is determined by the combined effect of how each life history stage fits within its ambient environment as it progresses throughout the life span, until the complete life cycle process is completed. We therefore propose to trace back the success of every major event of the life history, and to identify possible bottlenecks and failures.

The snow crab habitat

The stratification of water layers in Bonne Bay is a subsystem of the Gulf of St. Lawrence. Three layers of seawater exist in the Gulf as first described by Lauzier et al. (1957) and Lauzier and Bailey (1957). A top layer of desalted warm water (down to 20‰ and up to 20°C) forms in the spring, it reaches down to some 60 m in summer, and it disappears in winter. An intermediate layer of cold water (circa 33‰ and −1° to +1°C) is found down to some 100 m. The deepest layer reaches down to some 500 m at the deepest of the Gulf, it is warmer and saltier (some 35‰ and 6°C). Only the top two layers are found in Bonne Bay (Figure 4). The intermediate layer is generated in winter and is partially renewed in spring, summer, and fall by upwelling over the sills (Figures 5 and 6). The layers are stable and do not overturn. There is no anoxic water layer in Bonne Bay. In the winter the water column is extremely homogeneous, temperatures vary from year to year around −1° to +1°C. In summer, surface water temperature may occasionally reach +18°C. The salinity and temperature depth profiles provide similar information on water column structure (Figure 6). Bottom salinity remains around 33‰ all year round. Surface salinity may drop to 24‰ in the spring. The thermoclines and hyaloclines move downwards from spring to summer and finally oscillate around the depth of the sill of the fjord. The hyalocline in the fall may reach deeper (80 m) than the thermocline (45 m). Cold-blooded snow crab must move into a suitable layer of water to maintain energetically optimal body temperatures, and possibly osmolarity.

From January to March the fjord is usually covered with thick sea ice, and it is possible to use snow vehicles or to land helicopters on the ice for winter sampling. In certain years the ice cover is minimal. A strong phytoplankton bloom occurs a few weeks after ice break in the spring as the surface water layer forms (Figure 7). A rain of biogenic carbon particles can be traced down to the bottom of the fjord soon after the bloom (Figure 7). For an enhanced larval survival, the occurrence of snow crab larvae in the plankton should follow the occurrence of the phytoplankton bloom as per Cushing's (1975) match/mismatch theory.

The exchanges of water in and out of Bonne Bay are strongly affected by longshore winds that prevail over the shelf (Gilbert and Pettigrew 1993). During winter time ice cover limits the effects of wind on the water circulation. During the summer, winds tend to blow parallel to the coastline toward the NNE and cause a surface onshore Ekman transport and a downwelling. Occasionally the winds blow toward the SSW creating a surface offshore Ekman transport and upwelling. In the latter case the thermocline rises from an inflow of colder saltier water into the fjord over the sill as shown by temperature, salinity, and sigma-*t* (Figure 5). Upwellings appear to be more frequent in the spring than in the summer. Snow crab larvae must navigate the water exchanges to remain inside the fjord prior to metamorphosis into megalopae and early benthic stages.

Bottom sediments in Bonne Bay vary from fine mud at the bottom of the fjord to gravel, pebbles, boulders, and steep cliffs on the sides of the U-shaped fjord submerged valley. Clean sand can be found in the southern areas of the outer sill. As a function of their size snow crab may better survive on, or specifically elect certain types of sediment.

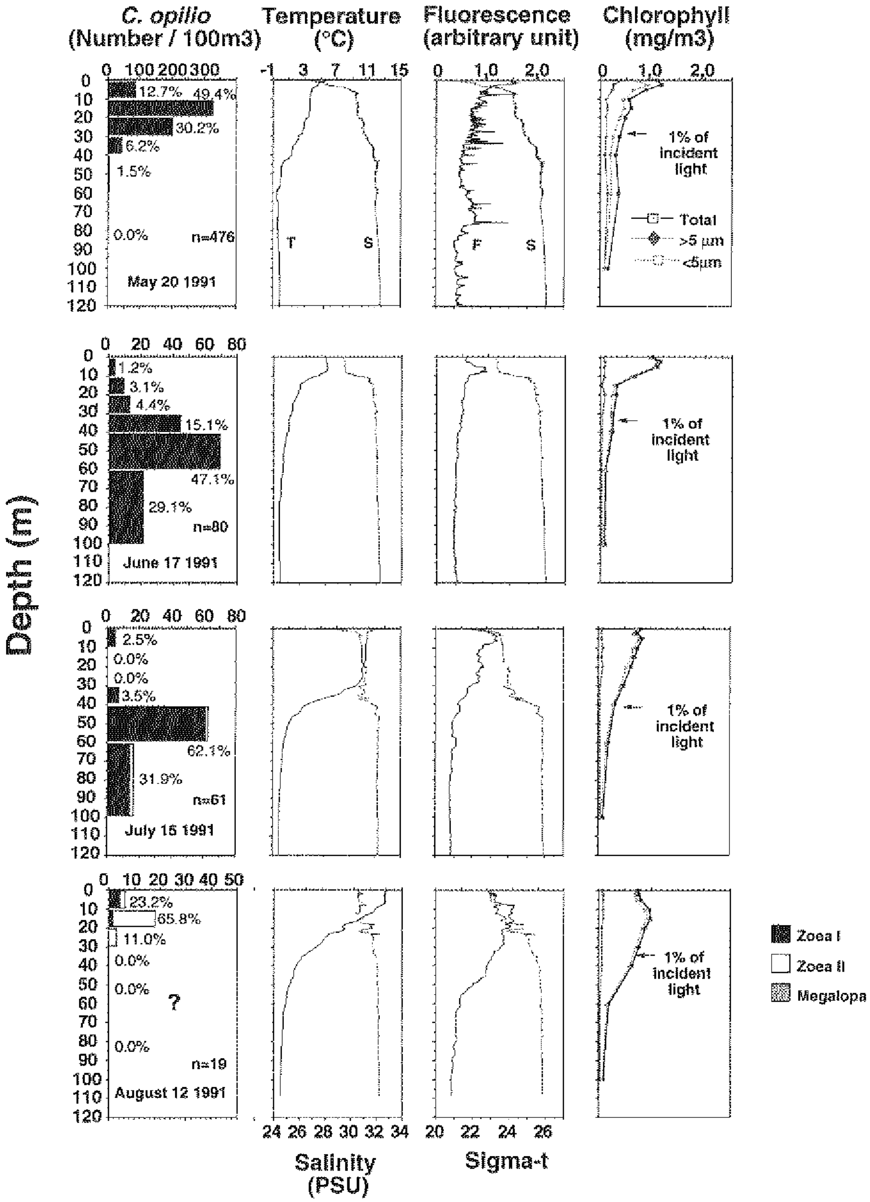


Figure 4. Some characteristic vertical distributions of snow crab larvae in Bonne Bay fjord concurrently with most important environmental factors. The larvae tend to remain just below the surface to intermediate water interface and are not affected by the wind-driven outward Ekman transport which sometimes affects the surface water.

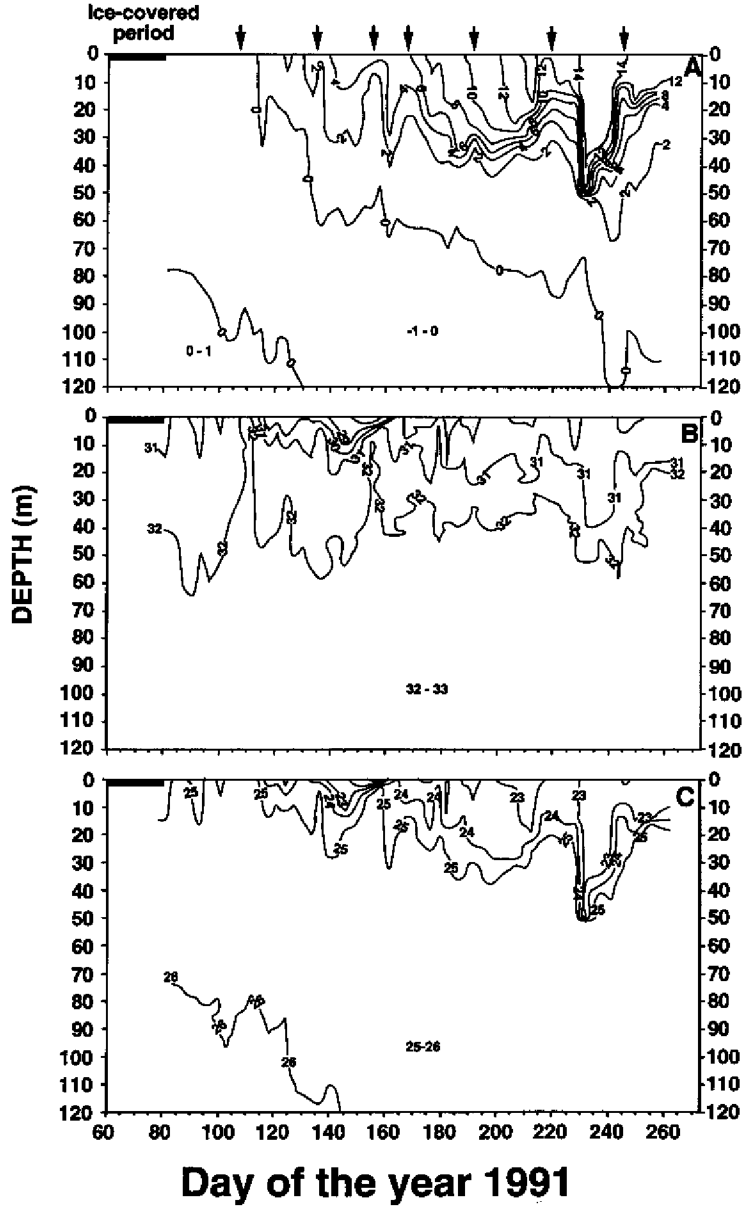


Figure 5. Temporal variations of temperature (a), salinity (b), and sigma-t (c) in the Bonne Bay fjord in 1991. Isopleths were fitted by kriging to CTD data sets taken twice a week from late March to early September. The arrows mark inferred periods of upwelling of intermediate water from outside the fjord, over the 50 m entrance sill, into the 100 meter deep basin (Michel Starr).

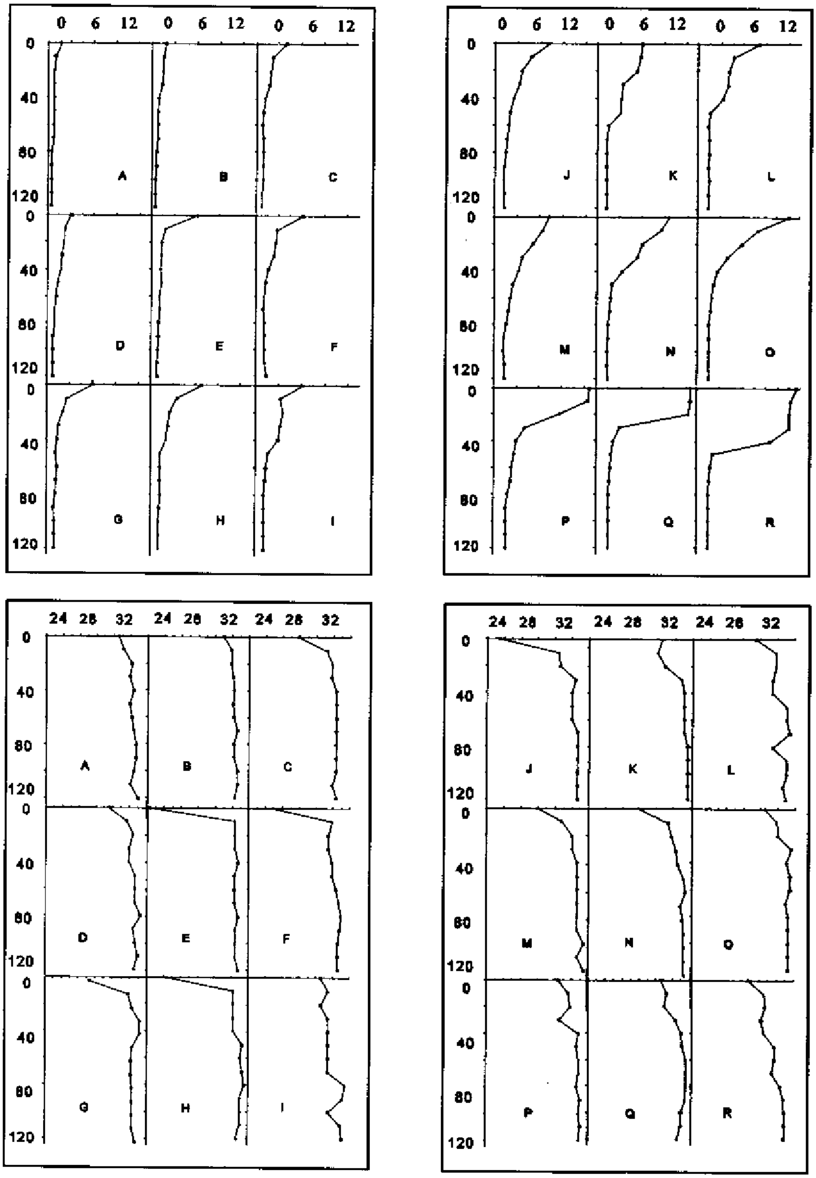


Figure 6. Temperature (top) and salinity (bottom) profiles in Bonne Bay. Depths from 0 to 120 m, temperatures from –2° to + 14°C, salinities from 22 to 34‰. Profiles taken by electronic probe every 10 days from April (A) to September (R). A layer of warmer, brackish water forms at the surface from spring to fall. The deeper layer (Gulf of St. Lawrence intermediate water, –1° to +1°C, 33‰ salinity) remains mostly unaffected beyond the 45 m fjord entrance sill depth.

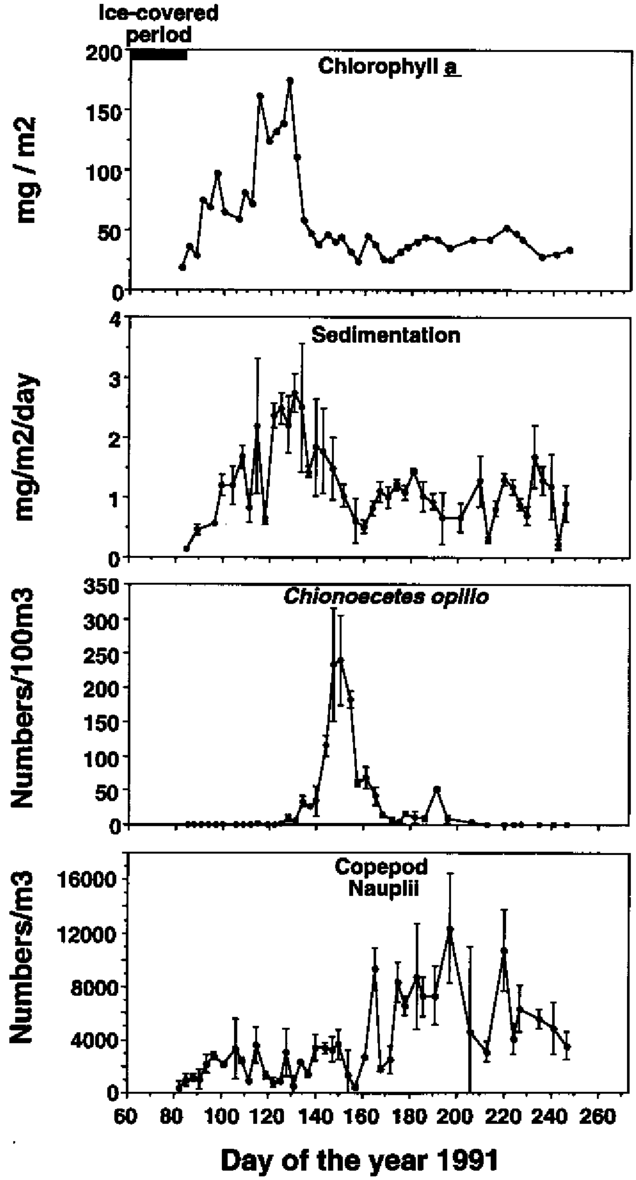


Figure 7. *Temporal variations of integrated chlorophyll a concentrations in the water column (0-100 m), chlorophyll a + phaeopigments concentrations in the sediment traps, and relative abundance of snow crab zoea 1 and copepod nauplii in Bonne Bay fjord in 1991. The hatching of the snow crab broods is triggered by the sinking excedent of organic material produced by the bloom. Snow crab larvae occur in the plankton at a most opportune time for feeding on copepod nauplii.*

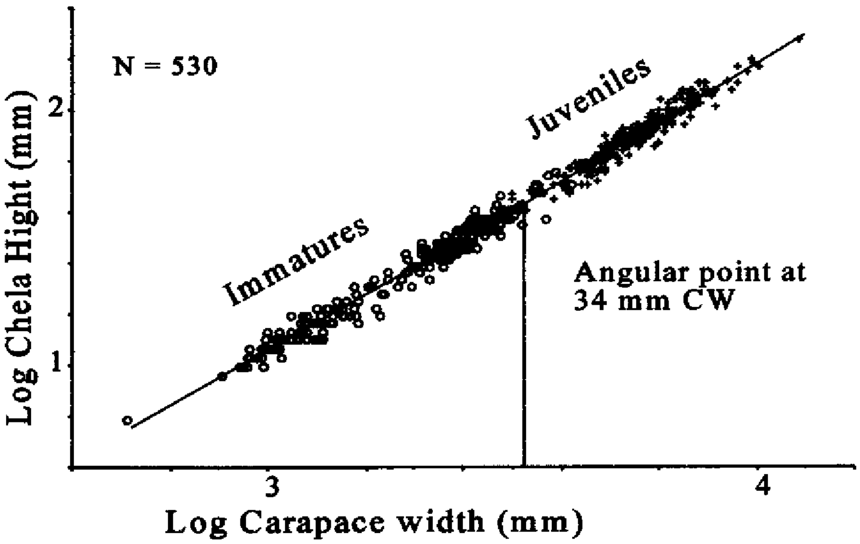


Figure 8. Morphometric identification of immature and juvenile male snow crab. On an allometric plot of log claw size vs log carapace size an angular point separates morphometrically immature from morphometrically juvenile males.

Snow crab major life cycle events

Our observations show that in Bonne Bay hatching of the eggs occurs in early May to early June. Zoea I larvae are liberated in the plankton where they metamorphose into zoea II and later into megalopae which settle to the benthos by late August to early September (Figure 4).

First benthic stages are found in early September. The benthic stages go through 3 different phases (Comeau and Conan 1992), immature (gonads are not differentiated, the external morphology of males and females is weakly differentiated), juvenile (the gonads are differentiated, the external morphology of males and females is incompletely differentiated), morphometrically mature (both the gonads and the morphometric secondary sexual characters are fully differentiated, males and females are fully functionally reproductive). The different phases of life cycle can be identified by morphometry (Figures 8 and 9). Both males and females achieve a terminal molt at onset of morphometric maturity (Conan and Comeau 1986). The phase of life cycle beyond the terminal molt is referred to as a terminal anecdysis. Terminal anecdysis and morphometric maturity are reached by different individuals over a wide range of ages (at least 5 years), and subsequently the terminal molt is achieved over a 3 to 4 fold range of sizes. The most obvious secondary

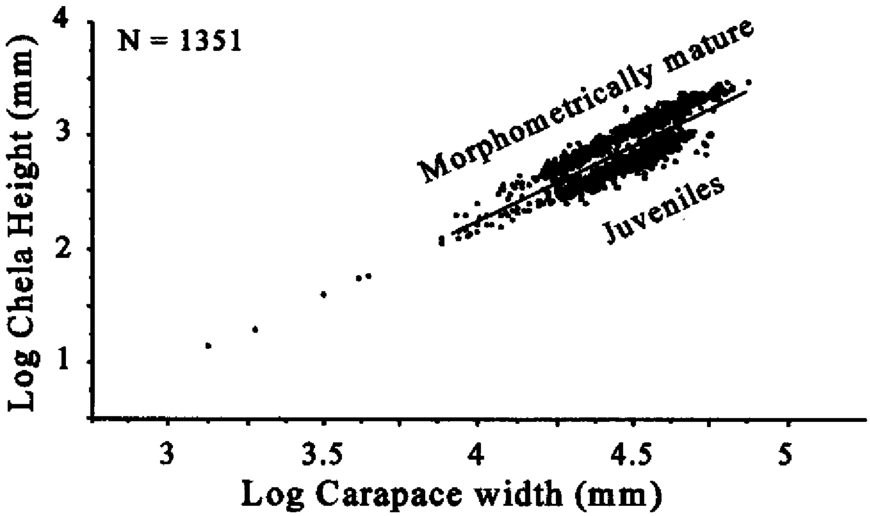


Figure 9. Morphometric identification of morphometrically mature and juvenile snow crab. On an allometric plot of log claw size vs. log carapace size a shift in ordinates separates morphometrically juvenile from morphometrically mature males.

sexual characters are the large claws of males and the wide abdomen of the females.

Early benthic stages and immature may molt several times a year. Juvenile males molt mostly once a year during a short season in March to April. In some years we observed that a fairly high proportion of juvenile males skipped the spring molt. There is some indication from radioisotope dating of carapaces and from reading molt stages on maxillipeds that some juveniles may molt in the fall. Morphometrically mature animals do not molt or regenerate.

Females mate for the first time shortly after the terminal molt possibly all year round. Each brood is incubated under the abdomen of the female for up to two years. Over subsequent years, the second and later matings take place immediately after hatching of the previous brood of eggs precisely in late May to early June.

Males start producing some spherical spermatophores containing spermatozoa during the juvenile stage (Comeau et al. 1992). Full production of spermatophores is achieved only by morphometrically mature males. In Bonne Bay we observed only the morphometrically mature males in constituted couples displaying precopulatory or copulatory embrace.

Most males and females die from senility 4 to 5 years after achieving the terminal molt as shown by one of us (G.Y. Conan) using radio isotope dating of carapaces. Old morphometrically mature individuals usually have abraded decalcified carapaces and numerous missing legs autotomized during the fights between males at the time of mating, as both males and females in terminal anecdysis have lost the ability to molt or regenerate.

Environment, life history, and success of recruitment

A stable recruitment to a commercial fishery would imply a sufficient supply of hatching eggs year after year, and thereafter cohorts successfully progressing throughout all of the life stages until they reach commercially harvestable sizes. We have identified some life cycle and environment characteristics which enhance snow crab survival from egg to adulthood.

Stable female fecundity

Egg counts vs. carapace size relationships have been checked since 1985 (Conan et al. 1989). The relationships remained quite stable during the period surveyed. There are no indications that environment fluctuations may affect production of hatching larvae by the females, and thereafter recruitment success. Parasites or commensal nemerteans are occasionally found in vestigial broods of senile females, but this appears to affect only a very minor part of the population.

No marked oxygen depletion

There is no evidence that oxygen may be a limiting factor in deep areas of the Bonne Bay fjord as it has been described off Sweden in the Kattegat for *Nephrops norvegicus* (Baden et al. 1990). The deeps of the Bonne Bay fjord are not anoxic and recruitment failures cannot be directly attributed to oxygen depletion.

Wide tolerance to sediment types

Snow crab are usually found on mud, at the bottom of the fjord. Underwater television work (Conan and Maynard 1987) has shown that snow crab may partially bury in bottom sediment. This was recently observed by Conan during mini-submarine dives that immature, juveniles, and possibly adult females may fully conceal in the sediment eyes only emerging. On the fjord banks large snow crab can be observed by diving in early spring on small pebbles bottoms and on fine sediment between rocks, but never on or among large boulders. Early benthic stages can be observed speeding away to avoid cameras and searching for shelter under small stones, however, when abundant they can be found on any type of bottom except large rocks and boulders. There appears to be no active search for a particular type of bottom at early stages, rather, they settle anywhere and survive wherever the location is the best for protection from predation and cannibalism. High density patches of early benthic stages are not necessarily found in the same location from year to year. The relationship with type of sediment is more opportunistic than actively directed.

Benthic stages adjust their depth distribution in relation to water masses

Snow crab may actively move along the slopes of the fjord to seek ambient temperatures optimal for their current activity. These optimal temperatures are likely to vary between different phases of life cycle, in relation with ambient dissolved oxygen. Experiments by Thompson and Haryluk (1989), Foyle et al. (1989), and Maynard (1991), the two latest in collaboration with us in Bonne Bay, confirm our field observations (Figure 10).

The depth range of snow crab in Bonne Bay varies according to the season. In early spring males and females can be found in shallow water, up to 15 m depths. Snow crab are found otherwise year-round down to 130 m and most likely down to the maximum depths of the fjord (230 m). As the season advances, the upper reaches of the distribution moves down to approximately 60 m, deeper than the fjord sill. Snow crab are therefore constrained into fjord deeps during the summer.

Salinity and temperature profiles indicate that the seasonal depth distribution of snow crabs is conditioned by the formation of the top layer thermocline and hyalocline from spring to summer. Snow crab are found almost exclusively below the upper layer thermocline and hyalocline. However, high concentrations of females were observed by one of us (G.Y. Conan) during mini-submarine dives in shallow water at the vicinity of the summer thermocline. These females were in their second and later reproduction cycles, appeared to move little and remain throughout the summer in shallower warmer water (3°C) than the males. Earlier observations by telemetry of acoustic tags attached while scuba diving to the male and the female of mating pairs (G.Y. Conan and D.R. Maynard 1984-1986) had shown that after mating the female remained in shallow water, while the male moved down to the deeps (Figure 10).

Hooper (1986) interpreted the occurrence of mating pairs in shallow water as a proof for a direct spring breeding migration. We believe that the occurrence of pairs within diving range early in the spring is simply due to the absence of a thermocline in this season (Figure 6). When shallow water starts warming up, crabs move down below the thermocline as can be observed by diving from April to June, trapping, and setting tangle nets. Pairs are present at any depth along the slope in early spring, while in shallow water the frequency of old males with missing limbs, or smallest morphometrically mature males is considerably higher than in the deep. It appears that weaker males are out-competed to-

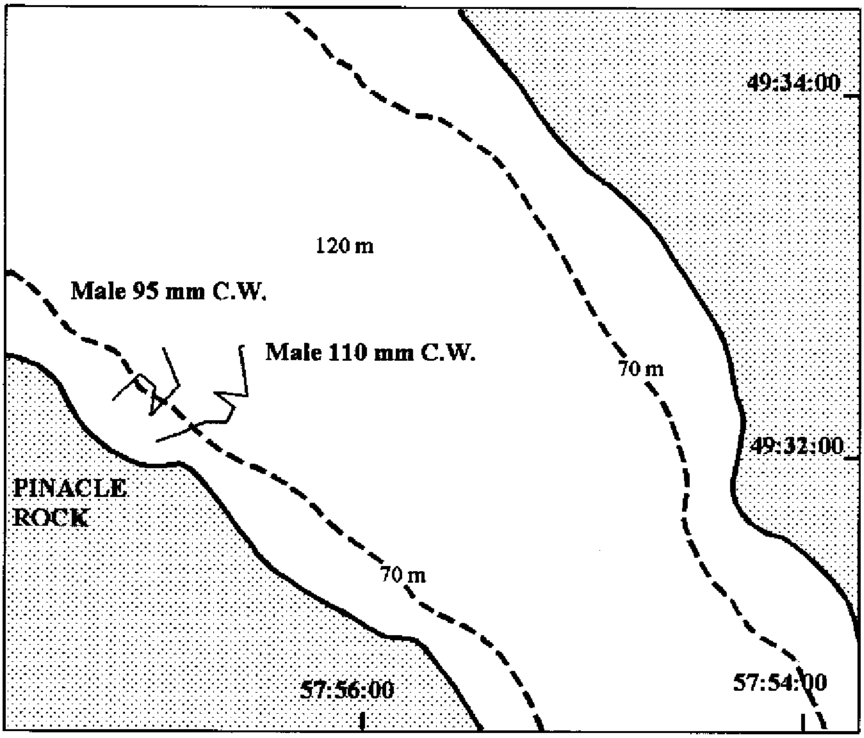


Figure 10. Tracking the behavioral response of male snow crab to warming up of surface water. Two morphometrically mature males were caught by scuba diving in shallow water in early spring during the mating period. They were tagged underwater with acoustic transponders. They were tracked remotely over a period of two weeks. As the thermocline between surface and intermediate water formed and deepened, the crabs moved down by trial and error and remained in the intermediate water layer (–1° to +1°C). Adapted from Maynard (1991).

ward shallow water during the pair formation process (Comeau et al. 1991).

Abundance of molting individuals in shallow water prior to the molting period or concurrently with the beginning of the molting period has been reported by Ennis et al. (1990) and Comeau et al. (1991). We have no information whether this may have been a pre-molt migration into shallow water in order to minimize cannibalism from non-molting morphometrically mature males or whether molting could have been simultaneously observed at any depth along the slope of the fjord. Molting occurs prior to formation of a thermocline, during and very shortly after ice breaking, and at a time it is impractical to set traps and tangle nets. There is some indication that females would molt shortly before the males.

Tracking berried females marked by sonic tags has shown that they do not move over large distance. By staying in the vicinity of the upper thermocline in warmer water they may shorten the development of their eggs from two to one year. Conan while conducting experimental trawling in 1994 has also detected concentrations of berried females in other locations on the Gulf in the vicinity of the thermocline separating intermediate from the warmer deep water layer. This deepwater alternative location of female concentrations may also be a strategy for reducing duration of egg development from two to one year. Aquarium observations further confirm that by changing temperatures from 1°C to 3°C it is possible to shorten egg development from two years to one year (Mallet et al. 1993). This could have major effects on enhancing production of eggs per female over a mature life span limited to some 5 years, and total production of eggs by the population.

Large morphometrically mature males can move over several miles in a few days when disturbed. Tracking acoustic tags has shown that after such a burst of activity, they tend to settle down. Such individuals have the potential to move all around Bonne Bay deeps in a few days, or up and down the fjord slopes (Figure 10), but will concentrate in selected sites, and will be encountered in similar spots from year to year. They need to remain in colder water around −1°C to +1°C to efficiently support their foraging activity. This may explain why they are seldom found outside of the intermediate layer, except for short incursions.

Small immature crab also appear to stay away from the thermocline. They probably cannot move over several miles to match water temperatures, and may die if they have settled as early benthic stages on grounds which are not all year round within the intermediate water layer.

The fluctuations of the depth of the intermediate water layer from year to year may open or close grounds suitable for successful recruitment or early benthic stages or foraging of juveniles and morphometrically mature stages. In the Gulf of St. Lawrence, variations of the top layer interface within the 40 to 60 meter depth range and of the deep layer interface within the 100 to 150 m can critically affect the extent of areas suitable for snow crab distribution, as the grounds are relatively flat at these depths. The effects are more limited in a U-shaped fjord where shallow areas exist only on the steep sides and at the fjord entrance sills.

Spatial structure of the benthic stages as a social and environmental response

Snow crab populations are highly aggregated into clumps which are specific to each biological category identifiable by sex, age, and morphometric differentiation (Conan et al. 1988c, Allard and Conan 1988). This is shown by analyzing data from underwater TV sledges (Conan and Maynard 1987), trawling (Conan et al. 1988c, Allard and Conan 1988).

Presence of aggregations in Bonne Bay was confirmed by using kriging to map the concentrations of crabs detected by trawling (Figure 12) and by visual information collected from TV sledges. Kriging and multivariate analyses such as principal component and correspondence analyses show that immature males and females are found in the same patches, but sexes tend to segregate as morphometric differentiation takes place, finally morphometrically mature males and females tend to congregate again seasonally at the time of mating, while senile individuals are found at the margin of the patches (Figure 11). Although this pattern of inter-group exclusion/aggregation remains similar from year to year, the actual geographic location of each of the concentrations may considerably vary from year to year (Figure 12). Only the mature berried females tend to remain in similar locations.

Using variogram ranges in the trawl data as an index of patch radius, it can be shown that the average size of the patches is quite stable in time and differs for males (6 km radius) and females (2 km radius or absent). From the mini-submarines, Conan (personal observations) was able to confirm the presence of high density, short range aggregations of females as he observed females forming heaps ("pods") in early May at the beginning of the mating season as "pairing" of males and females started to occur. The larger patch size of the males could be explained by the fact that they remain within foraging range of a small patch of females. The physical factors determining the location of the female concentrations are not fully understood. The presence of an eddy and, or a local downwelling or upwelling of warmer water could be determinant.

We have no indication that this organized population structure of a high density female concentration surrounded by a wider patch of males was affected by any natural effect during the series of years of observations. We have information showing that a female concentration remains stable over several years.

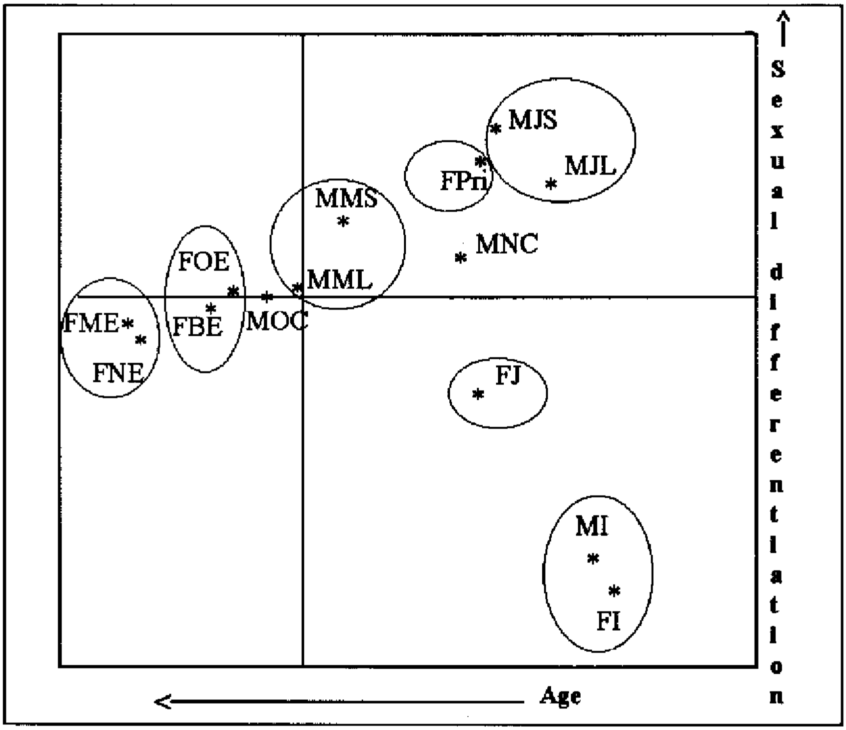
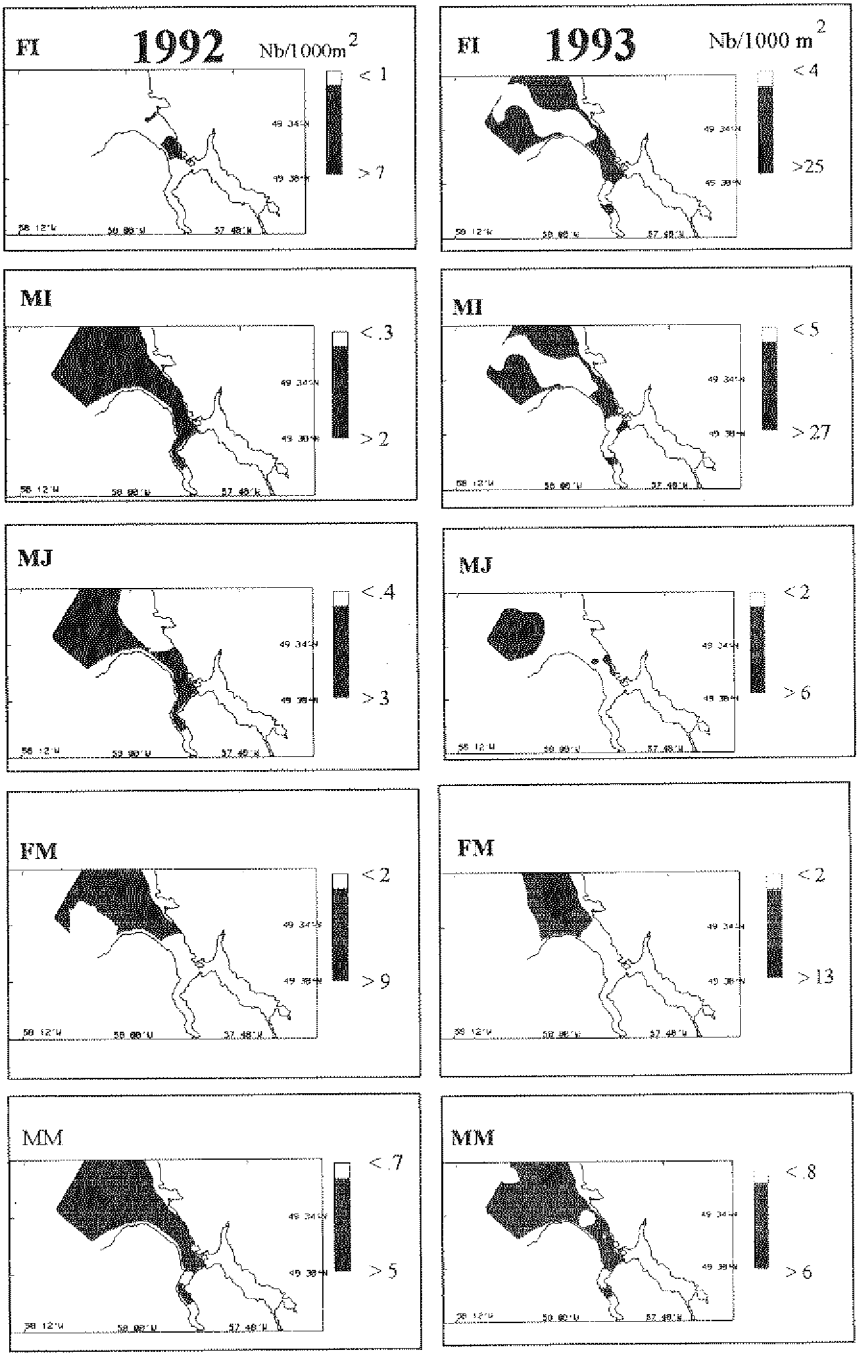


Figure 11. Correspondence analysis of snow crab spatial distribution. The catch from 13 Nephrops trawl stations was separated into 14 biological categories as a function of sex, size, state of maturity, state of development of the broods, and missing claws for the males. The two first principal factors explain 56% of the variance. They appear to be related respectively to age (here x axis, right to left) and to sexual differentiation (here y axis, bottom to top). Male and female snow crab aggregate or segregate into structured patches which change during their life cycle and can be explained by particular traits of their life histories. The variables are: 1. Females Immature (FI), Juvenile (FJ), Primiparous (FPri), Orange Eggs (FOE), Brown Eggs (FBE), Missing Eggs (FME), No Eggs (FNE), 2. Males Immature (MI), Small Juvenile (MJS), Large Juvenile (MJL), Morphometrically Mature Small (MMS), Morphometrically Mature Large (MML), One Claw (MOC), No Claw (MNC).


FI
1992
Nb/1000m^2
< 1
> 7
1993
Nb/1000 m^2
< 4
>25
MI
<.3
> 2
< 5
> 27
MJ
<.4
> 3
< 2
> 6
FM
< 2
> 9
< 2
> 13
MM
<.7
> 5
<.8
> 6
49 34'N
49 38'N
58 12'W
58 00'W
57 48'W

Phasing of individual life history events during benthic stages, in response to a seasonal environment

Phasing of life history processes involves detection of a seasonal external signal as well as exchange of information between individuals. In a seasonal environment there are strong advantages for having specific events synchronized among individuals and occurring at a most favorable time of the year.

Phasing of reproductive processes: Synchronizing individual reproductive processes between individuals and with the physical environment will allow more efficient male/female encounters and hatching of the larvae at the most opportune time to match food concentrations in the plankton.

The occurrence of pairs of crabs in precopulatory embrace had been first observed by Hooper (1986) in shallow water in Bonne Bay. Conan subsequently observed, while scuba diving, that pairs started to be found above 50 m always after a strong spring phytoplankton bloom. These observations have been documented over a sequence of years by Secchi disk readings (Figure 13) throughout the season (Comeau et al. 1991). The process was further studied by more sophisticated analytic field methods, and by experimental lab work. It appeared in the laboratory experiments that hatching of the brood from the previous year was triggered by the bloom (Starr et al. 1994).

High concentrations of pairs are restricted to a few areas of the fjord of Bonne Bay, possibly in the vicinity of permanent female concentrations. The duration of pairing in high concentrations is limited to May and early June. Pairing occurs year after year in the same areas. Mini-submarine and aquarium observations suggest that males would be ready for pairing all year round, and that it is the receptiveness of the female that would ensure successful pairing.

Pairing, hatching, and mating are initiated prior to the formation of the thermocline, it is not the warming of the water that initiates the receptiveness of the female. Recent observations from mini-submarines

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← *Figure 12. Examples of distinct spatial distributions for immature, juvenile, and morphometrically mature snow crab in Bonne Bay (1992 and 1993). Immature Males and Females (IM, IF) are not dissociated. Juvenile Males (JM) tend to spread apart and segregate from Morphometrically Mature Males (MM). MM are in the vicinity, but not confounded with the Mature (mostly multiparous here) Females (MF). The location of the patches differs from year to year, except for MF. The samples were taken using Devismes and Nephrops trawls, the data was processed using geostatistical techniques.*

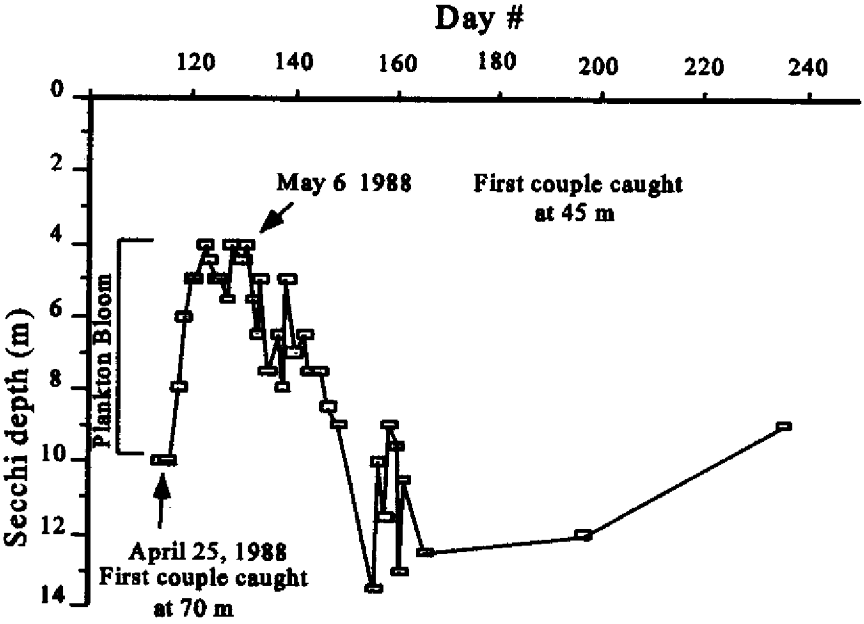

Figure 13. Detection of the spring plankton bloom by simple Secchi disks measurements in Bonne Bay. The snow crab couples consistently come into shallow water as the bloom forms a few weeks after ice break.

show that, in clear water, ambient light can be perceived by a human eye down to 100 m or more in the fjord. Light does not penetrate through snow-covered ice or through a bloom, it could therefore be used as a seasonal clue. We have shown however that a good candidate for an early spring seasonal clue is the rain of biogenic carbon residual from the spring phytoplankton bloom.

We have no indication that any natural physical process affected the success of pairing, hatching, and mating during the whole series of years of monitoring. The process was remarkably well timed year after year despite the annual variations in ice cover of the fjord.

Phasing of seasonal molting processes: The success of molting processes is highly critical for recruitment. It is during and shortly after molt that crab mortality by predation or cannibalism is prone to be the highest, while the carapaces are still soft, not fully calcified.

Small immature individuals may molt in phase several times a year as may be guessed from combined information from progression through time of modal sizes in Bonne Bay (Comeau et al. 1991) and from size increase at molt in aquaria (Moriyasu et al. 1987).

Field observations drawn from shallow water collections of carapace casts in the spring in Bonne Bay (Ennis et al. 1990, Comeau et al. 1991) and on direct observation of molters confirm dating of carapaces by radioisotopes indicating that most large males molt in early spring (April-May). Laboratory observations (Moriyasu et al. 1987) also confirm early spring molting of large males, and provide some indication that females may molt slightly earlier in the year. This is also corroborated by radioisotope dating (Conan et al. 1990b), with the additional information that females may reach the terminal molt throughout the year.

Although there appears to be mostly one seasonal spring period for molting in the year for male snow crab in their late benthic stages, a high proportion of juvenile males can in some years be found in an advanced stage of pre-molt in late fall. It is not clear whether such individuals will molt or remain in this stage until the next spring. They might also be the same individuals that occasionally skip the previous spring molt in certain years. One of us (M. Comeau) after analyzing the size composition of the catch over several years, suggests that such molt skipper individuals are affected by a very high natural mortality. Molting out of season could be very negative for recruitment success. We do not have a solid explanation for this molting out of phase, our observations show that the intermediate water layer was not colder in years of high incidence of molt skippers, rather we suspect that molt inhibition may have been induced by morphometrically mature dominant males in terminal anecdysis.

The spring synchronized molting of males in shallow water was not observed every year, it may occur only during years of high abundance of crab. It may be a mechanism of protection against predation and cannibalism from hard carapace crabs having gone through the terminal anecdysis in previous years. We have no direct observations providing information on the determinism of spring molting by external seasonal factors or indications that fluctuating environmental factors would have variable year to year effects on survival of the spring molters.

A stable survival of larval stages despite fluctuations of the environment

All larval stages of *Chionoecetes opilio* have been found in the fjord. The development from zoea to megalopa takes 3 to 4 months. The zoea 2 and megalopa stages have been difficult to encounter, even when corresponding early benthic recruitment is later found to be abundant. We have so far no proof that fluctuations in recruitment originate from the erratic success of larval stages. Several factors were considered as potential sources of recruitment failures, but none were retained.

Wind-driven larval advection: Larval behavior appears to be adapted to exploit predictable hydrodynamic regimes despite slow swimming speeds. Except shortly after hatching, the larvae tend to remain below the surface and mixing layer which is mainly affected by an Ekman

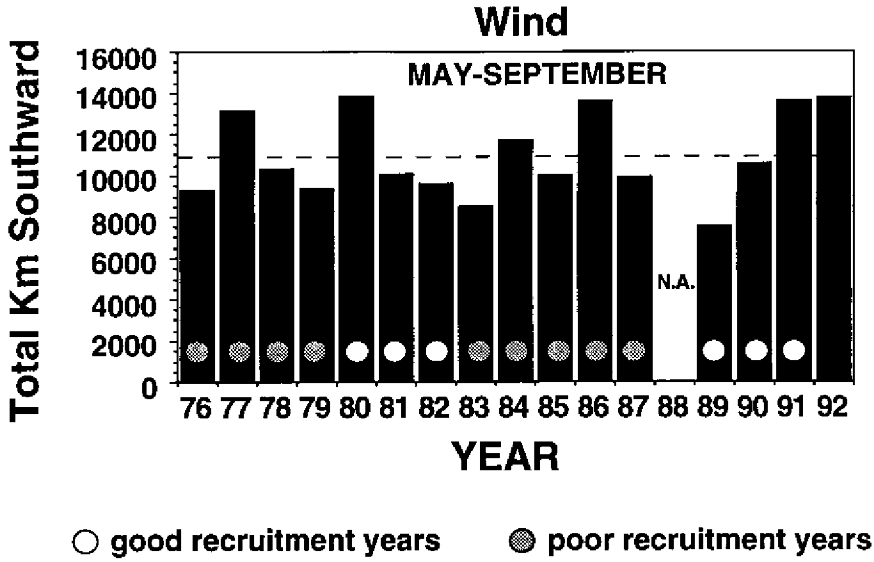

Figure 14. Cumulative southward transport of the wind blowing during 1976 to 1992 in the vicinity of Bonne Bay. Unshaded dots mark years during which the hatching larvae subsequently yielded strong cohorts when growing into early benthic to adult stages. There is no detectable negative effect on recruitment by wind induced Ekman currents out-flushing larvae out of the fjord.

transport component directed offshore (Figure 4). Subsequently Bonne Bay crab recruitment appears to be weakly affected by inter-annual variability in longshore winds (Figure 14).

Larval food limitations: Somerton (1982) suggested that seasonal sea ice cover may be an important factor controlling *Chionoecetes opilio* recruitment success in the North Pacific. He proposed that the timing of the release of *C. opilio* larvae was critical with respect to the occurrence of the plankton bloom forming in the spring at the breaking edge of the sea ice cap. Survival of larvae and thereafter success of recruitment would be determined by year to year asynchrony of the larvae appearance in the plankton with this spring phytoplankton bloom. This idea is similar to the hypothesis of match/mismatch proposed by Cushing (1975) as a general cause for fluctuations in recruitment success. The success of recruitment would be determined by the match/mismatch of larval releases in the plankton with abundance of food from phytoplankton blooms

Abundance of Gulf of St. Lawrence snow crab stocks, including Bonne Bay, do not appear to be affected by such environmental effects.

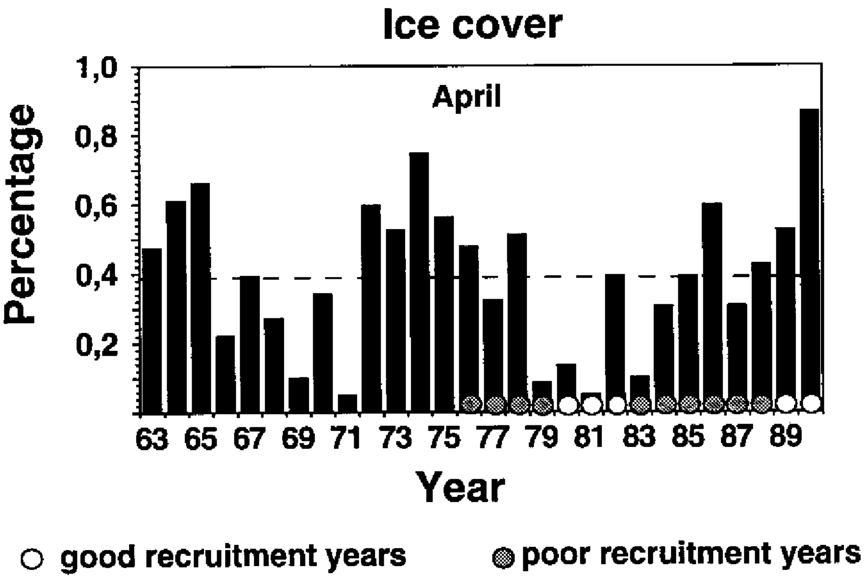

Figure 15. Annual average ice cover during the month of April in the northeastern Gulf of St. Lawrence from 1963 to 1990. Unshaded dots mark years during which the hatching larvae subsequently yielded strong cohorts when growing into early benthic to adult stages. There is no relationship between ice cover and recruitment success.

Conversely, snow crab seem to have developed means of matching larvae release with opportune bloom periods.

The ice extent anomalies calculated from a 27-year record of weekly ice cover charts for the spring months in the Northeastern Gulf of St. Lawrence demonstrate three well marked periods of longer seasonal extent of ice cover: 1972-1978, 1982, and 1988 onward. Stronger than usual cyclonic circulation over the Northwest Atlantic during winter months brought cold arctic air to coastal areas of Labrador and Newfoundland. Our analyses show that Bonne Bay crab recruitment was only weakly influenced by this inter-annual variability (Figure 15).

Starr et al. (1994) have shown that *C. opilio* have developed efficient mechanisms for synchronizing the release of their larvae with the spring secondary production cycle upon which they depend for food. In Bonne Bay, snow crab larvae releases are phased with the sedimentation peak of phytoplankton particles originating from the surface spring bloom, but with a delay of 2 to 3 weeks (Figure 7). In laboratory, a significant induction of hatching of the broods of egg-bearing females is obtained by applying extracts of senescent cultures of different phytoplankters as opposed to controls (Figure 16). These field and laboratory observations suggest that snow crab can detect the presence of decay products from the spring phytoplankton bloom. Whether the effect is direct on the eggs or relayed by the egg-bearing female, larvae are released when food zooplankters feeding on the phytoplankton are most abundant (Figure 7).

Occasionally when northeasterly winds cause upwellings of colder, nutrient charged intermediate water into the fjord during summer, one would expect secondary blooms and enhanced trophic production. But we found no positive effect of northeasterly wind components on the success of snow crab recruitment through enhanced survival of larvae.

Missing cohort dynamics, a natural intra-population source of recruitment fluctuations

The trawl samples taken in Bonne Bay over a period of 10 years show that complete sequences or cohorts are missing in the catch (Figure 17). The dynamics may be that over a period of 10 years a sequence of about three age groups will recruit successfully, grow to morphometric maturity in about 8 years or more, and disappear by natural mortality, mostly from senility. From 1985 to 1991, only three recruited cohorts (year classes 1980-82) have grown successfully but there was no subsequent replacement. From 1992 to 1994, as morphometrically mature individuals started to disappear by senility, nonregenerating damaged shells and lost appendages, a new flow of early benthic recruits started to appear. This sequence of events illustrates how recruitment can be highly variable from year to year in absence of a fishery. Some authors mistakenly stated that in Bonne Bay the snow crab stock had been cropped down by poachers, while as shown in Figure 17, the disappearance of commercial size 95-130 mm carapace width males was simply explained as a lack of renewal by early benthic recruitment in 1987-1988.

The dynamics of the population components juveniles and morphometrically mature males, represented by swarms of points in Figure 18, explains why certain authors relying on a one year static view of a snow crab population (Figure 18 A) may have been misled in interpreting snow crab growth. Such authors concluded that a terminal molt did not exist because individuals could not grow in one molt from the maximal size of juveniles to the maximal size of morphometrically mature. Figure 18 D represents a different stage of the population showing that such a growth did take place, and that the gaps disappear when the age groups are dynamically followed over several years.

The dynamics of the two population components juveniles and morphometrically mature males in Figure 18 also shows how pulsed recruitment generates shifts in the size distribution of the males (morphometrically mature) which participate in multiparous mating pairs. When a new age group reaches terminal anecdysis, the males participating in

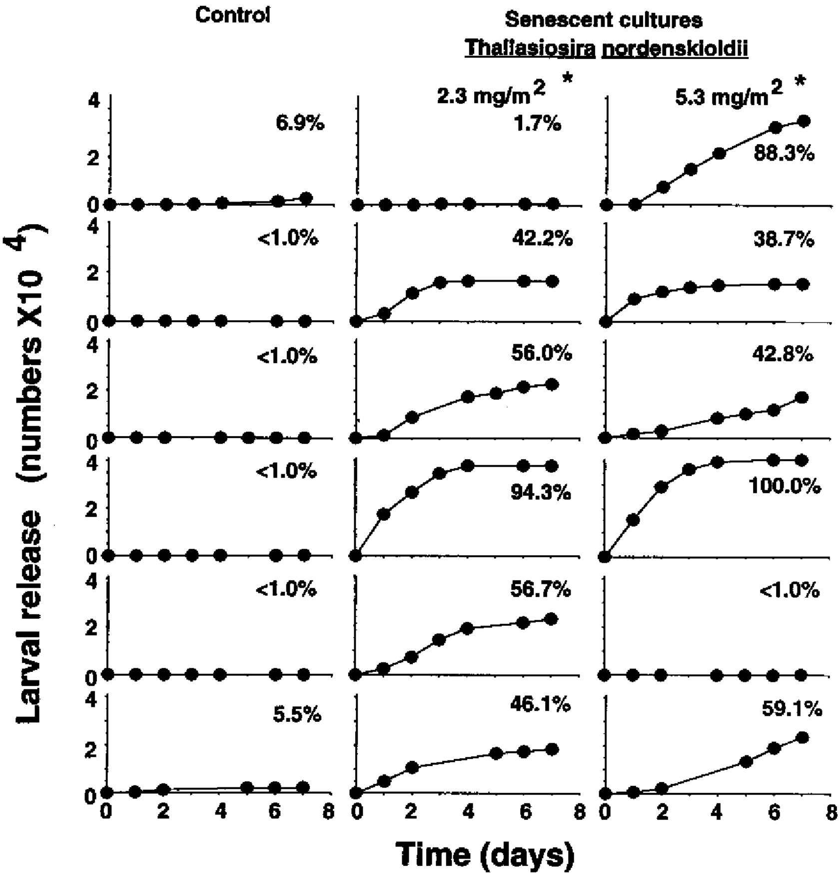

Figure 16. Results of laboratory experiments during which female snow crab carrying broods ready to hatch were exposed to seawater preparations mimicking winter and spring conditions. The rows are replicates. The replicates of the first column show how the broods reacted when control water collected in winter prior to any bloom was added to each tank containing a female. The sets in the second and third columns show how the broods reacted to winter seawater tinted with various concentrations of senescent cultures of a diatom commonly found in the Gulf of St. Lawrence. It appears that the senescent cultures mimicking residuals from a finishing bloom trigger quite efficiently the hatching of the eggs.

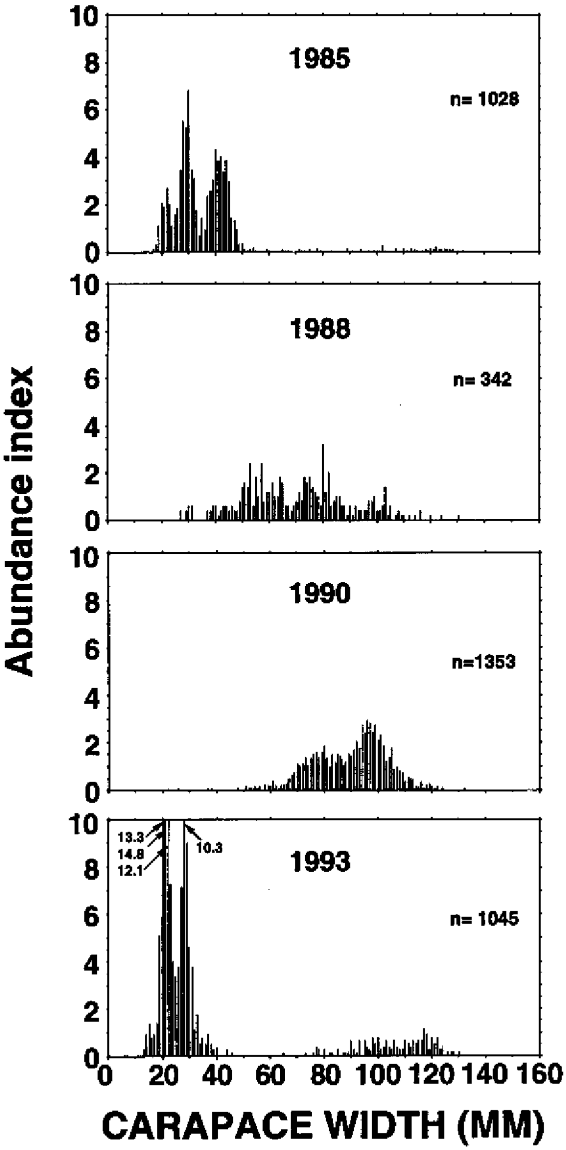

Figure 17. Characteristic changes in snow crab population structure inside the fjord of Bonne Bay from 1985 to 1993. The 1993 structure is similar to the 1985 and most likely 1984 structure. A sequence of high abundance of early benthic stages occurred twice over the lapse of time surveyed. The pulse grows to morphometrically mature stages and dies out from senility processes. A new wave of successful early benthic stages recruitment occurs only when the older animals start to disappear.

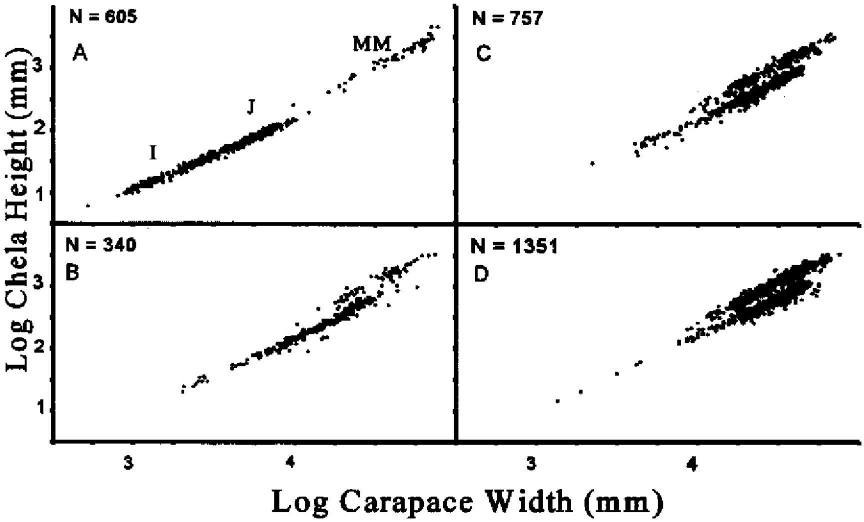

Figure 18. Characteristic changes in snow crab population structure inside the fjord of Bonne Bay from 1985 to 1993. Allometric plots show the dynamics of the missing cohorts. Immature individuals (I) grow into juvenile (J) which in turn grow into morphometrically mature (MM). When J molt into MM, very few I are found. It is inferred that MM prey on I and possibly also affect J.

mating with multiparous females are at first small, then over subsequent years the same cohort will produce larger and larger males reaching terminal anecdysis and mating, until the whole cohort has reached terminal anecdysis. Larger males exclude smaller ones from mating and the pairs over a sequence of years will be made of larger and larger males, until they disappear by natural effects of senility. Males who reach terminal anecdysis earlier and at smaller sizes mate earlier with multiparous females, but also have a shorter life expectancy.

These elements of information from Bonne Bay confirm fishermen records from other areas of the Gulf that the alternating sequences of good/poor recruitment years are a natural process. Intra-population regulations by cannibalism of terminal molters on molting immature and juvenile crabs, of juveniles on immature, or induced growth stunting resulting in molt skipping may be involved in generating the population oscillations, while some type of environmental factor would be required to phase these oscillations between partially isolated areas of the Gulf. Cannibalism by morphometrically mature males on immature was observed in situ by one of us (G.Y. Conan) during mini-submarine dives in Bonne Bay. The high concentration of females in structured pods, and the dispersion of the males around the pods, suggest exchanges of information by pheromones and metabolic regulations between individuals.

Conclusion

The Bonne Bay snow crab population and environment monitoring has allowed us to decrypt the major successive events taking place in the life history of snow crabs and to rectify previous erroneous interpretations on which some fishery management strategies were based. Our conclusions (Conan and Comeau 1986) were sometimes based on ancient basic biology knowledge (Teissier 1933, 1935), at first strongly criticized (see reply by Conan et al. 1988a) as nonconforming with the existing accepted trends of ideas, but have ever since frequently been confirmed by later work from different authors in different areas (Yamasaki and Kuwahara 1991, Sainte-Marie and Hazel 1992). It is important to stress that fisheries management cannot be efficiently achieved on the basis of simplified or erroneous biological assumptions. Modeling cannot supplement lack of information or inaccurate information, it can only help to think on the basis of sound initial information.

The major difficulty in fisheries management is presently the understanding of recruitment processes. Great effort has been set in the past on modeling relationships between parental stock and recruits, assuming that environmental factors have random effects on recruitment, and that natural populations tend to remain stable.

Our goal of decrypting step-by-step the recruitment processes of snow crab in Bonne Bay has shown that, at least in this case, environmental factors do not have random effects but are naturally responded to by a population. The assumption of a naturally stabilized recruitment destabilized by fishing is incorrect.

We have been able to show that some presumably important factors such as egg production, ice cover, or oxygen depletion did not actually seem to affect recruitment. In several cases such as match/mismatch of larvae release with phytoplankton blooms, and larval advection, we could identify a natural mechanism by which the population could react and avoid unnecessary losses. This does not imply that all environmental effects can be efficiently buffered by a natural population. But understanding the population response mechanism under normal circumstances may allow to understand and eventually correct in case of extreme effects overwhelming the buffering potential of a population.

Conversely, the important fluctuations in abundance of fishable crabs in Bonne Bay were not due to uncontrolled overfishing by poaching, as had been hastily concluded. The most logical interpretation of our observations is that the recruitment fluctuations are actually natural and result from intra-population regulations. There is some indication already that our Bonne Bay conclusions also apply to other areas of the Gulf (Sainte-Marie and Dufour 1995), and that there is a superimposed synchronization between areas by an external environmental factor. This environmental factor could be the fluctuations in available space for the extension of the species within ranges defined by depth of the intermediate water layer. Recent extension of snow crab on the Grand Banks of Newfoundland and into deeper water than usual (fishermen reports; to 500 m) seems to confirm this hypothesis.

The advantages of having oscillating population structures and well contrasted benthic life stages with different morphologies remain to be demonstrated. Changing population structure may be a protection against predators, that may not evolve to specialize on a species which is not available in stable quantities year after year. Cannibalism may also be a means of occupying the food chain simultaneously at several different levels for enhancing survivorship of reproductive adults.

The present major difficulty for managing the snow crab stock in the Gulf of St. Lawrence results from these wide fluctuations in recruitment that apparently cannot so far be regulated by any standard fishery management strategy. Our actions are still limited under our present state of knowledge. We can obtain reliable estimates and mapping of existing biological categories by quantitative trawling using the combined *Nephrops* trawl, SCANMAR, GPS, and kriging technology. Using growth schedules derived from following multiyear recruitment sequences in the Bonne Bay observations, we can predict several years in advance the occurrence of a successful recruitment to the fishery. We can decide over how many years this recruitment will be harvested knowing that the catch consists mainly of morphometrically mature males, that the first year the crabs are white and of low commercial quality, the second year of top quality and that afterward the quality degrades by loss of nonregenerating legs and fouling of the carapace. We can provide annual maps to the fishermen predicting where the best quality crabs and the low quality crabs are located.

However, we cannot yet stabilize recruitment and actually "protect" the stock from so-called "recruitment overfishing" because we have no elements to define such an overfishing. The goal of stabilizing fisheries yield year after year may be economically rewarding. Several strategies could be assayed in a relatively isolated location such as Bonne Bay by selectively removing certain components of the stock, such as the terminal molters and observing what structure of remaining standing stock would produce a steady flow of recruits. On the long run however, we have yet no elements allowing to predict whether this would increase the cumulative fishery yield over years. Only further experimental and basic population biology work would allow us to proceed.

We would recommend that the Bonne Bay fjord, which is located in the vicinity of the Gros Morne National Park, be used as a permanent monitoring and experimental base for snow crab research. Complementing the existing series of information and proceeding with planned fishing experimentation in situ would allow to further test our hypothesis of missing cohort dynamics and to solve many remaining unknowns in the process of recruitment of snow crab stocks.

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Development of an Expert Computer Vision-based Crab Classification System

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Abstract

Historically, Bering Sea fishermen, management, and research agencies have had difficulty in differentiating among Tanner *(Chionoecetes bairdi)*, snow *(C. opilio)*, and Tanner × snow putative hybrid crabs due to similarities in morphology. A computer vision-based crab classification system is under development which is highly accurate in identifying Tanner and snow crabs and hybrids of these two species. The system correctly classified all Tanner and snow crabs in samples of 120 crabs from each species. It misclassified 1 out of 120 hybrids examined.

Introduction

Tanner *(Chionoecetes bairdi* Rathbun) and snow crabs *(C. opilio* [O. Fabricius]) have comprised large commercial fisheries in the Bering Sea in recent years. Hybrids of the two species were first recognized in the eastern Bering Sea in 1969 (Karinen and Hoopes 1971). Genetic identification of the two species and hybrid was confirmed by Johnson (1976) and Grant et al. (1978). Estimates of total abundance of male hybrids in relation to total abundance of male Tanner and snow crab, has been estimated to approach 20% (Grant et al. 1978).

Both species are very similar in morphology to each other. The hybrid, due to a range of intermediate characteristics between the two species, can be very difficult to distinguish from either a true snow or Tanner crab. Hybridization has also been reported for this genus between *C. opilio* and *C. Japonicus* Rathbun in the Japan Sea (Nishimura and Mizusawa 1969).

The author, as contract administrator, developed this paper from reports prepared by Dr. A.H. Tewfik of the University of Minnesota who developed the system under contract to the Alaska Department of Fish and Game.

The Alaska Department of Fish and Game (ADF&G) manages fisheries for both species with separate seasons, catch quotas, and size limits. The difficulty in distinguishing the species and hybrids has led to problems for both industry and agencies managing and researching these fisheries (Gay 1991). Recently, in snow crab fisheries, the inability to separate Tanner, snow, and hybrid crab has resulted in the retention of sublegal Tanner crab, sold as snow crab (ADF&G Emergency Order No. 4-s-06-91).

Fishermen claim that in many instances it is impossible to discriminate between the species, especially when commingled with hybrid crabs, or when fishing in the Bering Sea in the winter and at night. Management of individual fisheries is difficult because of overlap in Tanner and snow crab habitat, the presence of a hybrid zone, and the recognition problem. For example, ADF&G estimated that as many as 10 million Tanner crabs were harvested during the snow crab fishery in 1991, a harvest equal to the directed fishery for Tanner crab.

There was a large economic cost associated with this crab identification problem. Fishermen were paid $0.50/lb for snow crab and $1.50/lb for Tanner crab in the respective 1991 fisheries. The 10 million Tanner crabs sold as snow crabs would have been worth approximately $10 million more ex-vessel had they been sold as Tanner crabs during the next Tanner crab season. Also fishers caught 10 million fewer snow crabs due to filling the snow crab quota with Tanner crabs, which would have been worth $5 million. So, fishers may have lost about $15 million during the 1991 season because of this problem.

This economic ex-vessel loss is multiplied when considering lost shoreside processing and employment opportunities. In addition, lost opportunities to harvest hybrid crab, which have been estimated to be as high as 20% of the Bering Sea population of snow and Tanner crabs, were not considered and would add to the overall loss.

From a species conservation and management perspective, the identification problem increases the potential for overharvesting Tanner crabs. Perhaps even more of a concern is the harvest of undersized Tanner crabs which have not reached sexual or functional maturity.

To overcome this identification problem ADF&G, in conjunction with InfoPet Identification Systems, Inc. (Minneapolis, MN) and the University of Minnesota, is researching electronic crab identification. This paper describes the consortium's efforts in developing a computer-based image acquisition system that uses visual features and measurements of visual features in differentiating between snow and Tanner crabs and their hybrids.

System Development

A four-phase approach is being used to develop this system: (1) collection of specimens, (2) genetic identification to species or hybrid, (3) carapace imaging, and (4) development of species identification system and training.

Collection of specimens

ADF&G personnel sampled crabs at the dock during the 1993-1995 Bering Sea Tanner and snow crab fisheries. Capture location, carapace width, shell age, and species morphological identification were recorded. A sample of muscle and heart tissue were collected from each crab as described by Merkouris et al. (in prep). The carapace from each crab was collected intact, labeled, and retained.

Genetic identification of specimens

Muscle and heart tissues were analyzed at the ADF&G genetics lab in Anchorage using standard horizontal starch gel electrophoresis methods. Merkouris et al. (in prep.) provide a thorough description of techniques employed. Results were compared to established genetic markers used to separate these two species and hybrids. Each carapace was then labeled as a Tanner, snow, or hybrid crab.

Crab carapaces, along with their genetic identification to species or hybrid, were sent to the University of Minnesota's Computer Science and Engineering labs where image analysis of the carapaces and system training were completed.

Carapace imaging—system overview

The system designed for this task consists of image acquisition, image processing, and classification. Image acquisition is accomplished by the use of a grayscale video camera which captures the image in a digital electronic form. The image is then processed in three stages (Figure 1):

1. Image correction: We need to correct blurs (due to motion, focus mismatch, etc.) and carapace position and tilt errors in image.
2. Feature enhancement.
3. Extraction: The identification software uses the outline of the carapace and certain measurements extracted from that outline to identify the crabs. This outline is extracted by performing various filtering operations on the acquired grayscale image.

These operations produce a sequence of edge images from which only the edge corresponding to the carapace outline is retained. The measurements (length, width, area, and perimeter) are then computed from the outline using pixel counting and direction estimation.

Image classification is accomplished by use of a tree classifier which involves two stages:

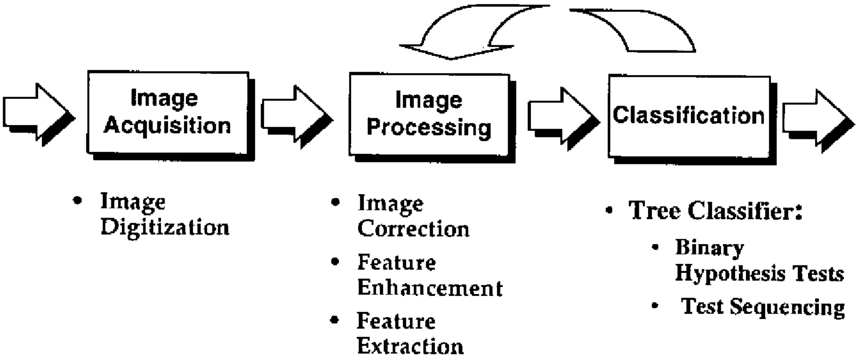


Figure 1. General overview of a computer vision-based crab classification system.

1. A binary hypothesis test identifies which of two hypotheses is correct; e.g., is this a snow crab or is it not? The test requires the computation of a single scalar (the test statistic) and compares it with a threshold determined during the testing stage.
2. To minimize the probability of a classification error, the system performs sequencing tests: ratios of length to width and the shape of the carapace, etc. Some tests are more complex than others. The software orders the tests by complexity and performs them sequentially. It stops when it has obtained a classification decision with the desired reliability.

Hardware overview

Image acquisition is accomplished using a Panasonic CCTV B/W video camera (model WV-BD400) with a Rainbow manual zoom lens (model s6x11-1.4-II). The camera is mounted on a stand with lighting and is cabled to an IBM PS/2 486 personal computer with 12 Mbytes RAM, 212 Mbytes of hard disk space with maximum access time of 15 msec (Figure 2). The configuration chosen uses an Intel 80486 DX2 CP unit running at 66 MHz and a precision frame grabber data translation board (model DT2867-LC). The computer is cabled to a color video monitor.

Software overview

The system's software consists of three levels (Figure 3).

Level 1 (lowest level) acquires and corrects images. This level uses image correction and enhancement routines developed by the University of Minnesota and found in the Global Lab Image package, a commer-

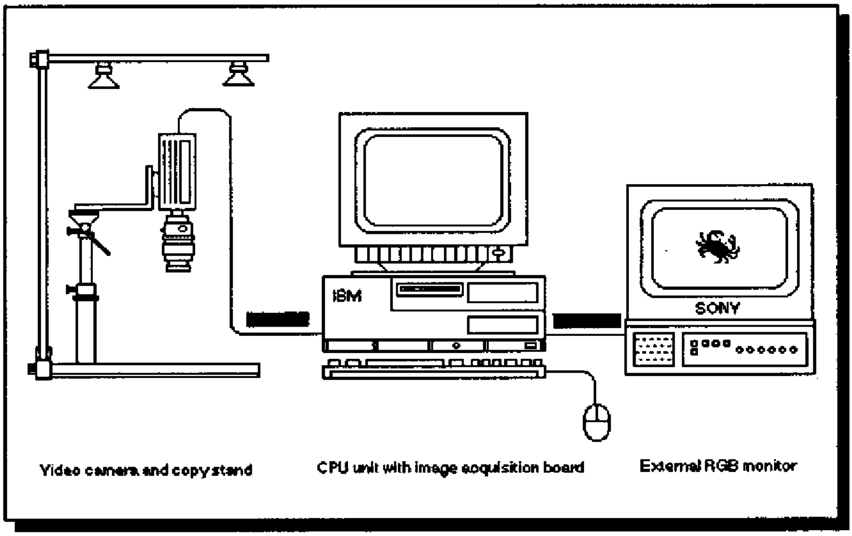


Figure 2. Hardware overview for a computer vision-based crab classification system.

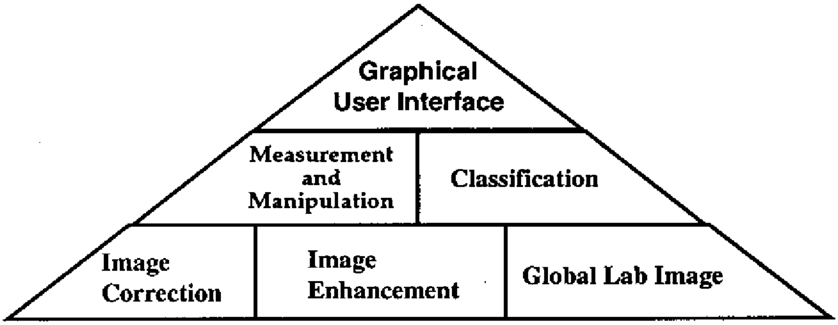


Figure 3. Software overview for a computer vision-based crab classification system.

cial software package written by Data Translation. The image correction and enhancement routines correct for blurs, and position and tilt errors in the crab carapaces and perform image transformations to facilitate edge detection. A final routine extracts the contour of the carapace after identifying the outer edge in the image produced by Global Lab.

Level 2 (middle level) is the heart of the software. In this level, measurements are taken from the carapace edge image and the signature of the image is also formed. The measurements are taken by integrating several low-level routines provided by Global Lab. These extracted features are then used by the tree classifier in conjunction with various tests to arrive at a crab classification decision.

Level 3 (upper level) provides a user-friendly interface allowing a user to run the system using plain English commands from automated pull-down menus.

Development of species identification system and training

Tree classifiers

The recognition software arrives at a classification decision by performing a sequence of tests. This sequence is described by a decision tree (Figure 4). Each test is based on a test statistic, s_1, and a threshold value, t_1. The threshold value t_1 is estimated during the training phase from the available crab carapaces. The statistic s_1 is computed from either a pair of measurements or a weighted difference between the carapace shape and average carapace shapes for the two species and hybrid. The test result determines the branch of the decision tree that the software follows. The branch can lead to a terminal node (square) indicating that the software has reached a classification decision with the desired certainty. It can also lead to an intermediate node (circle) that corresponds to another test that the system must perform next. The shape of the decision tree and the certainty associated with each terminal node are determined during the training phase.

The s_1 statistics that are based on a characterization of the carapace shape are computationally more expensive than those that are based on measurements. Therefore, the software first uses the computationally less expensive tests that are based on measurements. If these tests fail to identify the crab with the desired accuracy, it uses more complex tests that are based on the carapace shape.

Length/width discrimination

The ratio of the length to width of a carapace is one of the statistics conventionally used to identify and separate Tanner from snow crabs (Garth 1958, Takeshita et al. 1969, ADF&G 1992). The scatter plot (Figure 5) shows the distribution of this statistic for 120 crabs of each of the two

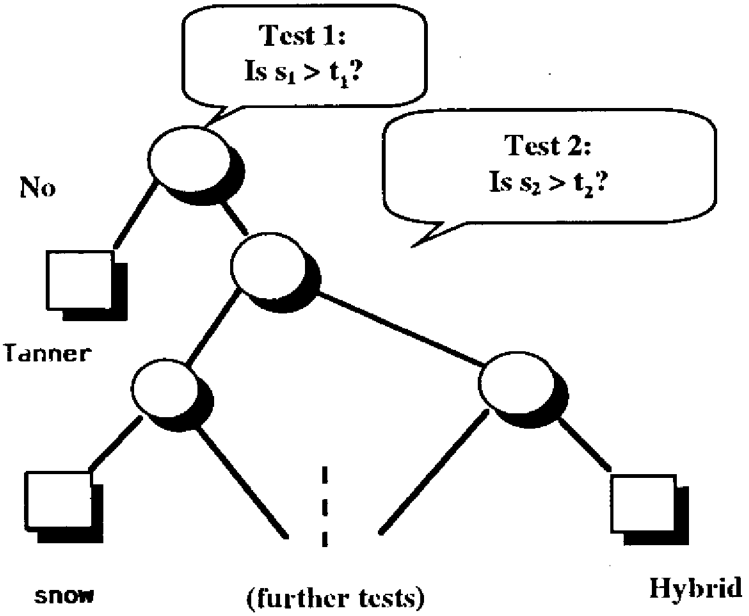


Figure 4. System tree classifiers for a computer vision-based crab classification system.

species and hybrids in this study. Figure 5 indicates that if this statistic is between the lower and upper threshold, unambiguous identification is achieved if the value is not within the spread of the other species or hybrid. If that statistic overlaps values within the spread of the other species or hybrid, then other tests have to be used. The exact thresholds are determined from the training set using cross validation techniques (Breiman 1984).

Cross validation is an approach that allows building a more reliable model with a small data set. It is based on a repeated decomposition of the sample set into different training sets and test (validation) sets. Using different training and testing sets, estimates of model parameters are fixed and their applicability to other data sets can be assessed.

Perimeter/area discrimination

The perimeter to area ratio of a carapace is another statistic used to identify crabs. The scatter plot (Figure 6) shows the distribution of this statistic for 120 crabs of each species and hybrid. Numbers 1 to 120 are Tanner crabs, 121 to 240 are hybrids and 241 to 360 are snow crab. The

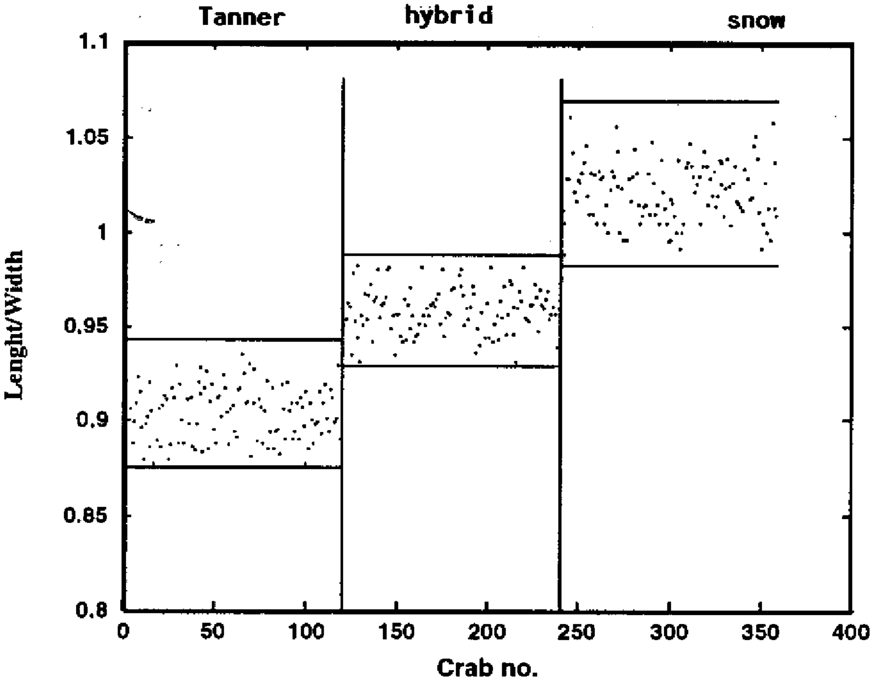


Figure 5. Length/width discrimination for a computer vision-based crab classification system. Tanner crabs are numbers 1-120, hybrid crabs are numbers 121-240, and snow crabs are numbers 241-360. The horizontal lines indicate the lower and upper limits of this statistic by species/hybrid. The vertical lines separate the species/hybrid.

horizontal lines indicate the lower and upper limits of this statistic for each species and the hybrid. Figure 6 indicates that if this statistic is between the lower and upper threshold unambiguous identification is achieved if the value is not within the spread of the other species or hybrid. If that statistic overlaps within the spread of the other species or hybrid, then other tests have to be used. Thresholds are determined from the training set using cross validation techniques.

Signature based recognition

The signature of an object is a one-dimensional representation of its contour (Figure 7). Specifically, it is a plot of the distance from a fixed point within the object to its contour as a function of angle. The angle is traced in a clockwise direction. The fixed point must be invariant to rotations and translation of the object. Normalized signatures were used to account for differences in carapace size.

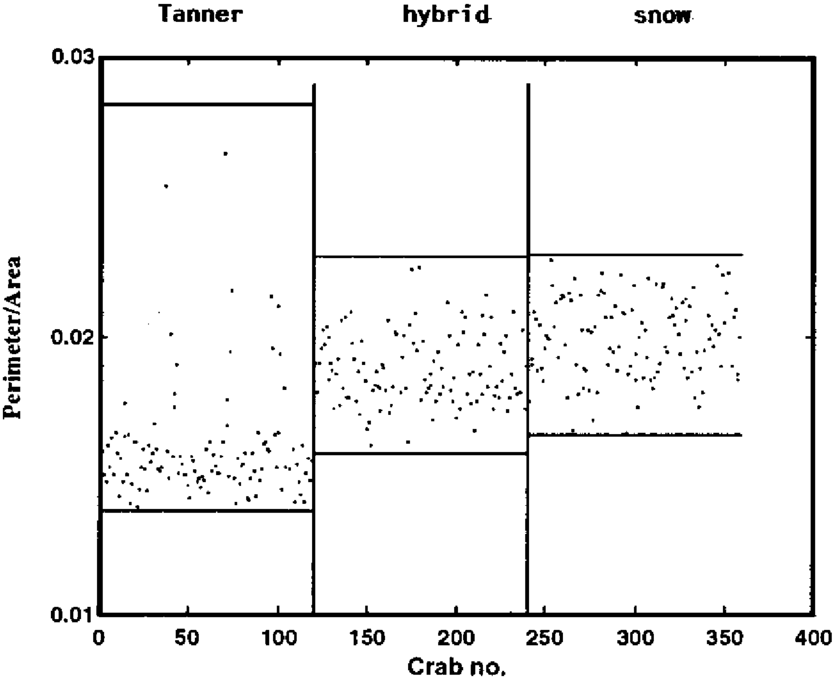


Figure 6. Perimeter/area discrimination for a computer vision-based crab classification system. Tanner crabs are numbers 1-120, hybrid crabs are numbers 121-240, and snow crabs are numbers 241-360. The horizontal lines indicate the lower and upper limits of this statistic for each species and the hybrid. The vertical lines separate the species/hybrid.

Signatures of crabs

Figure 8 shows the average ("prototypical") normalized signature for each species and hybrid. This signature is a plot of the distance from the center of mass of each carapace to its outer edge as a function of angle measured in a clockwise direction; 120 such plots were obtained for each species and hybrid and then averaged.

Signature based recognition involves acquiring the image of the carapace and computing the weighted distances between the signature of the carapace and the average signatures that correspond to the two species and hybrid. In particular, the system declares a given crab carapace to correspond to class A if the signature of this carapace is closest to the average signature of crabs in class A. Closeness is measured using a weighted distance that emphasizes certain directions and de-emphasizes or ignores other directions.

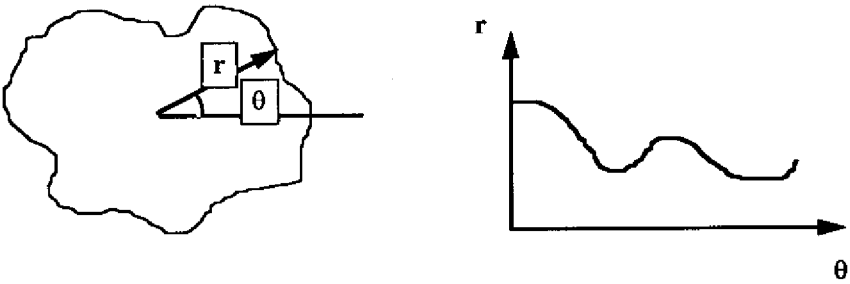


Figure 7. Signature based recognition. The signature of the carapace is derived by a series of measurements from the center of mass to the contour of the carapace as a function of angle. The measurements are then plotted as a one-dimensional representation of its contour.

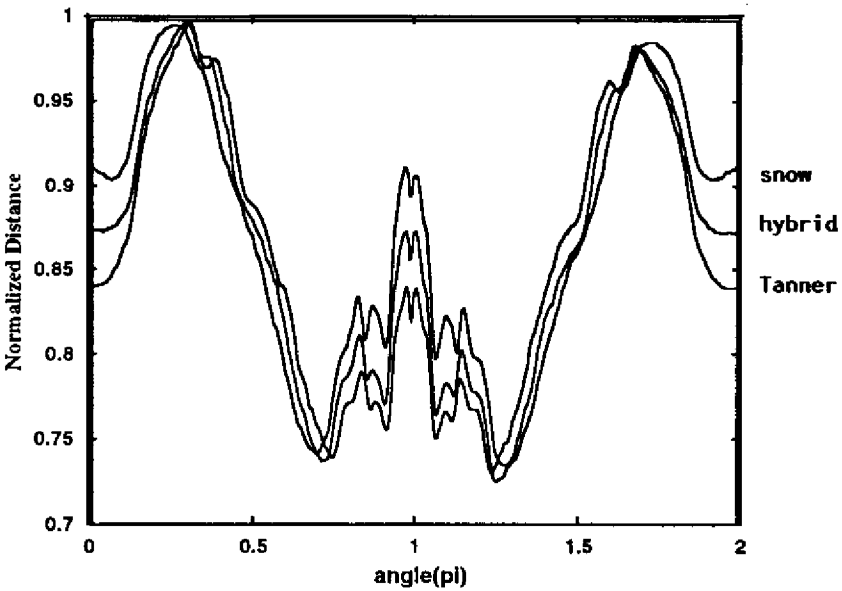


Figure 8. Signatures of crabs. The average ("prototypical") normalized signature corresponding to the two species and hybrid is depicted. This signature is a plot of the distance from the center of mass of each carapace to its outer edge as a function of angle measured in a clockwise direction. N = 120 for each species and hybrid.

There were several technical concerns addressed by the consortium:

1. Speed of computation: To increase computational speed we attempted to simplify signature computation, because computing signatures by measuring distances from the center of mass of the carapace to its outer edge is computationally expensive. The main costs of this operation are associated with the identification of the center of mass of the carapace. A simple alternative approach to compute distances from the center of the smallest rectangle that encloses the carapace was unfortunately less reliable because of the sensitivity of the shape of the enclosing rectangle to small changes in the contour of the carapace.
2. Directions to emphasize or ignore in computing distances: When computing distances between signatures, variability of the signatures about each average signature must be considered. In particular, changes along certain directions must be de-emphasized, whereas changes along other directions need to be neglected because they would correspond essentially to inaccuracies in the image.

Figure 9 shows the two points that we can use to determine signatures. These two points are the center of mass of the carapace or the center of the smallest enclosing rectangle. Note that this latter point can be unambiguously determined because the software automatically rotates the carapace so that the eye orbits point upwards.

An illustration of why the distribution of signatures around each average signature must be taken into account when computing distances is provided in Figure 10. The ellipse represents the scatter of signatures from that class around the average of a crab class (the center of the ellipse). The distance from the center of the ellipse to its edge along a particular direction indicates the amount of variability in the signature values along that particular direction (note that all signatures are normalized signatures).

Three cases are shown. In Figure 10a, variability is the same in all directions for the two species and hybrid. In Figure 10b, variability is different in different directions but is the same for all three classes. In Figure 10c, variability is a function of both class and direction.

As mentioned before, the system declares a given crab carapace to correspond to a class (A, B, or C) that is closest to the average signature of crabs in the class. Closeness is measured using a weighted distance that emphasizes certain directions and de-emphasizes or ignores other directions.

To determine whether a signature is closest to the average signature corresponding to class A, B, or C, the distribution of signatures in the clusters around each average signature is considered. Directions that correspond to wide variability must be de-emphasized. Directions that

- **Signatures computed from the center of mass or the center of rectangle that encloses the carapace?**

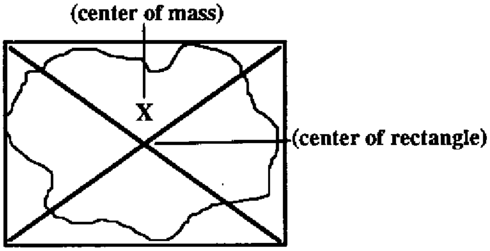


Figure 9. Generalized depiction of signature computation from centers of mass (x) and smallest enclosing rectangle.

- **Weighting distance measurements: how is the data distributed?**

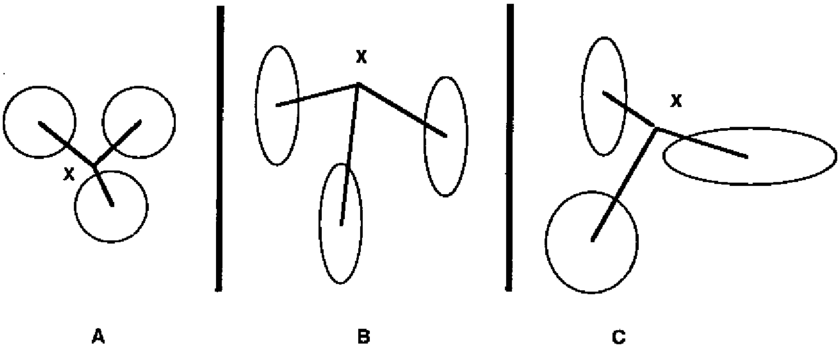


Figure 10. Generalized signatures and data distribution. Each ellipse represents the scatter of signatures from a distinct crab class (Tanner, hybrid and snow) from the average of a crab class (center of ellipse). In 10a the variability is the same in all directions, in 10b the variability is different in different directions but is the same for all classes, and in 10c the variability is a function of both class and direction.

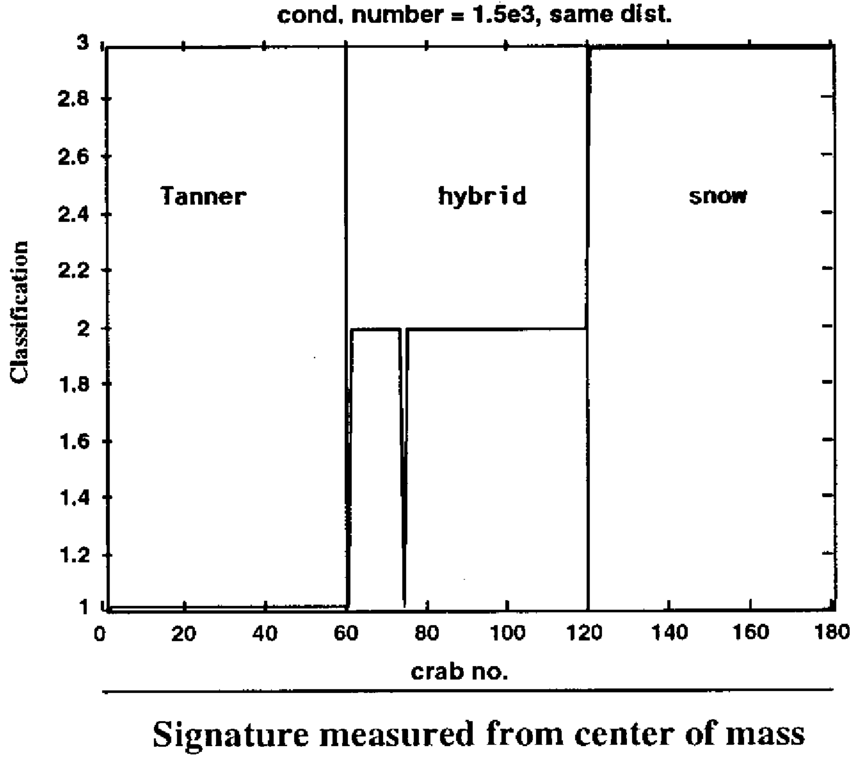
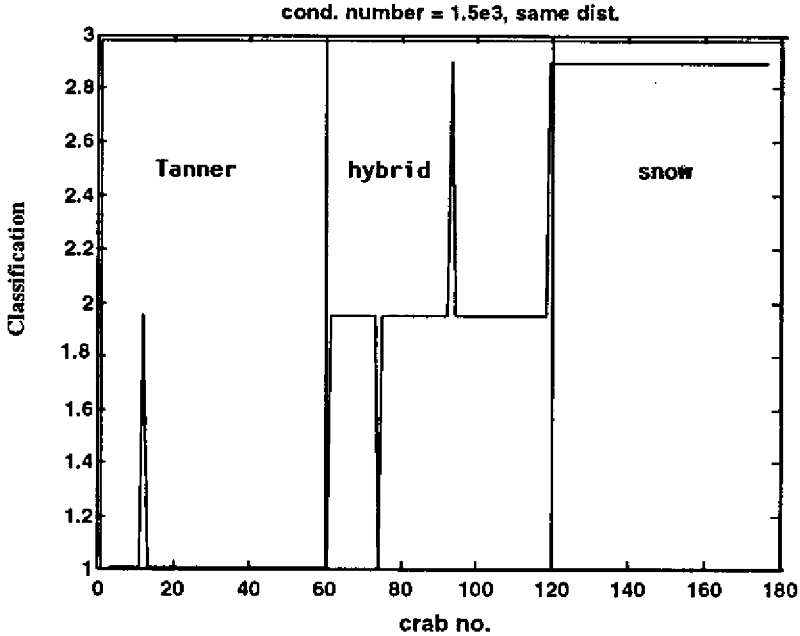


Figure 11. Signatures measured from the center of mass. The vertical axis denotes the crab class. Number 1 denotes the Tanner crab class, 2 denotes hybrid, and 3 denotes snow crab. The horizontal axis indicates the number associated to each crab carapace in the testing set. Numbers 1-60 were Tanner crabs, numbers 61-120 were hybrids, and numbers 121-180 were snow crabs. Signatures measured from the center of a rectangle.

correspond to no or little variability must be treated with care because that could emphasize noise. On the other hand, some of these directions may provide the best discrimination between the three classes. Part of the experimental work involved determining which directions of small variability to retain and which to ignore.

Signatures from center of mass

Figure 11 summarizes the accuracy of the discrimination test based on signatures computed from the center of mass of the crab carapace. Numbers 1 to 60 were Tanner crabs, numbers 61 to 120 were hybrids, and numbers 121 to 180 were snow crabs. Sixty crabs from each class



Signature measured from center of enclosing rectangle

Figure 12. Signatures measured from the center of a rectangle. The vertical axis denotes the crab class. Number 1 denotes the Tanner crab class, 2 denotes hybrid, and 3 denotes snow crab. The horizontal axis indicates the number associated to each crab carapace in the testing set. Numbers 1-60 were Tanner crabs, numbers 61-120 were hybrids, and numbers 121-180 were snow crabs.

were used to train the system (i.e., determine the average signature corresponding to each crab class and the variability around the signature). The plot indicates that only one hybrid was misclassified as a Tanner crab. All other 179 crabs were correctly classified.

Signatures from center of enclosing rectangle

Figure 12 summarizes the accuracy of the discrimination test based on signatures computed from the center of the smallest rectangle that encloses the crab carapace. We used sixty crabs from each class to train the system. The plot indicates that two hybrids were misclassified as a Tanner and one Tanner was misclassified as a hybrid. All other 177 crabs were correctly classified.

Comparing Figures 11 and 12 indicates that the test based on the signature measured from the center of mass of the crab carapace is more reliable than the method using the center of the smallest rectangle that encloses the crab carapace. This is due to the sensitivity of the shape of the enclosing rectangle to small changes in the crab contour that may be due to errors in the acquisition process, e.g. noise, shadows, etc.

Continuing Investigations and Goals

An expert computer vision-based crab classification system has been developed that is highly accurate in identifying Tanner, snow, and Tanner × snow putative hybrids. The system, once launched, automatically takes a picture of the crab carapace, and produces its classification decision based on features that it has acquired or measured from images taken by the video camera.

The system, as it now exists, correctly classifies all Tanner and snow crabs in the current sample (120 crabs from each species). It misclassifies one out of 120 hybrids in the current sample. The initial version of this system is deemed usable onboard research vessels and in a laboratory setting.

The system accuracy is as good as the sample size used to train it. The carapaces of an additional 1,080 genetically typed crab of Tanner, snow, and their hybrids will be used to train and refine the system.

Continuing investigations include (1) study of the effect of carapace size variability on recognition accuracy, (2) king crab *(Paralithodes camtschaticus)* carapaces may be examined for intraspecific morphological differences between geographical areas, (3) study possible intraspecific morphological differences between Atlantic and Bering Sea snow crab, and (4) produce a weather-resistant field system which can be used on fishing vessels.

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Impact of Uncertainty on ITQ Management of the Bristol Bay Red King Crab Fishery

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Introduction

Individual transferable quotas (ITQs) have become an increasingly popular means for managing fisheries because they offer the potential to solve the common property problems of overcapitalization and rent dissipation. These ubiquitous commercial fisheries problems were first described in a seminal article by H. Scott Gordon (1954). Thirty years later, Munro and Scott (1985) classified two types of common property problems. Class I common property problems occur when there is no regulation of the fishery. In this situation, there is excessive entry into the fishery, resulting in a race-to-fish with its associated dissipation of resource rents and also depletion of the resource. Class II common property problems occur when the fishery is managed to prevent the depletion of the resource, but the regulation fails to adequately control the intensity of the fishing effort. The resulting race-to-fish and dissipation of resource rents follow from excessive investment and competition for the limited resource.

The Bristol Bay red king crab fishery is an example of a Class II common property fishery, which is why it and other North Pacific crab fisheries are being considered for ITQ management. Once a multiple month-long fishery, the Bristol Bay red king crab has been reduced to a week-long derby, if the season is not closed altogether. ITQs might offer the potential to reverse this race-to-fish and restore economic health to this industry.

Any new management proposal, however, needs thorough consideration before implementation to ensure that promised benefits are realized. Careful prior analysis of ITQ management in the Bristol Bay red king crab fishery is especially prudent given the historical commercial importance of this fishery to both the state of Alaska and the nation (see Otto and Dyson 1985, Blau 1985). But there is another reason why the efficacy of ITQ management should be examined in the context of this or other North Pacific crab fisheries. ITQ management is predicated upon managers being able to establish an annual total allowable catch (TAC) consistent with maximum sustainable yield or other conservation oriented goal. To date, crab managers have not been able to define such a TAC, despite a preseason trawl survey to assess stock abundance and harvestable surplus. Both the initial biomass and the TAC remain uncertain. Consequently, the fishery is managed for maximum sustainable yield with two principal tools: (1) a guideline harvest level (GHL) based on a preseason estimate of the harvestable surplus from the trawl survey, and (2) in-season management that ostensibly monitors catch per unit effort (CPUE) in order to close the fishery by emergency order. The inevitable catch quota or TAC is not actually known until after the season is closed and all crabs are landed. Input controls (e.g., gear restrictions) also are used by managers to limit fishing effort. However, input substitution tends to undermine or negate the impact of these controls.

This paper provides a preliminary examination of the role of uncertainty in managing the Bristol Bay red king crab fishery with ITQs. Since the research is ongoing, the purpose of this paper is to illustrate potential consequences of uncertainty. We do this by comparing ITQ models with and without uncertainty.

ITQs with Certain TAC

It is instructive to see why a certain TAC is important to realizing all of the purported economic efficiency benefits of ITQ management. ITQ management is a form of rights-based fishing. Individual fishers are awarded a share of the overall quota or TAC, normally based upon historical catch performance in the open access fishery. These quota shares ω_f^0 then act as an output constraint on the fishers, such that no fisher can catch more than (ω_f^0)TAC amount of fish. Each operator then can decide whether and how to fish his/her quota shares. This simple assignment of rights to a percentage of the TAC prevents the race-to-fish because fishers now know the quantity of fish they are allowed to catch. With no need to race to catch fish, operators should use the most economical (minimum cost) mix of capital, labor, and other inputs so as to maximize profit.

Operators who decide not to fish their quota shares are free to transfer (sell or lease) part or all of them to other fishers. This transferability feature makes ITQ management akin to an industry sponsored buyout program. Profit maximizing fishers will weigh their earnings potential if they remain in the fishery versus exiting the fishery by selling or leasing their quota shares to more efficient vessels. The more efficient (lower production cost) vessels will be willing and able to purchase (lease) the fishing rights from the less efficient (higher production cost) vessels. Surplus fishing capacity is voluntarily eliminated which assures additional economic rents will be generated. The less efficient operators will be bought out by the more efficient operators such that the sellers are fully compensated for leaving the fishery. Maximum overall efficiency will be attained simply because an ITQ system allows the fisher to choose *both* the catch level and the corresponding quantity of quota shares so as to maximize profit, subject to the constraint that the quantity harvested cannot exceed the initial quota share endowment adjusted by the purchase or sale of quota shares.

This promise of maximum efficiency can be shown more formally. The amount of fish that can be harvested by the fisher is given by $Y_f = (\omega_f^0 + \omega_f)TAC$ and the transfer of quota is constrained by $\omega_f^0 + \omega_f \geq 0$, where $\omega_f > 0$ is the amount of quota the fisher leases from others, while $\omega_f < 0$ is the amount the fisher rents out to others. [Note: For the sake of analytical simplicity, we consider only annual quota transfers (renting/leasing) for the remainder of this paper. This representation causes no loss in generality.] Letting *s* represent the annual quota share rental price, the individual fisher's profit maximization problem (absent fixed costs) is given by the Lagrangian expression in equation (1).

$$\max_{Y_f,\omega_f,\lambda_f} L = \max_{Y_f,\omega_f,\lambda_f} PY_f - C_f(Y_f) - s\omega_f TAC + \lambda_f\left[\left(\omega_f^0 + \omega_f\right)TAC - Y_f\right] \tag{1}$$

The composite term $PY_f - C_f(Y_f)$ represents fishing revenues, PY_f, minus direct fishing costs, $C_f(Y_f)$. This composite term normally is thought of as profit in the absence of ITQ management. The next term, $s\omega_f TAC$, is the value of the leased/rented quota share, assuming the TAC is known with certainty. Since quota may be acquired by leasing it from other vessels ($\omega_f > 0$) or transferred to another vessel by leasing out quota shares ($\omega_f < 0$), the value of traded quota may add to costs or revenues, respectively. The final term, $\lambda_f[(\omega_f^0 + \omega_f)TAC - Y_f]$, is the constraint that restricts the harvest of the f^{th} fisher to equal the post-trade quota position.

The market equilibrium solution to (1) is characterized by the corresponding Kuhn-Tucker conditions.

$$\frac{\partial L}{\partial Y_f} = P - \frac{\partial C_f}{\partial Y_f} - \lambda_f \begin{Bmatrix} = 0 \\ \leq 0 \end{Bmatrix} \text{ for } \begin{Bmatrix} Y_f > 0 \\ Y_f = 0 \end{Bmatrix} \tag{1.1}$$

$$\frac{\partial L}{\partial \omega_f} = [\lambda_f - s]TAC = 0 \tag{1.2}$$

$$\frac{\partial L}{\partial \lambda_f} = (\omega_f^0 + \omega_f)TAC - Y_f \begin{Bmatrix} = 0 \\ \geq 0 \end{Bmatrix} \text{ for } \begin{Bmatrix} \lambda_f > 0 \\ \lambda_f = 0 \end{Bmatrix}. \tag{1.3}$$

These simultaneous equilibrium conditions provide economic insight into individual fisher behavior under ITQ management. The Lagrangian multiplier λ_f represents the marginal value of a unit of quota share to the fisher. Condition (1.2) implies that the marginal value of quota share must equal its market rental price if the fisher is in a profit maximizing equilibrium. It follows from equations (1.1) and (1.2) that the profit maximizing fisher will lease out all of his/her initial quota share endowment ω_f^0, if the net value of fishing that quota share is less than the value that could be earned by leasing it to someone else,

$$P - \frac{\partial C}{\partial Y_f} < s.$$

Conversely, the profit maximizing fisher will acquire more quota share if each unit of landed fish yields a profit greater than the cost of leasing additional quota share from someone else,

$$P - \frac{\partial C}{\partial Y_f} > s.$$

Equation (1.3) states that quota shares have value only if the final share of the TAC exactly equals the catch. This one-to-one mapping of quota shares into catch requires the TAC to be known with certainty. If the TAC is uncertain, as in the case of Bristol Bay red king crab, one thing is known for sure; the Kuhn-Tucker conditions stipulated in (1.1)-(1.3) do not characterize profit maximizing behavior under ITQ management.

This conclusion poses something of a policy conundrum. Despite decades of economics literature espousing the efficiency merits of ITQ management, none of that literature addresses the behavioral implications of uncertainty of stock and TAC. Yet, as Charles (1988) notes, one ought to regard such uncertainty as the norm.

> For fishery managers charged with the responsibility for operating the fishery in a manner which most closely achieves management goals, it is in-season decision making which is most critical. Typically, the inherent conflict faced by the manager centers on the balance between maximization of harvest levels for the fishermen and achievement of resource stock management objectives. This problem is complicated by the very nature of fish stocks—namely, that they are not observable, and are difficult to evaluate, particularly prior to the start of the fishing season. (P. 599)

Incorporating Uncertainty

Baseline uncertainty model

Uncertainty related to the compelling need for in-season crab management begs the question whether ITQ management will, in fact, eliminate the race-to-fish and deliver promised economic efficiency benefits. These questions can be answered only by reformulating the conventional, "certain" model specified in equation (1). Equation (2) characterizes the same behavioral model given in equation (1) except that: (a) discrete fishing periods within a season (e.g., days) are introduced, and (b) harvest is expressed in its more elemental components of catch per unit of effort (CPUE), which is conditional on the biomass at the beginning of the period, times effort (*e*).

$$\underset{e_{1,f},\ldots,e_{Jf}}{\mathrm{Max}}\,\pi = \sum_{j=1}^{J}[P(CPUE_{jf}\,|\,X^{j-1})e_{jf}] - VC(e_{jf}) - s\omega_f TAC \qquad f = 1,2,\ldots,F \qquad (2)$$

subject to:

$$X^{j-1} = X^0 - \sum_{k=1}^{j-1}\sum_{f=1}^{F}(CPUE_{kf}\,|\,X^{k-1})e_{kf}$$

$$\sum_{j=1}^{J}(CPUE_{jf}\,|\,X^{k-1})e_{jf} \le (\omega_f^0 + \omega_f)TAC \quad f = 1,2,\ldots,F$$

$$\sum_{f=1}^{F}\omega_f = 0$$

where:

e_{jf} = fishing effort of the f^{th} firm in the j^{th} period
J = total number of fishing periods, $j = 1,2,\ldots,J$
P = ex-vessel price
$CPUE_{jf}$ = catch per unit of effort for the f^{th} firm in the j^{th} period
Xj^{-1} = biomass at the end of the j-1 period
VC = variable costs
F = total number of firms, $f = 1,2,\ldots,F$
s = market price for quota
ω_f^0 = initial quota share allocation to the f^{th} firm
ω_f = amount of quota traded by the f^{th} firm
($\omega_f > 0$ is purchase, $\omega_f < 0$ is sale)

It is apparent from equation (2) that uncertainty has a profound impact on the behavior of individual fishers, and thus the fleet. Since the initial stock, X^0, is unobservable, both X^0 and TAC are uncertain. It follows that CPUE also is uncertain because at any point in time it is a function of an uncertain biomass. [Note: CPUE is defined as the number of legal crabs per potlift. Even if biomass were certain the relationship between CPUE and stock (X) is not exact.] In-season management adds to the fishers' uncertainty. The fishery may be closed by emergency order at any point in time so that the total number of periods, J, is stochastic. Finally, it should be noted that these various sources of uncertainty are not all independent of each other.

The implications of uncertainty in equation (2) is that this behavioral model is a discrete time stochastic control problem. No analytical solutions analogous to equations (1.1)-(1.3) exist. Insight into firm behavior can be gained through numerical simulation, however. Such computer simulation involves tracking the evolution of the system (as reflected in this model) as time is sequentially increased. In essence, the values of random variables are generated on a computer, yielding the necessary information to obtain estimates of the quantities of interest (Law and Kelton 1991). The advantage of simulation is that it allows analysis of realistic models of real-world systems that are too complex to evaluate analytically. Examples of other numerical simulations to study fisheries include Dudley and Waugh (1980) and McDaniels (1995).

Extensions to the baseline uncertainty model

Meaningful and informative simulations must incorporate available information to both fishers and managers. We contend that most fishers do not literally attempt to implement the equation of motion specified in equation (2) because it would require the individual fisher to know the behavior of every other fisher in the fleet. Instead, we assume that fishers form expectations on the trajectory of the crab stock by using a more "myopic" equation of motion. A myopic equation of motion is based on the assumption that the total catch by the fleet in any period will be proportional to the stock level. Johnson (1991) found evidence of a linear relationship between CPUE and biomass levels for red king crab in the Kodiak fishery. This linear relationship supports our assumption that the total catch will be proportional to biomass levels. While Johnson's study was based on seasonal averaged CPUE and yearly biomass levels, it is our intention to use an intra-seasonal CPUE function.

Use of a myopic equation of motion combined with accumulating information as the fishing season progresses will allow both fishing firms and managers to update their decisions sequentially as the season progresses. Although CPUE may not be a good indicator of biomass (Morrison 1995, Kruse 1995), CPUE data and estimates of harvest-to-date currently are the basis for in-season management/emergency closure. This same information also can be used by fishers to update their myopic equation of motion, and therefore revise their level of fishing effort and quota trading decisions (subject to market clearing conditions). The sequential updating process is illustrated in Figure 1. Formal mathematical representation of this process was still under development at the time this paper was written.

The goal of fishery managers is to allow the GHL to be harvested, unless there are reasons to do otherwise. The managers use the daily CPUE data from a sample of vessels in the fleet along with estimates of catch-to-date. If the CPUE falls rapidly to a lower than expected level and stays at that level, the stock is presumed "at risk" and the season may be closed by emergency order before the GHL is obtained. Alternatively, if the GHL is almost caught and the CPUE remains above a critical CPUE, the season may be allowed to continue beyond the GHL. Currently, the Alaska Department of Fish and Game (ADF&G) tries to inform the fleet of the estimated catch-to-date by announcing its estimate every other day. This information allows fishers to update their myopic equation of motion.

An additional consideration must be addressed when attempting to simulate firm or fleet behavior under ITQ management, given the presence of uncertainty. ITQ management may induce firms and policy makers, alike, to fundamentally alter current harvesting practices and regulations. For example, pot limits were imposed by the Alaska Board of Fish in 1993 in an attempt to reduce effort and gear loss, and to redistribute effort by vessel length. Vessels less than or equal to 125 feet may fish up to 200 pots, whereas vessels greater than 125 feet may fish a maximum of 250 pots. This pot limit policy had the ancillary effects of decreasing soak time and increasing variable costs of harvesting. Relaxing the pot limit could increase the soak time and decrease variable costs. Perhaps more important, sufficiently long soak times (5-7 days) combined with larger escape panels should lessen by-catch of smaller crabs, decrease handling mortality, further reduce the variable costs of crabbing, and help promote greater overall stock vitality and conservation. Simulation affords an opportunity to examine each of these possibilities prior to implementing or rejecting ITQ management of red king crab.

Conclusions

It is premature to draw conclusions concerning the efficacy of ITQ management in North Pacific crab fisheries—Bristol Bay red king crab, in particular. One thing seems certain, however. The presence of uncertainty and its associated use of in-season management raises questions as to the extent to which ITQ policies can help rationalize overcapitalized crab fisheries. The extent to which promises of fleet consolidation will proceed is unclear as is whether the race-to-fish will be minimized, or even lessened.

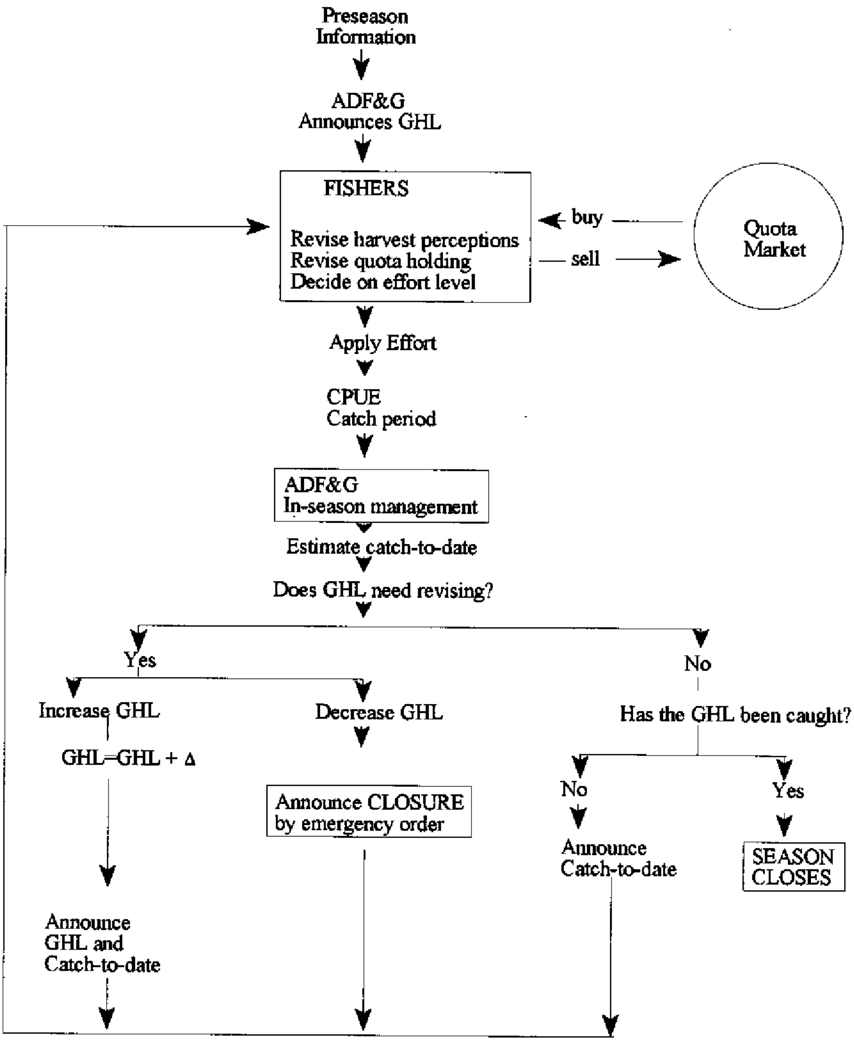

Figure 1. Fishing process under ITQs. GHL = guideline harvest level.

It is equally unclear whether there are effective or necessary ways to lessen the impact of uncertainty. For example, the season could be divided into two seasons. A certain TAC less than the GHL could be established for the first season of a specified length. A second season then could be established after first season closure, and managers update and refine their stock forecast and determine whether the allowable catch can be increased. Any uncertainty would occur only in this second season. Such a potential management structure should be evaluated for its policy merits. This evaluation would include establishing appropriate decision criteria for determining the first TAC and season length, and whether the second season should be governed by a certain TAC or a GHL combined with in-season management.

Acknowledgments

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Fisheries Biology of the Giant Crab (*Pseudocarcinus gigas*, Brachyura, Oziidae) in Southern Australia

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Abstract

The giant (or king) crab *Pseudocarcinus gigas* (Milne Edwards) is distributed along the southern margin of the Australian continent, principally in the depth range 119-366 m and at temperatures of 10-18°C. Maximum weight attained is 13.6 kg for males and 6 kg for females. Crabs are taken using modified lobster pots incorporating long-life baits and employing soak times of 48 to 72 hours. Crabs are exported live to Asia. The fishery has expanded rapidly over the last 4 years due to strengthening markets and a shift of fishing effort from southern rock lobster (*Jasus edwardsii*). The basic biology of the species is not known. The data upon which this study is based has been generated by a network of cooperating fishermen across the four southern Australian states. Population structure has been assessed in fished and unfished areas across the geographic range of the species. A unique "double T-bar" tag has been developed to study growth and movement, and 7,000 tags were inserted in 1994.

The fishery appears to consist of a single stock across southern Australia. Changes in population structure attributable to fishing mortality can be detected in some populations after a year. Movement of animals is related to reproduction (berried females move into shallower water) and molting (larger males move into deeper water to molt and possibly to mate). Females store sperm in spermathecae and may spawn in consecutive years without molting. In virgin stocks only 50% of mature females spawn in a given year. Mating first occurs in June/July soon after molting. Spawning first occurs in June/July with clutch size varying from 0.5 to 2 million eggs depending upon female size. Berried females migrate to the top margin of the continental shelf break as hatching approaches in November/December. Size at sexual maturity has been established. Fecundity appears to be high and the species may have large molt increments. The features of the life history of *P. gigas* are discussed with reference to possible effects on the stability of the fishery. On the basis of data collected to date, legislative constraints on the taking of berried females, vessel numbers and gear quantity, seasonal fishing, and minimum size at first capture have been introduced.

Introduction

Pseudocarcinus gigas is distributed across the southern coast of Australia from the Perth canyon in southwestern Western Australia (WA) to central New South Wales (NSW) (Kailola et al. 1993) (Figure 1). It is found at depths from 18 to 400 m (Winstanley 1979) with the greatest concentration of the population occurring on the shoulder of the continental shelf break at depths between 140 to 270 m (unpublished data). This is somewhat deeper than recorded by Jones and Morgan (1994) as previously most crabs were taken as a bycatch from rock lobster fishing operations in shallower water. Maximum size recorded for a male of the species is at least 13.6 kg (Hale 1927-1929, Kailola et al. 1993). Maximum size recorded for a female of the species is 6.0 kg (unpublished data). The most common sizes taken by fishermen range between 2 to 8 kg; even in areas that have been subjected to very little fishing effort, the bulk of the catch is composed of individuals in the 130 to 190 mm length range, equivalent to a weight range of 1.6 to 5.4 kg.

The species has been little studied, with scant reference to distribution in the literature (Hale 1927-1929, Kailola et al. 1993, Jones and Morgan 1994). Prior to this study no published information was available on life history, population structure, or feeding ecology of the species. The species shows the morphology typical of xanthoids (after Warner 1977, Jones and Morgan 1994) with a heavy exoskeleton, relatively large body, and large crushing claws. *P. gigas* shows sexual dimorphism with males developing an enlarged right cheliped after the onset of sexual maturity.

Over the last 5 years, *P. gigas* has become the target of increasing fishing effort. This has been due to improvements in capture technology, principally baiting and depth fished, and an expanding live domestic and export market, the latter to Asia. These developments have seen a shift of effort from southern rock lobster (*Jasus edwardsii*) to giant crab. Concern by fishermen over sustainability of stocks led to the industry developing a national strategy to contain effort and provide the foundation for knowledge-based management decisions. This strategy involved (a) the introduction of interim protective regulations based around ex-

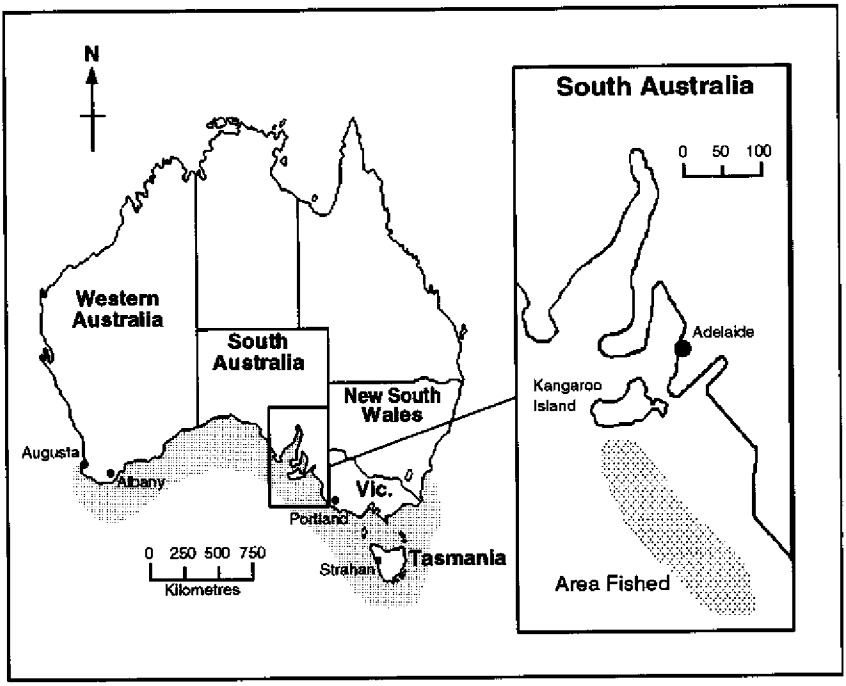


Figure 1. The geographic range of P. gigas across southern Australia, and the site of research fishing in South Australia.

isting rock lobster regulations which constrained fishing gear, fishing season, and area of access, and (b) the development of a research program to determine biology and stock structure of the species. The objectives of the study, the preliminary findings of which are reported in this paper, include obtaining basic biological information (reproductive cycle, size at maturity, fecundity, growth, distribution, and movement), determining stock structure across southern Australia, and undertaking preliminary stock assessment.

This paper presents initial findings, based on preliminary analysis of selected data, of stock structure across southern Australia, population structure in selected fishing areas, reproductive cycle, size at sexual maturity, molt increment based upon tag returns, and diet of crabs from the deeper part of their distribution. It must be stressed that figures presented represent unweighted means and that, at this stage, tests of significance have not been performed on the data. The data is used to propose hypotheses concerning life history and annual movement cycles, and to describe initial impacts of fishing on population structure. Data collection has commenced very early in the history of the fishery and it is therefore possible to compare fished and virgin stocks and observe the effects of fishing. Legislative controls have been introduced very early in the development of the fishery, meaning that data collection and interpretation are not confounded by high fishing mortality.

Development of the Fishery

P. gigas were once considered a nuisance by lobster fishermen in that they damaged pots and deterred the entry of lobsters into pots. For the reasons outlined above, crabs are now a valuable catch. Fishermen have learned to target them on soft sand/mud substrates away from the hard reef areas preferred by lobster. Nearly all deepwater pots are of steel frame construction covered with a resilient synthetic mesh netting. Unlike the lobster fishery where pots are hauled once or twice a day, the crab fishery requires immersion of pots for 48 to 72 hours, and sometimes up to 4 days, to maximize the catch. A lice resistant bait such as hock [cow's foreleg] or hide is used. Whereas most of the catch was formerly males taken as bycatch on hard substrates, many females are now taken off the softer substrate, a habitat they appear to favor. The shift of fishing from shallower reef bottom to deeper sand/mud has resulted in new fishing techniques being developed, where 10-20 pots are set connected to a longline which may be up to 4 km long and anchored at either end to prevent the tide sweeping the assembly away. The advent of Global Positioning Systems allows floats at either end of the longline to be easily detected.

Wharf prices in South Australia, Victoria, and Tasmania during 1993-1994 have varied from $30 per kg (winter) to $5 per kg (summer) for crabs less than 5 kg. Larger crabs, mainly males, are negatively discounted by about 30%. In Western Australia a fixed price structure of $12-$14 per kg for all sizes appeared to prevail during 1993. Chinese communities, both domestic and in Southeast Asia, provide the major markets. A number of market initiatives to mainland China occurred during the latter half of 1993.

Currently 194 operators are licensed to take giant crab. Not all of these are actively targeting giant crab, and of those actively fishing 25 take 80% of the total catch. Many fishermen have taken out a license to ensure retention of the crab bycatch during rock lobster fishing operations or in anticipation of future management changes in access. The catch history for all states across southern Australia is summarized in Figure 2. Crabs are primarily targeted from early summer (December) through to late winter (August), with catches peaking in mid-summer. Closed seasons vary according to state jurisdiction, with 10 week closures from September in the two most productive states, Victoria (VIC) and Tasmania (TAS). The total value of the catch across southern Australia has risen from $0.12 million in 1991 to $5 million in 1994.

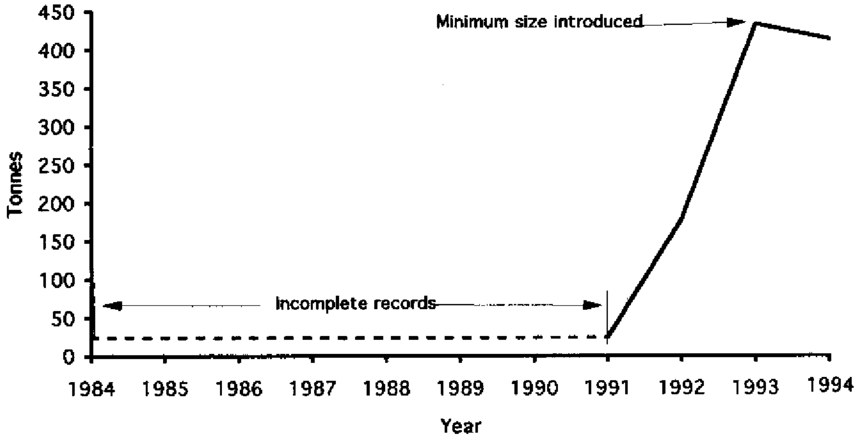


Figure 2. Catch history for P. gigas across all southern Australian states from 1984 to 1994 (compiled from state fisheries agencies records).

Materials and Methods

Catch Records

Aggregated catch records have been obtained from the recently upgraded commercial catch monitoring programs of state fisheries agencies in TAS, VIC and WA, and directly from fishermen's records in South Australia (SA).

Stock Structure

Tissue samples (leg muscle) were obtained from Augusta and Albany in WA and Portland in VIC, the most widely separated geographic areas of the distributional range of *P. gigas*, and stored in liquid nitrogen. Muscle tissue was screened for genetic markers at 20 enzyme loci to determine the degree of heterozygosity using standard allozyme electrophoresis techniques.

Biological Information

Biological information on giant crab, collected from 1993 to 1995, has been derived from two sources. The first source was at-sea commercial catch sampling and the second was subsampling of landed commercial catch onshore. While attempts were made to stratify sampling of commercial catch onshore, it must be acknowledged that some sorting of catch by fishermen is a potential source of bias. Most data (n = 20,000) has been collected at sea from SA (Figure 1), and this has been complemented by data (n = 10,000) from at-sea sampling during research fishing in VIC and TAS. Data has also been collected by observers on commercial fishing vessels in WA (n = 5,000) and from onshore sampling of landed catch (n = 5,000). Research fishing was undertaken during the closed season in VIC and TAS and attempted to stratify catch by area, depth, and time. This included sampling a wider depth range than is normally targeted in commercial operations. However, closed season fishing was conducted under permit with sale of catch to cover costs. This meant that most productive areas and depths had to be targeted. This situation was compounded by movement of berried females which meant specific depths needed to be targeted to ensure adequate samples were obtained. The history of fishing at the sites sampled was as follows:

- Augusta, WA: virgin stock.
- Albany, WA: 10 years by one operator in some areas, virgin stock in others.
- South of Kangaroo Island, SA: six months fishing.
- Portland, western VIC: three years fishing.
- King Island, northwest TAS: three years fishing.
- St. Helens, northeast TAS: six months fishing.

Data collected and presented here include:

- Date, depth, and location of catch.
- Sex and female reproductive state based upon carrying of eggs.
- Shell state, described as degree of fouling with encrusting organisms and rated (after Hoggarth 1993) as "clean" shelled (less than 5 encrusting organisms) or "old" shelled (more than 5 encrusting organisms and with wear on the tips of the walking legs).
- Carapace length measured as the shortest distance from the anterior margin of the carapace between the eyestalks to the posterior margin of the carapace at the joint with the abdomen, using 300 mm Mitotoyu vernier calipers (0.01 mm accuracy).
- Individual weight using certified accurate processors electrobalances (0.100 kg accuracy).
- Egg clutch mass as wet weight (to nearest gram) after stripping eggs from pleopods and blotting dry with tissue paper using electrobalances (0.100 gm accuracy).

- Indicators of mating based on abrasions on the ventral somites of the anterior abdominal segments of females (after Melville-Smith 1987).

This paper relies heavily on the data set obtained from SA.

Diet

Fifty-four animals were collected from March to July 1995, from Bass Strait, Western VIC, by commercial finfish trawling operators at depths between 300 m and 420 m over a substrate of fine gravel and silt. Animals were immediately frozen to avoid excretion or digestion of stomach contents. Animals were then sexed and weighed, and a pleopod was removed which was fixed in 10% formalin for 24-48 hours and then preserved in 70% ethanol. Molt stage was determined on the basis of pleopod setal development after Vigh and Fingerman (1985) and Burton and Mitchell (1987). Molt stage was categorized as postmolt (stages A-B), intermolt (stage C), and premolt (stage D). After animals had thawed stomachs were removed, relative degree of fullness assessed, and then each stomach was opened and the contents removed and preserved with 10% buffered formalin. Food items were sorted into representative taxa and quantified using ranks based on the points method (Pollard 1973) using estimated percentage volume. This gives information on both relative dominance and association of food items.

Tagging

Crabs were tagged using the epimeral suture line site at the rear of the branchial chamber as employed for *Cancer magister* after Butler (1957) and for *Cancer pagurus* after Bennett (1974). However, to avoid the use of loop tags requiring two holes to be punctured in the suture line, a double T-bar tag was developed by Hallprint Ltd. (South Australia). The tag consisted of a conventional T-bar tag with an additional T-bar inserted into the barrel with a gap of 10 mm between the cross bars of the Ts (Figure 3). The second T-bar prevented the tag from being drawn into the branchial chamber. Trials to assess tag loss were conducted in laboratory tanks. Double T-bar tags were applied to 25 animals (size ranging from 88 mm to 147 mm carapace length) using Dennison 08958 Tagfast II tag guns with a heavy duty stainless needle. Animals were housed in a recirculating seawater system at 11°C, in individual mesh cages, and fed a diet of squid and mussels.

No mortality was associated with application of the double T-bar tags and the shell around the tag remained in a healthy state. To date, of the animals tagged, 5 have molted; tags were retained through the molt in all cases. The urgency for the commencement of a full-scale tagging program at sea precluded a full tag-loss study prior to widespread application of tags. To date 7,000 tags have been applied across all fishing

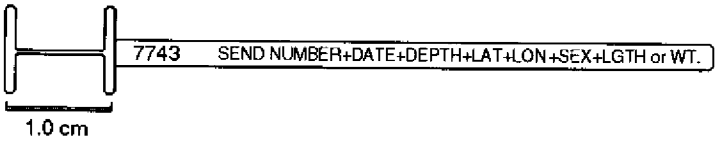


Figure 3. Double T-bar tag developed for use in P. gigas.

states with approximately 500 recaptures after 1 year. Eleven recaptured animals have molted with only 4 reports of tag loss by fishermen.

Results

Stock Structure

The degree of heterozygosity exhibited by enzymes in muscle tissue of *P. gigas* was very low both within and between samples from different geographic areas. At the level of resolution provided by allozyme electrophoresis there is no evidence of isolation of stocks across southern Australia. On the basis of this it is assumed that *P. gigas* represents a single stock across southern Australia; however, it cannot be concluded that gene flow is unrestricted across the range of the species.

Depth Distribution

Catches showed stratification of size classes with depth and time across the species range with smaller animals of both sexes in deeper water during winter, spring, and summer. During autumn the size of animals of both sexes increased in deeper water suggesting movement down the continental slope. These larger animals displayed an old, worn shell state. Crab bycatch by lobster fishermen has generally shown a high proportion of large males in catches from shallow waters (from 25 to 120 m) over rocky substrates. Targeted fishing for giant crab in deeper water suggests that females favor softer substrates at depths between 120 and 270 m.

Population Structure

The length-frequency distribution of *P. gigas* from SA (Figure 4) consistently showed a single peak; multiple modes were not apparent. Effects of fishing on population structure at a single site can be discerned from the SA data set over the period from autumn 1994 to autumn 1995. As fishing proceeded the size structure of the population changed, particularly among the larger size classes above 150 mm; the larger size classes were lost from the population, particularly the animals around 165 mm carapace length which changed in proportion from approximately 12% in autumn 1994 to 8% in autumn 1995. A seasonal change in mean

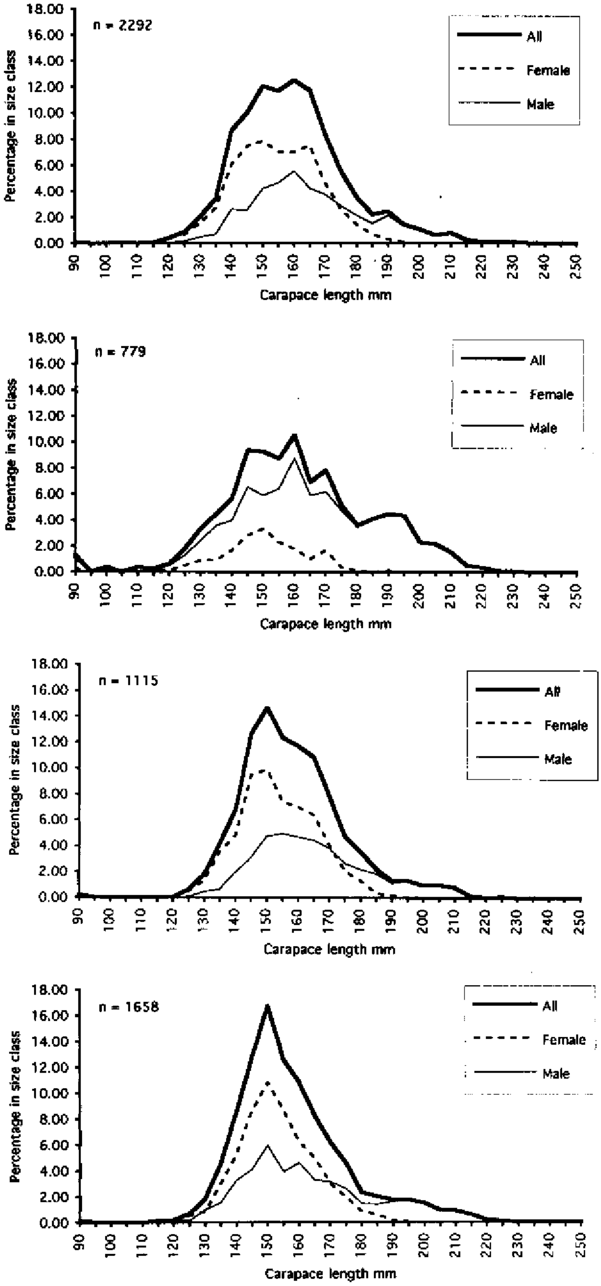


Figure 4. Length-frequency distributions for P. gigas in 1 mm carapace length classes from South Australia. (top) autumn 1994; (upper middle) winter 1994; (lower middle) summer 1994-95; (bottom) autumn 1995.

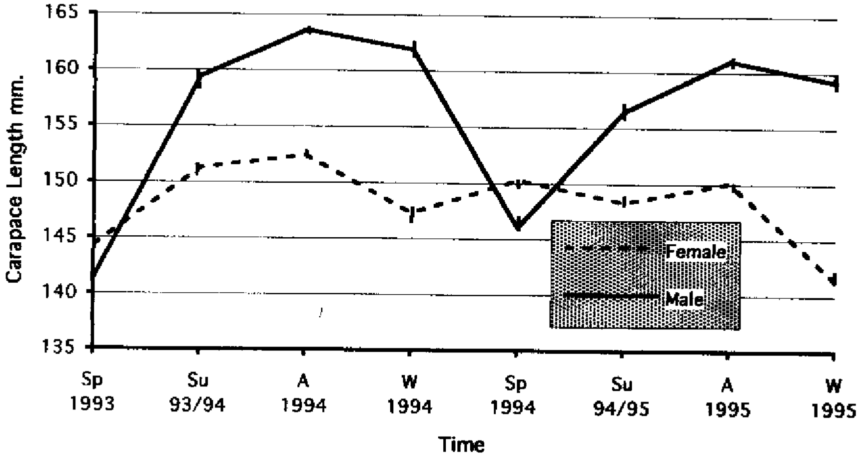


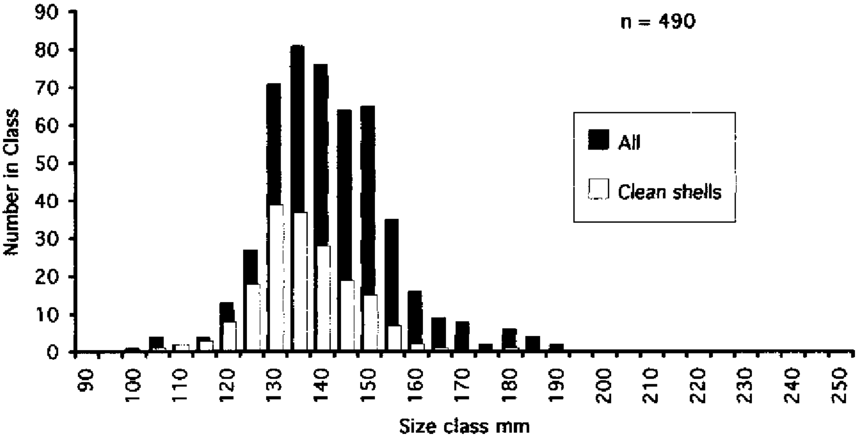
Figure 5. Mean size (plus standard error) of P. gigas from South Australia over the period spring 1993 to winter 1995.

size, especially among males, was evident in SA (Figure 5). Mean size of males increased from spring through to summer and autumn and then decreased from autumn to winter and spring. This trend was not pronounced in females. Mean size of males in catches generally exceeded that of females except during spring.

The proportion of the catch made up of females exceeded that for males in size classes below about 170 to 175 mm (reflecting the larger number of males in larger size classes) in all seasons with the exception of winter 1994 where the proportion of males increased and exceeded that of females (Figure 4). This reflected a change in the availability of males (due to movement off the shelf and down the slope into deeper water) and reduced activity of females (due to either molting or spawning activity).

The 1993 spring catch from northwestern TAS (Figure 6a) showed that the proportion of females with "clean" shell state rarely exceeded 50% for any length class while for males the proportion was always greater than 50% across all size classes (Figure 6b). This suggested that molting was less frequent in females than in males.

A comparison of mean and maximum carapace length across all sites in spring 1994 (Table 1) shows that both maximum and mean size varied across sites for both sexes in order of descending size: western TAS > SA > WA. In general terms this correlated negatively with sea bottom temperatures which varied from 8 to 10°C off Strahan (western TAS) to 15 to 18°C at Augusta (WA). This relationship between temperature and size has been reported in other brachyurans (Dugan et al. 1994),



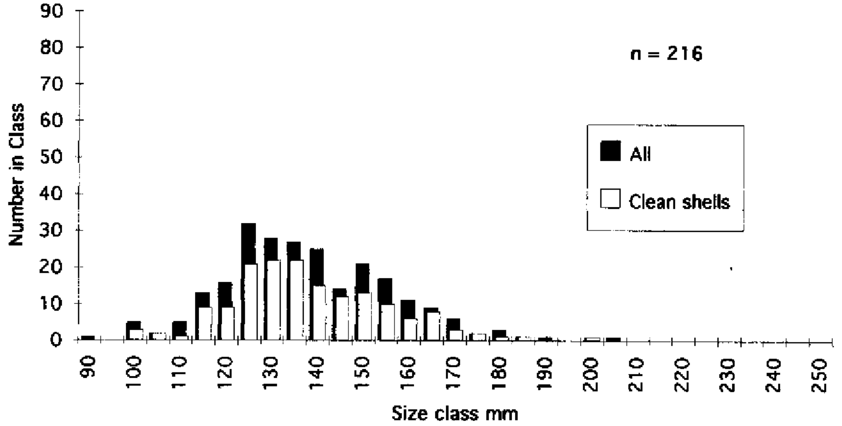


Figure 6. Number of clean-shell P. gigas in 5 mm carapace length classes from northwest Tasmania in spring 1993. (above) females; (below) males.

Table 1. Mean and maximum carapace length, and sex ratio (expressed as proportion of catch) of *P. gigas* across all southern Australian states in spring 1994.

	Female				Male			
Site[a]	Max. length (mm)	Mean length (mm)	N	% of catch	Max. length (mm)	Mean length (mm)	N	% of catch
W-Vic	209	149.8	751	67.2	223	139.4	367	32.8
SA	191	150.3	2018	75.6	220	146.0	653	24.4
NW-Tas	201	143.0	254	72.2	224	143.0	98	27.8
NE-Tas	203	149.0	1093	90.0	220	148.0	122	10.0
Aug	181	142.3	1428	53.6	199	155.9	1237	46.4
Alb	179	130.6	1157	48.8	203	144.0	1216	51.2

[a] W-Vic = western Victoria; SA = South Australia; NW-Tas = northwestern Tasmania; NE-Tas = northeastern Tasmania; Aug = Augusta, Western Australia; Alb = Albany, Western Australia.

and probably reflects reduced growth rate at lower temperature, longer life, and larger final size as has been reported in *Lithodes aequispina* (Somerton and Otto 1986).

Sex ratios across sites in spring 1994 are presented in Table 1 and showed that the proportion of sexes varied between sites from 39% females in western TAS to 89% females in northeastern TAS. Sex ratio is highly variable in crabs and local variation from 1:1 reflects differential mortality, migration, and habitat selection (Cobb and Caddy 1989). Seasonal changes in sex ratio within a population from SA (Table 2) showed that the proportion of females increased from spring to summer and decreased from autumn to winter. The winter sex ratio was highly skewed in favor of males. Temperature differences between sites may modify the timing of seasonal patterns in the proportions of sexes, and interannual variation is also likely to occur.

Reproduction

The morphology of the genital tract in *P. gigas* is yet to be determined and when vaginal structure is compared to Hartnoll (1969) should identify the pattern of molting and mating exhibited by females of the species. The pattern is likely to be pre-ecdysial courtship and mating after molting, with males guarding recently molted females, as has been reported in other xanthoids, for example *Menippe* sp. (Wilber in Kruse 1993). This is supported by field records of clean shelled females with signs of recent mating manifested as discoloration around the vulvae and abrasion on ventral surface of second and third abdominal segments of the female. This is caused by the abrasive action of the male pleopods and/or last abdominal somite during copulation (Melville-

Table 2. Sex ratio (expressed as % of total catch) in a population of *P. gigas* from South Australia (spring 1993 to autumn 1995).

Sampling date	% Females	% Males
Spring 1993	42.7	57.3
Summer 1993/94	65.7	34.3
Autumn 1994	57.9	42.1
Winter 1994	18.2	81.8
Spring 1995	75.6	24.4
Summer 1994/95	78.7	21.3
Autumn 1995	49.9	50.1

Smith 1987). No observations of mating in the species have yet been recorded in the wild or in captivity.

It appears that *P. gigas* females store sperm and the apparent layering of sperm deposits in spermatheca (C. Gardner, Tasmanian Fisheries, pers. comm.) suggests that serial mating with several males by a single female also occurs. The timing of molting, mating, and spawning is hypothesized to follow the sequence: female molts, mates immediately, then spawns 12 months later. Validation of this pattern will be dependent upon determination of vaginal morphology and recaptures of tagged individuals. That this pattern occurs in *P. gigas* is supported by the fact that clean-shell females have not been observed to carry eggs. Females appear to spawn more than once, in successive years, without subsequent molting or mating. This is supported by collection of females from the wild with remnants of hatched eggs on pleopods and with ripe ovaries preparatory to spawning; captive females have spawned in successive years without access to males (C. Gardner, Tasmanian Fisheries, pers. comm.).

Based upon field observations in western VIC the proposed reproductive cycle of *P. gigas* is summarized below:

```
            J   F   M   A   M   J   J   A   S   O   N   D
molting              -----------____---------
mating                  --------______----------
spawning                      ---____--
incubation                       ---____________----
hatching                                        ____--
```

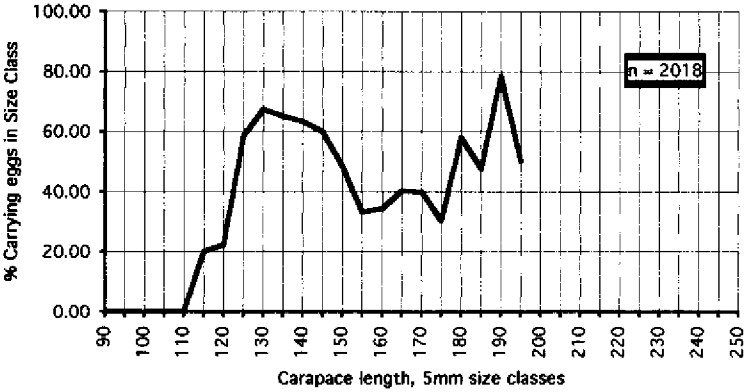
The dashed line is the period over which animals have been recorded in each stage of the reproductive cycle. The solid line is the main period (in which the largest number of animals is recorded) for each stage of the reproductive cycle.

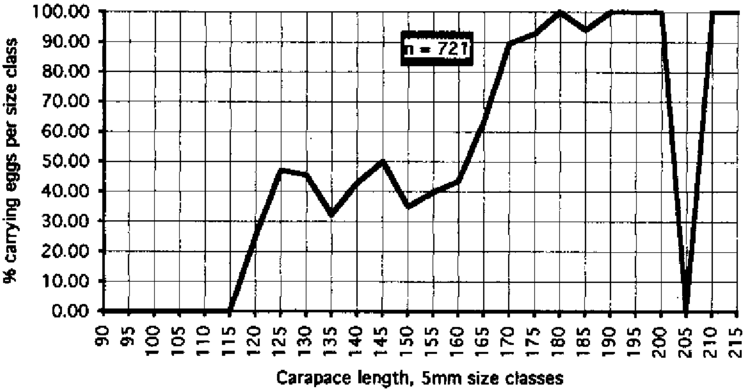
Movement of berried females carrying eyed eggs from deeper water, approximately 270 m, upslope to shallower depths, approximately 210 to 140 m, was apparent as the egg incubation period proceeded. Hatching occurred in shallower water on the shoulder of the continental shelf as evidenced by the high proportion of reproductive females with empty egg casings attached to pleopods at these depths and the low numbers of females taken at other depths during October. Catchability of females increased in October due to increased movement, and the proportion of berried females to non-berried females in catches remained fairly constant throughout this period.

Female size at the onset of sexual maturity was determined from plots of percentage carrying eggs against length class. This relationship, determined in spring 1994, is presented for three populations (SA, western VIC, and Augusta, WA) in Figure 7. The relationships showed a characteristically flat shape with asymptotes at approximately 40 to 60% across a wide range of sizes. There is some suggestion of a reduction in the proportion carrying eggs in larger size classes but this may reflect variability due to low sample size. The form of the relationship suggests that once reaching sexual maturity females do not necessarily spawn each year; that is, a large proportion of females in a given mature size class are not berried in any given year. Based upon the observations described above, both with regard to spawning activity and shell state in the wild, it is proposed that some female *P. gigas* may molt only once every 3 years; in larger animals the intermolt period may be longer. Comparison of graphs for Augusta and SA showed a decline in the percentage carrying eggs from 145 to 180 mm in the SA population. This probably reflected loss of larger size classes through fishing mortality and recruitment of newly molted animals into larger size classes (as discussed below). Minimum size at the onset of maturity (first berried) across all sites was Augusta 115 mm, Albany 90 mm, SA 110 mm, western VIC 115 mm, and northeastern TAS 115 mm. That is, variation in size at the onset of maturity was evident.

Figure 7 may also show the effects of fishing as the curves for spring catches of virgin stock at Augusta and for more heavily fished stock in South Australia over the same period are quite different. Catches from the fished population in SA (presented in more detail in Figure 8) showed that the proportion of berried females in larger size classes (above 150 mm) declined markedly. This appeared to reflect (a) increased abundance of females less than 150 mm due to the introduction of an ILMS (interim legal minimum size), and, (b) fishing effort on larger females over the preceding 18 months which resulted in an influx of new recruits into 150 mm plus size classes.

To determine the relative contribution of mature female size classes to reproductive effort the relationship between egg mass and carapace





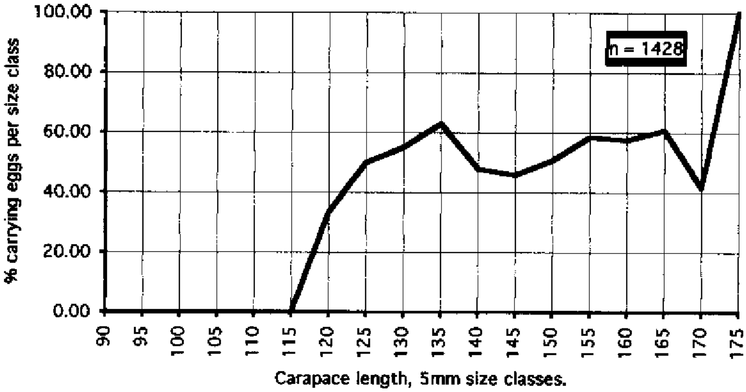


Figure 7. Percentage of female P. gigas carrying eggs in 5 mm carapace length classes in spring 1994. (top) South Australia; (middle) western Victoria; (bottom) Augusta, Western Australia.

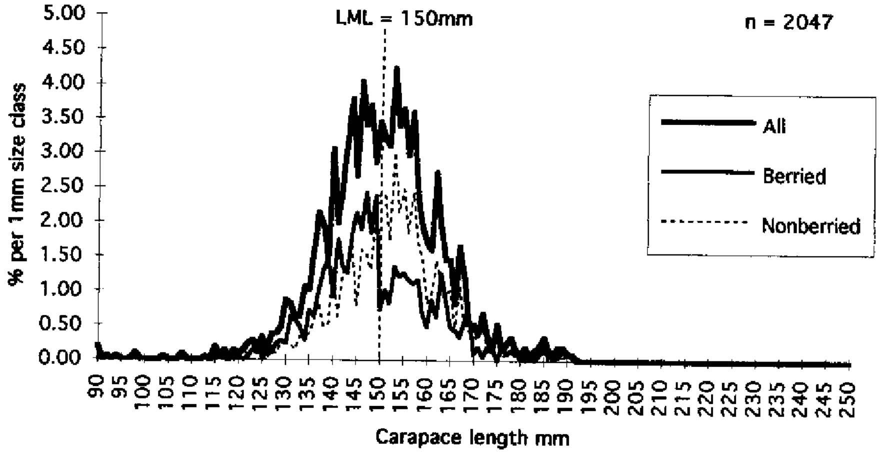


Figure 8. Proportion of female P. gigas carrying eggs in 1 mm carapace length classes from South Australia in spring 1994.

length was determined by regression analysis. The relationship, up to a carapace length of 188 mm (the largest female for which egg mass has been determined), took the form:

$$\textit{egg mass} = 3.179 \times \textit{length} - 296 \ (n = 48, R^2 = 0.71).$$

Egg number also varies as a function of size from approximately 500,000 for a female of 126 mm carapace length to approximately 1,400,000 for a female of 170 mm carapace length (C. Gardner, Tasmanian Fisheries, pers. comm.). Based upon egg mass as a function of female length, the number of females in each length class, and the proportion of females carrying eggs in each length class, cumulative egg production across all size classes was determined for each population. From this analysis size to protect 50% of egg production was determined for each population; the selection of 50% of egg production for determination of an ILMS was arbitrary and is conservative for decapod fisheries (J. Prescott, South Australian Fisheries, pers. comm.). Size at 50% of egg production across all sites was: Augusta 148 mm, Albany 135 mm, SA 151 mm, western VIC 160 mm, northwestern TAS 149 mm, northeastern TAS 149 mm. Based upon this analysis an ILMS of 150 mm has been recommended across all states.

Diet

Forty percent of crabs had food items in their stomachs. Most crab stomachs contained a single food item; the mean number of items per

Table 3. Mean percentage composition of the diet of *P. gigas* from 300 to 420 m depth range, western Victoria, autumn 1995.

	Food item[a]								No. of
	Aster	Brach	Carr	Anom	Gast 1	Gast 2	Osteic	UM	crabs
Overall	22	8	5	3	24	14	4	21	22
Male	46	0	4	4	18	11	7	11	10
Female	8	12	6	2	28	16	2	26	12
Size < 2.5 kg									
Overall	18	5	7	0	30	16	2	23	13
Male	44	0	5	0	30	17	0	4	4
Female	0	8	8	0	32	18	3	32	9
Size > 2.5 kg									
Overall	33	14	0	10	10	10	10	14	9
Male	38	0	0	13	0	0	25	25	6
Female	33	25	0	8	17	8	0	8	3
Molt Stage									
A-B, overall	50	17	6	6	11	11	0	0	17
< 2.5 kg	36	21	7	7	14	14	0	0	3
> 2.5 kg	100	0	0	0	0	0	0	0	2
C, overall	13	5	5	2	28	15	5	27	17
< 2.5 kg	13	6	6	0	32	17	2	25	10
> 2.5 kg	14	0	0	14	0	0	29	43	7
D, overall	0	0	0	0	0	0	0	0	7

[a] Food items: Aster = Asteroidea; Brach = *P. gigas*, Majidae; Carr = carrion (including equine/bovine hair and feathers); Anom = Paguroidea; Gast 1 = Gastropoda species 1; Gast 2 = Gastropoda species 2; Osteic = Osteichthyes; UM = unidentified material.

stomach was 2 and the maximum number was 4. Mean percentage composition of food items in the diet of *P. gigas* is presented in Table 3.

Dominant food items were two species of gastropod mollusks, a single species of asteroid echinoderm and decapod (other *P. gigas*, spider crabs of the family Majidae, or hermit crabs of the order Paguroidea) fragments. Carrion comprised less than 5% of diet and stomachs did not contain sediment or other material inadvertently ingested during feeding. Males consumed more asteroids than females (46% of diet composition compared to 8%) while females consumed more gastropods than males (total of 44% of diet composition compared to 29%). Smaller crabs (less than 2.5 kg) fed mainly on gastropods while larger crabs (over 2.5 kg) consumed more asteroids and decapods. Large males did not contain gastropod fragments. Larger males consumed a narrower range of

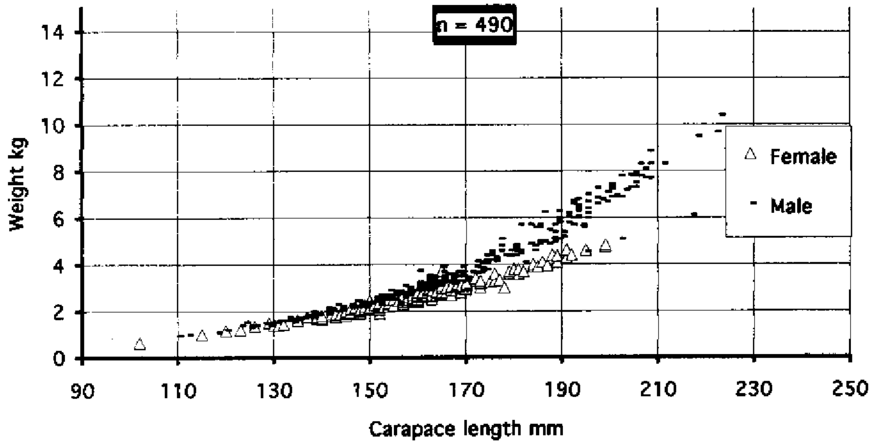


Figure 9. Wet weight of P. gigas from western Victoria plotted against carapace length.

food items than comparably sized females. Premolt animals all had empty stomachs. Postmolt animals consumed mostly asteroids, this being the only item in larger postmolt animals. Intermolt animals consumed more gastropods with larger animals including significant proportions of fish and decapods. Diet diversity was very low and was dominated by slow moving benthic forms.

Growth

To date the data available on growth of *P. gigas* is limited. As discussed above, the observation that the proportion of clean-shell males (always greater than 50%) exceeds that of clean-shell females (generally less than 50%) in spring catches suggests that the rate of molting in females is less than that of males and that not all females molt each year. This is in spite of the fact that indefinite post puberty molting has been recorded in xanthids (Hartnoll 1985). Length-weight relationships for males and females from western Victoria are presented in Figure 9 and showed divergence in the form of the relationship between the sexes at approximately 130 mm carapace length. This could reflect reduced growth of females after the onset of sexual maturity and/or accelerated growth of the right male cheliped after the onset of maturity.

Molt increment data from the recapture of tagged individuals is limited; the data available on percent molt increment is plotted against premolt carapace length in Figure 10. The data suggested a decrease in molt increment with increasing size in males but female molt increments at a given premolt length were variable. All increments were re-

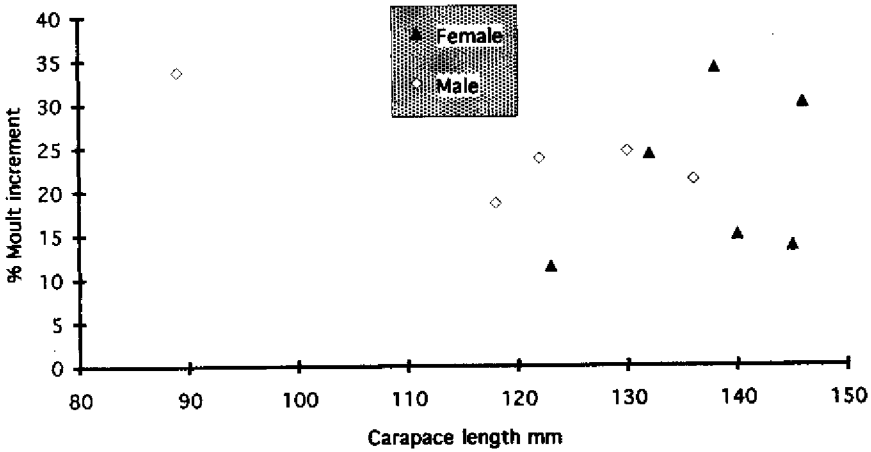


Figure 10. Percent molt increment plotted against premolt carapace length for P. gigas (all increments based upon recaptures within 12 months of tagging).

corded within 12 months of tagging. Increments were quite large (up to 34%) in *P. gigas*.

Discussion

P. gigas appears to consist of a single stock across southern Australia. Low levels of allozyme variation within and between populations of *P. gigas* is consistent with the findings for other large marine crustaceans (Hedgecock et al. 1982). However, it needs to be acknowledged that the failure to find differences among stocks on the basis of allozyme electrophoresis does not necessarily mean that stocks are genetically homogeneous. It is therefore planned to use more sensitive DNA techniques to further explore the question of stock structure of the species across southern Australia.

Based on the data obtained to date, two models relating size distribution and movement to depth, and reproductive stage and movement to depth can be proposed for *P. gigas*. The models are:

1. *P. gigas* stocks are stratified by depth. In spring smaller males and females occur in deeper water, medium females on the shoulder of the continental shelf, large females just inside the shelf break, and large males in shallow water on the continental shelf. Fishermen target the area giving largest yield; in spring this is the shoulder of the continental slope which yields large numbers of medium-size females. As animals mature both sexes move from deeper water to

shallower water just inside the shelf break. In autumn the entire distribution appears to shift downward and results in an influx of larger males and females to deeper water; catchability in shallower water decreases.

2. Spawning/molting/mating cycles affect distribution with depth. Females molt in deeper water and subsequently mate with larger males. Females spawn in deeper water and then berried and nonberried females migrate upslope in spring, with hatching occurring just inside the shelf break (near the shoulder).

These two migratory patterns interrelate growth, mating, and spawning. Seasonal patterns of movement related to spawning and molting cycles may partially explain the seasonal change in sex ratio observed in the SA population. The decline in relative abundance of females in autumn-winter may reflect simultaneous downslope migration of males and reduced activity of females preparing to molt and/or spawn. Behavior and depth distribution are important for the fishery; fishermen target areas where catches are high and this contributes to the high proportion of females in spring catches. Prior to the introduction of the ILMS medium-size females were targeted on the shoulder of the continental slope; after the introduction of the ILMS in 1994 fishing effort shifted to shallower water inside the shelf break. Spring movement of berried females to just inside the shelf break means that a seasonal closure during October-November would protect aggregated berried female stock during a period of high catchability. For this reason closure of the crab fishery during the closed period of the rock lobster season (October and the first two weeks of November) has been recommended.

The reproductive cycle and pattern of movement relative to breeding in *P. gigas* show similarities to other species. Deeper water is the site of mating in many deepwater crab species (for example, Hoggarth 1993, Diesel 1991, Sainte-Marie and Hazel 1992, Stevens et al. 1993). Upslope migration of berried females carrying eyed eggs in spring has been recorded in other crab species (for example, Jamieson et al. 1990, Diesel 1991) and may be a strategy to take advantage of warmer water to accelerate egg development as suggested by Diesel (1991). This movement often explains the dominance of females in shallow water catches in spring (Jamieson et al. 1990). Female *P. gigas* move downslope into deeper water in autumn; this behavior is also common in brachyurans prior to mating and spawning (Diesel 1991).

Molting/mating and spawning cycles are yet to be confirmed for *P. gigas*. Preliminary examination of dissected animals suggests that a series of spawning years is punctuated by one or more years when females molt without spawning. Female *P. gigas* may not spawn in all post puberty instars, however, the number of spawnings per instar is undetermined at this stage.

Variation in size at the onset of sexual maturity between locations, even those geographically adjacent, has been reported in lobster (Annala et al. 1980) and crabs (Somerton 1981; Dugan et al. 1994). These studies have shown that female size at maturity is a function of growth rate and is negatively correlated with temperature and positively correlated with food availability. Differences in size at maturity evident for *P. gigas* are not easily related to temperature; the difference between Augusta and Albany populations, subject to different patterns of fishing mortality, warrants further attention as it has been shown in the lobster *Panulirus marginatus* that five to ten years of fishing pressure can reduce size at onset of sexual maturity (Polovina 1989).

P. gigas females showed a characteristically flat relationship between carapace length and proportion carrying eggs with asymptotes at about 40 to 60%. Asymptotic values at 20 to 40% have been reported in *Panulirus marginatus* (Polovina 1989). Hoggarth (1993) has reported a non-sigmoidal relationship between length and proportion in berried female *Paralomis granulosa* and, like *P. gigas,* the proportion of berried females declined in larger size classes. Hoggarth (1993) proposed that this might reflect breaks from reproduction in females due to molting without spawning or large females being unable to find suitable larger male partners during the receptive period following molting.

Although the molt increments recorded for *P. gigas* were quite large, similar increments have been recorded in other brachyurans (for example, Edwards 1965, Warner 1977, Tweedale et al. 1993, Gonzalez-Gurriaran et al. 1995). The data is limited but compares to the mean molt increment of 18% reported in the oziid *Menippe mercenaria* (Tweedale et al. 1993). Edwards (1965) recorded unusually high increments as 34 to 49% in *C. pagurus* and noted that all high increments occurred in females. Variable molt increments in females of the same length class as observed in the present study may reflect individual state at the time of molting or may be related to reproductive cycle in that females molting prior to mating and spawning may show smaller increments than females molting without spawning. Hartnoll (1985) reported that reproductive and non-reproductive brachyurans of the same size may show different molt increments with nonreproductive females having larger increments. Determination of the linkage between molting/mating and spawning is important and will be reliant upon correlation of molt increment with other information from recaptures, for example, the presence of spent egg shells on pleopods.

Based upon molt increments of *P. gigas* observed in the field, the increase in size of males from spring through summer in SA can be interpreted as reflecting the molt increment of animals newly recruited to the fishery. Molt increments across a wide size range approximate 20%

for males; this is equivalent to an increase of 30 mm for a 150 mm length animal and would account for the seasonal shift in mean size recorded for SA animals. Molt increment in females may vary with reproductive state and the seasonal shift is less clear.

Two pieces of evidence suggest that larger *P. gigas* males (above 165 mm) may warrant special attention as regards management. First, larger males may be targeted during fishing; the bycatch from the rock lobster fishery is largely larger males. This reflects the distribution of larger males on the harder and shallower substrates, where rock lobster are targeted. Secondly, sex ratio data from SA in spring of 1993 and 1994 suggests a shift in favor of females. This may reflect reduced catchability of females during incubation of eggs with consequent increased effort on males. This may predispose males to greater fishing mortality.

There is evidence for other crab species that larger males are important in mating. Kruse (1993) has suggested that low numbers of males in xanthoid species characterized by male guarding of recently molted females may increase female mortality post-molting. If, as in other crab species (for example, Blau 1986, Sainte-Marie and Hazel 1992, Kruse 1993, Stevens et al. 1993) male size is important in mating success of *P. gigas*, with females only mating with males larger than themselves and broods from matings with larger males having a higher percentage of viable eggs, then loss of large males may reduce spawning in, and subsequent recruitment from, intermediate-large female size classes. This factor interacts with female size to influence spawning and recruitment. It was formerly held that intermediate sized female crabs made the greatest contribution to egg production due to their greater abundance and more frequent spawning than larger females (Campbell and Robinson 1983, Cobb and Caddy 1989). However, evidence from lobsters suggests that larger females may contribute relatively more to recruitment due to the higher energy content and earlier hatching time of their eggs (Attard and Hudson 1987). Waddy and Aiken (1986) have shown that consecutive spawning in *H. americanus*, wherein larger females spawn without intervening molts, results in larger females spawning more frequently than smaller animals. This combined with their increased fecundity means that very large females may have a greater relative fecundity than previously assumed. If, as it appears, female *P. gigas* spawn intermittently then intermediate-large female size classes may make the largest contribution to reproduction (after Waddy and Aiken 1986). The loss of males large enough to mate with these larger female size classes could impact upon spawning.

The diet of *P. gigas* was composed of mostly sedentary organisms as expected for xanthoids which have small eyes and are unable to move quickly or capture fast moving prey (Warner 1977). The number of food items in *P. gigas* stomachs was very low compared to studies of other species from similar depths, for example, *Paromola cuvieri* (38 items) and *Geryon longipes* (17 items) (Cartes 1993). Crabs from shallower habitats tend to have more diverse diets (Comoglio et al. 1990, Jewett et al. 1990). The latter study showed that *Paralithodes camtschaticus* trawled from 16-31 m depths consumed similar diet items to *P. gigas* with bivalves, gastropods, brittle stars and brachyurans being most common. The apparent preference of *P. gigas* for asteroids has not been recorded elsewhere in other species; if echinoderms are ingested they are generally echinoids or holothuroids (Jewett et al. 1990, Cartes 1993).

The low diversity of diet items in *P. gigas* could reflect one or more of three situations. *P. gigas* may feed selectively on the diet items recorded as they offer the greatest energy return for the amount of energy invested in capture. Diet would also be influenced by the body form of *P. gigas* and it may be restricted to relatively slow moving prey. The majority of prey items recorded are slow moving. Seasonal availability of prey would also be involved in these two hypotheses; stomachs were sampled during autumn and this may influence food availability. Restricted diet diversity may also reflect reduced food availability in the crab's habitat, potentially as a result of trawling operations; the natural diversity of benthic communities in this region is currently being assessed. These alternative hypotheses will be further evaluated by comparing inshore diets and evaluation of benthic community diversity from previous studies.

Female *P. gigas* consumed more gastropods than males and larger males had fewer food items in their stomachs than females of similar size. These differences could be attributable to sexual dimorphism in cheliped morphology. *P. gigas* has large crushing chelipeds with rounded denticles typical of xanthoids (Warner 1977). In males the right cheliped becomes larger than the left after the onset of sexual maturity. Larger males thus have only one actively mobile cheliped and may be unable to forage for mollusks. Females may be better able to use their chelipeds to forage for food. This hypothesis is supported to some degree by the fact that the stomachs of smaller males contained equivalent proportions of mollusks to that of similar sized females. The absence of food in the stomachs of premolt animals correlates with the cessation of feeding in preparation for molting which involves the digestive tract.

Some conjecture on the capacity of *P. gigas* to sustain a fishery can be offered based upon the limited findings to date. The fishery for *P. gigas* in southern Australia appears to be the only xanthoid fishery not based substantially upon the harvest of claws. The life cycle characteristics of *P. gigas* will determine management requirements for the fishery. *P. gigas* is possibly more r-selected than anomuran deep sea crabs but less so than *C. magister* (after Kruse 1993). Particular features are that the species appears to store sperm, and this may mean that consecutive spawning occurs, the species appears to have high fecundity for crabs (after Kruse 1993), and the species appears to have fairly large molt increments. These features would tend to compensate to some degree for adverse reproductive effects due to reduced male abundance and mortality of spawning stock due to fishing pressure (Kruse 1993). However, the population structure of *P. gigas* from SA shows that length-frequency distributions are bell-shaped; a long lived species might be expected to show more than one mode and a gradual decrease in proportion of the older age classes. This may relate to the frequency of recruitment. These features will affect harvest strategies and *P. gigas* may be able to sustain more liberal harvest than, for example, red king crab or Tanner crab, but this will be dependent on features such as age at maturity, age at recruitment, size-dependent molting frequency, and natural mortality rates. Should *P. gigas* prove to be more r-selected then natural mortality could be high and year class strength variable (after Otto 1986); this is likely to mean that any stock-recruitment relationship would be weak. Differences in size at the onset of female maturity between populations of *P. gigas* require investigation and, depending upon their origin, may require differences in management strategies (e.g., Kruse 1993).

A deliberately conservative management approach has been adopted with regard to *P. gigas*, and legislative constraints on the taking of berried females, vessel numbers and gear quantity, seasonal fishing, and minimum size at first capture have been introduced by the Australian Fisheries Management Authority in collaboration with state fisheries agencies. Further consideration of the life history of *P. gigas* and the degree to which it is r-selected must await completion of the study. It is a significant question as it has implications for the long-term stability of the fishery; r-selection is likely to increase variability in year class strength, increase variability in catches, and reduce the strength of the linkage between active management and the stability of the fishery (after Jamieson 1986, Otto 1986, Kruse 1993).

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Economic Evaluation of Superexclusive Designation for the Summer Norton Sound Red King Crab Fishery

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Abstract

The Norton Sound summer red king crab fishery has recently become the only federally managed Alaska king crab fishery designated as superexclusive. Under this designation, any vessel that participates in this fishery is barred from participating in any other federally managed king crab fishery. The new designation has fundamentally changed the industry structure of the Norton Sound summer red king crab fishery. The fishery, which was previously dominated by a highly capitalized distant water fleet, has become a small scale local fishery. Moreover, the localization of the fleet has fostered the development of support industries in Nome. The down-scaling of the fishery is unique in Alaska's crab industry. This paper presents a methodological framework for estimating the economic impacts of this "new" fishery to the Norton Sound region through input/output analysis.

Introduction

Communities in Alaska are experiencing diverse and significant economic changes. The economies of urban Alaska appear to be on a path of expansion and long-term growth. In contrast, a significant portion of rural Alaskan economies are experiencing stagnation and decline. These economies are characterized by both high levels of unemployment and low per capita incomes. If these economies are to be revitalized it is important that potential economic opportunities be identified and evaluated.

One potential economic opportunity has emerged in the Norton Sound region. Recent regulation changes by the North Pacific Fishery Management Council (Council) to the Norton Sound Summer Red King Crab (NSSRKC) fishery have profoundly affected the fishery's structure and links between the fishery and the economies of the Norton Sound region. In 1993, the fishery was designated superexclusive by the Alaska Board of Fisheries (Board). And while this adoption of superexclusive status for the fishery was initially overturned in 1993 by the U.S. Secretary of Commerce (Secretary), superexclusive status was reinstated in 1994 by the Council. Under superexclusive status, any vessel that participates in the NSSRKC fishery is barred from participating in any other federally managed king crab fishery. This change in management designation has fundamentally altered the way the NSSRKC fishery is prosecuted. A once distant water, highly capitalized fleet was replaced by small local vessels primarily from the Nome and Yukon Delta regions.

The localization of the fleet has created direct employment opportunities for local residents. Moreover, economic benefits from the fishery to the Norton Sound region extend beyond those accruing from the directed harvesting sector. Support industries have emerged, expanding economic activity throughout the region.

The assessment of the economic impacts of the NSSRKC fishery to the regional economies of Norton Sound requires that economic benefits occurring through links between various economic sectors be incorporated in the evaluation process. In this paper, regional economic modeling is presented as the appropriate framework for comprehensive economic impact analysis of the NSSRKC fishery to the Norton Sound region. Specifically, a regional economic model is being developed for impact analysis of the 1994 NSSRKC industry to the Norton Sound regional economies.

The methodology employed in model development is as follows:

- Provide an economic description of the Norton Sound red king crab fishing industry. This description will clearly detail the primary sectors of the industry: harvesting and processing. Furthermore, the structures of support industries will be incorporated in the description.

- Develop a Norton Sound regional economic model that focuses on contributions of the summer Norton Sound red king crab fishery to the regional economies. This model will be constructed within an input/output framework.

- Utilize the developed model to estimate the impacts of the Norton Sound red king crab fishery to the regional economy.

Proposed Research

Regional economic analysis provides a methodology for describing regional economies, identification of economic opportunities, and impact assessment. The IMPLAN input/output model (USFS 1993) will be employed in conjunction with the Fisheries Economic Assessment Model (FEAM) (Jensen 1995) to perform the analysis of economic impacts to the Norton Sound region associated with the superexclusive fishery designation. The Norton Sound region for analysis purposes will represent the Nome U.S. census district. However, the reader should be aware that localization of the NSSRKC fishery has also had important economic impacts to the Yukon Delta region (Wade Hampton U.S. census district); and only due to fiscal and time constraints is the proposed analysis limited to the Nome census district. This limitation can be mitigated once the model is constructed through impact analysis—"what if" scenarios can be developed to estimate economic affects of the fishery to the entire Norton Sound region.

History of Fishery

Until 1977, the only king crab harvested in the Norton Sound was for subsistence purposes. The commercial fishery was initiated in 1977 on the basis of a petition to the Board by local subsistence fishers who wanted to supplement their limited incomes. The Board allowed an experimental commercial fishery in both the winter and summer of 1977 and an open summer season in 1978. The winter commercial fishery has been minor in comparison to the summer fishery, with total winter harvest ranging from a few crabs to nearly 10,000 (ADFG 1993).

The NSSRKC fishery, the focus of this project, occurs in water close to Nome, approximately 20-40 miles offshore (see Figure 1). Historically, the fishery has operated under an open-access policy and was exploited on a first come, first serve basis. Similar to numerous fisheries worldwide, open access management contributed to a "race for fish." Seasons which once lasted months became seasons lasting a few days. Furthermore, the short duration of the seasons created a fishery which managers did not believe could be effectively managed (ADFG 1993). Over and under harvesting of the resource became common.

Until recently, the NSSRKC fleet was dominated by highly capitalized, distant water crab vessels that participated in other Bering Sea

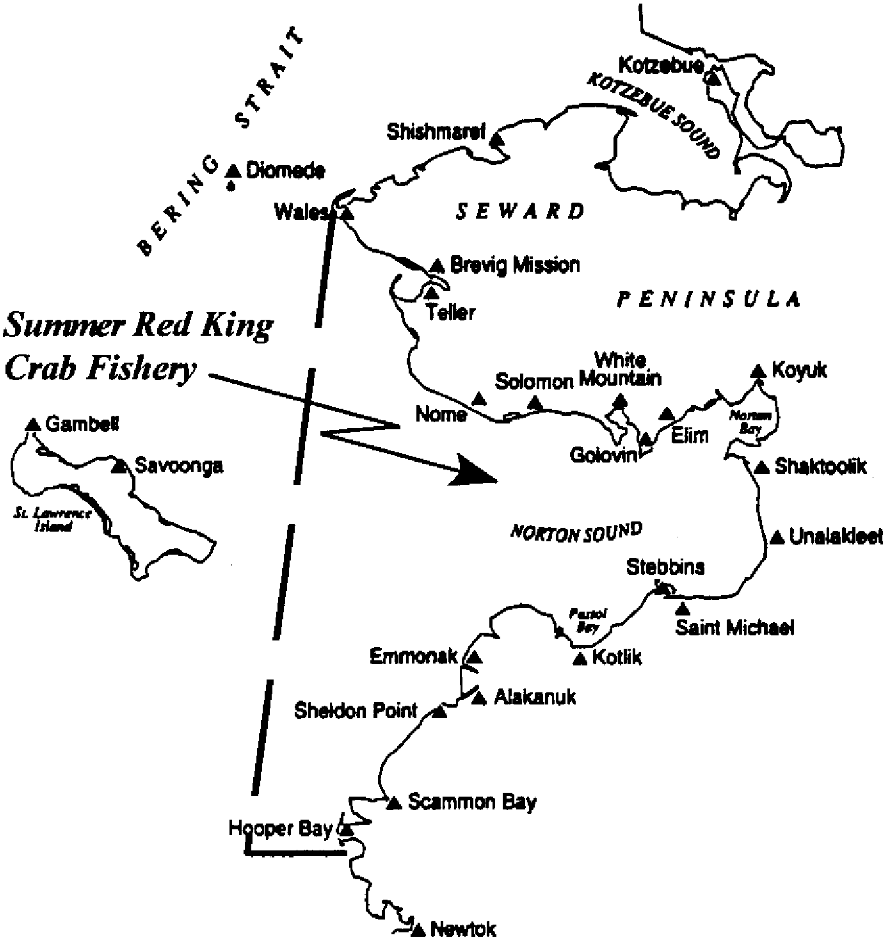

Figure 1. Location of Norton Sound summer red king crab fishery, in western Alaska.

Aleutian Island (BSAI) king and Tanner crab fisheries. Local participation did not develop, despite apparent interest, because small local boats were unable to compete with the more effective "outside" vessels. These outside vessels were attracted to the fishery by its summer opening when other BSAI crab fisheries are closed.

Beginning in 1979, the fishery experienced a series of fluctuations in vessel participation as shown in Table 1. The highly variable nature of this fishery is also apparent by examining average harvest and total fishery harvest. In general, high average harvests and limited participation has been followed by low average catches and high participation.

Table 1. Summer red king crab harvest and effort summary, Norton Sound, 1977-1995

Year	Days	Vessels	Pots	Average pots	Pot lifts	Crabs/ pot	Ex-vessel Price	Total harvest	Average harvest
1977	60	7	-	-	5,457	36	.75	0.52	-
1978	60	8	-	-	10,817	64	.95	2.09	-
1979	16	34	-	-	34,773	28	.75	2.93	-
1980	16	9	-	-	11,199	29	.75	1.19	-
1981	38	36	-	-	33,745	11	.85	1.38	-
1982	23	11	-	-	11,230	6	2.00	0.23	-
1983	3	23	3,583	156	11,195	12	1.50	0.37	16,087
1984	13.6	8	1,245	156	9,706	14	1.02	0.39	48,750
1985	21.7	6	1,116	186	13,209	11	1.00	0.43	71,667
1986	13	3	578	193	4,284	38	1.25	0.48	160,000
1987	11	9	1,430	159	10,258	10	1.50	0.33	36,667
1988	9.9	2	360	180	2,350	32	N/A	0.24	120,000
1989	3	10	2,555	256	5,149	15	3.00	0.25	25,000
1990	4	4	1,388	347	3,172	19	N/A	0.19	47,500
1991					*SEASON CLOSED*				
1992	2	27	2,635	98	5,746	4	1.75	0.07	2,593
1993	58	14	560	40	7,063	16	1.28	0.33	23,571
1994	31	34	1,165	35	11,729	9.3	2.02	0.33	10,000
1995	67	48	1,778	32	18,782	5.6	2.87	0.32	6,666

Source: ADFG

While this uncertainty reduced the fishery's attractiveness, the summer opening continued to attract participants.

Table 1 also provides average ex-vessel price paid for Norton Sound summer red king crab. The ex-vessel price is substantially lower than that for red king crab from other BSAI fisheries because of the crab's smaller size. For example, the ex-vessel price for Bristol Bay red king crab was $5.00/lb. in 1992 compared to $1.75/lb. for Norton Sound red king crab (ADFG 1994).

There were several management actions in the early 1980s which affected the fishery's structure. In 1981, the Board enacted a 15 mile closure along the Norton Sound coast to protect sublegal and female crabs that congregate near shore (ADFG 1993). The Board also changed the fishery's seasonal opener from July 15 to August 1. These actions presented further barriers to local participation because small local vessels were unable to safely navigate the Norton Sound in August when the weather worsens.

Finally, the guideline harvest level (GHL) was reduced in 1982 to assure subsistence availability. The reduction in GHL coupled with inadequate local markets caused a shift from a predominantly catcher fleet to a predominantly catcher/processor fleet. Catcher/processors, on average had greater fishing capacity than catcher vessels. The combination of small quotas and a highly capitalized fleet led to seasons too short to manage effectively (ADFG 1993). The season's length fell from 21 days in 1985 to 3 days in 1989 (see Table 1).

The fishery was closed in 1991 due to management concerns that the fishery could not be effectively managed given the excessive fleet capacity. Management problems continued in 1992, when the season was closed after 2 days with only 76,000 pounds harvested out of a 300,000 pound GHL. ADFG estimated that the fleet, consisting of 27 catcher/processors fishing in excess of 2,600 pots, could have harvested the GHL in just a few days (C. Lean, Area Biologist, ADFG, Nome, pers. comm. 1996). ADFG closed the fishery after 2 days to evaluate the harvest. In spite of the harvest being substantially below the GHL, reopening the fishery was not considered an option due to the fleet's high level of fishing power.

Superexclusive Designation

In the fall of 1992, local residents requested that the Board reclassify the fishery as superexclusive. As noted, under superexclusive registration, vessels participating in the Norton Sound fishery would be ineligible to participate in any other federally managed king crab fishery. The Board, noting a range of fishery problems, adopted the superexclusive designation for the 1993 season. However, a group of vessel owners appealed the Board's decision. The group cited that under the Fishery Management Plan (FMP) for the commercial BSAI king and Tanner crab fisheries (NPFMC 1989), superexclusive registration could only occur through a plan amendment approved by the Council. The Secretary upheld the appeal, overturning superexclusive registration. However, in 1994 the Council voted to reinstate the superexclusive registration.

Even though the superexclusive registration was not formally in place for the 1993 season, the late date of the Secretary's ruling led to the 1993 fishery being treated as de facto superexclusive by fishery participants. Distant water crab vessel owners who might have participated in the NSSRKC fishery were unwilling to risk being excluded from more lucrative BSAI king crab fisheries. Consequently, major changes in the fishery's structure began in 1993 with the de facto superexclusive registration. These changes are evident in Table 1 and also Table 2, which provides the home port and average vessel lengths for 1991-1995 NSSRKC fishery participants.

Table 2. Point of origin and average vessel length for vessels participating in the Norton Sound summer red king crab fishery, 1991-1995.

	Nome region	Yukon Delta	Alaskan nonlocal	Non-Alaskan	Total	Average length
1991			*SEASON CLOSED*			
1992	1	0	6	20	27	119
1993	2	1	6	5	14	41
1994	18	9	3	4	34	31
1995	25	14	3	6	48	31

In 1992, the fishery season lasted 2 days with only 23% of the GHL harvested. A total of 27 vessels participated in the season with 20 of the vessels originating from outside Alaska. The average 1992 vessel was 119 feet and fished 98 pots. In contrast, the 1993 fishery attracted 14 vessels with only 5 originating from outside Alaska. The average vessel was 41 feet and only fished 40 pots. As a result of the reduced level of effort, the season lasted 58 days and the GHL was harvested.

The changes, which were noted in conjunction with the 1993 de facto superexclusive registration, have remained in place. In 1994, 34 vessels participated in the fishery with 18 vessels originating from the Nome region and an additional 9 vessels from the Yukon Delta area. Only 4 vessels originated from outside Alaska. The average vessel was 31 feet and fished 35 pots. The 1994 fishery season lasted 31 days and the fishery harvest was 327,858 pounds (ADFG 1994).

As noted, support industries to the NSSRKC fishery have developed within the region in response to the localization of the fleet. A significant portion of the fleet harvest is being processed in Nome. A Community Development Quota (CDQ) nonprofit corporation, the Norton Sound Economic Development Corporation (NSEDC), has become one of the primary local processors, through a for-profit company it formed, the Norton Sound Crab Company. Additional businesses in the Nome area have benefited from the fishery through the sale of supplies, gear, and equipment. For example, fuel is now being provided locally to the fleet. Also, Nome restaurants are now featuring locally caught red king crab.

Norton Sound

Current participants in the NSSRKC fishery are principally from Western Alaska communities located on the southern portion of the Seward Peninsula and the Northwestern Yukon Delta region. These regions share many characteristics with other rural Alaska communities. The region comprises small villages, with populations under 750, and a single city, Nome (population 4,559). The region is the ancestral home of the Inupiat Eskimos and currently most of the villages have predominately Native Alaskan populations. The area is isolated due to geographic remoteness from major urban areas of Alaska and also the absence of surface transportation systems. There are no road or rail corridors that connect the area to other Alaska regions, and while there is a road system around the city of Nome, in most villages the road system is strictly local.

The economies of the Norton Sound region are experiencing either stagnation or in many cases decline, which can be attributed to the lack of employment opportunities in the cash economy, not atypical of the circumpolar north (Stabler 1990). High unemployment rates in the cash sector reflect the limited number of developed industries throughout the region. The majority of jobs that do exist are directly related to government agencies and educational services. Most of the residents participate in the non-cash subsistence component of the regional economies. Subsistence is vital both economically and culturally to the residents of the Norton Sound region, and has been the major industry in rural Alaska for thousands of years. In contrast to local subsistence production, most manufactured goods are imported into the Norton Sound region. Many households in rural Alaska engage in a mixed cash-subsistence economic strategy. Subsistence production supplements or replaces market purchases, and cash income is used to purchase necessary inputs for subsistence production. Subsistence, over time, has become increasingly capital intensive (Geier et al. 1992).

Communities

The problems faced by the communities of the Norton Sound are impressive, and all too prevalent in rural Alaska. The superexclusive designation of the NSSRKC fishery has provided an economic stimulus to regional economy, creating a new industry and encouraging further development of the region's fishing industry. Two Norton Sound communities in particular experienced significant economic activity from the localization of the fishery, Unalakleet and Nome.

Unalakleet is the second largest town in the Norton Sound region, with a 1990 population of 714. The community is predominantly Native (82%) with a minority white population (17%). A 1990 study by Northern Economics estimated that 70% of all full-time jobs were in the public sector (including schools). Within the private sector, the Unalakleet Village Corporation and the airline industry are the major employers. The median 1990 per capita income was $12,027 and 11.6% of the residents had incomes below the poverty level (NPFMC 1994).

Eleven vessels from Unalakleet participated in the 1994 and 1995 NSSRKC seasons (see Table 2). The average 1994 gross revenue per vessel was $3,350. Prior to the 1994 superexclusive designation, no vessels from Unalakleet participated in the fishery. In addition to the direct harvesting participation, Unalakleet residents also engage in vessel building and repair, and the town is one of the few places in western Alaska to provide these services.

Nome has been a principal recipient of economic activity generated by the superexclusive designation of the NSSRKC fishery. The economic activity has emanated from several sources. Seven vessels from Nome participated in the 1994 directed fishery and twelve vessels participated in the 1995 fishery. As with Unalakleet, no vessel from Nome participated in the directed fishery prior to superexclusive management.

Nome, as noted, has become the processing center for the NSSRKC fishery. NSEDC has operated the Norton Sound Crab Company in Nome since 1994. The Norton Sound Crab Company processed 36% of the NSSRKC harvest in 1994 and 98% of the harvest in 1995. In 1994 the company employed approximately 75 local residents. Prior to the superexclusive designation of the fishery, virtually all crab harvested in the NSSRKC were processed either onboard catcher/processors or outside the region.

Nome's location near the fishing grounds has led to it becoming the staging area for the fishery. Nome provides lodging, supplies, and docking facilities for local and non-local vessels. For example, the Yukon Delta fleet docked their vessels in Nome and also purchased many of their supplies from local merchants. There has been discussion in Nome of expanding the city's dock to accommodate growth generated by the NSSRKC fishery (N. Stiles, crab vessel owner, Nome, pers. comm.). Benefits from the fishery have even extended to the tourist industry, with many restaurants featuring locally caught crab, and tour operators including stops at the dock facilities on their local tours (N. Stiles pers. comm.).

Basic Input/Output Theory

The economic methodology employed to evaluate the economic impact of the superexclusive designation is input/output analysis. Input/output (I/O) models are operational analytical tools that have a variety of uses: measuring the economic interdependence of a region's industrial structure, providing a set of disaggregated multipliers, calculating the effects on economic activity in individual regions of changes in final demand, and as a technique for long-run projections and forecasts (Richardson 1972). Input/output models were first developed by Wassily W. Leontief during the 1930s and are constructed from observed economic data for a particular region (Miller and Blair 1985). The economic activity in a region is divided into a number of industry sectors. I/O analysis is concerned with the flow of products from each industry sector considered as a producer to each of the sectors considered consumers. The flow of products is tracked in monetary terms for a specific period (usually a year) and tabulated (Miller and Blair 1985).

IMPLAN

Two I/O models will be employed in the impact analysis of the NSSRKC fishery. The first is IMPLAN, which is a standard I/O model originally developed by the U.S. Forest Service. It was employed as a tool for supporting economic analyses within the land management planning procedures required of the Forest Service by the National Forest Management Act of 1976 (Cordell et al. 1992). IMPLAN is a non–survey-based regional I/O model that consists of 21 economic and demographic variables at a 528 industrial sector level for all counties (boroughs in the case of Alaska) of the United States. It is recognized as one of the best available sources of U.S. secondary economic data. IMPLAN has two basic functions. First it is used to create regional and national I/O models along with the corresponding multipliers and response coefficients. Second, the model is used to estimate regional economic impacts resulting from changes in final demand. Impact analysis involves posing a change in demand for commodities and using the multiplier model to examine the effects that producing and delivering the commodities may have on a region's employment, income, and production (USFS 1993).

Limitations of IMPLAN

A limitation of IMPLAN is that it does not provide for support industries in its estimation of economic impacts. Consequently, IMPLAN in isolation lacks sufficient detail for impact assessment from shocks to the commercial fishing industry and needs to be augmented by a more detailed representation of the industry. Furthermore, the IMPLAN model is demand driven. That is, IMPLAN estimates economic impacts based on changes in final demand. For example, IMPLAN is designed to estimate the effects on the regional economy if household consumption of commercial fishing output increased by $1 million. IMPLAN is not designed to estimate the economic impacts from an increase or decrease in industry output. Therefore, IMPLAN is unable to estimate the effects of policy changes with regard to the output of the commercial fishing industry.

FEAM

The second I/O model utilized in this project, FEAM, not only provides the additional detail for the commercial fishing industry but also affords a structure for organizing the impact assessment information. Moreover, this model is production oriented and is therefore able to estimate the impacts of policy changes with regard to the commercial fishing industry.

FEAM is an I/O model developed by Radke and Jensen (1995) to assess the impacts of commercial and recreational fishing industries to regional economies. FEAM utilizes the response coefficients and secondary economic data generated by IMPLAN to account for inter linkages in regional coastal economies, through production and consumption patterns. FEAM, through its I/O framework, explicitly accounts for links in regional coastal economies between various economic sectors, according to production and consumption patterns.

FEAM is referred to as a disaggregated I/O model. IMPLAN, an aggregated model, divides an economy into 528 basic sectors. The sectors are aggregated national industry composites based on the SIC classification system. A disaggregated model further divides the basic sectors into numerous supporting sectors, thus providing a greater level of detail in industry operations. Consequently, disaggregation provides greater detail in analyzing the economic impact from changes in final demand.

Model Development

The IMPLAN and FEAM models will be used interdependently in the development of the Norton Sound regional model. Both of these models are being modified to accurately reflect the Norton Sound region. First, this involves updating IMPLAN's database to accurately portray the regional economy. The process is community intensive and involves presenting the IMPLAN employment estimates to individuals familiar with the Nome regional economy. The individuals are asked to review the data to verify its accuracy. Revisions are then made when discrepancies occur. Once updated, the corrected IMPLAN data relevant to the commercial fishing industry is entered into the FEAM model.

The FEAM model is updated by acquiring the operating costs of the harvesting and processing sectors. This data is obtained through surveying the fishers and processors that participated in the 1994 NSSRKC fishery and is subsequently used to estimate the participants' cash flows. Thereafter, the primary data is entered into the FEAM model and the economic impact statements are generated

Model Output

The developed Norton Sound I/O model will be utilized for impact analysis to estimate direct, indirect, and induced effects on income by industry and aggregated industries using the constructed FEAM model. A direct effect is the income generated from production changes fundamental to the superexclusive designation. The indirect effect is the income generated from changes in inputs in the production process. Finally, the induced effect is the income generated from changes in household spending patterns resulting from the direct and indirect income effect.

To illustrate the three types of economic effects, suppose there was an increase in the demand for crab bait. The direct effect would be an increase in income realized by the bait sector resulting from the increased demand for bait. There would also be an accompanying indirect effect as the demand for inputs by the bait producing sector increased. For example, bait producers might increase their demand for netting in response to the increased demand for bait. This provides a further stimulation to the economy. Finally, the increase in demand for inputs would cause income and employment to increase, consequently causing an increase in spending throughout the economy. This represents the induced effect.

The FEAM model is also used to estimate the impact of different harvesting and processing scenarios. The model allows for the creation of different harvesting and processing possibilities. Given these perturbations to the regional harvest and/or processing, FEAM then estimates the impacts to the regional economy.

Conclusion

The superexclusive designation of the NSSRKC fishery has represented an important development in Alaska fishery management. The fishery was beset with an impressive series of problems. The chosen management option alleviated many of the problems by downsizing the fishing fleet. Not only has this change in management policy achieved management's objectives, but it also appears to have led to significant economic development in an economically depressed region of Alaska. The fishery has provided employment opportunities to local residents as well as serving as the basis for new business development.

This paper provides a structured approach for developing a regional model to evaluate the impact that the NSSRKC industry had on the Norton Sound coastal communities. Moreover, the approach outlined presents a methodology for assessing the impact of changes in resource allocation resulting from regulatory changes. This is especially significant to the numerous communities in rural Alaska that rely on commercial fishing as source of employment and income. Today, when resource allocation is a key issue in the management of many fisheries, it is critical for economist to be able to address economic impacts to the various affected parties. Regional economic modeling, and more specifically input-output analysis, provides a methodology to accomplish this task.

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High Latitude Crabs: Biology, Management, and Economics
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Distribution of Golden King Crabs by Sex, Size, and Depth Zones in the Eastern Aleutian Islands, Alaska

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Abstract

In 1991 Alaska Department of Fish and Game (ADF&G) conducted its first systematic survey on golden king crabs *Lithodes aequispinus* in Alaska. It was conducted around three Aleutian Islands (midpoint 52°30′N latitude, 171°W longitude) and encompassed an area of 2,750 km^2. Data collected by mandatory observers on three catcher-processor vessels, which fished in the same area in the ensuing commercial season, were compared with survey findings. Crabs were captured using baited pots fished in a longline fashion. Conical pots (594) were fished on the survey, and larger king crab pots (143) were used on the commercial vessels. There were 12,543 crabs captured on the survey, a catch per unit of effort (CPUE) of 21.1, and 7,582 crabs sampled by observers, a CPUE of 53.0. Survey pots had shorter soak times, mean 3.2 days, than commercial pots, mean 5.9 days. Effort and crab data were grouped into nine different 91 m depth categories for analysis. The percentage of survey and commercial pots lifted were within 10% of each other in each of the seven shallowest depth zones fished. Pots were retrieved from 128 to 853 m (all data); but no commercial pots were set deeper than 673 m. Survey pots, on average, were fished 121 m deeper than commercial pots. Small crabs ($\leq$ 100 mm CL) were abundant at 103 per pot on the survey in the deepest depth group fished, 823-913 m, but only 10 pots were fished. Length frequency distributions of females $\geq$ 100 were dissimilar between survey and commercial pots but were remarkably similar for males > 115 mm CL. Crabs were captured at all depths fished and were represented by both sexes and all size categories throughout their

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vertical distribution, except > 548 m which were dominated by small crabs. Greatest concentrations of juvenile and adult females on ADF&G's survey were markedly deeper than those reported for British Columbia. An additional 5,000 pot lifts containing data on 350,000 golden king crabs has been recorded by observers since 1988 but has not yet been analyzed in detail. This database will continue to grow and will be ADF&G's major source of information to estimate relative abundance of larger sublegal and legal males, and monitor adult female reproductive condition, and provide new insights into golden king crab life history.

Introduction

Commercial fishing for golden king crabs *(Lithodes aequispinus)* in the Aleutian Islands is managed by the Alaska Department of Fish and Game (ADF&G) using two separate management areas: Adak and Dutch Harbor, which are divided at 171°W longitude (ADF&G 1993a). Exploratory fishing for golden king crabs in the Aleutian Islands began in 1975, but full development of the fishery did not start until the 1981/82 season (Morrison and Gish 1996). From 1981 to 1994, 46,100 tonnes of golden king crabs, with an ex-vessel value of $307 million, have been landed from the Aleutian Islands. During 1990-1994, this fishery was the fourth largest shellfish fishery in Alaska; only the snow crab *(Chionoecetes opilio)*, red king crab *(Paralithodes camtschaticus)*, and Tanner crab *(C. bairdi)* fisheries of the Bering Sea have been greater in value and tonnage landed (Figure 1).

Despite the value of the fishery, Aleutian Islands golden king crabs are not regularly surveyed to assess stock status. The first and only systematic survey of Aleutian Islands golden king crabs performed by the ADF&G occurred in 1991 (Blau and Pengilly 1994). That survey covered 2-10% of this species' estimated habitat (40,000-80,000 km^2) in the Aleutian Islands (Blau 1987). Due to the vast golden king crab habitat and distribution in the Aleutian Islands, in combination with no ADF&G dedicated funds to survey the area, regular population assessment surveys are unlikely in the future.

Lacking regular surveys, biologists from ADF&G and National Marine Fisheries Service (NMFS) have collected biological data on golden king crabs from trawlers and crab vessels fishing in the Aleutian Islands (McBride et al. 1982, Ronholt et al. 1982, Otto 1983, Otto et al. 1983, Otto and Cumminskey 1985, Sommerton and Otto 1986). Since 1988, the Alaska Board of Fisheries (BOF) has required mandatory observers on all catcher-processor vessels participating in Alaska's king, Tanner, and snow crab fisheries. Biological data collected on Aleutian Islands golden king crabs under that program have been summarized and reported annually (Beers 1991, 1992; Tracy 1994, 1995a, 1995b). In 1995, recognizing that a decrease in catcher-processor participation in the fishery had resulted in a decrease in biological data collected, the BOF

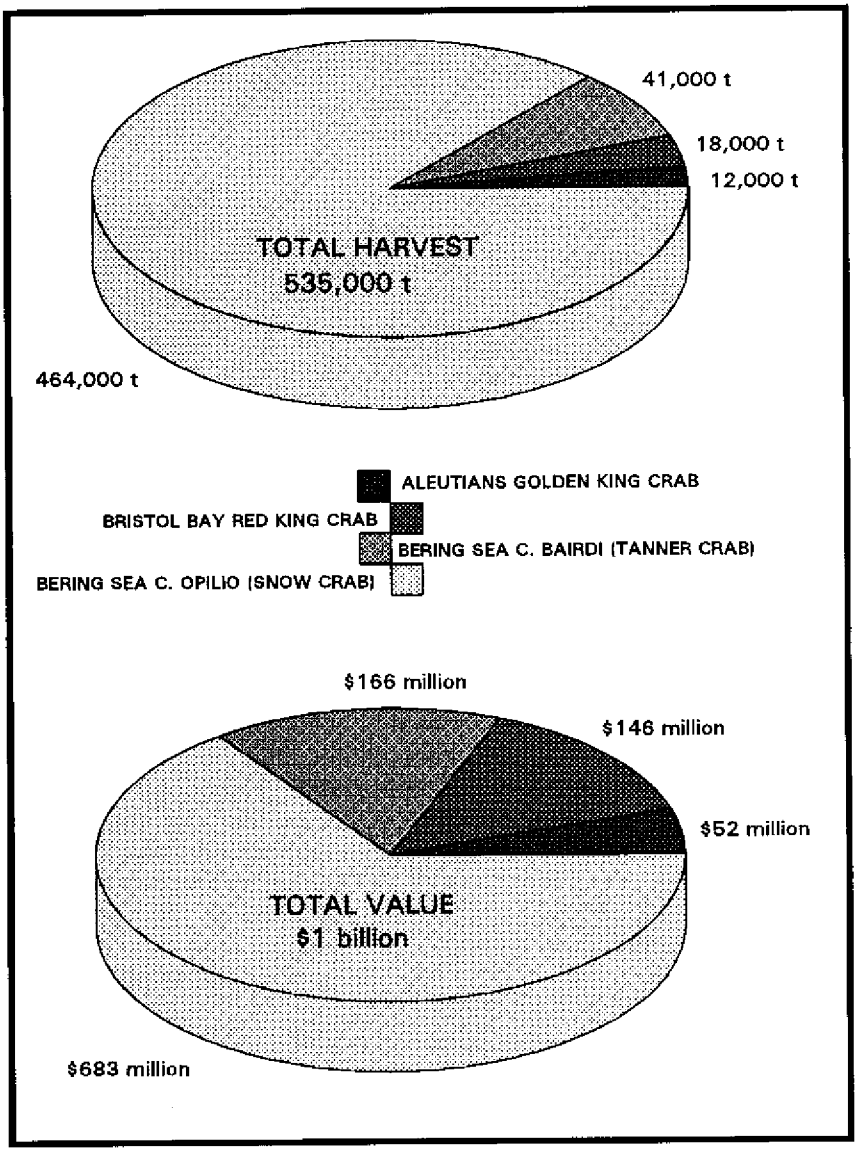

Figure 1. Harvest and ex-vessel value of the four largest shellfisheries in Alaska, 1990-1994 (Morrison and Gish 1995).

mandated observer coverage for all vessels fishing golden king crab in the Aleutian Islands.

Since observers collect data from fishing vessels that target legal-sized male crabs and use unstandardized gear and methods, inferences on distribution and sex-size composition based on these data may differ from those based on data from a standardized systematic survey. This report compares sex-size composition and depth distribution data of golden king crabs collected on the 1991 ADF&G survey in the Aleutian Islands with data collected by mandatory observers stationed on catcher-processor vessels fishing in the same area during the ensuing 12 months. Goals of this research were to increase knowledge on this species' biology and explore the usefulness of observer data to assess general stock status in lieu of regular surveys.

Methods

Survey area and design

Selection of the 1991 survey area was based on commercial catch data from the previous four commercial seasons in each management area (Blau 1992). Four of the seven statistical areas with the greatest combined catches of golden king crabs in the Aleutian Islands adjoined at the 171°W longitude line, which divided the Dutch Harbor and Adak Management Areas.

Sixty stations for the 1991 survey were drawn on National Oceanic and Atmospheric Administration charts 16480 and 16500 using a 9.3 km systematic spatial grid pattern. Stations were oriented in an E-W direction within the survey area. Only stations occurring entirely within the 137-913 m target depth range were selected because that covers the area inhabited by most golden king crabs (Blau 1990). The survey area was located between 52°18′ and 52°57′N latitude and 170°17′ and 171°50′W longitude (Figure 2).

Timing of data collections

The 31 m FV *Western Viking* was chartered by ADF&G from August 21 to September 19, 1991. Comparative observer data were gathered from golden king crab fisheries conducted after the survey: the 1991 Dutch Harbor fishery (September 1-November 15) and the 1991/92 Adak fishery (November 1, 1991-August 15, 1992).

Fishing techniques

Golden king crabs were captured using baited pots fished in a longline fashion. Ten conical pots were fished per station (Blau and Pengilly 1994). Each pot was baited with 3.8 L of frozen herring and either one Pacific cod *(Gadus macrocephalus)* or an equivalent amount of another bottomfish. Each pot weighed 50 kg and was covered by webbing with a

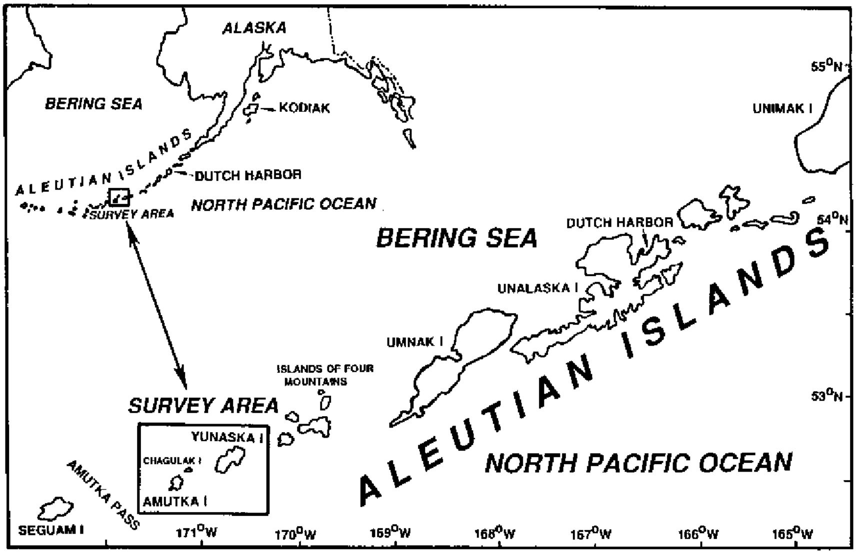

Figure 2. Location of the 1991 ADF&G golden king crab (Lithodes aequispinus) pot survey in the eastern Aleutian Islands, Alaska.

stretched mesh size of 9-11 cm. Each pot had two opposing tunnels with two one-way triggers to prevent crabs from escaping. Pots were spaced 183 m apart on each longline. A nonbaited king crab pot was attached as an anchor to ends of each longline. Exact time that each pot was deployed and retrieved were recorded.

King crab pots (approximately 200 × 200 × 84 cm, weighing 295 kg) were used in the Dutch Harbor and Adak commercial fisheries but exact specifications and fishing methods were not recorded by observers (i.e., mesh size, amount and kind of baits use, distance between longlined pots). Observers recorded pot soak time to the nearest whole day. All pots that soaked for > 21 days were grouped together. Pot soak times were not used to adjust crab numbers in either data set.

Data collected

Similar data were obtained from survey and commercial vessels with observers. Individual crab pot locations were recorded (longitude, latitude, depth). All crabs captured were sexed. Crab exoskeleton ages were categorized as new shell, old shell, or very old shell based on the amount of scratches on the ventral side of the coxa and presence of visible epibonts on the exoskeleton (Weber and Miyahara 1962). Observers followed methods described in the ADF&G observer field guide (ADF&G

1993b). Measurements on crabs were made with Vernier calipers to the nearest millimeter. Carapace length (CL) was taken from the right eye orbit to the midpoint of the posterior margin of the carapace. Size and shell condition were recorded for all crabs captured on the survey. Reproductive condition of females were noted such as clutch size and state of pleopodal setae (clean or with embryos or empty embryo cases). Observers recorded the number of all females, and sublegal and legal males in sampled pots. Occasionally crabs were subsampled for size, shell, and reproductive condition.

Legal size measurement

Minimum legal size of male golden king crabs was 152.4 mm carapace width (CW), measured as the greatest straight line distance across the carapace, including the spines. This measurement is at a right angle to a line midway between the eyes and the midpoint of the posterior portion of the carapace. Legal size was confirmed on most males by using a fixed measuring "stick" having standard width equivalent to minimum legal size. Carapace width was also measured with calipers on the survey to document male length-width relationship (Blau and Pengilly 1994).

Juvenile/adult female categories

Females were defined as juveniles if they were without embryos or funiculi (egg stalks) on their pleopodal setae and were less than the estimated size (carapace length) at 50% maturity (SM50). Adult females either had embryos or empty egg cases and funiculi on their pleopodal setae, or they were barren but ≥ SM50. Female SM50 was estimated from survey data using a logistic model (Cox and Snell 1989). Female SM50 for the Dutch Harbor and Adak Areas were estimated to be 109 and 107 mm CL, respectively (Blau and Pengilly 1994). Female SM50 for the observer data was not calculated but was estimated to be 108 mm CL by simply averaging the survey data since the observer data came about equally from both management areas.

Prerecruit/legal male categories

Each male golden king crab sampled was placed into one of four categories. Prerecruit ones and recruit-sized crabs were based on growth per molt information (Koeneman and Buchanan 1985; Robert Otto, National Marine Fisheries Service, Kodiak, AK 99615, Apr. 1992, pers. comm.). Prerecruit ones were estimated to be one molt away from reaching legal size and had carapace lengths from 121 to 137 mm but carapace widths less than minimum legal size. All other sublegal males ≤ 120 mm CL were grouped together as prerecruits 2-5 (estimated as 2-5 years from reaching legal size). Recruits were defined as new-shell males ≤ 153 mm

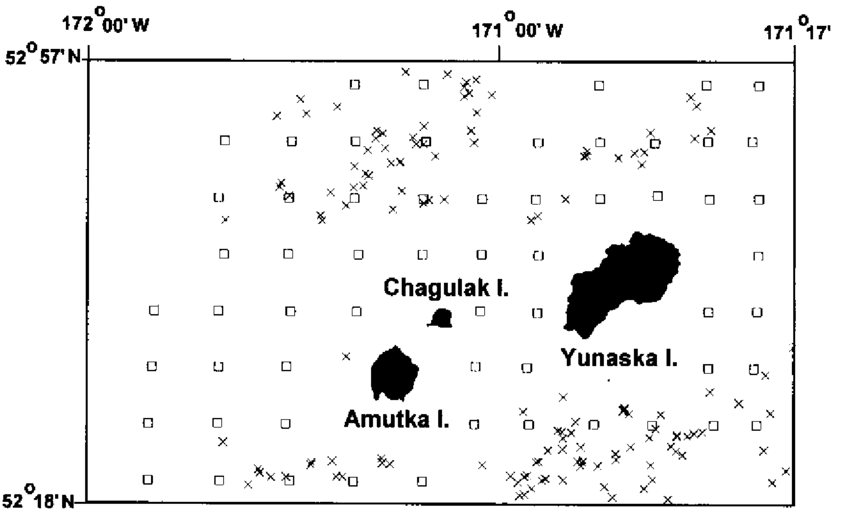

Figure 3. Locations of the 60 stations fished (squares) during the 1991 ADF&G golden king crab (Lithodes aequispinus) survey and of 143 commercial pots sampled (X) by observers within the survey area.

CL that had reached legal width. Postrecruit males were ≥ 154 mm CL, as well as all legal-sized anexuviants (old and very old-shell crabs).

Depth zones defined

Catch per unit of effort (CPUE) for male and female groups were calculated for nine different depth zones. Each depth group spanned 91 m (50 fathoms), except the shallowest zone had a vertical range of 45.5 m (25 fathoms).

Results

The 1991 golden king crab survey encompassed 2,750 km^2 and included Amutka, Chagulak, and Yunaska Islands (Figure 3). Sixty stations were fished, 594 pots were retrieved, and 12,543 golden king crabs were captured. Mean CPUE was 21.1 crabs per pot. Observers sampled the contents of 143 pots from three commercial vessels fishing within the survey area. These pots captured 7,582 golden king crabs of which 81.6% were measured. Mean CPUE was 53.0 crabs per pot. Most commercial pots sampled were clustered either south of Yunaska Island or north of Chagulak and Amutka Islands (Figure 3). Survey pots were fished in

August and September; 74% of the commercial pots were fished in September-December. The remaining commercial pots were fished up to 12 months later than survey pots.

Soak times and distribution of pots by depth

Mean soak time of pots was 3.2 days from survey stations and 5.9 days from commercial pots (excluding four pots sampled that were soaked > 21 days) (Figure 4a). Pot soak times ranged from 1.1 to 7.7 days per station on the survey and from 1 to 21 days or > 21 days for pots sampled by observers. Soak times for survey pots were generally shorter than observed for commercial pots. Sixty-six percent of survey pots were soaked for 2-3 days, while 56% of commercial pots which were sampled soaked 3-5 days. Survey pots were fished an average of 121 m deeper than the commercial pots. Mean depth fished was 460 m for survey pots and 339 m for commercial pots. Survey fishing ranged from 137 m to 852 m and from 128 m to 673 m for sampled commercial pots. In each of the seven shallowest depth zones, the percentage of survey and commercial pots fished were within 10% of each other, except in the two deepest depth zones (> 731 m) where no commercial pots were sampled (Figure 4b). The greatest effort in both the survey and commercial fishery occurred in the 274-364 m depth range where 24% of the survey and 31% of the observed commercial pots were deployed. Eighty-three percent of the survey and 97% of the observed commercial pots were fished in depths < 548 m. Commercial pot samples were taken every month from September 1991 to August 1992 although, most (106, 74%) were sampled from September to December 1991, which encompassed the start of the fishery in each management area.

CPUE by sex-size groups

Overall golden king crab CPUE by sex-size groups for survey/commercial pots were: juvenile females 5.6/4.9, adult females 5.3/20.7, prerecruits twos-fives 6.1/6.1, prerecruit ones 2.0/6.1, legal males 2.1/10.2, recruit males 1.6/8.3 and postrecruit males 0.5/1.9. Golden king crab sex ratios, female/male, were 51.7%/48.3% for the survey catch, and 48.3%/51.7% from sampled commercial catch.

Length frequencies

Female length frequencies were dissimilar between survey and commercial data < 120 mm CL, and most similar at lengths ≥ 135 mm CL (Figure 5a). Dominant carapace length mode for females captured on the survey was 115-120 mm compared to 130-140 mm from observer sampled pots. Male carapace length frequencies were dissimilar < 115 mm, but remarkably similar for sizes above 115 mm (Figure 5b). Small crabs (≤ 100 mm CL) made up a much larger proportion of the catch on the survey at depths ≥ 730 m compared to observer measured crabs (Figure 5).

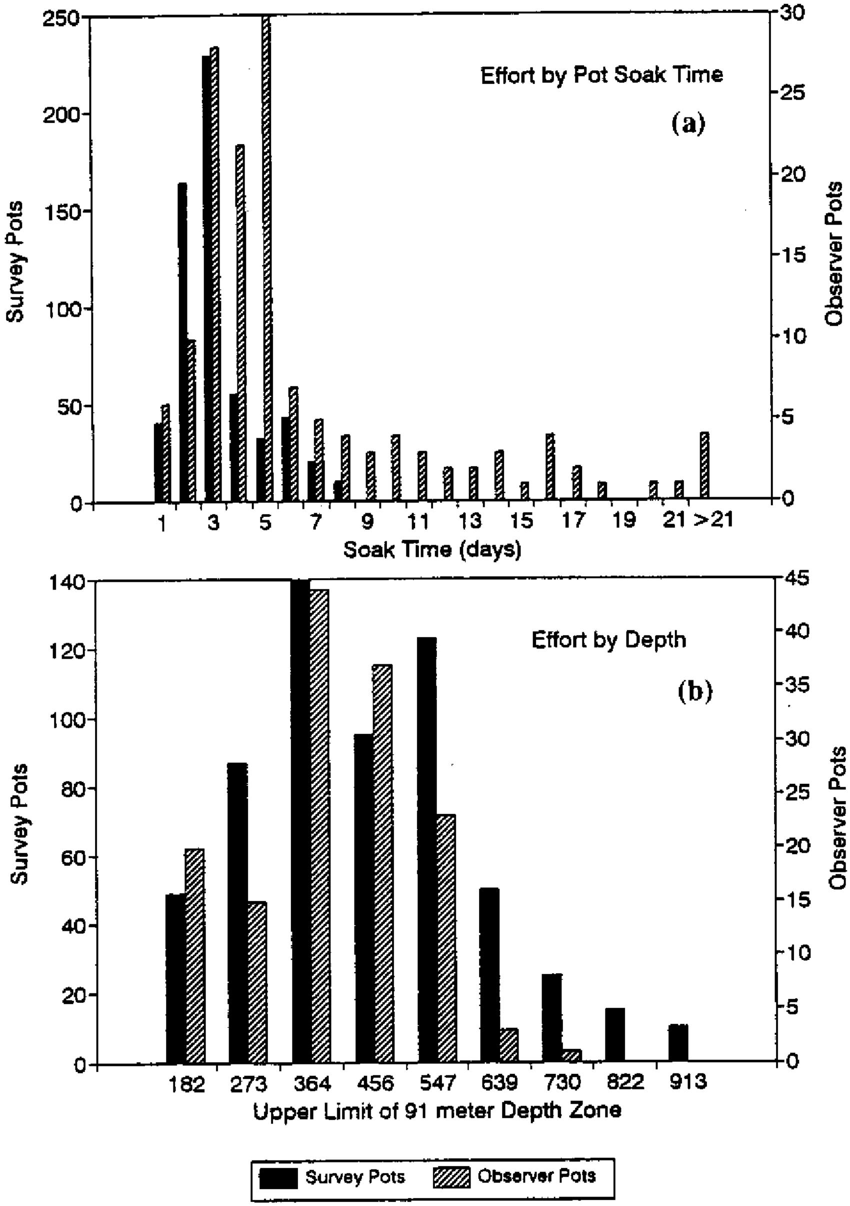

Figure 4. Comparison of pot soak times (a) and depths fished (b) from 594 potlifts from the 1991 ADF&G golden king crab survey and from 143 pots sampled by observers during the 1991 Dutch Harbor and 1991/92 Adak Management Areas golden king crab fisheries.

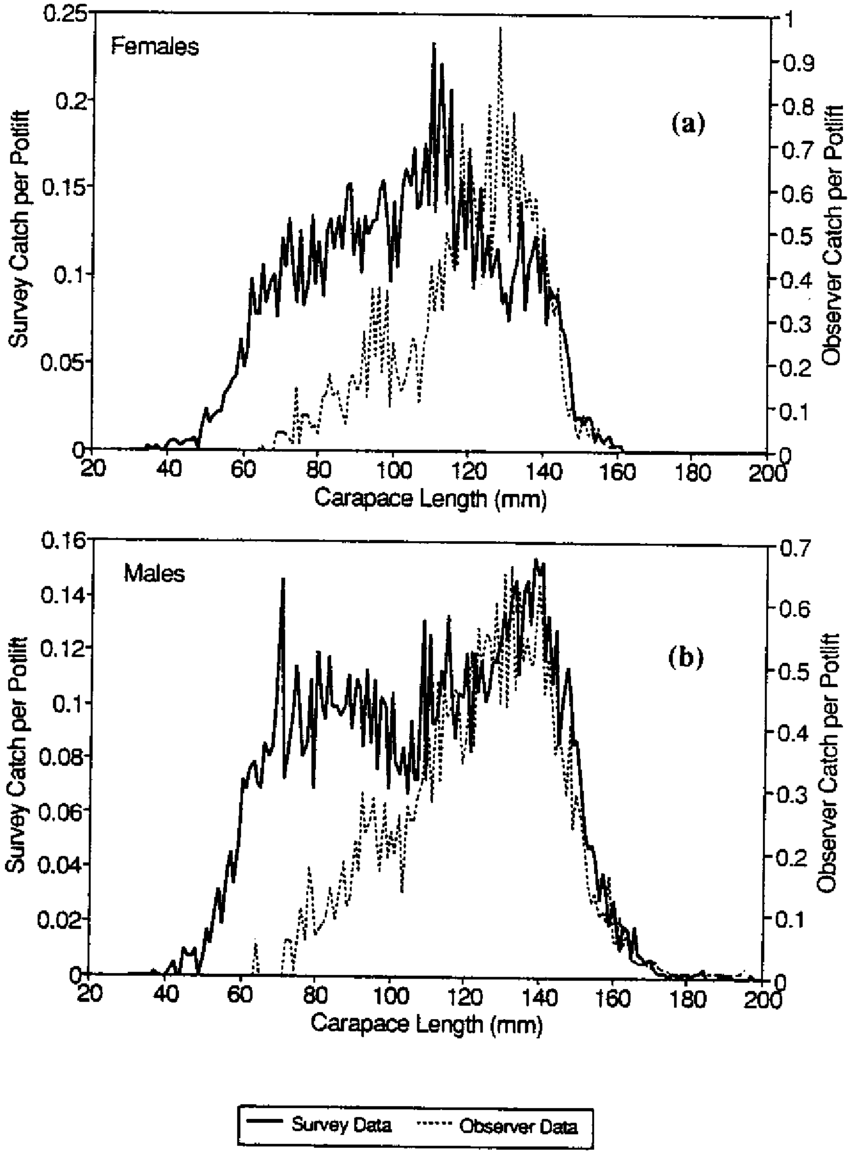

Figure 5. Comparison of female (a) and male (b) golden king crab length frequencies from the 1991 ADF&G golden king crab survey and from commercial vessels fishing golden king crabs in the survey area during the 1991 Dutch Harbor and 1991/92 Adak Management Areas fisheries.

Male categories by CPUE and depth zone

There was little similarity in the overall CPUE distribution by depth among the three male categories (Figure 6a and 6b). CPUE for prerecruits 2-5, prerecruit ones, and legals was greater for observed commercial catch data than survey data for every depth zone except those at which no commercial pots were sampled (> 620 m; Figure 6). CPUE for prerecruits 2-5 increased with depth on the survey, but was similar throughout most of the depths commercially fished. CPUE was low for legal crabs (< 4) on the survey, generally half as great as observer data in each depth zone sampled. CPUE for legal crabs was very low at < 1 at depths > 640 m on the survey (Figure 6a). Legals were captured from 148 to 725 m on the survey and from 128 to 549 m in observer sampled pots. CPUE for legal crabs from commercial sampled pots was greatest in depths < 183 m, although effort was greater in the adjacent deeper three depth categories (Figure 6b).

Female categories by CPUE and depth zone

CPUE increased with depth for juvenile females (< 1 in depths < 183 m but > 52 at depths > 822 m) (Figure 7a). Commercial fishery CPUE for juvenile females was lower than obtained during the survey with no juvenile females captured at depths > 547 m in the observer sampled pots (Figure 7b). Low CPUE for juvenile females occurred in shallower depths (< 274 m) during the survey and commercial fisheries. CPUE for adult females captured on the survey was greatest abundance (8.8 to 9.0 CPUE) in depths between 274 and 456 m, while adults captured during the commercial fishery had higher CPUEs (≥ 15) over a larger depth range (128 to 547 m). No adult females were captured at depths > 730 m on the survey or at depths > 639 m during the observed commercial fishery.

Rank correlation with legal males

There are similarities between the survey and observer data in the association of catch of legal males with catch of the sublegal male and female size classes. Rank correlations of catch of legals with other sex-size classes is highest for prerecruit ones in both the survey and commercial fishery data (Table 1). Although somewhat lower, the association of legal males with adult females is also similar in the survey and observer gathered data. Prerecruits 2-5 and juvenile females had the poorest association with legals in both the survey and commercial sampled data. Similarities between the survey and commercial fishery data in the association of catch of legals with catch of the sublegal male and female size classes are increased when survey stations > 730 m were excluded from the comparison (Table 1). Survey stations > 730 m were produced the highest catches of small males and juvenile females, but no commercial catch was sampled from those depths.

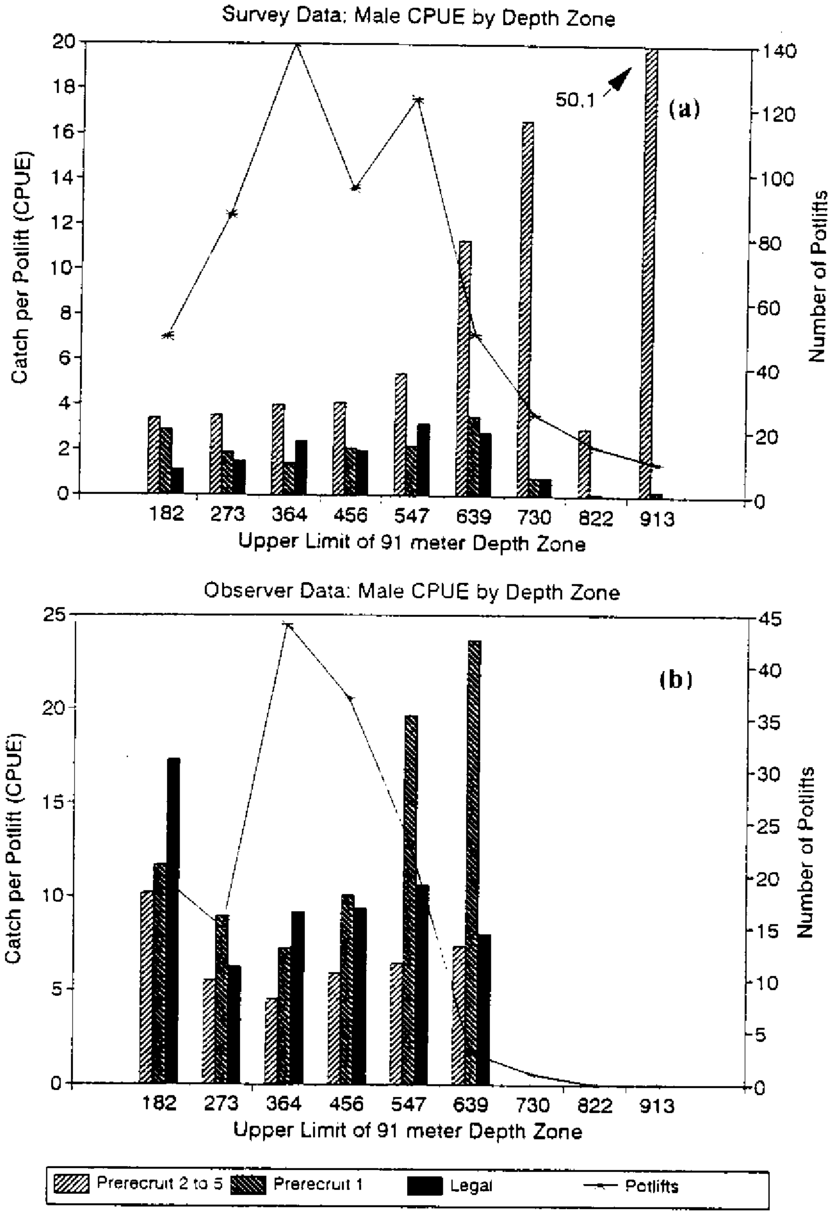

Figure 6. *Comparison of male golden king crab catch per unit of effort (CPUE) by depth zones and pot lifts from (a) the 1991 ADF&G golden king crab survey, and from (b) commercial vessels fishing golden king crabs in the survey area during the 1991 Dutch Harbor and 1991/92 Adak Management Areas fisheries.*

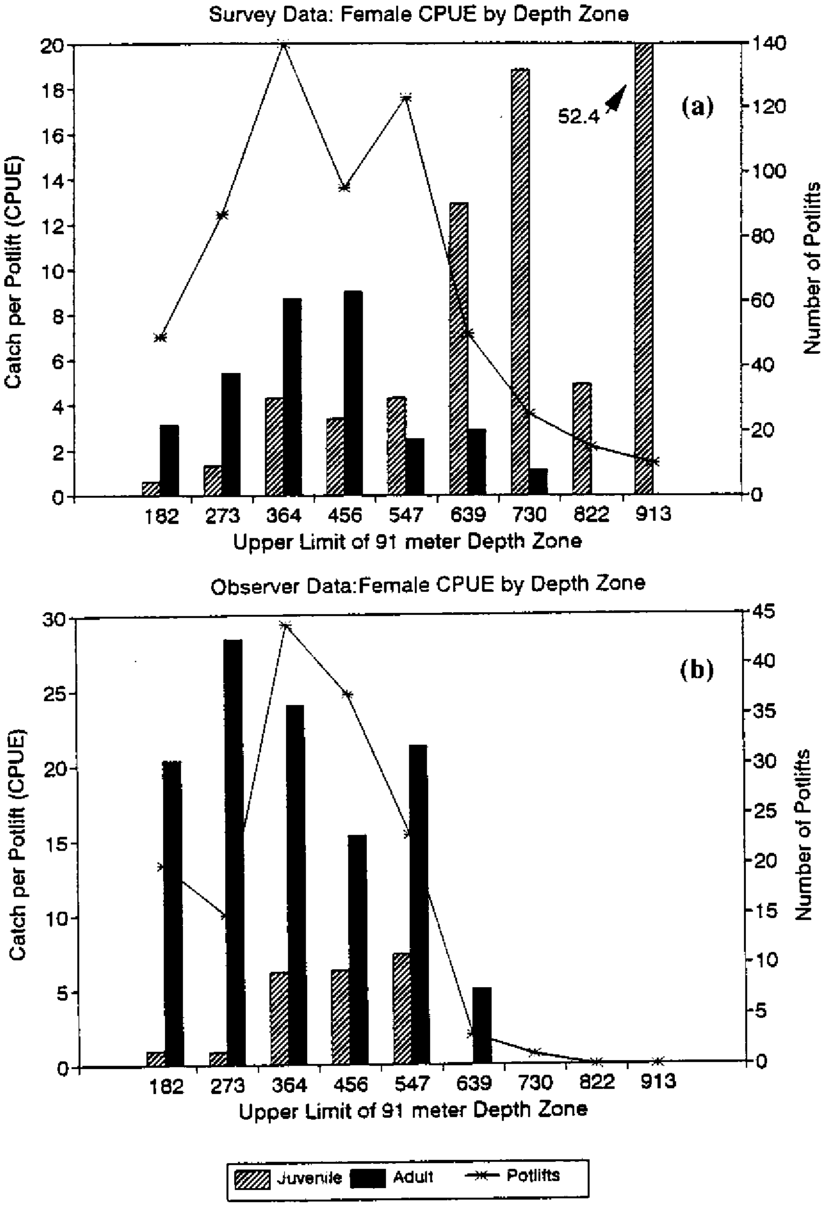

Figure 7. Comparison of female golden king crab catch per unit of effort (CPUE) by depth zones and pot lifts from (a) the 1991 ADF&G golden king crab survey, and from (b) commercial vessels fishing golden king crabs in the survey area during the 1991 Dutch Harbor and 1991/92 Adak Management Areas fisheries.

Table 1. Spearman rank correlations for catches of legal golden king crabs, and sublegal male and female size classes in 1991 survey and observer data.

	Male prerecruits		Females	
	Twos-Fives	Ones	Juveniles	Adults
Total survey	0.220*	0.70*	0.167	0.479*
Survey < 730 m	0.304*	0.676*	0.259*	0.429*
Commercial fishery data	0.349*	0.589*	0.297*	0.416*

"Total survey" correlations are for data from all 60 stations and "Survey < 730 m" correlations are for the 58 survey stations with mean depth < 730 m (* = rank correlation significant at $P < 0.05$).

Discussion

A stock assessment survey should be designed to provide an estimate or standardized index of species density over the range of the stock, as well as provide information on stock distribution (Hilborn and Walters 1992). Data from commercial fisheries can provide misleading information because fishing effort is usually concentrated in areas supporting high abundance of the targeted species. Several features of the Aleutian Islands golden king crab fisheries can cause problems in using these data for stock assessment. In Alaska only male crabs that exceed a minimum size are allowed to be harvested. Therefore commercial fishing effort targets areas where legal-sized males are abundant. In the Aleutian Islands golden king crab fisheries, fishermen often attempt to minimize capture of nonlegal crabs by using escape rings to reduce bycatch with the long soak times typically employed. In addition, because golden king crabs occur in deep water, fishing effort may be concentrated at depths that support densities that can be efficiently fished, rather than at depths that support the highest densities of legal-sized crabs. Problems with using data collected from commercial fisheries for biological and stock assessment purposes must be weighed against costs of performing standardized stock assessment surveys. Conducting surveys that would provide information throughout the vast distribution of Aleutian Islands golden king crabs is not feasible with existing management agency resources.

Although golden king crabs were nearly ubiquitous over the survey area, occurring at 90% of the survey stations, locations of commercial fishing pots sampled by observers were concentrated only south and north of Chagulak, Amutka, and Yunaska Islands (Figure 3). Observer data were rarely collected from pots fished > 547 m and no pots were fished > 673 m, the depth at which the greatest CPUE of crabs were obtained during the survey.

Differences between survey and observer data reflect dissimilarity in fishing goals, effort distribution, soak times, and fishing gear (i.e., presence or absence of escape mechanisms). CPUE in observer-sampled pots was 2.5 times greater than that from survey pots. Prerecruits 2-5 were the most common size class of males captured in the survey and dominated the survey catch of males at depths > 547 m. That size class was the most poorly represented male size class in all depth zones for observer-sampled pots. Similarly, juvenile females were less abundant in observer samples than in survey data. This was the only sex-size class for which CPUE was greater in the survey than in the commercial fishery.

Because of escape mechanisms used in commercial pots, long soak times, and limited range of depths at which pots are fished, the commercial fishery data does not provide information of the same detail or quality as does survey data. Survey data allowed us to examine the depth distribution of golden king crabs during August and September. The general pattern of increasing CPUE with increasing depth shown in survey data was principally due to increasing CPUE for prerecruits 2-5 males and juvenile females. That trend is of particular interest because it contrasts sharply with findings on golden king crabs in Portland Inlet, British Columbia. Portland Inlet data show the greatest concentrations of juvenile females were in relatively shallow waters (< 150 m in depth) (Sloan 1985). Also, in contrast to the results from the 1991 golden king crab survey in the Aleutian Islands, where greatest densities of adult females occur at moderate depths (274-364 m), the greatest concentrations of adult females in Portland Inlet were found at much shallower depths (151-250 m).

Despite differences between survey and observer data, results from both sources did reveal important areas of agreement. Both data sets show similar CPUE trends for legal and prerecruit ones in relation to depth. Legal males occur over a wide range of depths (spanning 644 m vertically) and coexist with all sex-size classes of golden king crabs. CPUE for legal males varied little among the four depth zones between 274 m and 639 m. Where commercial effort was poorly represented in the observer data, at depths > 639 m, survey data showed a sharp decrease in legal male CPUE. It is only for the shallowest depth zone that survey and observer data show different trends for legal male CPUE. CPUE for this size-sex category was greatest at depths < 182 m in the commercial fishery observed, but relatively low at similar depths in the survey. Both data sets also showed that increasing CPUE for prerecruit ones over the four depth zones between 274 m and 639 m.

Effort by depth zone seen for commercial vessels was consistent with expectation based on the survey depth distribution by sex-size class. From a commercial fisher's perspective it would be wise to fish pots as shallow as possible while maintaining an acceptable CPUE of legal crabs. In addition to using gear with escape mechanisms, commercial fishers would also be expected to decrease time spent to sorting out small females and sublegal males by concentrating effort where densities of nonlegal sex-size classes are lowest. The survey showed: (1) greatest CPUE for legal males between 274 m and 639 m, (2) low CPUE for legals captured > 639 m, (3) and an increase in CPUE of sublegal males and juvenile females at depths greater than 364 m.

Composition of males > 120 mm CL from both data sets were similar. Legal crabs in both data sets were dominated by the recruit class. Although the ratio of prerecuit ones to legal crabs in the survey were higher than that observed in the fishery, prerecruit ones were still well represented in the observer data. Relative size frequencies for males > 120 mm CL from the two data sets were very similar. The association of prerecruit ones with legals in both data sets indicates that reasonable information on relative abundance of prerecruit ones can be gained from sampled commercial pots targeting on legals.

Amendment 1 to the Bering Sea/Aleutian Islands King and Tanner Crab Fishery Management Plan (FMP) of the North Pacific Fishery Management Council (McKean 1991, NPFMC 1989) defines overfishing of golden king crabs in the Aleutian Islands as an annual fishing mortality rate on mature male crabs in excess of 0.3. ADF&G does not conduct regular stock assessment surveys in the Aleutians for golden king crabs; therefore we cannot estimate fishing mortality or set preseason harvest guideline levels based on estimates of stock abundance. The present study does suggest, however that observer data from the commercial fishery can serve as a proxy for survey data in determining trends in relative abundance of prerecruit ones, recruits, and postrecruits. This information can show trends in the relative abundance of legal-sized crabs and the prospects for future recruitment into the fishery. Observer data may also provide the means for setting preseason guideline harvest levels and avoiding overfishing (as defined in the FMP), if it can be incorporated into catch-length models (e.g., Zheng et al. 1996).

In this paper we have only considered data on composition and depth distribution of golden king crabs collected from a single survey and ensuing commercial fishing seasons in a portion of their habitat. There is much more fishery data available that has not yet been analyzed. Observers have sampled over 5,000 commercial pot lifts and recorded biological data from nearly 350,000 golden king crabs captured in the Adak and Dutch Harbor fisheries since 1988. Despite problems using commercial catch data (e.g. unstandardized gear, variable and long soak times, uncontrolled distribution of effort) observer data from the Aleutian Islands golden king crab fisheries can provide information that is not economically feasible for ADF&G to obtain through surveys. Observer data has been collected from locations spanning approximately 1,500 km across the Aleutians Islands and can provide a broad base of information on the distribution of golden king crabs. Although observer data cannot be relied on to identify the geographic boundaries of a stock or areas where densities of the target species are low, data from the commercial fishery can be used to identify geographic areas where densities of legal crabs are high. Data from the two golden king crab fisheries in the Aleutian Islands are collected nearly year-round by observers and contain valuable information regarding the crabs' biology, including temporal changes in their distribution and female reproductive condition.

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Ecology of the Snow Crab *(Chionoecetes opilio)* from an Isolated, Unfished Bank in the Sea of Japan

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Abstract

Snow crabs *(Chionoecetes opilio)* are found in the shallow waters of the Yamato Bank (shallowest depth: 246 m) in the central area of the Sea of Japan; however, the Japanese Government prohibits their commercial catch. We have randomly collected snow crabs using longline traps at depths of 296 to 380 m during 1982 to 1995. Subsequently, we have recognized several different features of the ecology of this crab and compared them with data from Wakasa Bay, a heavily fished area in the southwestern waters of the Sea of Japan.

We estimate that the optimal depth of the breeding area (296 to 318 m) where adult female crabs are densely distributed is approximately 50 m deeper than that in the southwestern waters. The extent of the patchy aggregations formed by adult female crabs on the breeding area is larger than that in the southwestern waters. The diameter of the largest patchy aggregation observed in the Yamato Bank is over 2.6 km. The mean carapace width of adult female crabs (61.8 to 69.7 mm) is smaller than the crabs (78.8 to 82.0) in the southwestern waters, with the carapace width on the Yamato Bank becoming larger year by year. In 1995 3.1% of adult female crabs and 4.2% of male crabs were infected with the black mat syndrome (BMS), and 1.2% of adult female crabs and 0.9% of male crabs had black scars on the surface of the exoskeleton, respectively. Specimens infected with BMS or having black scars are, however, very rare in the southwestern waters.

Introduction

Snow crab *(Chionoecetes opilio)* are found abundantly in the shallow waters of the Yamato Bank in the central area of the Sea of Japan. The Japanese government, however, prohibits the commercial catch of them, because they are thought to be a source of recruitment to the stock near the Japanese archipelago. Fukui Prefectural Fisheries Experimental Station have been collecting crabs, mainly adult females, and releasing them for restocking the resources in the waters off Fukui Prefecture.

The Yamato Bank is over 100 nautical miles both from the Asian continent and from the Japanese archipelago. Furthermore, the depth of the sea between the Yamato Bank and the continent or the archipelago is more than 1,000 m. Therefore, it may be thought there are few direct interchanges between the resources of the Yamato Bank and the resources nearer the continent or the archipelago. Research on the resources of the Yamato Bank is sparse (Kobayashi and Yamaguchi 1978, Japan Marine Fishery Research Center 1989). We have compared the ecological data of this isolated, virgin resource on the Yamato Bank with data from the heavily exploited southwestern waters of the Sea of Japan, which has been utilized for a long time.

Materials and Methods

At its shallowest depth the Yamato Bank is 246 m, and the area shallower than 500 m in depth extends over about 50 km^2 (Japan Marine Fishery Research Center 1989) (Figure 1). Snow crabs are found here in high densities. We have operated 1-3 times every year using longline traps at a depth of 298 to 380 m between May and July during 1982 to 1995. We investigated the number of crabs collected in each trap, carapace widths, and the presence or absence of the black mat syndrome (BMS) and scars on the exoskeleton. The data and the results of each operation is shown in Table 1.

The shape of the trap used is a truncated cone (lower diameter 1.5 m and upper diameter 0.8 m, high 0.7 m) and has an entrance 0.3 m in diameter on the upper surface. Fourteen (minimum) to 100 (maximum) traps were tied to a longline at intervals of 50 m and the longline was laid in a straight line across the seabed. The maximum mesh size of the trap was 6.6 cm and mean mesh size of the bottom was 5.0 by 4.4 cm.

Carapace width of adult female crabs collected on the Yamato Bank were compared with those collected off Wakasa Bay, southwestern waters of the Sea of Japan. The comparative samples off Wakasa Bay were collected during 1986 to 1992 with the same longline traps.

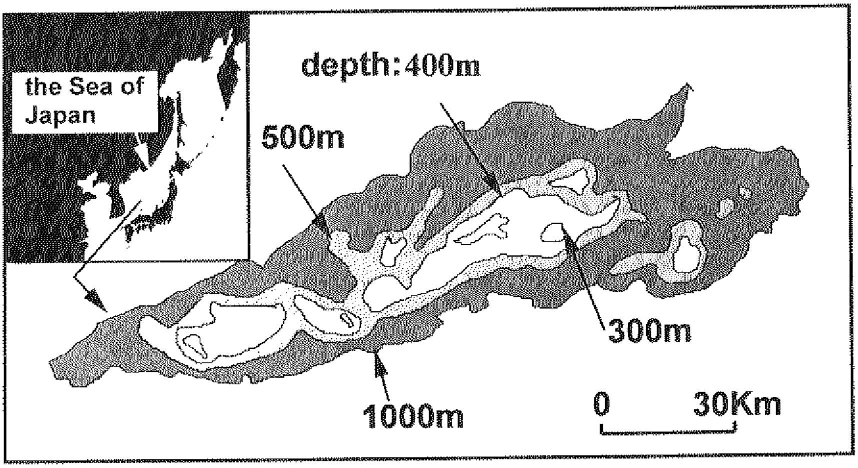

Figure 1. Location and depth profile of the Yamato Bank in the Sea of Japan.

Results

Density distribution

The mean number of adult female crabs collected per trap showed large fluctuations within the range of 0.2 to 233.0 crabs (Table 1). The relation between the numbers of females caught and the depth of each operation is consistently more than 27.6 crabs per trap when collected in waters shallower than 318 m; the numbers collected at depths of 321-334 m fluctuated between 0.2-77.0 crabs; and deeper than 338 m constantly fewer than 5.5 crabs were taken. Male crabs collected per trap in each operation showed a smaller fluctuation within 2.0-29.7 crabs, and there is no relation between the number caught and the depth of each operation. Although the carapace width of 10th instar female (juvenile, prior instar to adult) is larger than the mesh size of the trap and therefore will be retained in the trap, their numbers collected are extremely few in all operations.

Aggregation

In all operations the number of male crabs collected in each trap were less than 40 crabs and were relatively constant, so the relation between the number caught and the trap number on the longline is not recog-

Table 1. Mean depth and duration of immersion of longline traps and mean catch per trap of adult female, juvenile female and male *Chionoecetes opilio*.

Year	Duration traps laid	Mean depth (m)	Number of traps	Mean number of crabs per trap: Adult female	Juvenile female	Male
1982	5/19-5/22	350	100	5.5	–	25.3
	5/22-5/27	323	95	77.0	–	29.7
	6/24-6/28	315	93	100.2	–	27.1
1986	6/24-6/25	318	50	65.4	–	14.0
	6/24-6/26	338	50	2.4	–	14.7
	6/25-7/02	311	31	233.0	–	13.5
	6/26-7/02	324	14	0.2	–	9.3
	7/02-7/03	374	50	0.4	–	2.8
	7/09-7/10	314	60	75.3	–	10.2
1987	6/23	318	22	40.0	–	3.7
	7/01-7/02	343	50	2.3	–	6.2
	7/02	318	50	79.2	–	7.6
	7/07-7/08	325	50	40.3	–	16.8
1988	6/21-6/22	330	50	2.8	2.6	4.7
	6/22-6/23	309	49	28.1	0.1	8.7
	6/28-6/29	321	53	4.4	0.6	4.4
1989	6/20-6/21	311	49	27.6	0.4	5.7
	6/27-6/28	313	50	37.2	0.2	9.0
1991	6/25-6/26	298	60	46.6	0	14.6
	7/02-7/03	322	59	66.7	0.1	6.0
1992	6/16-6/17	305	54	107.0	0	14.7
	7/07-7/08	315	60	44.2	0	12.6
1993	7/13-7/20	306	51	111.8	0	12.3
1994	6/23-6/24	313	49	38.5	1.0	6.2
	6/24-6/28	318	49	104.6	0.5	2.0
1995	7/05-7/06	319	64	19.3	0.5	6.6
	7/06-7/07	334	64	42.5	0.3	15.8
	7/07-7/11	330	64	57.0	0.5	16.3

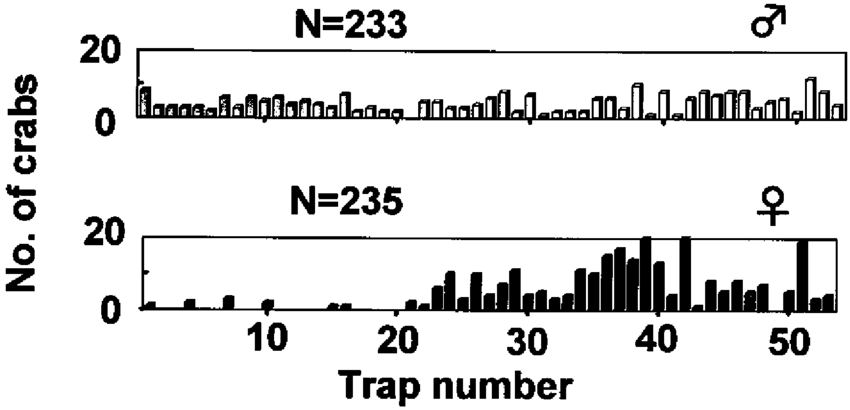

Figure 2. Number of snow crabs caught per trap (consecutively numbered from start to finish of the longline) at a mean depth of 321 m on June 29, 1988, on the Yamato Bank, Sea of Japan.

nized (Figures 2, 3, 4, 5). However, in the case of adult female crabs there are three patterns between the numbers collected in each trap and the location of the trap along the longline, namely, the first is very few crabs in any traps (June 29, 1988) (Figure 2), the second is very few in the start or the end of the longline but many crabs at either the end or start of longline (June 26, 1991; July 8, 1992) (Figures 3, 4), and the last is many crabs in all traps (June 17, 1992) (Figure 5). The first pattern is recognized only in the area deeper than 321 m. On June 17, 1992, at a mean depth of 305 m each of 54 traps laid straight over a distance of 2.65 km collected high numbers between 67 and 269 individuals. So it may be concluded that adult female crabs make aggregations, some of which are in the range of, or larger than, 2.65 km in the breeding area of the Yamato Bank.

Carapace width of adult female crabs

The annual mean carapace widths of adult female crabs collected on the Yamato Bank ranged from 63.9 to 71.0 mm (Figure 6). As the annual mean carapace widths off Wakasa Bay in 1986 to 1992 range from 78.8 to 82.3 mm, adult female crabs on the Bank are smaller than that off Wakasa Bay. The carapace width on the Bank, however, has become larger from year to year in almost the same rate of increase as off Wakasa

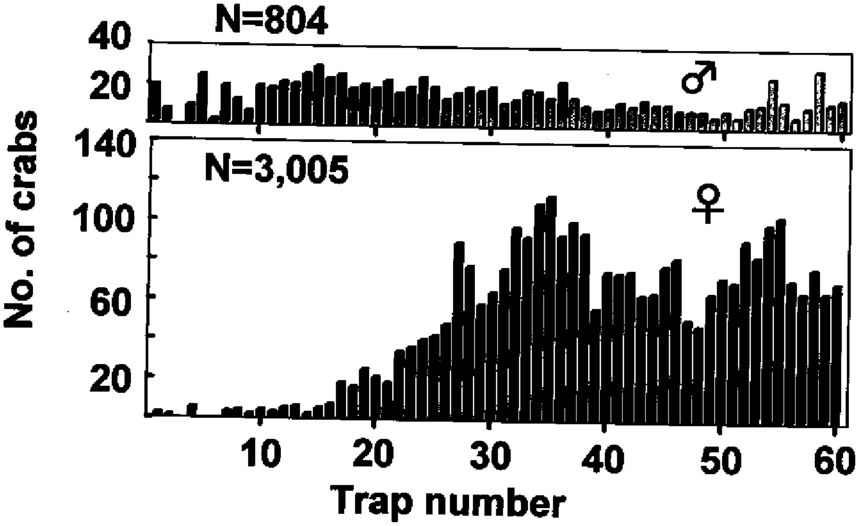

Figure 3. Number of snow crab caught per trap (consecutively numbered from start to finish of the longline) at a mean depth of 305 m on June 17, 1992, on the Yamato Bank, Sea of Japan.

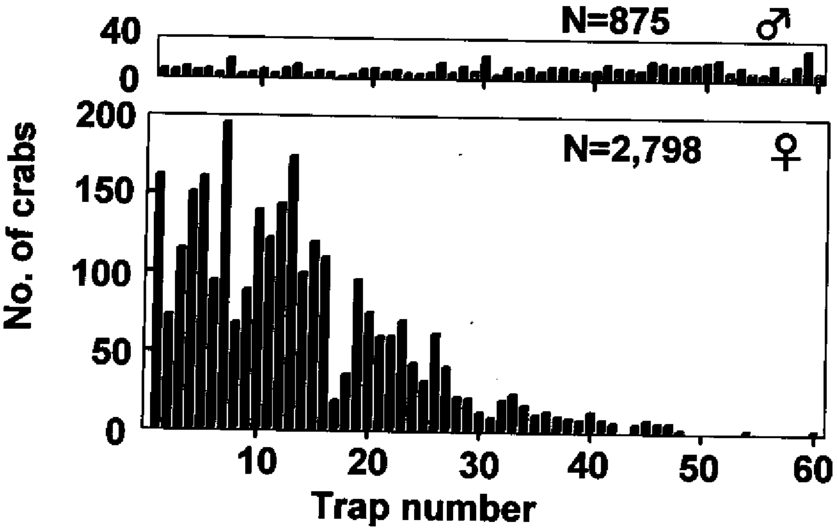

Figure 4. Number of snow crabs caught per trap (consecutively numbered from start to finish of the longline) at a mean depth of 315 m on July 8, 1992, on the Yamato Bank, Sea of Japan.

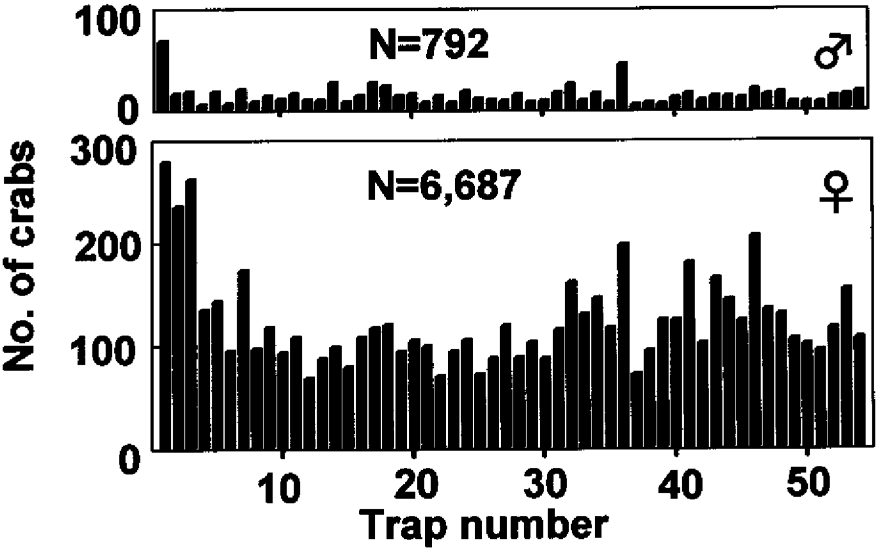

Figure 5. Number of snow crab caught per trap (consecutively numbered from start to finish of the longline) at a mean depth of 305 m on June 17, 1992, on the Yamato Bank, Sea of Japan.

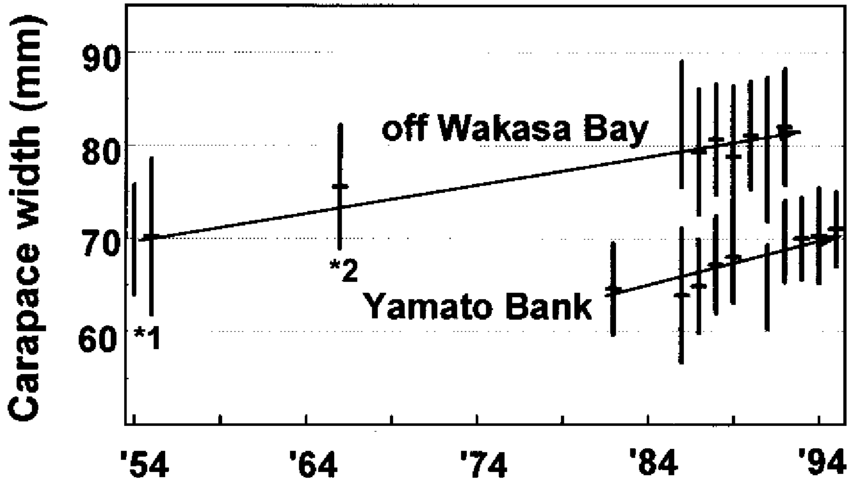

*Figure 6. Annual changes of the mean carapace widths (± standard deviation) of adult female snow crab collected on the Yamato Bank and off Wakasa Bay in the southwestern waters of the Sea of Japan. *1. Data of Minamizawa (1955), *2. Data of Kon et al. (1968)*

Table 2. Rate of snow crabs having black spots (BMS or scars) on the surface of the exoskeleton collected on the Yamato Bank, Sea of Japan.

Year	Operation	Number of catch		Percentage	
		Adult female	Male	Adult female	Male
1991	1	2,798	875	21.0	11.2
	2	4,355	430	9.7	10.5
1992	1	6,687	792	27.2	32.6
	2	3,005	804	10.7	14.7
1993	1	5,701	625	18.9	20.0
1994	1	1,887	306	3.0	6.5
	2	5,127	311	41.6	19.3
1995	1	1,237	1,656	1.9	3.1
	2	2,721	1,013	4.1	5.3
	3	3,518	1,046	8.3	10.0
Total	10	37,036	7,858	(14.6)	(13.3)

( ): Mean.

Bay (Figure 6). The following formulas are calculated for between the year (X) and the carapace width (Y: mm) for both Yamato Bank and off Wakasa Bay (including the data of carapace widths in 1954 and 1955 [Minamizawa 1955] and in 1966 [Kon et al. 1968]) (Figure 6).

Yamato Bank: $Y = 0.562\ X - 1{,}050.607$
(correlation coefficient: 0.836, $1982 \le X \le 1995$)

Wakasa Bay: $Y = 0.278\ X - 472.889$
(correlation coefficient: 0.941, $1954 \le X \le 1992$)

BMS and scars

It is reported that many crabs collected on the Yamato Bank have black material on the surface of the exoskeleton (Kobayashi and Yamaguchi 1978). In 1986 the black materials were clarified (Hatai et al. 1986) as BMS encrusting fungus, *Trichomaris invadens*, which was first reported by Hibbits et al. in 1981. Furthermore, we have found since our first collection in 1982 that some crabs have many black scars on the surface of the exoskeleton (Figure 7). It is presumed that some of the scars on the females' legs are caused by the mating embrace of the male, and some of the scars on the abdomen are by scraping along the rocky sea bed.

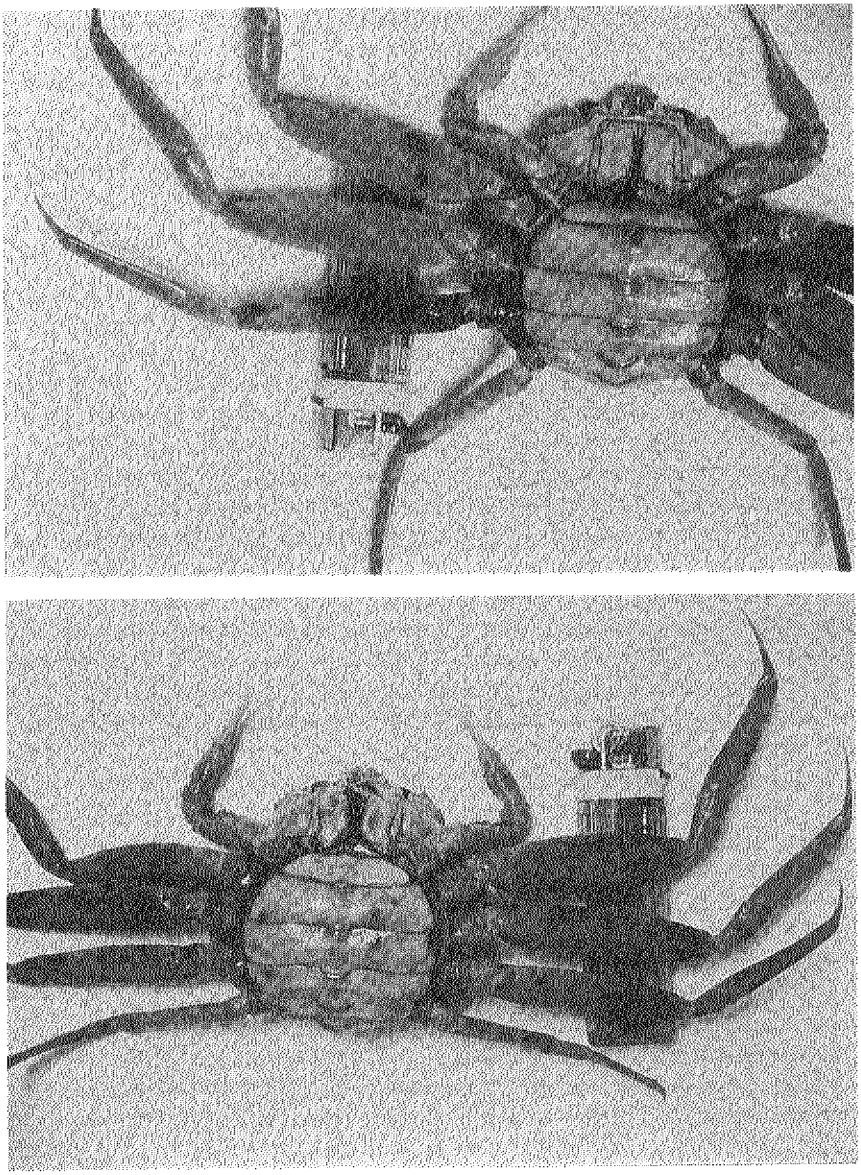

Figure 7. Adult female crabs with many black scars on the legs, collected on the Yamato Bank, Sea of Japan.

Many of these scars are not merely scars but have festered and sometimes lack a part of the exoskeleton. The rate of crabs having black spots (BMS or scars) on each operation shows a large fluctuation which ranges from 1.9 to 41.6% in adult females and from 3.1 to 32.6% in males (Table 2). In 1995, 3.1% of adult females and 4.2% of male crabs were infected with BMS, and 1.2% of adult females and 0.9% of male crabs had black scars.

Discussion

It is well known that the depth distribution of snow crab is limited by temperature. In the southwestern waters of the Sea of Japan, they are found at depths ranging from 200 to 450 m, and especially adult female crabs are distributing at a 240-260 m depth stratum (Ito 1968) which is called the breeding area. On the Yamato Bank, adult female crabs are constantly caught more than 27.6 crabs per trap at 296-318 m depth. So it is presumed that the breeding area on the Bank occurs in this depth stratum, and this depth stratum is approximately 50 m deeper than that in the southwestern waters.

In the southwestern waters of the Sea of Japan, it is also reported that adult female crabs occur as a large aggregation over 1,500 m in diameter (depth: 242-244 m) (Yamasaki and Kuwahara 1991). As a general pattern of distribution, adult female crabs make aggregations in a breeding area, but size in distance of the aggregations may differ with the density of the female crabs.

For the southwestern waters of the Sea of Japan, the molt stage of adult female crab has been estimated to be the 11th instar (Kon et al. 1968), or most adult female crabs are the 11th instar but some are the 10th and the 12th instar (Ito 1970). In the southeastern Gulf of St. Lawrence, it is reported that the molt stage of adult female is the 10th instar (Robichaud et al. 1989), and the mean carapace width is 68.7 mm which is similar to that of the 10th instar (66.2 mm) of the southwestern waters of the Sea of Japan (Kon et al. 1968). It is presumed that the mean carapace width of adult female crabs distributed in waters which have not been exploited or recently have begun to be exploited are smaller than those in waters which have been exploited for many years and the resource has decreased markedly. The density distribution of adult female crabs may affect the size and/or molt stage.

We believe that for the two areas, an intense, long-term crab fishery is responsible for the differences in snow crab ecology, such as the extent of patchy aggregation formed by adult female crabs, mean carapace width of adult female crabs, and the percent of crabs infected with BMS or having black scars.

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High Latitude Crabs: Biology, Management, and Economics
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Larval Distribution of *Chionoecetes* (Majidae, Brachyura) in the Sado Strait, Sea of Japan

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Abstract

Dispersal and settlement of *Chionoecetes* crabs were investigated in the Sea of Japan. Larvae of *C. opilio* and *C. japonicus* were collected monthly in the Sado Strait from March to May 1993, and juveniles in September. Among four stages of samples in this study, we successfully identified zoea 1 and juveniles of both species.

Only zoeal were collected in March and they occurred only around the Sado Basin. In April, zoea 1 and zoea 2 were distributed widely throughout the study area at a high density, except the stations into which fresh and cold water flowed. It is suggested that larvae were carried and dispersed to coastal areas too shallow for adult crabs to inhabit, mainly because of the Tsushima Warm Current flowing along the coast of Honshu. These two species occurred together at the stage of zoea 1, and *C. japonicus* was the dominant of the two; zoea 2 in May and megalopa both in April and May did not occur inshore in water shallower than 100 m along Honshu, other than Sado Island.

Though both species occurred together at the stage of zoea 1, the juvenile crabs were nevertheless found on the bottom at different depths, which were almost the same bathymetric distribution as adult crabs. From this, it is inferred that juveniles might choose the bottom of the depth appropriate for each species when they settle.

Introduction

Three species of *Chionoecetes*, *C. opilio*, *C. japonicus*, and *C. bairdi*, inhabit the waters around Japan. *C. opilio* and *C. japonicus* are mainly found in the Sea of Japan and their bathymetric distributions are known to be different (e.g. Yosho and Hayashi 1993). *C. opilio* lives at depths of about 200-500 m, and is mainly fished by Danish seine in waters shallower than 350 m (e.g. Sinoda 1982, Yosho and Hayashi 1993). It mainly occurred in the western area, where the continental shelf is well developed, unlike the northern area in the Sea of Japan. But the annual catch in the western area has recently decreased drastically to less than that of the northern area. Some projects have been started to catch live *C. opilio* from Yamato Bank or the Maritime Provinces, and release them in the coastal water along Honshu, aiming at fisheries enhancement. It becomes more important to clarify larval transport and the process of dispersal because genetic exchange between these areas has not been determined.

The other species, *C. japonicus*, has been found in waters between 400 and 2,700 m deep, and fished by baited traps at the bottom deeper than 800 m (e.g. Sinoda 1980, Yosho and Hayashi 1993). *C. japonicus* has been regarded, without any well-grounded arguments, as one population whenever its management was discussed. So far, there have been some studies using mark and recapture methods to estimate their movement after settlement (unpublished). All those results suggested that adult crabs move within 50 km, which is a very short distance considering the size of their range.

The dispersal of *C. opilio* and *C. japonicus* in pelagic stages, during which they are expected to disperse most widely, has hardly been studied. Few studies on larval distribution and vertical migration of *Chionoecetes* have been done, with distinction of both species (Fukataki 1969, Ito and Ikehara 1971, Kon 1982). Moreover, although there are some studies on distribution pattern and vertical migration, very little is known about horizontal transport and dispersal and not at all about the distance they travel during the period from hatching to settlement. In this study, we sampled larvae and juveniles of *Chionoecetes* around the Sado Strait in the Sea of Japan, to get information on their dispersal and settlement.

Materials and Methods

Sampling area

The Sado Strait is located between Sado Island and the Honshu coast in the Sea of Japan (Figure 1). Sado Basin, the deepest part of the strait, is 530 m at the center. In the west part of the basin, the deep-sea bottom (deeper than 1,000 m) comes close to the shore, penetrating into Toyama Bay. In the west, there is a shallow area where the continental shelf

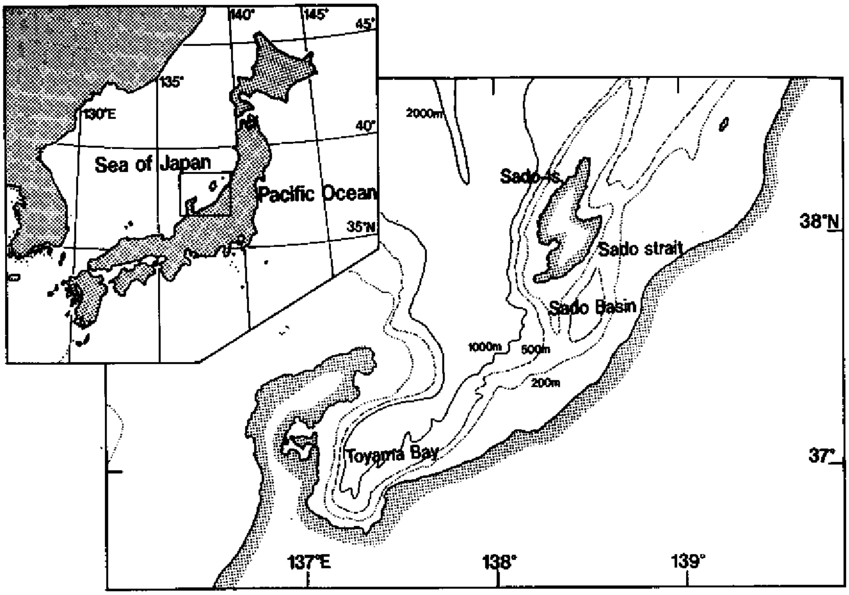

Figure 1. Maps of the Sado Strait area.

is well developed. *C. opilio* and *C. japonicus* live mainly in the center of the Sado Basin and in the western area because in the demersal stage they are known to live in the depth of 200-500 m and 400-2,700 m, respectively (e.g. Sinoda 1982, Yosho and Hayashi 1993). The water around the study area flows from the southwest to northeast under the strong influence of the Tsushima Warm Current.

Sampling of larvae

Planktonic *Chionoecetes* larvae were collected monthly by oblique tows from 100 m deep to the surface with a Bongo net, at 52 stations in and around the Sado Strait in the Sea of Japan, during a cruise of the R/V *Mizuho-Maru* of the Japan Sea National Fisheries Research Institute, from March to May 1993 (Figure 2). Water temperature and salinity were measured by CTD at all the stations.

Sampled larvae were fixed in 5% neutralized formalin seawater, and then taken into the laboratory and *Chionoecetes* larvae were sorted out. Only for zoea 1 was it possible to separate *C. opilio* from *C. japonicus*, by the number of spinules on the long posterolateral spines of the third abdominal somite (Konishi and Yosho in prep.). Both zoea 2 and megalopa were treated as *Chionoecetes* larvae. The number of larvae per 1,000 m^3 seawater at each station was estimated by the amount of water passing through the sampling net, which was measured with a flow meter.

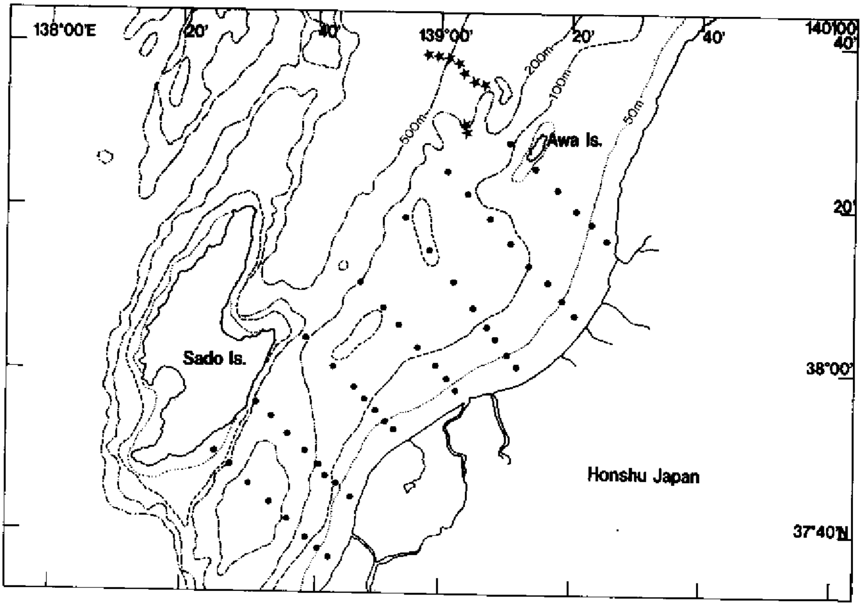

Figure 2. Map of the study area; closed circles are the stations where larvae were collected, and closed stars are the stations where juvenile crabs were sampled.

Sampling of juveniles

Juveniles of *Chionoecetes* were collected from nine stations on the bottom at the depth of between 200 and 700 m in the northwest off Awa Island by the T/V *Tanshu-Maru*, the Kasumi High School, Hyogo Prefecture (Figure 2). The sledge net with a 2.3 m span, which is the same type of gear as used by Ito (1984), was used for sampling. The collected crabs were fixed in 10% neutralized formalin seawater. In the laboratory, they were identified to species and their carapace width (CW) was measured by a caliper to the nearest 0.1 mm. For convenience, we refer to small crabs less than 10 mm in CW as juveniles, which corresponds to the fourth instar of both crabs as reported by Ito (1970), Kon (1980), and Watanabe and Suzuuchi (1982). These juveniles were difficult to distinguish between male and female. The density was calculated from the width of the sledge net and the distance it traveled in order to compare crab abundance among sampling stations. Because the hauls were, as a rule, operated for 10 minutes, during which they traveled the distance ranging from 370 to 722 m with a mean of about 574 m, the density was expressed by the number of individuals per 1,300 m^2 for convenience.

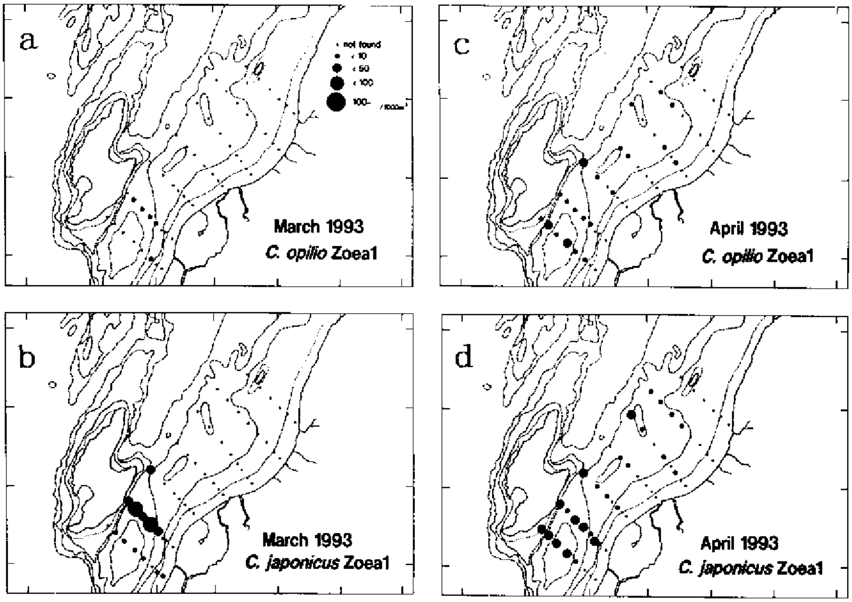

Figure 3. The distribution of zoea 1 of C. opilio and C. japonicus in March and April.

Results

Physical environment

The vertical profile of both temperature and salinity showed almost the same pattern in March and April. The temperature was 10-11°C and hardly changed vertically and horizontally in the study area, except 8-9°C at the coastal stations on the most eastern transect, into which cold water seemed to flow. However, such cold, fresh water affected the physical environment of the water above 20 m deep at most. In May, it was 12-13°C at the surface and 10-11°C at a depth of 100 m. The effects of fresh water in this period was much less than in April.

Occurrence of Larvae

Zoea 1 and zoea 2

In March, only zoea 1 occurred in the study area. Zoeae of both *C. opilio* and *C. japonicus* were found at the stations around the Sado Basin, which was the upstream region of the Tsushima Warm Current and deep enough for adult crabs to live at the bottom (Figure 3a, b). However,

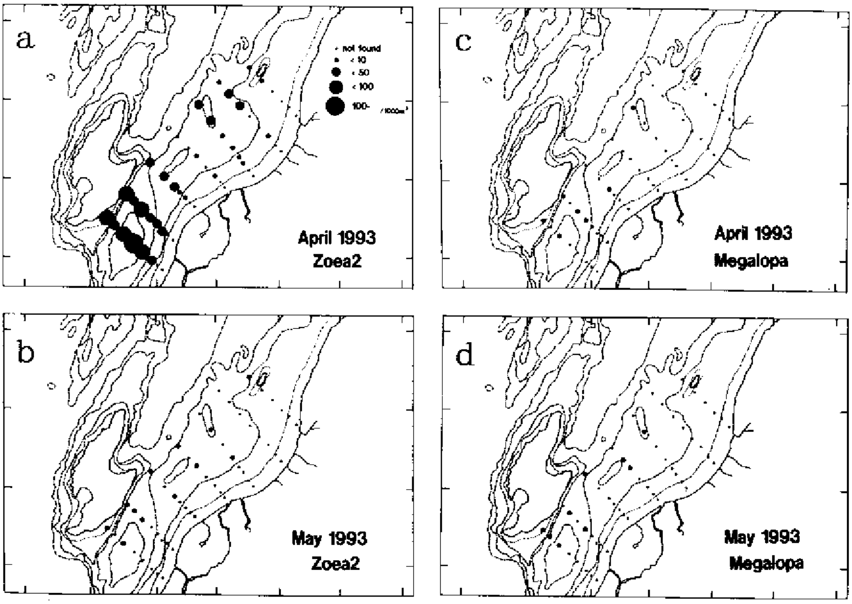

Figure 4. The distribution of zoea 2 and megalopa of Chionoecetes in April and May.

none was collected from the stations on any of the farther eastern transect. Among the total of 206 zoea 1 collected, 137 and 10 samples were identified into *C. japonicus* and *C. opilio*, respectively. The highest density of 59.1 ind./1,000 m^3 was recorded for *C. japonicus*, which was collected at more stations than *C. opilio*.

In April, in addition to zoea 1, many zoea 2 larvae appeared. Two hundred and forty-three zoea 1 were collected; many concentrated near the Sado Basin, and some occurred in the shallow and coastal area, where adult crabs hardly live (Figure 3c, d). *C. japonicus* zoea 1 was also dominant in this month; the mean densities for all the station were 6.0 and 2.4 for *C. japonicus* and *C. opilio* respectively. For zoea 2, 422 larvae were collected from the study area. They were abundant at the stations near the Sado Basin and not a few in the eastern part of the study area as found for zoea 1 in this month (Figure 4a).

In May, no zoea 1 were collected. Few zoea 2 were sampled and the mean density of all the stations was 0.7, which was only 4.3% of that in April. They did not occur inshore along the Honshu coast other than at Sado Island (Figure 4b).

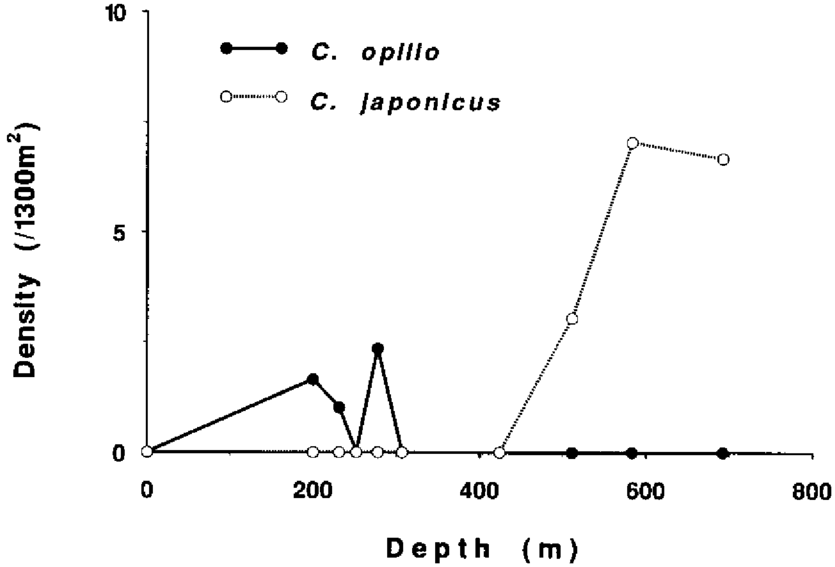

Figure 5. The bathymetric distribution of juveniles of C. opilio and C. japonicus.

Megalopa

Megalopae were collected in April and May (Figure 4c, d); mean densities were much lower than that of zoea 2 in April but almost the same as in May. The highest density was recorded at 7.9 and 3.9/1,000 m^3 in April and May respectively. Megalopae occurred only offshore in these months, like zoea 2 in May. The distributional pattern of megalopae did not change between April and May.

Occurrence of juveniles

The bathymetric distribution of juveniles is shown in Figure 5. Because we did not conduct any samplings on the bottom shallower than 200 m and deeper than 700 m, it was not possible to determine the entire bathymetric range of juveniles of *C. opilio* and *C. japonicus*. However, bathymetric separation between the species was obvious; *C. opilio* were collected from the bottom shallower than 300 m with the highest density of 2.4 ind./1,300 m^2 at 278 m, while *C. japonicus* were from deeper than 500 m, and the density recorded 7.0 ind./1,300 m^2 at the depth of 583 m, which was higher than that of *C. opilio*.

Discussion

Both *C. opilio* and *C. japonicus* at a zoea 1 stage occurred in the wider area than those in the demersal stage. In particular, many zoea 1 of *C. japonicus*, which is one of the deepest species, were found in very shallow coastal waters, where the adult crabs do not live. More larvae of *C. japonicus* were found than those of *C. opilio* in all the samples collected. However, many previous studies on the distribution of *Chionoecetes* larvae have been made without identification of the two species (e.g. Fukataki 1967, Ito and Ikehara 1971). These suggest that the two species, which show the apparent difference in their bathymetric distribution at a demersal stage, should be treated separately in studying larval distribution.

Zoea 1 of both *C. opilio* and *C. japonicus* co-occurred in March and April. This may mean that they come near the surface a short time after hatching because the presence of zoea 1 coincided with their hatching period from February to April in the Sea of Japan (e.g. Ito 1976, Kon 1980, Kobayashi 1989). Generally, crabs at zoea 1 are known to show negative geotaxis and swim up near the surface (Sulkin 1984). The speeds of upward migration have been measured in the laboratory; for some intertidal and brackish crabs the speed was 0.1-0.3 cm/sec (Sulkin 1984), and for species of Geryon, which is one of the deep-sea crabs, the speed was 1.5-2.0 cm/sec in various temperatures (Kelly et al. 1982). The calculation for the time taken for upward migration was made by referring the lowest value of 0.1 cm/sec because it has not been reported for *Chionoecetes*, and taking into account the main depth at which the adults live (Yosho and Hayashi 1993). From this, the hatching larvae would only take 4.6 days from 400 m deep and 11.6 days from 1,000 m deep for *C. opilio* and *C. japonicus*, respectively. This supports quick larval migration to the surface after hatching.

Both zoea 1 and zoea 2 showed a much wider distribution than adults in April. This could be explained by the Tsushima Warm Current carrying and dispersing these larvae downstream. But it is not clear from this study how long and how far they are dispersed passively in their zoeal stage. No larvae were collected in the coastal water on the most eastern transect, into which cold, fresh water flowed. The cold, fresh water might affect survival of larvae.

Two possible reasons can be considered why the densities of zoea 2 in May and megalopa in April and May were quite low. One is the high mortality when zoea 2 molt to megalopa. The other is the offshore migration beyond the study area, and vertical migration beyond the survey depth; Kon (1982) reported downward migration of *C. opilio* larvae according to ages. Because megalopae would be capable of moving actively in comparison with zoeae (Shanks 1994), they might migrate to the bottom where they molt to juveniles. For *Chionoecetes*, the process from the pelagic stage to settlement has hardly been studied. The juveniles of these two crabs showed distributional separation whereas they occurred together in a zoea 1 stage. This implies that they would selectively settle on the bottom where adult crabs live. The detailed process for settlement and the distributional segregation have remained unknown and should be solved in future studies.

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High Latitude Crabs: Biology, Management, and Economics
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Dispersion of Adult *Cancer magister* at Glacier Bay, Alaska: Variation with Spatial Scale, Sex, and Reproductive Status

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Abstract

Patterns of micro- to mesoscale distribution of Dungeness crabs (*Cancer magister*) in nearshore habitats at five locations in and near Glacier Bay National Park were revealed using subtidal transects. Sampling was conducted in April and September 1992 and 1993 and April 1994. Divers censused crabs by sex and reproductive status (ovigerous/nonovigerous females) along belt transects (2 m × 100 m) perpendicular to shore in the depth range 0 m (mean lower low water) to 18 m. A sample estimator of Morisita's index ($\hat{I}_\Delta^*$) was used to quantify crab dispersion at 10 scales of measurement ranging from 20 m^2 to 200 m^2 at each location during each sampling period.

Values of $\hat{I}_\Delta^*$ in ovigerous female *C. magister* deviated significantly ($P < 0.05$) from 1.0 (random distribution) toward contagion more frequently than did $\hat{I}_\Delta^*$ for nonovigerous female and male crabs. Ovigerous crabs also usually had higher $\hat{I}_\Delta^*$ than did nonovigerous female and male crabs, especially at smaller measurement scales (20-80 m^2). Morisita's index for all three groups of crabs decreased more frequently than it increased with an increase in measurement scale. We observed no relationship between $\hat{I}_\Delta^*$ and crab density in nonovigerous female and male crabs, whereas $\hat{I}_{\Delta}^{*}$ was positively correlated with the density of ovigerous crabs. A total of 13 dense aggregations of ovigerous *C. magister* were observed nearshore (depth range 0-10 m) at the five study locations. About half of these were repeatedly observed at the same microsite over the course of this study. Ovigerous Dungeness crabs at Glacier Bay were usually aggregated, often forming dense aggregations with high site fidelity. These dense aggregations may concentrate a significant proportion of the brood stock of this species in a limited number of patches of optimal brooding habitat at Glacier Bay.

Introduction

The micro- to mesoscale dispersion (i.e., the positions of individuals relative to one another; Ricklefs 1979) of members of a population is fundamentally important to the study of population biology because it provides valuable clues to the behavioral and ecological influences on the population. Knowledge of the spatial distribution of individuals in a population is also of great practical significance in designing sampling programs for estimating species abundance in benthic ecology and is useful in developing some stock assessment models in fishery science (Downing 1979, Mangel and Smith 1990). The precision of estimates of stock size depends heavily on the pattern of spacing of individuals in the population and how realistically the design of a sampling program to assess stock size accounts for that spatial pattern.

The dispersion of marine benthic organisms ranges from uniform through random to highly aggregated. Although many marine benthic invertebrates display aggregated distributions, some (including some decapod Crustacea) are randomly or uniformly distributed (Clark and Milne 1955, Connell 1963, Kosler 1968, Gage and Geekie 1973). Among the decapod Crustacea, several authors have reported dense aggregations (pods, heaps, or mounds) of lobsters or crabs associated with mating, molting, egg extrusion, or brooding (see Stevens et al. 1994 for review). Because most of the observations on these aggregations have been short-term and small-scale, we do not know how widespread, persistent, or predictable the aggregations are in these species. Where longer-term studies have been conducted the degree of dispersion varies over space and time (Dew 1990, Stone et al. 1993). Aggregations of ovigerous Dungeness crabs (*Cancer magister* Dana 1852) have been observed in Washington and Alaska (Armstrong et al. 1987, Dinnel et al. 1987, O'Clair et al. 1990), but hitherto, no attempt has been made to systematically quantify dispersion in *C. magister*.

Here we present results of a study of the spatial distribution of adult male, and ovigerous and nonovigerous female *C. magister* at Glacier Bay, Alaska. Our objectives were to: (1) determine whether differences exist in the degree of dispersion of crabs depending on sex and female reproductive status, (2) determine the extent to which dispersion changes with increasing spatial scale of measurement and crab abundance, (3) to compare the degree of dispersion of crabs between study locations at Glacier Bay, and (4) to characterize dense ovigerous crab aggregations at Glacier Bay.

Methods

Five locations in or adjacent to Glacier Bay National Park were chosen for study (Figure 1). Four study sites (North and South Beardslee islands, Berg Bay, and Bartlett Cove) were located within the park. One site (Gustavus Flats) was outside and adjacent to the park.

Divers censused Dungeness crabs on 2 m × 100 m belt transects in the depth range 0 (mean lower low water) to 18 m. Because the transects did not extend below 18 m some transects were less than 100 m long. (Divers were prevented from going deeper than 18 m to avoid excessive buildup of nitrogen in their blood from many repetitive dives each day.) The transects, positioned randomly (with the aid of a random number generator on a computer), were laid perpendicular to shore and divided into quadrats 2 m × 10 m in size within which crabs were counted. We recorded the depth range of each quadrat. Usually, 15 transects were laid at each site during each sampling period. The number of quadrats per site per sampling period ranged from 107 to 150 (Table 1). A total of 369 transects and 3,408 quadrats were searched for crabs.

Adult crabs (carapace width [CW] > 116 mm for males; CW > 100 mm for females) were counted separately by sex and female reproductive status (ovigerous or nonovigerous). A crab was considered to be ovigerous if she bore an egg clutch beneath her abdominal flap. Virtually all Dungeness crab egg clutches can be observed without lifting the abdominal flap. Because of limited dive time, nonovigerous females were not examined further for matted pleopodal setae (a sign of recent larval hatching), sperm plugs, or other indications of female reproductive status beyond the two categories identified above.

We sampled all sites in April 1992-1994 and September 1992 and 1993 (Table 1). These periods were chosen, in part, to limit sampling to the period when ovigerous crabs would be available for study. In southeastern Alaska most females extrude their eggs from August to October; larval hatching usually occurs from April to June (Shirley et al. 1987, O'Clair unpublished data). Sample periods were further restricted to avoid the commercial Dungeness crab fishery and thereby preclude mutual interference between our sampling activities and the fishery and avoid compromising diver safety. (The commercial fishery was open in the part of southeastern Alaska that includes Glacier Bay between 15 June and 15 August and between 1 October and 30 November [Alaska Department of Fish and Game 1994]).

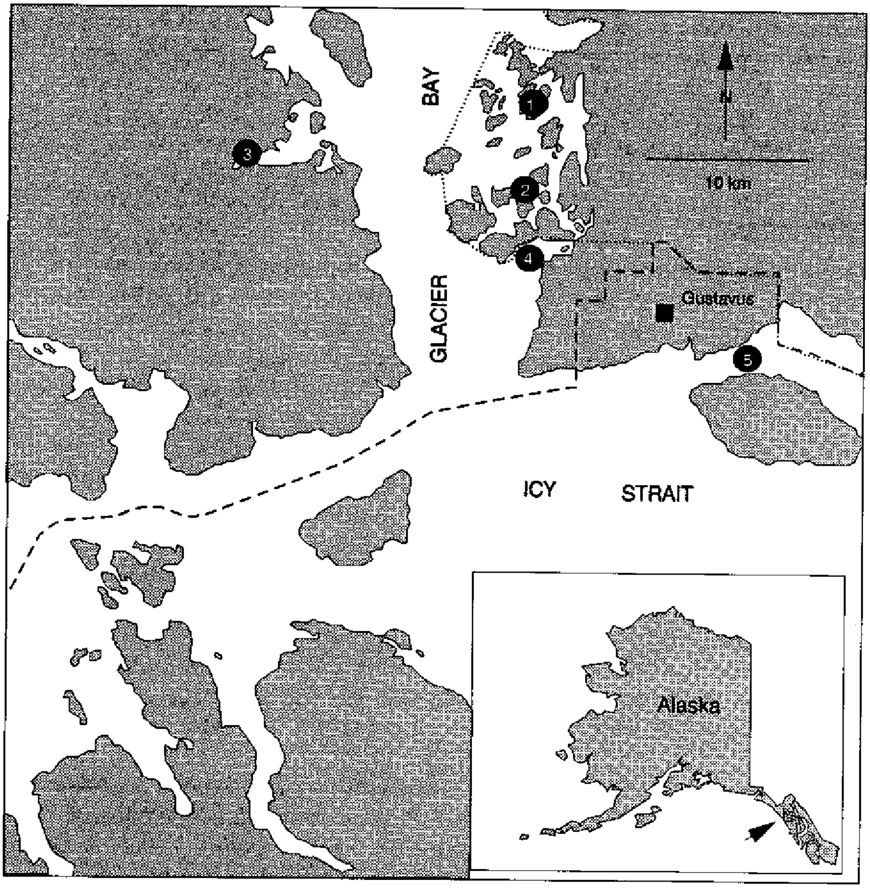

Figure 1. Study locations in and adjacent to Glacier Bay National Park. Numbered locations are (1) North Beardslee Islands, (2) South Beardslee Islands, (3) Berg Bay, (4) Bartlett Cove, and (5) Gustavus Flats. The dashed line marks the border of the park; dotted line marks the border of the wilderness area within the park.

Table 1. Number of transects and quadrats sampled at five locations at Glacier Bay, Alaska.

Location	Date	Number of transects	Number of quadrats
North Beardslee Islands	4/7-8/92	14	140
	9/17/92	15	145
	4/20/93	15	150
	9/24/93	15	142
	4/22/94	15	148
South Beardslee Islands	4/8-9/92	15	114
	9/18/92	15	107
	4/19-20/93	15	137
	9/23/93	15	122
	4/23/94	15	112
Berg Bay	4/9-10/92	14	129
	9/19/92	15	141
	4/21/93	15	136
	9/25/93	15	147
	4/24/94	15	139
Bartlett Cove	4/11/92	15	141
	9/20/92	15	148
	4/22/93	15	137
	9/26/93	15	150
	4/25/94	15	149
Gustavus Flats	4/12/92	11	109
	9/21/92	15	131
	4/25/93	15	145
	9/27/93	15	146
	4/21/94	15	143

Dispersion was quantified by Morisita's (1959) index:

$$I_\delta = q\frac{\sum_{i=1}^{q} x_i(x_i - 1)}{N(N-1)}$$

where q = total samples, x_i = number of individuals in the ith sample, and N = the total number of individuals in all samples. The value of I_δ approaches 0 when the distribution is uniform, equals 1 when the distribution is random, and exceeds 1 when the distribution is contagious (i.e., aggregated). Morisita's index was chosen because it is not appreciably influenced by sample size, whereas such indices of dispersion as Green's (1966) and the standardized Morisita coefficient of Smith-Gill (1975) are strongly influenced by sample size (Hurlbert 1990). When evaluated under the criterion of "effect of random death," I_δ, unlike most other indices, is independent of population density (Pielou 1969, Hurlbert 1990). This does not exclude the possibility that the degree of aggregation may correlate with population density in nature as a consequence of the biology of the species under study (Hurlbert 1990).

The sample estimator of the population dispersion index ($\hat{I}^*_\Delta$) used here is that of Morisita (1971):

$$\hat{I}^*_\Delta = \frac{s^2 - \bar{x}}{(\bar{x})^2 - \frac{s^2}{q}} + 1$$

where s^2 and $\bar{x}$ are the variance and mean, respectively, of the number of individuals per sample. The index $\hat{I}^*_\Delta$ was calculated at 10 measurement scales, increasing from 20 m^2 to 200 m^2 in 20 m^2 increments. Sample surface was increased from 20 m^2 by randomly combining from 2 to 10 adjacent 20 m^2 quadrats depending on the intended measurement scale.

We tested the significance of the departure of $\hat{I}^*_\Delta$ from 1 with a two-tailed F-test, comparing

$$F_I = \frac{\hat{I}^*_\Delta(N-1) + q - N}{q-1}$$

with the critical value in the F-table where $v_1 = q - 1$ and $v_2 = \infty$ when $\hat{I}^*_\Delta > 1$ (Southwood 1966). The reciprocal of F_I with $v_1 = \infty$ and $v_2 = q - 1$ degrees of freedom was compared with the critical value of F when $\hat{I}^*_\Delta < 1$. The index $\hat{I}^*_\Delta$ was judged significantly different from 1 if $P < 0.05$.

Because of the irregular relationship of the mean $\hat{I}^*_\Delta$ to its variance when we compared $\hat{I}^*_\Delta$ between groups of crabs (averaged at each measurement scale over all study locations and sample periods), variance-stabilizing transformations could not be employed. We therefore used the Kruskal-Wallis test to test for differences between values of $\hat{I}^*_\Delta$ for male, nonovigerous, and ovigerous female crabs. The significance of the relationship of $\hat{I}^*_\Delta$ to measurement area was determined with regression analysis; that of $\hat{I}^*_\Delta$ to crab density with correlation analysis. The relationship of $\hat{I}^*_\Delta$ to measurement area was judged to be linear, logarithmic, or exponential based on the value of the coefficient of determination (r^2). The regression model with the highest r^2 was considered to be the "best fit."

Results

Frequency and degree of aggregation

In general, ovigerous Dungeness crabs were more frequently and more strongly aggregated than were males or nonovigerous females. The frequency (expressed as a percentage of the total number of significance tests on ovigerous crabs) with which Morisita's index ($\hat{I}^*_\Delta$) for ovigerous crabs significantly exceeded 1 (F-test, $P < 0.05$) ranged from 50% to 94%, depending on the scale of measurement (Figure 2). The average frequency of aggregation in ovigerous crabs exceeded that of both males and nonovigerous females at all measurement scales except 160 m^2 where the frequency of nonovigerous females exceeded that of ovigerous females. Ovigerous crabs tended to be more frequently aggregated at smaller scales than at larger scales (Figure 2).

Although males and nonovigerous females were frequently aggregated at the spatial scales studied (range of frequency, 44-69% and 53-73%, respectively), in general, they were randomly distributed more frequently than ovigerous crabs. Depending on measurement scale, $\hat{I}^*_\Delta$ did not differ significantly from 1 (F-test, $P > 0.05$) for 31-56% of the statistical tests in males and for 27-47% of the statistical tests in nonovigerous females. In ovigerous crabs, $\hat{I}^*_\Delta$ did not differ significantly from 1 in 6-44% of the statistical tests. None of the three groups of crabs exhibited a significant tendency toward a uniform distribution (i.e., $\hat{I}^*_\Delta$ significantly < 1). We observed no consistent differences in the frequency of aggregation between males and nonovigerous females (Figure 2).

Ovigerous crabs were usually more strongly aggregated than males and nonovigerous females (Figure 3). Average values of $\hat{I}^*_\Delta$ for ovigerous crabs (range of mean $\hat{I}^*_\Delta$, 14-21.8, depending on scale of measurement) were significantly (Kruskal-Wallis test, $P < 0.05$) greater than those for males (range, 2.4-4.5) and nonovigerous females (range, 4.4-31.9) at all scales of measurement less than 120 m^2. At scales $\geq$ 120 m^2 the average $\hat{I}^*_\Delta$ for ovigerous crabs (range of mean $\hat{I}^*_\Delta$, 6.9-13.6) was usually greater than that for males (range, 2.1-2.6) or nonovigerous females (range, 6.1-24.8) or both. Only at 160 m^2 did we observe no significant difference in the value of $\hat{I}^*_\Delta$ between all three groups of crabs. (Extremely high values of $\hat{I}^*_\Delta$ were obtained for ovigerous crabs at 140 m^2, 160 m^2, and 200 m^2 at Gustavus Flats in September 1993. To not obscure the generally decreasing trend in the values of $\hat{I}^*_\Delta$ for ovigerous crabs with increasing

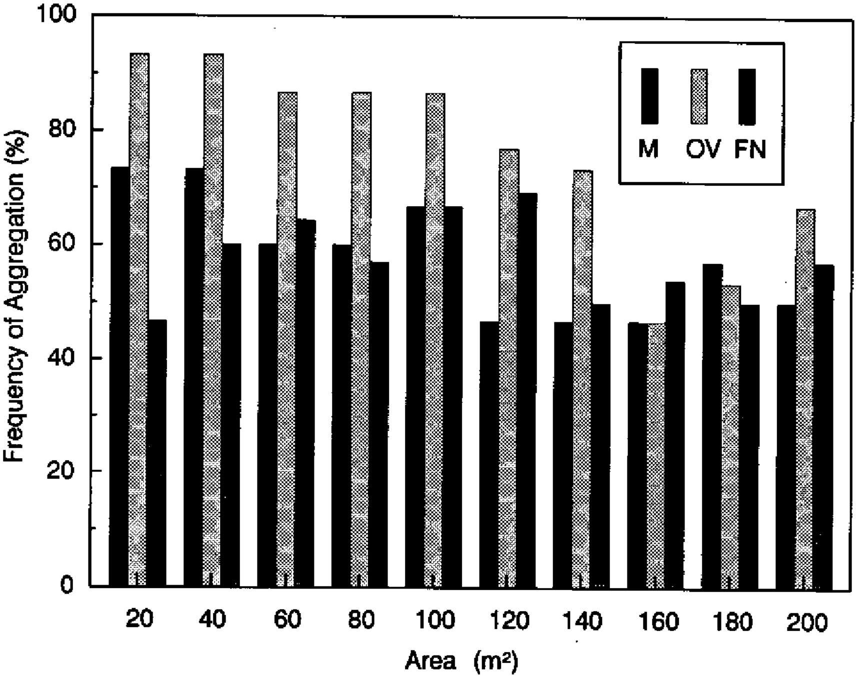

Figure 2. Frequency (%) of aggregation (Morisita's index of dispersion [$\hat{I}_{\Delta}^{*}$] significantly greater than 1.0) of male (M), and nonovigerous (FN) and ovigerous (OV) female Dungeness crabs at 10 measurement scales. Indices for five locations in and near Glacier Bay sampled during five sampling periods were combined at each measurement scale.

sample area in Figure 3, these extreme values were excluded from calculations of the means shown in Figure 3. Results of significance tests were identical whether the extreme values were included or not.) Ovigerous crabs tended to be more strongly aggregated at smaller spatial scales (20-80 m^2) than at larger scales (Figure 3). Values of $\hat{I}_{\Delta}^{*}$ for males and nonovigerous females did not differ significantly at any measurement scale (Figure 3).

When values of $\hat{I}_{\Delta}^{*}$ were averaged over all spatial scales and sampling periods ovigerous females were more strongly aggregated ($P <$ 0.05, Kruskal-Wallis test) than males and nonovigerous females at all locations except Berg Bay (Figure 4). At Berg Bay there was no significant difference between the values of $\hat{I}_{\Delta}^{*}$ for the three groups of crabs. A single large value of $\hat{I}_{\Delta}^{*}$ for nonovigerous crabs and the absence of ovigerous crabs from the transects at Berg Bay during two sampling periods, by reducing sample size, may have been responsible for this result. At

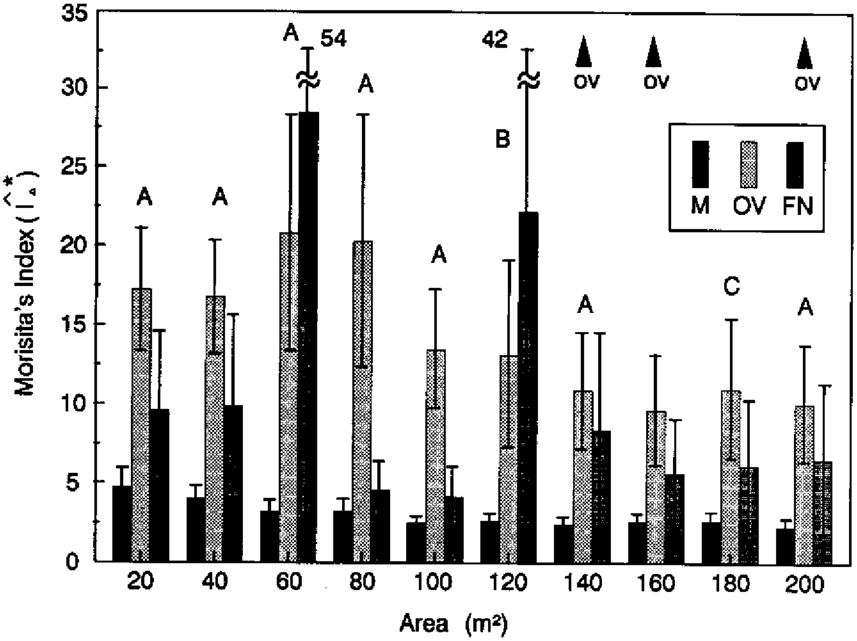

Figure 3. Mean values of Morisita's index of dispersion ($\hat{I}^*_\Delta$) for male (M), ovigerous (OV) and nonovigerous female (NF) Dungeness crabs at 10 measurement scales at Glacier Bay, Alaska. Indices for five locations in and near Glacier Bay sampled during five sampling periods were averaged at each measurement scale. Bars are one standard error of the mean. Letters above each cluster of bars summarize statistical tests of $\hat{I}^*_\Delta$ between crab groups: A, OV > M & FN; B, OV > M only; C, OV > FN only. Outlier $\hat{I}^*_\Delta$ values ($\hat{I}^*_\Delta = 1\text{-}2 \times 10^{20}$) not used in the calculation of index means for ovigerous crabs at 140, 160, and 200 m^2 are depicted by arrows. See text for a discussion of the treatment of these outliers.

Gustavus Flats the mean value of $\hat{I}^*_\Delta$ for nonovigerous females appeared greater than that for ovigerous crabs, but the rank sum $\hat{I}^*_\Delta$ of the latter significantly exceeded that of the former ($P < 0.001$, Kruskal-Wallis test; Figure 4).

Dispersion and spatial scale

The relationship of dispersion and spatial scale showed several patterns when $\hat{I}^*_\Delta$ was regressed against sample area. The most common pattern observed was an exponential or logarithmic decrease in $\hat{I}^*_\Delta$ with increasing sampling area, depending on sex and female reproductive class (Figure 5, Table 2). Male and ovigerous female crabs more frequently exhibited a logarithmic decrease with increasing area. Nonovigerous fe-

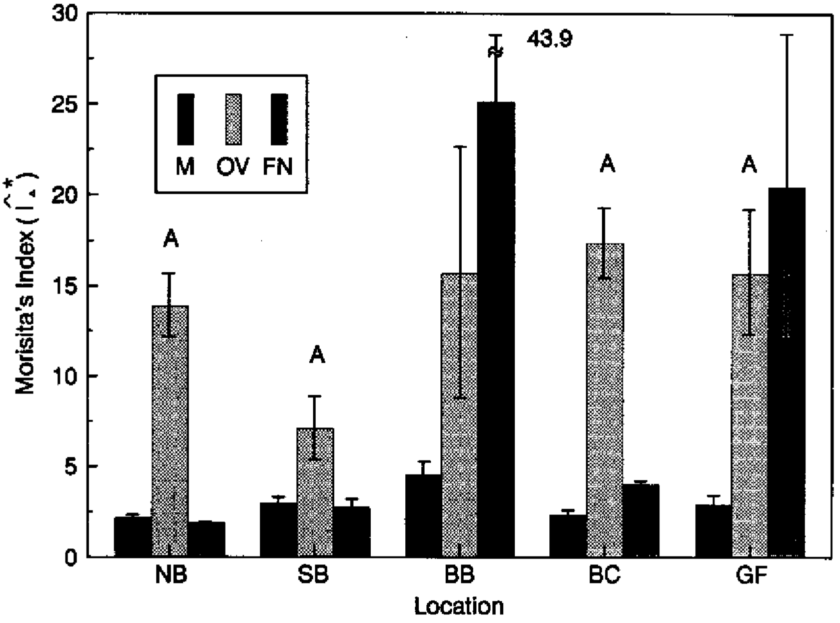

Figure 4. Mean values of Morisita's index of dispersion ($\hat{I}_\Delta^*$) for male (M), ovigerous (OV) and nonovigerous female (NF) Dungeness crabs at five locations (NB, North Beardslee Islands; SB, South Beardslee Islands; BB, Berg Bay; BC, Bartlett Cove; GF, Gustavus Flats) at Glacier Bay, Alaska, averaged over five sampling periods and 10 measurement scales. Bars are one standard error of the mean. Letters above each cluster of bars summarize statistical tests of $\hat{I}$ between crab groups (A, OV > M & FN).*

males more frequently exhibited an exponential decrease with increasing area (Table 2). Linear decreases in $\hat{I}_\Delta^*$ with increasing area were less frequent as were increases in $\hat{I}_\Delta^*$ with increasing area (Table 2). For all three groups of crabs the greatest proportion of the total variation explained by the regression (as measured by the coefficient of determination, r^2) of $\hat{I}_\Delta^*$ on area occurred when $\hat{I}_\Delta^*$ decreased exponentially with increasing measurement area (Table 2).

Dispersion and density

Ovigerous crabs usually exhibited the greatest variability in density both within (as indicated by the magnitude of the standard error of the mean density) and between sample periods, depending on sample location (Table 3). Because ovigerous crabs at Berg Bay were confined chiefly to two small, discrete areas, none were observed on the random transects in April and September 1993. By contrast, high densities of

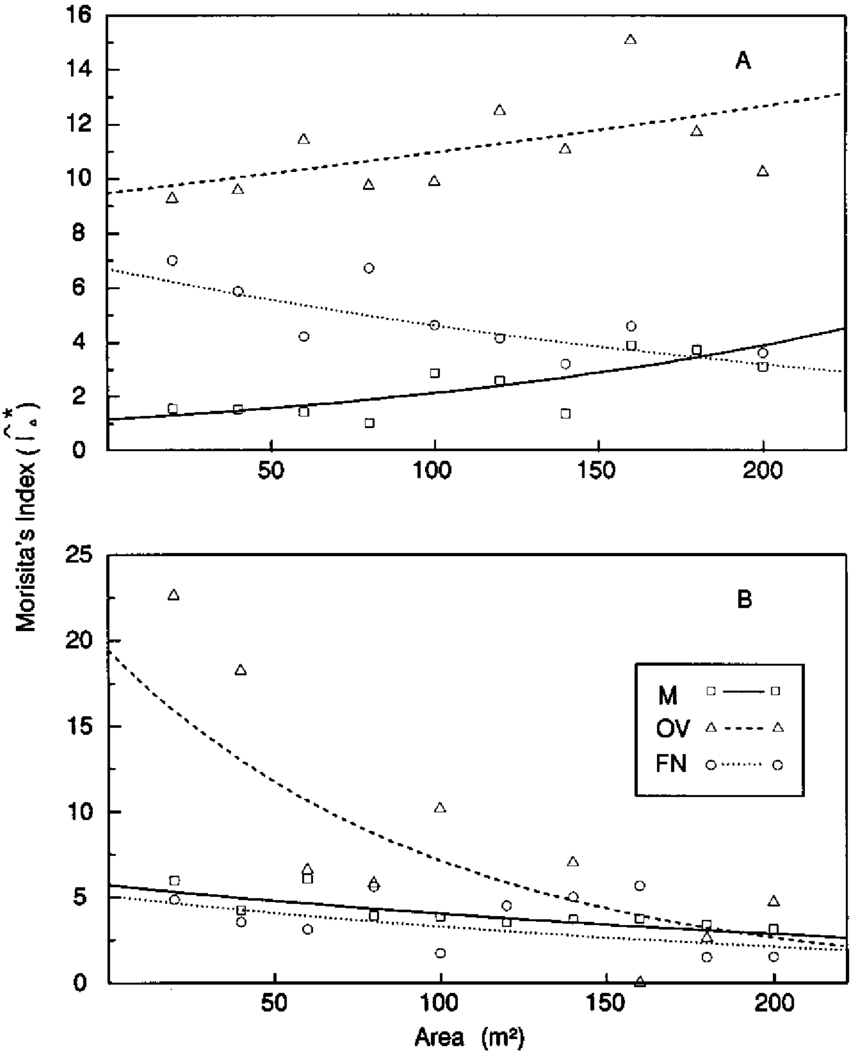

Figure 5. Representative curves showing the types of relationships between Morisita's index of dispersion ($\hat{I}^*_\Delta$) and sample area obtained for male and nonovigerous and ovigerous female Dungeness crabs in April (A) and September (B) 1992 at Bartlett Cove, Glacier Bay.

Table 2. Dependence of Morisita's index ($\hat{I}^*_\Delta$) on measurement scale (m^2) for three groups of Dungeness crabs at Glacier Bay, Alaska.

Crab	Positive regression						Negative regression					
	lin		exp		log		lin		exp		log	
group	%	r^2	%	r^2	%	r^2	%	r^2	%	r^2	%	r^2
M	12	0.40	–	–	12	0.47	19	0.62	19	0.82	38	0.67
OV	–	–	7	0.28	7	0.12	7	0.36	33	0.69	47	0.53
FN	–	–	6	0.26	12	0.12	–	–	50	0.59	31	0.34

lin = linear; exp = exponential; log = logarithmic. Males (M) and ovigerous (OV) and nonovigerous (FN) females. Frequency of occurrence (%) and mean coefficient of determination (r^2) by type of "best fit" regression are shown for each direction of regression. The index increased with increasing scale when the regression was positive.

ovigerous crabs were observed at Bartlett Cove (BC) and Gustavus Flats (GF), especially in April. Average density at these locations ranged up to 1,858 ovigerous crabs/ha (BC) and 1,177 ovigerous crabs/ha (GF), in April 1993 (Table 3). The density of male and nonovigerous female crabs exhibited less extreme variation than did ovigerous crabs over the course of the study. Average male density ranged from 0 to 207 crabs/ha; that for nonovigerous female crabs ranged from 7 to 228 crabs/ha (Table 3).

The value of $\hat{I}^*_\Delta$ tended to increase ($P < 0.01$) with increasing crab density in ovigerous crabs (Figure 6A). However, the proportion of the variation of $\hat{I}^*_\Delta$ explained by the variation in density was small ($r^2 = 0.40$). Variation in crab density accounted for even less of the variation in $\hat{I}^*_\Delta$ in males ($r^2 = 0.11$) and nonovigerous females ($r^2 = 0.10$). No significant relationship was observed between $\hat{I}^*_\Delta$ and density in males and nonovigerous females ($P > 0.05$; Figure 6B).

Ovigerous crab aggregations

Distinct aggregations of ovigerous crabs occurred at all study locations over the course of this study. These aggregations were characterized by a high density of crabs distributed over areas of a few m². Dense aggregations occurred at 13 sites at the five study locations. Most of these aggregations (77%) occurred more than once. On all but one occasion virtually all of the crabs in the aggregation were partially to completely buried in the sediment. Often the crabs would be stacked one on top of the other in the sediment. Although the aggregations occasionally occurred in substrates composed primarily of silt and finer sediments, the highest densities of ovigerous crabs usually occurred in sand. The depth of the aggregations extended from just below mean lower low water to a depth of about 10 m on gently to steeply sloping bottoms. Four

Table 3. Mean ($\bar{x}$) and standard error of the mean (se) of the density (individuals/ha) of adult male (M), ovigerous female (OV), and nonovigerous female (FN) Dungeness crabs at five locations in or adjacent to Glacier Bay, Alaska from April 1992 to April 1994.

		Density		
		M	OV	FN
Location	Date	$\bar{x}$ ± se	$\bar{x}$ ± se	$\bar{x}$ ± se
North Beardslee Islands	Apr 1992	168 ± 53	46 ± 21	107 ± 28
	Sep 1992	129 ± 33	37 ± 30	122 ± 34
	Apr 1993	130 ± 34	220 ± 188	60 ± 46
	Sep 1993	40 ± 14	10 ± 5	71 ± 21
	Apr 1994	104 ± 22	40 ± 28	73 ± 21
South Beardslee Islands	Apr 1992	65 ± 24	70 ± 30	63 ± 25
	Sep 1992	63 ± 22	159 ± 105	51 ± 17
	Apr 1993	102 ± 29	130 ± 46	77 ± 28
	Sep 1993	110 ± 39	91 ± 73	93 ± 33
	Apr 1994	147 ± 45	146 ± 41	79 ± 29
Berg Bay	Apr 1992	67 ± 16	23 ± 10	87 ± 26
	Sep 1992	167 ± 99	27 ± 13	15 ± 9
	Apr 1993	85 ± 32	0	19 ± 7
	Sep 1993	121 ± 71	0	15 ± 7
	Apr 1994	73 ± 49	297 ± 282	228 ± 225
Bartlett Cove	Apr 1992	53 ± 20	305 ± 215	94 ± 44
	Sep 1992	207 ± 83	20 ± 12	125 ± 61
	Apr 1993	42 ± 13	1858 ± 1517	112 ± 46
	Sep 1993	100 ± 38	3 ± 3	73 ± 25
	Apr 1994	51 ± 12	442 ± 310	30 ± 14
Gustavus Flats	Apr 1992	0	45 ± 27	33 ± 16
	Sep 1992	45 ± 17	107 ± 48	187 ± 48
	Apr 1993	3 ± 3	1177 ± 1085	20 ± 10
	Sep 1993	30 ± 18	23 ± 23	41 ± 15
	Apr 1994	17 ± 8	412 ± 200	7 ± 4

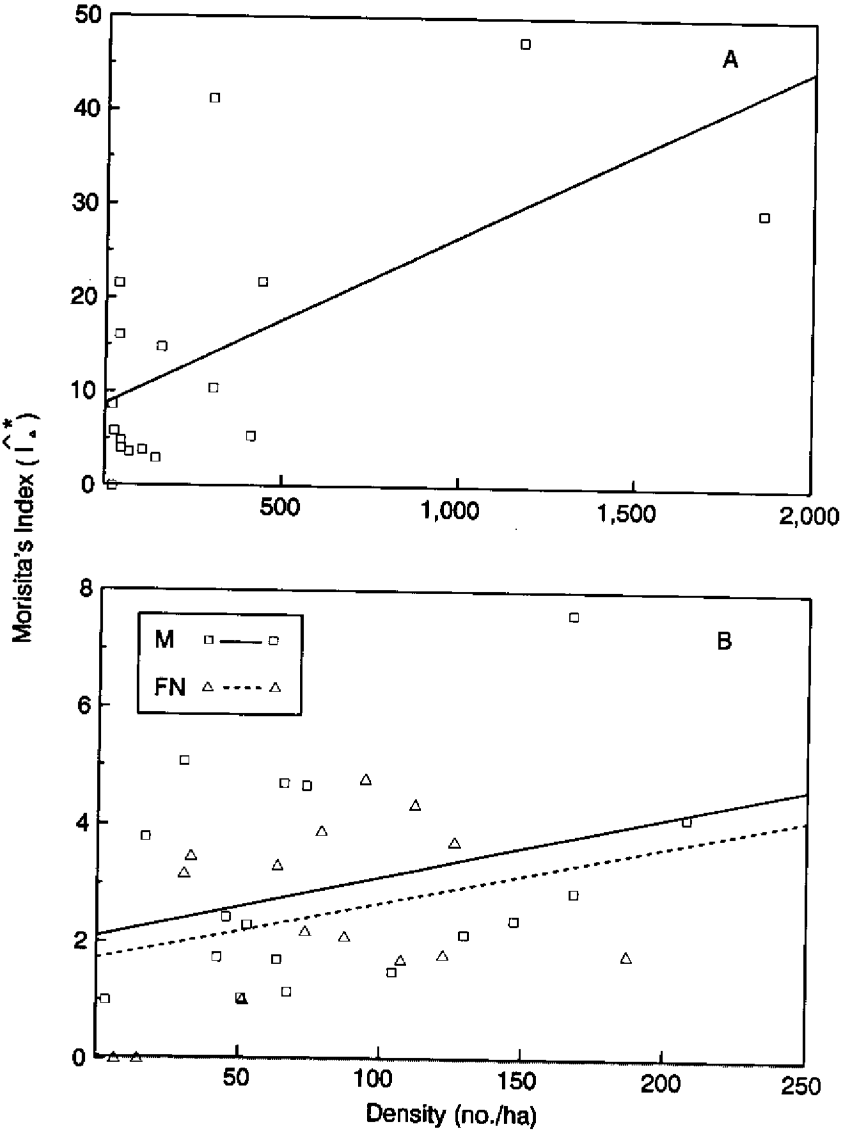

Figure 6. Correlation of Morisita's index of dispersion and crab density for (A) ovigerous and (B) male (M) and nonovigerous female (FN) Dungeness crabs sampled during five periods at five locations in and near Glacier Bay.

aggregations (31%) were located near the mouths of streams emptying into bays. Over one-half (54%) of the aggregations repeatedly occurred at the same micro-site. One of us (CEO) collected ovigerous crabs for another project from these aggregations during each sampling period of this study, and therefore confirmed the location of the aggregations during each sample period. The distribution of aggregations of ovigerous Dungeness crabs observed in the present study was also evident in crab pot collections made synoptically in the same bays. Ovigerous crabs were uncommon in pots, but, when present, usually occurred in pots nearest the aggregation sites recorded by divers (Schultz et al. 1996). Although male and nonovigerous female Dungeness crabs occasionally occurred in discrete aggregations, these aggregations invariably contained fewer crabs and were much less predictable than were the aggregations of ovigerous crabs.

Discussion

The distribution of *Cancer magister* in or near Glacier Bay, Alaska, was usually contagious. This is a frequently observed and well-documented distributional pattern in benthic invertebrates (Kosler 1968, Gage and Geekie 1973, Downing 1979). Less well documented are the differences that we observed in the distributional patterns of subpopulational groups of *C. magister*, specifically differences between the distributional patterns of males, nonovigerous females, and ovigerous crabs. Ovigerous crabs were clearly more frequently and more strongly aggregated at most measurement scales we examined than were male and nonovigerous female crabs. Males and nonovigerous females were also frequently aggregated but were more likely to be randomly distributed than were ovigerous crabs.

Ovigerous crabs were often in dense aggregations in shallow water (0-10 m) at Glacier Bay. Over one-half of these aggregations were observed repeatedly at the same sites over the course of this study. Others have reported aggregations of ovigerous cancroid crabs at depths ranging from 1 to 40 m in England, Washington, and Alaska (Howard 1982, Armstrong et al. 1987, Dinnel et al. 1987, O'Clair et al. 1990). None of these authors offered explanations of the function of these aggregations or why they occurred where they did. McKoy and Leachman (1982) found aggregations of ovigerous female rock lobsters, *Jasus edwardsii*, in circular formations, on open shelly-sand bottom, in New Zealand. They suggested that the function of these aggregations was defensive. The sites of these aggregations were in areas of strong tidal water movements. Newly hatched lobster larvae at these sites would be rapidly dispersed by the water movements. As a result, predation on the larvae may be minimized (McKoy and Leachman 1982). Campbell (1990) found aggregations of ovigerous lobsters (*Homarus americanus*) in shallow waters off Grand Manan, eastern Canada. He did not ascribe a function to these aggregations, but considered the question of habitat selection by the lobsters. He suggested that some areas may be preferred by ovigerous lobsters. The aggregations occurred in areas relatively sheltered from major storm surges and with a soft sand-clay substrate into which the lobsters "bulldozed" depressions. In these areas, lobsters would be exposed to warm surface waters which would increase the rate of egg development and hatching in a region where waters are generally cold for most of the year. The areas harboring aggregations of ovigerous lobsters were characterized by strong tidal currents which would promote rapid dispersal of newly hatched larvae (Campbell 1990).

In the present study Morisita's index of dispersion for ovigerous crabs tended to decrease in value with increasing sample area. Because smaller measurement scales more likely encompass areas within the same habitat type than do larger scales, aggregation in ovigerous *C. magister* probably does not reflect differences in habitat quality between broad habitat types. However, differences in habitat patch quality at the micro-scale level may promote the establishment of dense aggregations of ovigerous crabs similar to those at some sites at Glacier Bay.

Sediment type probably plays an important role in determining habitat quality for ovigerous *C. magister*. Female *C. magister* that do not have suitable substrate into which to burrow suffer high losses of freshly extruded eggs (Fisher 1976). Uncompacted fine sediments may be the easiest to burrow into, but a large silt-clay fraction may interfere with oxygenation of the eggs. Considering the sediment type associated with the dense aggregations of ovigerous crabs that one of us (CEO) has observed in Glacier Bay, sand may be the preferred substrate for ovigerous crabs. Particles finer than sand may be more likely to foul crab egg clutches; coarser substrates may be more difficult for crabs to penetrate. Increased interstitial water flow in sand may enhance oxygenation of crab eggs and remove crab waste products such as ammonia.

In a glacial fjord system like Glacier Bay with a high rate of sedimentation of fine (silt-clay) particles, most bottom sediments are probably composed of fine particles. Areas of sand may be limited. The sediment sorting that takes place on the alluvial fans of rivers and streams may provide patches of sand for ovigerous crabs. At least a one-third of the dense aggregations observed in our study were on or near alluvial fans. However, dense aggregations also occurred in sandy substrates that were not near alluvial fans.

One function of the dense ovigerous aggregations at Glacier Bay may be mutual enhancement of the brooding (interstitial) environment. Small movements of the legs and abdominal flaps of large numbers of densely packed crabs may prevent sediment compaction around egg clutches and may induce resuspension of fine particles which then become subject to export from the site of the aggregation by bottom currents.

Aggregations of ovigerous *C. magister* may also function in group defense against predation, as has been suggested for aggregations of lobsters and other species of crabs (McKoy and Leachman 1982, Stone et al. 1993, Stevens et al. 1994). Ovigerous *C. magister* seem reluctant to abandon their burrows. If dug up, they will attempt to escape but are encumbered by their large egg clutches. As a result, ovigerous crabs cannot escape as quickly and presumably evade predators as effectively as nonovigerous female and male crabs. If one or more individuals in an aggregation of ovigerous crabs is removed from her burrow, nearby crabs will often erupt from their burrows simultaneously. This behavior usually continues throughout the aggregation until all of its members have abandoned their burrows and are running in all directions. The behavior may serve to confuse a potential predator. In addition, the burrow-abandonment and escape behavior of these crabs resuspends fine sediments, reducing near-bottom visibility to a few centimeters, thereby further interfering with prey capture by a visual predator. In this way, individual crabs may obtain cover through the activities of conspecifics reacting to the same predator. This may increase the fitness of the individual in an aggregation over that of an isolated individual (Hamilton 1971).

Our results indicate that aggregation in ovigerous *C. magister* at Glacier Bay is commonplace and that ovigerous crabs are usually more strongly aggregated than nonovigerous females and males. Moreover, observations by one of us (CEO) indicate that dense aggregations of ovigerous *C. magister* occur elsewhere throughout southeastern Alaska. This suggests that a large percentage of the brood stock of a Dungeness crab population at Glacier Bay and probably elsewhere is restricted to small, nearshore areas. Because these aggregations usually occur in sheltered bays near shore, locations with anthropogenic disturbances such as log transfer facilities, shoreline developments including docking facilities and marinas, dredge and fill operations, and oil spills, the aggregations are vulnerable to these disturbances (Howard 1982, Armstrong et al. 1987). In bays proposed for shoreline development that harbor a population of Dungeness crabs, care should be taken to locate aggregations of ovigerous crabs so that major impacts to the population can be avoided.

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Behavioral Basis of Depth Regulation in the First Zoeal Stage of the Giant Crab (*Pseudocarcinus gigas*, Brachyura, Xanthoidea, Oziidae)

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Abstract

The responses of the first zoeal stage of the deepwater crab *Pseudocarcinus gigas* (Lamarck) to stimuli affecting vertical migration were determined. Larvae are negatively buoyant and sink passively at 0.61 cm/s at 35 ppt salinity. Negative geotactic response was weak in larvae immediately after hatching; however, larvae exhibited strong negative geotaxis in tests at 15 and 20 hours. This pattern was less evident in subsequent samples up to day 13. It is suggested that a strong negative geotactic response is important initially to induce upward migration of larvae from the site of release, at approximately 350 m depth, to the surface. Light-adapted larvae were sensitive to change in light intensity from overhead lighting with both decreases and increases in intensity inducing downward migration; this negative phototactic response was only induced at lower light intensities (below 230 lux). It is suggested that this may be a shadow response which has not been previously reported for increases in intensity. Distributions of larvae in angled testing columns suggest that the larvae are actively swimming away from the light source when negative phototaxis occurs. Where positive phototaxis occurred, larvae appeared to orient with gravity while light provided the stimulus for increased locomotory activity. Larvae did not appear to respond to small changes in pressure (0.24-2.70 cm water/s, at surface) of a similar magnitude to that which they would experience by vertical swimming. They appeared to detect currents and most larvae could maintain position in currents of 1.12 cm/s.

Introduction

Giant crabs *Pseudocarcinus gigas* are distributed along the southern coast of Australia and have recently begun to be commercially harvested. They are a large, deepwater species with ovigerous females captured at greatest density along the edge of the continental shelf, at approximately 350 m. Ovigerous females appear to migrate up the shelf before hatching of the eggs occurs, so that larval release may take place in shallower depths of 160-240 m (Andrew Levings, Deakin University, Warrnambool, Austl., pers. comm., Sept. 1995).

Development of the larvae of giant crabs consists of a prezoea, 5 zoeal stages, and a megalopa (Gardner 1996). The vertical migration of these larvae and their response to currents may be an important behavioral mechanism in larval dispersal, survival, and growth. The mechanism controlling migration in planktonic crustaceans is highly complex and can be influenced by a range of stimuli including pressure, polarization of light, gravity, absolute light intensity, salinity, change in light intensity, predator fields, prey fields, and temperature (Knight-Jones and Morgan 1966, Umminger 1969, Latz and Forward 1977, Forward et al. 1984, Gliwicz and Pijanowska 1988, and Forward 1990). While many stimuli may be perceived by brachyuran larvae, and contribute to vertical migration, it appears that migration is predominantly controlled by phototaxis in the presence of light (Thorson 1964), and geotaxis (gravity) and barokinesis (pressure) in the absence of light (Sulkin 1973).

The response to external stimuli varies between species so that widely different migration strategies exist in relation to depth and diel cycle. Plankton, including decapod larvae, do not show a clear general diel pattern in oceanic water off Tasmania; some species exhibit nocturnal upward migration while others are found on the surface during daylight hours (Barry Bruce, Div. Mar. Sci., CSIRO, Hobart, Austl., pers. comm., Sept. 1995). Consequently, no assumptions can be made on the general pattern of larval movement in *P. gigas*. Further, it is not possible to predict larval movements of the giant crab based on other studies as deepwater crabs, or those with oceanic larval stages, have received scant attention in behavioral research. Most other studies on brachyuran larval behavior have focused on estuarine species with only one other deepwater species, *Geryon quinquedens*, having been studied (Kelly et al. 1982).

The aim of this research was to provide behavioral information to assist with understanding movement of giant crab larvae and to contribute to research on deepwater crabs in general. An additional aim was to identify larval environmental preferences to assist with small-scale production of juveniles. The responses of stage 1 larvae to several stimuli influencing vertical migration were assessed; gravity, spectral sensitivity, absolute light intensity, change in light intensity, orientation of light, and change in pressure. Larvae were also tested for their response to lateral current movement.

Methods

Source of larvae

Thirty ovigerous females were collected from depths of 300–380 m off the east coast of Tasmania (41°15'S; 148°40'E) in May 1994 by a commercial fisher. These females ranged in size from 2.2 to 3.5 kg and were held in two 4 m^3 tanks with flow-through, unfiltered water supply. Crabs were fed twice weekly with abalone (*Haliotis* spp.) or mackerel (*Trachurus* sp.) and food remains were removed after 48 hours.

Hatching of larvae commenced in November 1994 and continued for three weeks. Stage 1 zoeae were collected for behavioral experiments by first flushing the system of any zoeae present in the tanks, and then reducing flow so that only newly hatched larvae could be drawn from the tanks. Zoeae were mixed by drawing samples from each of the two holding tanks, so that no female contributed more than 50% of the larvae in any trial. Further mixing of larvae was achieved within tanks, as daily monitoring of the egg masses indicated that on any day where larvae were collected, hatching occurred in the egg masses of at least three females.

Sinking and swimming rates

Sinking rates were determined for 30 stage 1 zoeae collected from each of the two holding tanks and narcotized until immobile in a solution of 0.05% 2-phenoxyethanol in seawater. The larvae were then allowed to sink through a seawater-filled Plexiglas column and their rate of descent measured for 25 cm after an initial decent of 25 cm.

Swimming rate was measured for 30 larvae which were introduced to a clear, horizontal Plexiglas column with illumination from one end (500 lux). The time required for larvae to swim 15 cm without stopping or turning was measured.

General experimental procedures for geotaxis, phototaxis, and barokinesis experiments

Zoeae were discarded after use in an experiment and were replaced if held for more than four hours after collection before use in a behavioral trial (with the exception of geotaxis experiments where zoeae up to 13 days old were used).

All experiments were replicated four times with each replicate staggered between other treatment levels. For instance, the behavioral responses of zoeae to each level of light intensity were tested with a single trial at each level and then the entire set of trials was repeated to a total of four times. Trials were conducted at 13°C in a temperature controlled room. All water used was 0.2 μm filtered seawater of consistently 35 ppt salinity.

The movement of larvae was measured by placing approximately 30 larvae into a clear Plexiglas column divided into eleven 5 cm segments (30 mm internal diameter × 550 mm length) and recording their position after subjecting to a stimulus. Larvae were introduced into the middle of the column with a transparent 60 ml syringe. The light intensity that larvae are adapted to has been shown to influence their behavior in response to light stimulus (Forward 1974). To prevent confounding of experiments from previous light exposure, larvae were acclimatized to the lighting for 10 min within the transparent syringe. Preliminary trials established suitable duration of trials to be 2 min. Longer periods than this resulted in all the larvae gathering at either end of the testing chamber. Also, no change in the nature of the larval response occurred in trials of 15 min compared to 2 min trials. Barokinesis trials were reduced to 1.5 min due to constraints on the apparatus used to alter pressure.

Injection of larvae into the testing column caused currents which tended to move the larvae vertically upward. To compensate for this effect, the initial position of the larvae was determined by repeatedly introducing larvae into the testing column and recording their position immediately (433 zoeae in the angled column, 394 in the vertical column). The mean column position of these larvae was used as the point of origin in all trials.

Significant difference between treatments was determined using the method outlined by Sulkin et al. (1980). "Mean position value" was calculated by assigning weights from 1 to 11 for each of the sections along the testing chamber, multiplying the weights by the number of larvae in each section, and dividing the product by the total number of larvae. The mean position value was calculated for each replicate and these values were then used to compare treatments with the non-parametric Mann-Whitney U test (Zar 1974). Differences in means were considered significant at $P < 0.05$.

Geotaxis

Significant upward movement of the larvae in the absence of light or pressure changes was attributed to negative geotaxis. The apparatus used to study geotactic response is illustrated in Figure 1. Geotactic response of larvae was tested at: immediately post-hatch, 15 h, 20 h, 2 d, 6 d, 9 d, and 13 d. Larvae were maintained in a 1,000 L tank on a recirculating water system with UV sterilization and biofiltration. Larvae were fed *Artemia salina* nauplii enriched with Protein Selco™; they molted to second stage zoeae after 7 days. At the culmination of the geotaxis trials (13 d), larvae were still at second stage zoea.

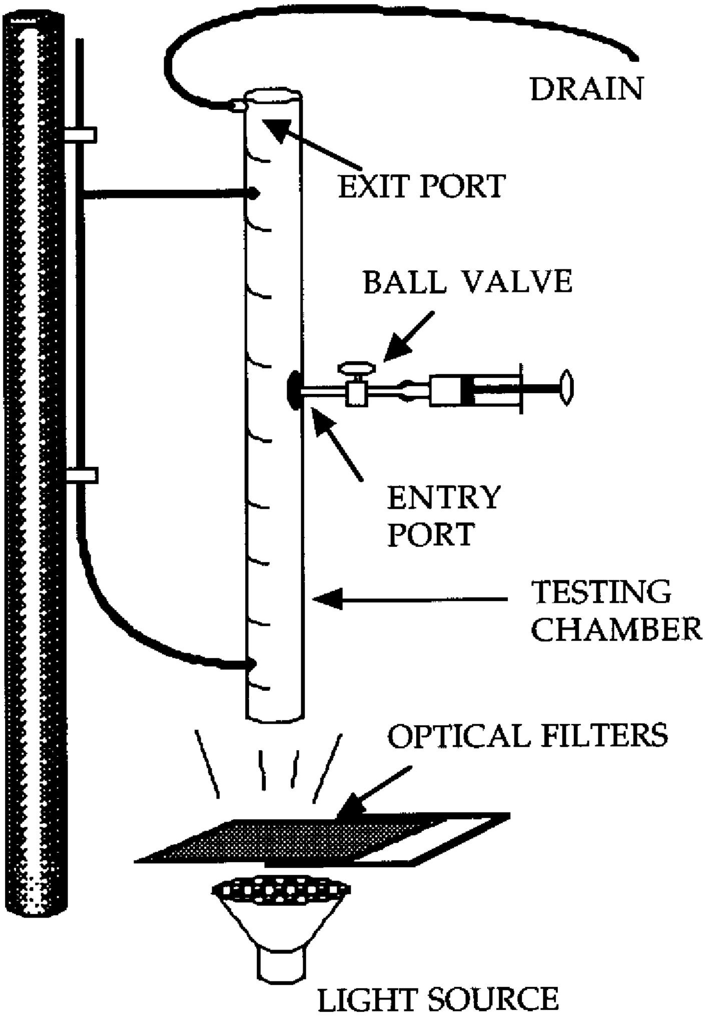


Figure 1. Detail of testing chamber and experimental apparatus used to measure larval response in darkness and also to light of 617 nm and 478 nm. Wavelength and light intensity was altered with optical filters held in a rack between the light source (quartz halogen floodlight) and the testing chamber. Larvae were introduced through the entry port and water and air bubbles displaced through the exit port.

Phototaxis

Several aspects of phototactic response were investigated: spectral sensitivity, response to constant light intensity, response to change in light intensity, and the effect of incident angle of light source. All lighting was from quartz halogen globes which was diffused through neutral density optical filters. Generally, intensity of lighting was altered between treatments by changing the wattage of the globe or the neutral density filter although, for change in light intensity trials, the intensity was altered by moving the light source away or toward the testing chamber. Light intensity was measured in lux with a Gossen Profisix™ plan-diffuser light meter.

The apparatus used to study spectral sensitivity is illustrated in Figure 1. Lighting was from beneath and wavelength was altered with red (Kodak #25, dominant wavelength = 617 nm) and blue (Kodak #47A, dominant wavelength = 478 nm) gelatin filters.

Response to constant light intensity, response to change in light intensity, and the effect of incident angle of light source were determined with the apparatus illustrated in Figure 2. Natural underwater distribution of light was approximated by submerging the testing chamber in a 400 L tank, using angled light and diffusing the light source with neutral density filters. The walls of the outer tank were blackened walls and the tank was filled with 0.2 μm filtered seawater. All trials with constant light intensity were conducted with the light source in the lower position. Test intensities ranged from 3 lux to 40,000 lux, recorded from the top of the testing chamber.

To test the effect of change in light intensity, the light source was moved toward or away from the testing chamber by a variable speed 12 V electric motor (Figure 2). The change in intensity commenced as the larvae were introduced to the column, and continued for the duration of each trial. The effect of change in light intensity was examined for both increasing and decreasing intensities for intensities between 6 and 2,000 lux. The range of intensities experienced by larvae for each treatment is given in Figure 8. Rates of change in light intensity, under natural conditions at sunset, were determined by measuring decline in light intensity on two days in September. Readings were taken every two minutes and rates of change averaged for the two days. Simulated declines in intensity were considerably faster than that which occurs at sunset (Table 1).

The effect of incident angle of light source was tested by comparing larval distributions in a testing chamber angled directly toward the angled light source with a testing chamber oriented vertically (Figure 2). The angle of light incident on the testing chambers was 45° to vertical after refraction through the water surface. Trials conducted to compare the effect of incident angle of light source were conducted simultaneously for the vertical and angled testing chambers.

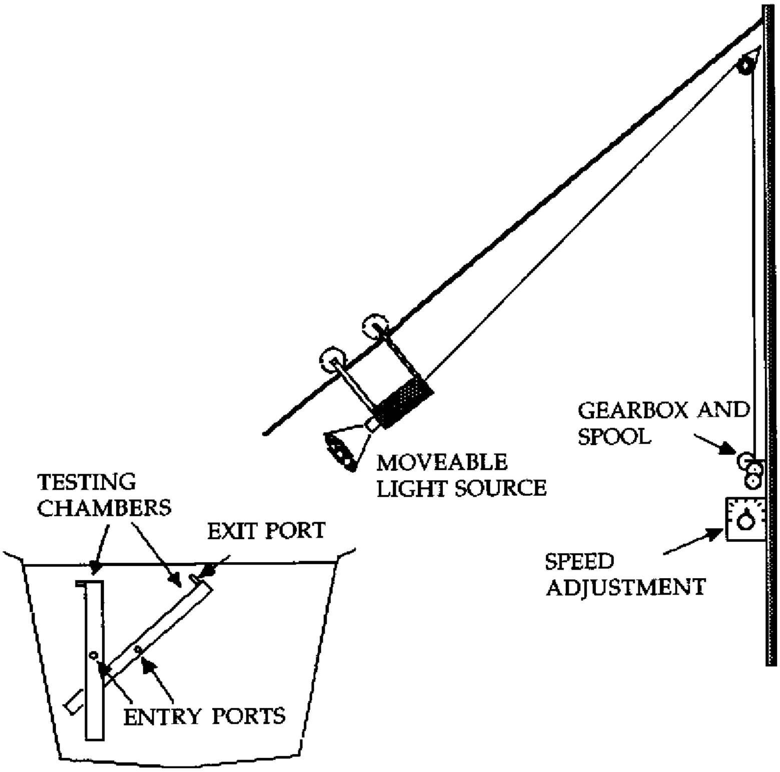


Figure 2. Experimental apparatus used to measure larval response to fixed intensity white light and change in light intensity. The light source was moved up or down the track to adjust intensity with a variable speed, 12 V electric motor connected to a gearbox to reduce speed of revolution and increase torque. Initial light intensity was adjusted with neutral density filters or by changing the wattage of the quartz halogen globe.

Table 1. Change of light intensity during natural sunset compared with experimental rates of intensity decline.

Initial intensity (lux)	Natural[a] (lux/min)	Simulated change in intensity	
		Slow (lux/min)	Rapid (lux/min)
15	2.8	3	4.5
230	20.9	60	95
900	57.5	175	395
2,000	103.9	450	875

[a] Values for natural change in intensity at sunset are derived from a regression fitting recorded intensity changes.

Barokinesis

As with phototaxis experiments, the testing chamber was submerged in a water-filled, blackened tank (Figure 3). The testing chamber was oriented vertically and the response of larvae to change in pressure was measured in darkness and also with 800 lux lighting, angled at 45°. Larvae were introduced to the testing chamber through a ball valve which could be closed to seal the chamber. Silicon tubing was connected to the testing chamber and filled with seawater so that the water was continuous with that in the testing chamber. Pressure was then altered by raising or lowering this tubing with a variable speed electric motor and the rate of pressure change recorded as vertical cm per second. This method of recording change in pressure allowed pressure change to be directly related to potential larval movement in surface waters.

Rheotaxis experimental method

Rheotactic responses of individual zoeae were measured within a 10 mm internal diameter glass tube connected to a peristaltic pump to provide current (Figure 4). Larvae were introduced to the apparatus with a 60 ml syringe and pulsation was largely removed by constricting the 1.5 m length of expandable silicon tubing, feeding from the pump, with a screw valve. Current speed was adjusted with the peristaltic pump and measured by recording the speed of passage of bubbles through the apparatus. The rheotactic responses of larvae were tested for current speeds from 0.35 to 1.87 cm/s. Lighting was at 90° to the current flow and oriented horizontally to produce an intensity of 80 lux incident on the testing chamber. A positive rheotaxis response was recorded when larvae actively oriented themselves and swam into the current or maintained position; a negative response was recorded if the larvae were swept along the testing chamber or swam indifferently to the current. At least thirty larvae were used for each current speed tested.

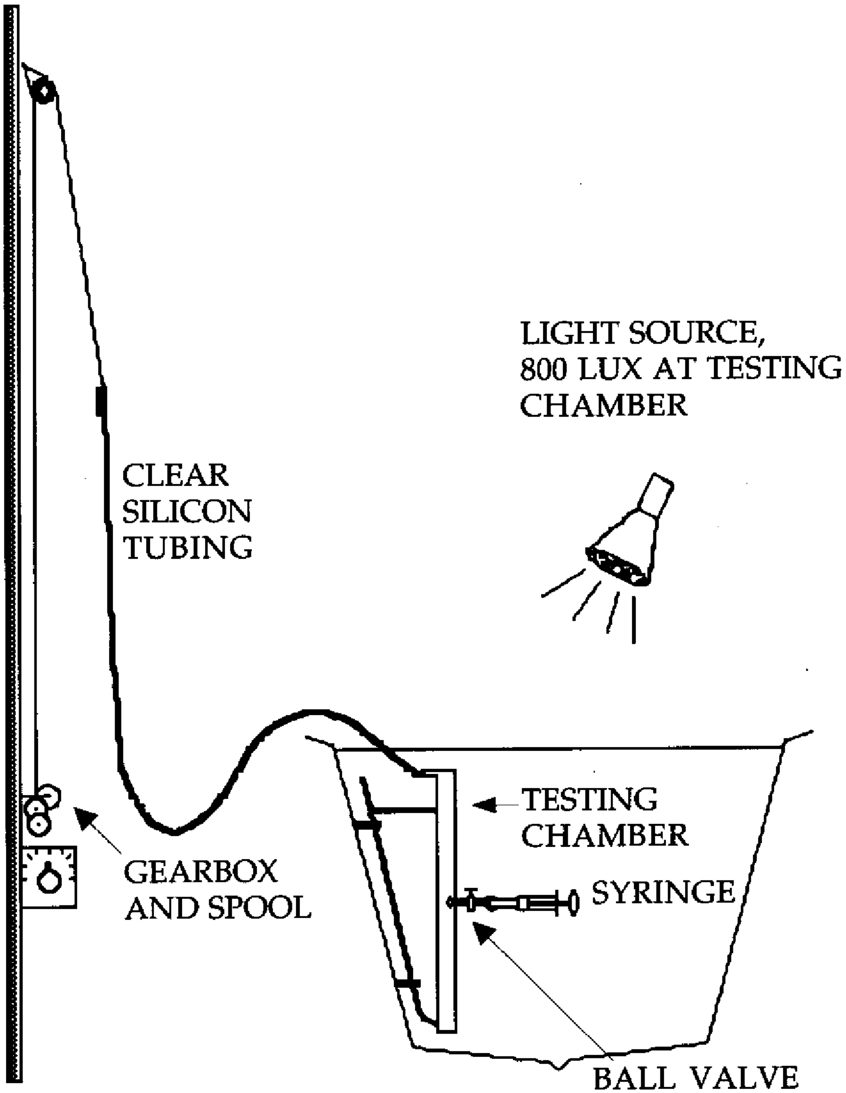


Figure 3. Experimental apparatus used to measure larval response to rate of change in pressure. Pressure in the testing chamber was regulated by the height of the silicon tubing, as the water in the tubing was continuous with that in the testing chamber. Change in pressure was achieved by raising or lowering the silicon tubing at different rates with a variable speed, 12 V electric motor. Lighting was with a 50 W quartz halogen floodlight. The ball valve was opened to introduce larvae into the testing chamber with the syringe, and then sealed for pressure trials. The syringe and testing chamber supports were oriented away from the light source to prevent shadowing.

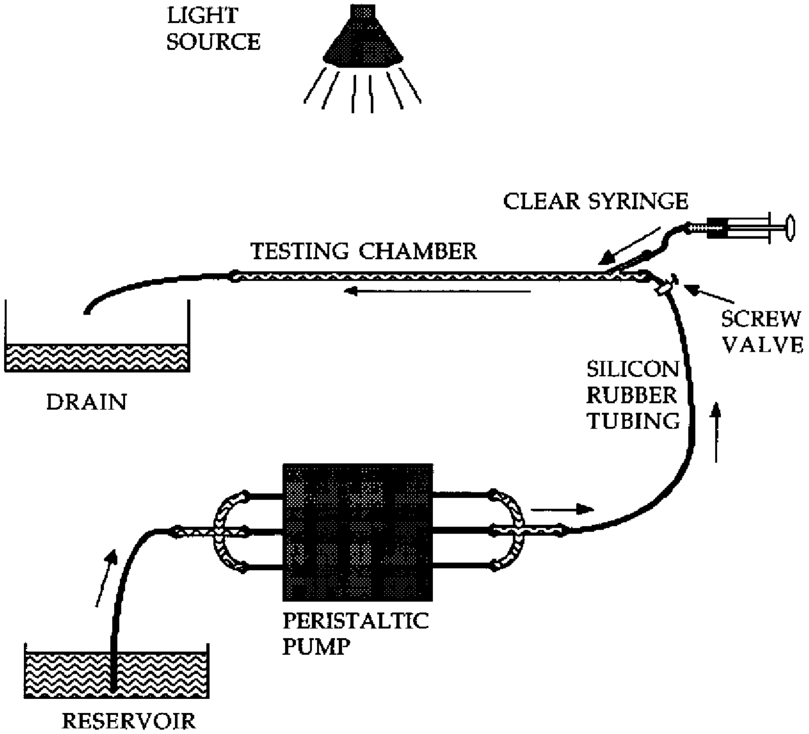


Figure 4. Apparatus used for rheotaxis experiments. Pulsation in flow from the peristaltic pump was reduced by including 1.5 m of silicon tubing between the pump and the glass testing chamber and then constricting tubing immediately before the testing vessel. This caused the silicon tubing to expand and contract, which removed pulsation. Lighting was from a 50 W quartz halogen floodlight, 2.5 m distant and angled at 90° to the testing chamber to produce 80 lux incident on testing chamber.

Results

Swimming and sinking speeds

The mean vertical upward swimming speed of larvae, without pausing, was 1.61 (± 0.382 s.d., n = 30) cm/s. Assuming that larvae did not pause in swimming and also chose to swim vertically upward, this rate of swimming would enable larvae released at 350 m depth to reach the surface waters in about 6 hours. Larvae swam with the dorsal spine foremost and sank in the opposite manner, with the dorsal spine trailing. The average sinking rate for anesthetized larvae was 0.61 (± 0.084 s.d., n = 30) cm/s.

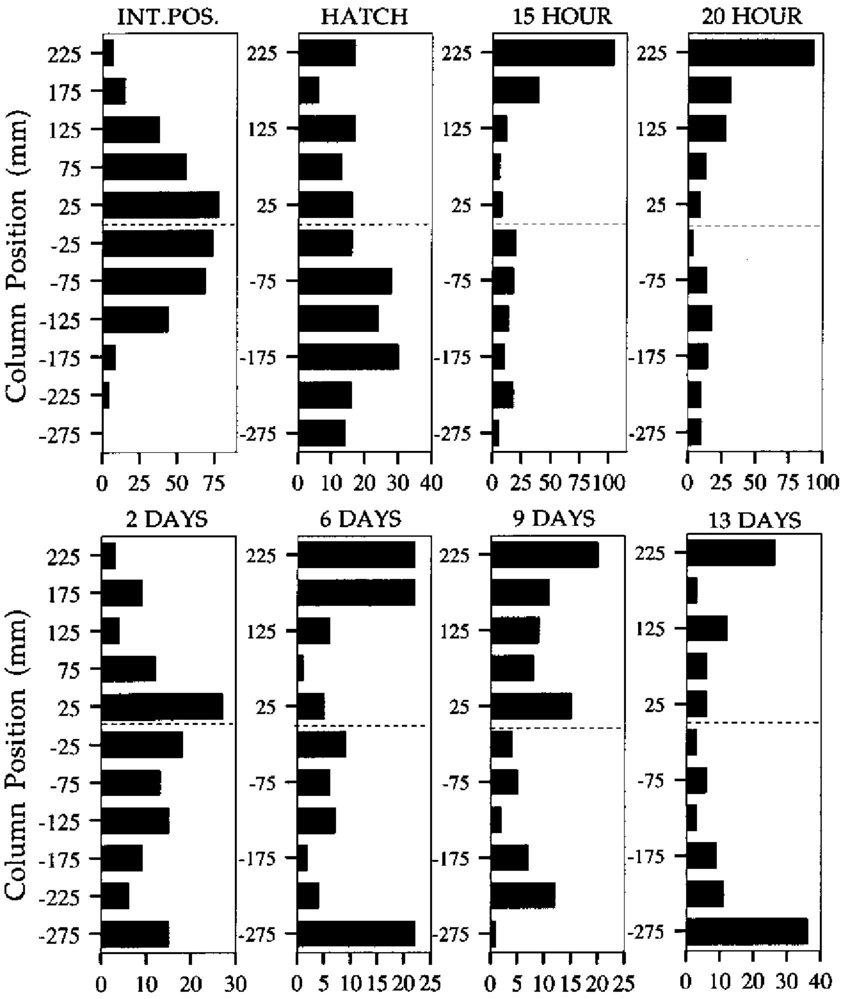


Figure 5. Ontogenic change in geotactic response of stage 1 and 2 zoeae. "Int. Pos." is the distribution of larvae immediately after introduction to the testing column; the mean of this distribution was used to define the zero position of column height in the subsequent geotactic response plots. "Hatch" plot is for larvae collected and tested within 10 minutes of release.

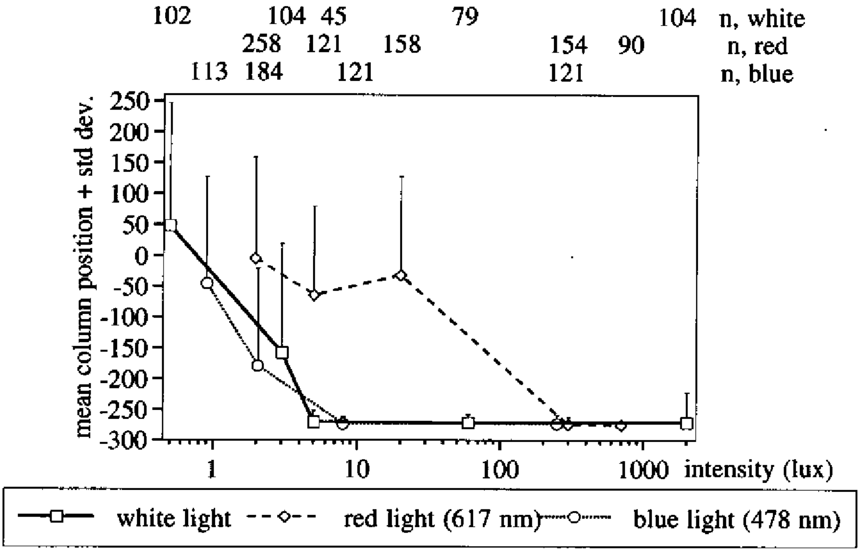


Figure 6. Vertical migration of Z1 larvae in response to white, red (617 nm), and blue (478 nm) light directed from below the vertical testing column. The response of larvae in darkness was measured and has been plotted as the lowest intensity reading for the white light series. This point has been artificially allocated an intensity of 0.5 lux so that light intensity could be plotted on a logarithmic scale. Negative values indicate positive phototaxis, i.e., movement toward the light below the testing chamber (see Figure. 1).

Geotaxis

There was a tendency for stage 1 zoeae to be negatively geotactic but this appeared to be influenced by the age of the larvae, or possibly time of day (Figure 5). Immediately after hatching the larvae did not exhibit any clear geotactic response. Larvae exhibited strong negative geotaxis in tests at 15 h and 20 h but the strength of response declined in older larvae. The mean response of larvae tested at 2 d and 13 d was positively geotactic although the pattern of movement for all larvae tested was not clear with some larvae moving upward in the column and others downward.

Phototaxis

Fixed intensity

In the experimental situation shown in Figure 1 (results Figure 6.), downward movement is positive phototaxis. There was strong phototaxis to blue light of 2 lux while larvae failed to exhibit a strong phototactic

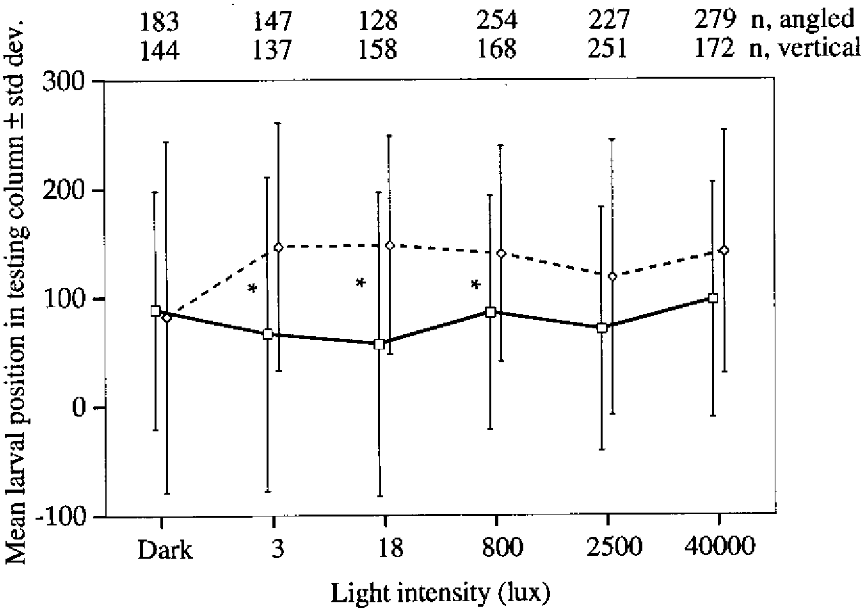


*Figure 7. Migration response of Z1 larvae, in vertical and angled testing columns, to light of different intensities. Means have been artificially displaced sideways to prevent overlap of error bars. Significant differences between distributions of angled and vertical tests are denoted by * at $P < 0.05$. Solid lines = angled column, dashed line = vertically oriented column. Positive values indicate positive phototaxis, i.e., movement toward the light above the testing chamber (see Figure 2).*

response when exposed to red light of 11 lux (Figure 6). In the experimental situation shown in Figure 2 (results Figure 7), a positive phototactic response will result in upward movement. Larvae were phototactic to all intensities tested for white light (3-40,000 lux, Figure 7) and at no intensity were larvae induced to swim or sink downward. There were no significant differences between larval responses to any intensities tested ($P < 0.05$), in both the angled and the vertical columns.

Effect of change in intensity

There was a significant ($P < 0.01$) effect of change in light intensity on column position of larvae (Table 2). This was most apparent at lower light intensities; downward movement (negative phototaxis, Figure 2) was most evident in larvae exposed to changes in intensity between 9-15 lux and 6-15 lux (Figures 8 to 10). In the vertical column, there was a significantly greater movement away from the light source at slow rates

Table 2. Statistical comparisons of the effect of different light intensity changes under different regimes of: rate of change; increasing or decreasing intensity; and angled or vertical testing column.

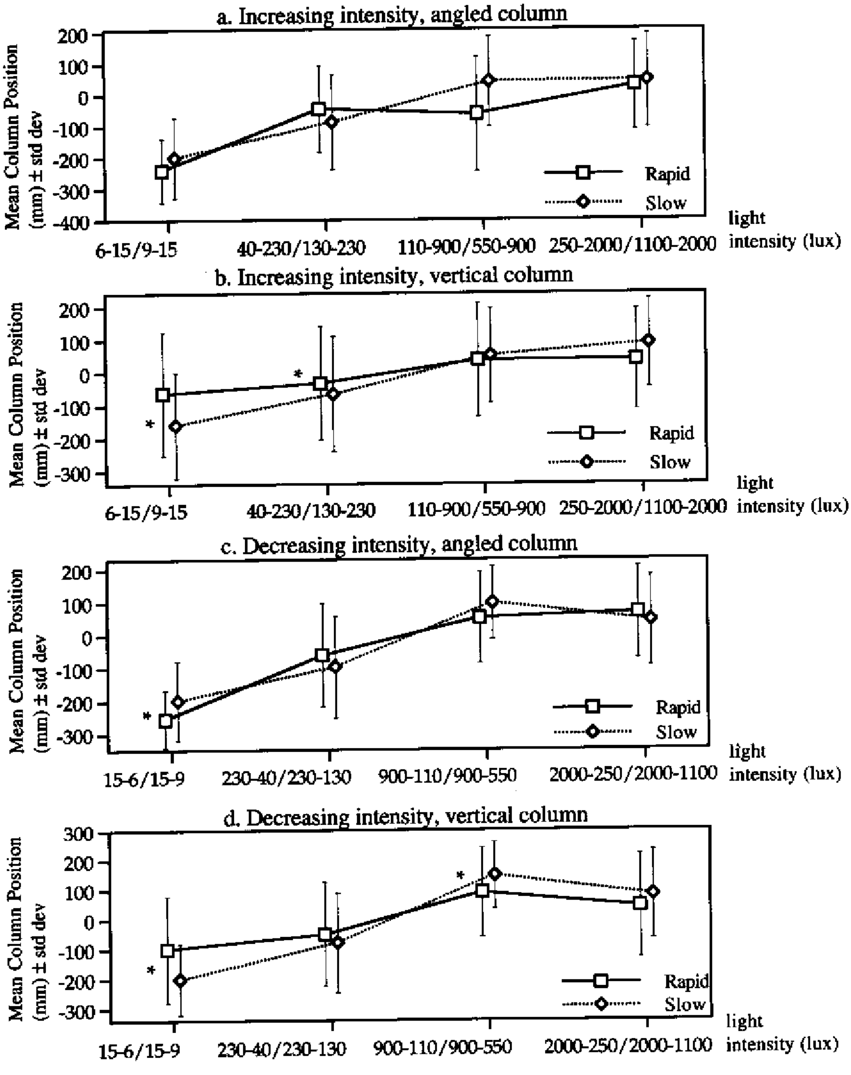
Treatment	Intensity range (lux)				N
Rapidly increasing intensity (angled)	6-15	40-230	250-2,000	110-900	1,098
Rapidly decreasing intensity (angled)	15-6	230-40	900-110	2,000-250	728
Slowly increasing intensity (angled)	9-15	130-230	550-900	1,100-2,000	838
Slowly decreasing intensity (angled)	15-9	230-130	2,000-1,100	900-550	938
Rapidly increasing intensity (vertical)	6-15	40-230	110-900	250-2,000	1,001
Rapidly decreasing intensity (vertical)	15-6	230-40	2,000-250	900-110	1,012
Slowly increasing intensity (vertical)	9-15	130-230	550-900	1,100-2,000	985
Slowly decreasing intensity (vertical)	15-9	230-130	2,000-1,100	900-550	860

Light intensity changes are ranked from lowest to most positive phototactic response, left to right respectively. Bars beneath intensity ranges denote significance by joining non-significant tests ($P < 0.01$). See Figure 2 for experimental apparatus. N = number of larvae per treatment level.

of changes in intensity than at faster rates ($P < 0.05$; Figure 8). There appeared to be no effect of direction of light change (increasing or decreasing intensity) on larval movement (Figure 9).

Effect of orientation of light source

The effect of orientation of light source was investigated by exposing the larvae to an angled light source and comparing the distribution of larvae in a vertical and an angled testing chamber (Figure 2). This was trialed with larvae exposed to white light of fixed intensity (Figure 7) and also with varying intensity (Figure 10). In the fixed light experiments, there was significantly greater movement of larvae along the column in the vertically oriented column than in the column angled directly toward the light source ($P < 0.05$; Figure 7). This trend was not significant at the higher light intensities measured, 2,500 and 40,000 lux, or in darkness ($P > 0.05$).



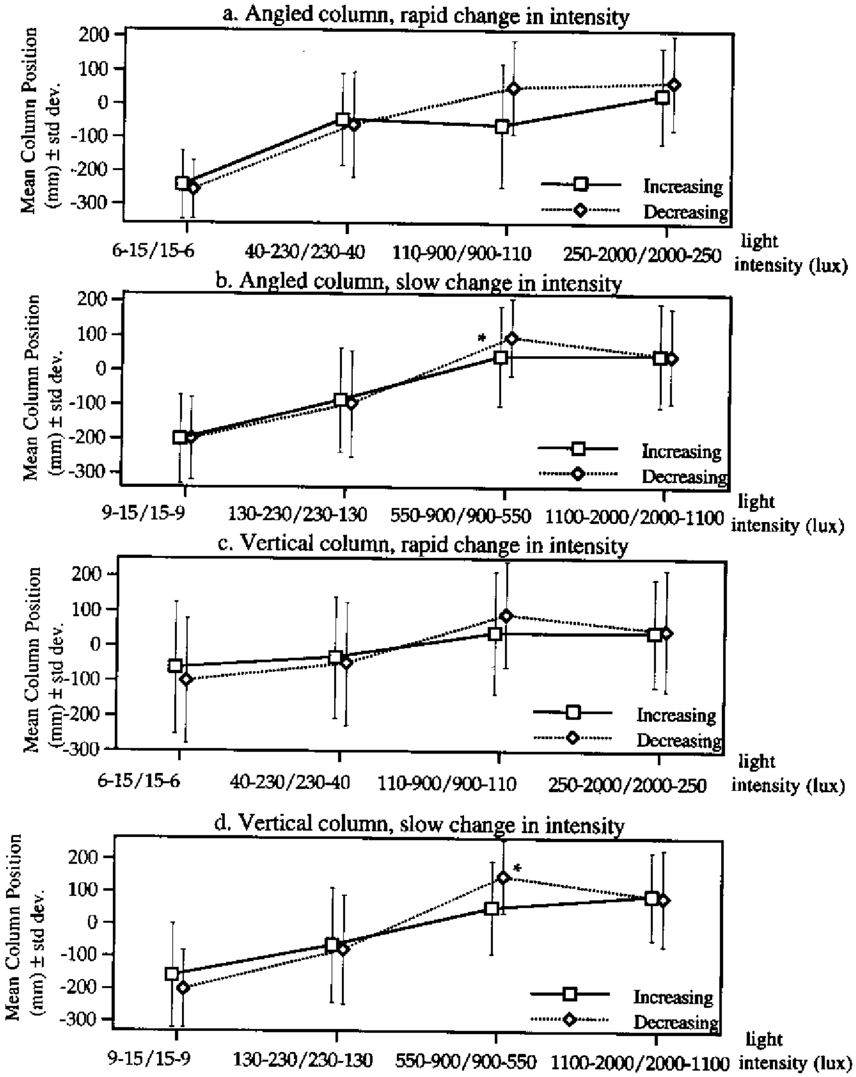
a. Increasing intensity, angled column

b. Increasing intensity, vertical column

c. Decreasing intensity, angled column

d. Decreasing intensity, vertical column

*Figure 8. Effect of rate of change of light intensity on vertical migration in Z1 larvae exposed to different varying light intensities. The effect of fast and slow rates of change were tested in combinations of decreasing/ increasing intensity and with the testing column oriented directly toward the angled light source (angled) or else oriented vertically (vertical). Plot symbols have been artificially displaced sideways to prevent overlap of error bars. Positive values indicate positive phototaxis (see Figure 2). * indicates significance at $P < 0.05$.*


a. Angled column, rapid change in intensity

b. Angled column, slow change in intensity

c. Vertical column, rapid change in intensity

d. Vertical column, slow change in intensity

*Figure 9. Effect of direction of change (increasing or decreasing) of light intensity on vertical migration in Z1 larvae exposed to different varying light intensities. The effect of direction of change was tested in combinations of rapid/slow change in intensity and with the testing column oriented directly toward the angled light source (angled) or else oriented vertically (vertical). Plot symbols have been artificially displaced sideways to prevent overlap of error bars. Positive values indicate positive phototaxis (see Figure 2). * indicates significance at $P < 0.05$.*

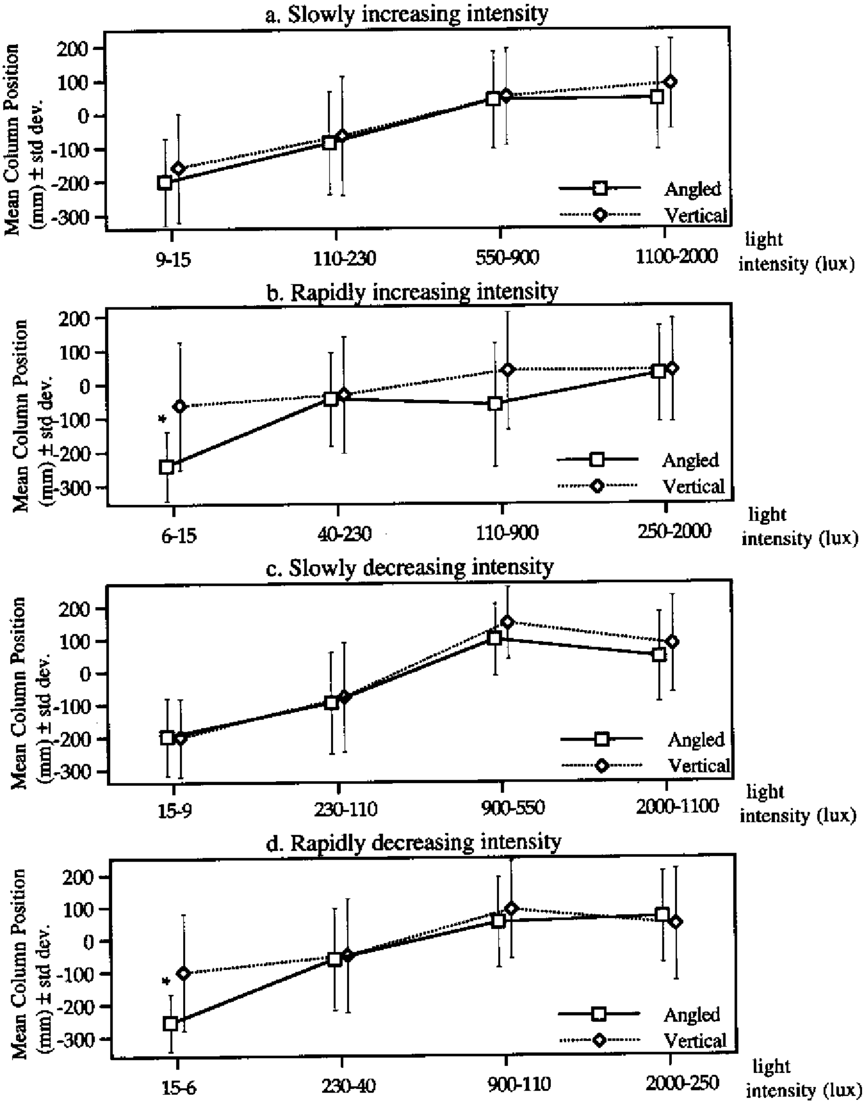


*Figure 10. Effect of orientation of testing column to light source on vertical migration in Z1 larvae exposed to different varying light intensities. The effect of orientation was tested in combinations of decreasing/increasing intensity, at rapid/slow rates. Plot symbols have been artificially displaced sideways to prevent overlap of error bars. Positive values indicate positive phototaxis (see Figure 2). * indicates significance at $P < 0.05$.*

In the varying light intensity experiments, significantly different movement between the vertical and angled columns occurred only when larvae exhibited negative geotaxis in response to rapidly changing light intensity ($P < 0.05$; Figure 10).

Barokinesis

Larvae did not clearly respond differently to increasing or decreasing pressure under conditions of total darkness or with 800 lux overhead lighting (Figure 11). There was no clear effect of the rate of change of pressure on larval movement. However, the mean upward movement of larvae when exposed to overhead lighting was smallest, although still upward, when the water column was lowered (decreasing pressure) at 1.85 cm/s (Figure 11b). This rate of change was the rate closest to the observed swimming speed of stage 1 zoeae, 1.61 cm/s.

Rheotaxis

Larvae exhibited positive rheotaxis with the greatest proportion of larvae responding at a current speed of 1.12 cm/s (Figure 12). At lower current speeds (0.35 & 0.59 cm/s), many larvae appeared to be unaware of the current and swam back and forth along the testing column apparently in response to the lighting. At current speeds greater than 1.12 cm/s (1.4 and 1.87 cm/s) larvae tended to swim into the current but failed to maintain position.

Discussion

The pattern of vertical swimming resulting in upward movement was the same as that described by Sulkin (1984); larvae are negatively buoyant which is countered by upward orientation and locomotion to produce upward swimming. Passive sinking rates of *P. gigas* ($x = 0.61$ cm/s) were similar to that of stage 1 zoeae of several other brachyuran species: *Cancer magister*, 0.64 cm/s (Jacoby 1982); *Ebalia tuberosa*, 0.60 cm/s (Schembri 1982); and *Hemigrapsus oregonensis*, 0.67 cm/s (Arana and Sulkin 1993). The upward locomotory force of these species is sufficient to counter sinking and produces similar mean upward swimming speed to that of *P. gigas* (1.61 cm/s): *Cancer magister*, 0.95 cm/s (Jacoby 1982); *Ebalia tuberosa*, 0.96 cm/s (Schembri 1982); and *Hemigrapsus oregonensis*, 1.78 cm/s (Arana and Sulkin 1993). As discussed by Sulkin (1984), depth regulation relies on the interaction between passive sinking, active swimming, and orientation. Orientation and the speed of swimming are then adjusted in response to external stimuli, such as gravity, light, and pressure, to induce depth regulatory response.

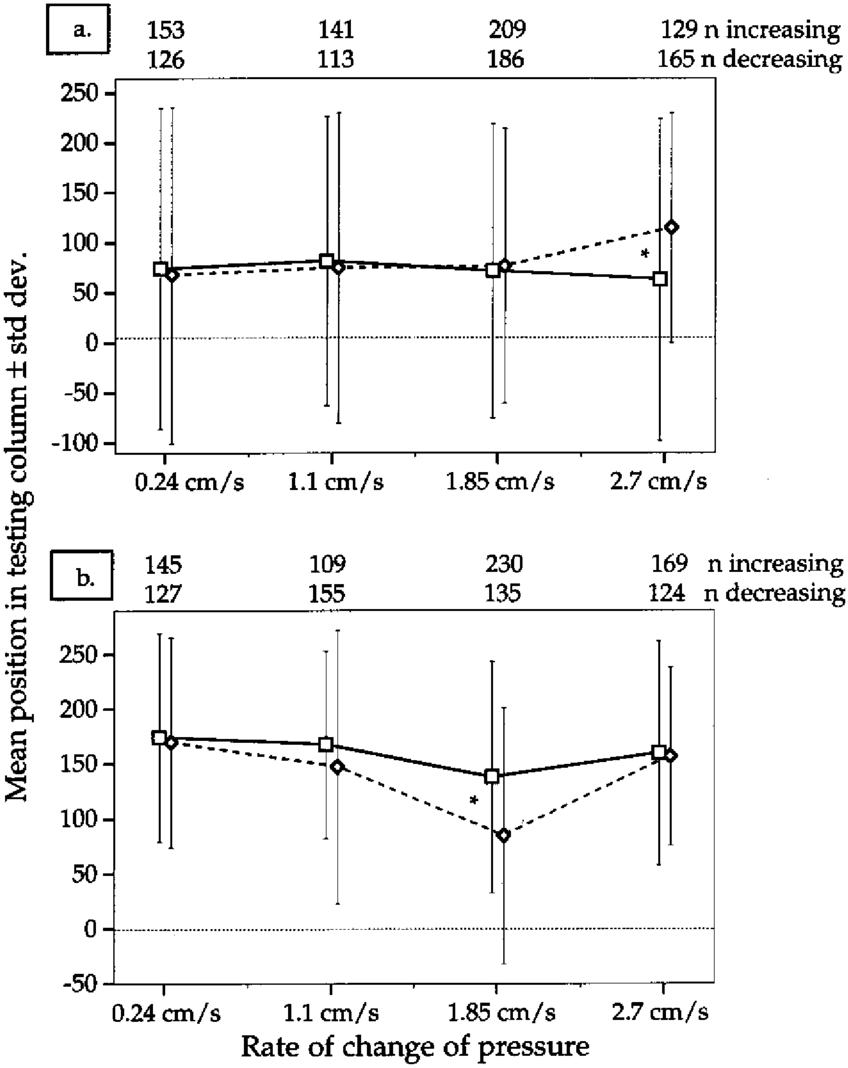


Figure 11. Comparison of the effect of increasing and decreasing pressure of different rates on the vertical migration of Z1 larvae held in darkness (a) or with 800 lux overhead lighting (b). Means have been displaced sideways to prevent overlap of error bars. Solid line = increasing pressure, dashed line = decreasing pressure.

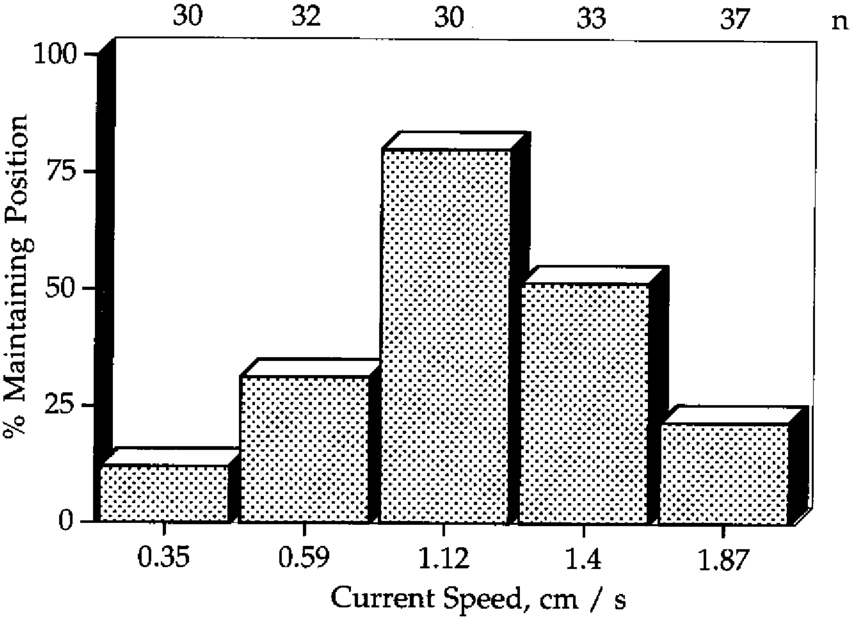


Figure 12. Rheotactic response of stage 1 larvae to current velocities of 0.35-1.87 cm/s. Values represent percentage of total larvae responding to stimuli so no measure of error is presented.

Geotaxis

The observed pattern of geotaxis suggests that larval swimming is not clearly affected by gravity immediately after hatching. After this initial period the larvae exhibit strong negatively geotaxis which would suggest that larvae migrate upward to the surface waters. The speed of larval swimming suggests that this would be accomplished in a period of around 6 hours if the larvae were released at 350 m and did not rest. A negative geotactic response was also observed in the first zoeal stage of the deep sea crab, *Geryon quinquedens* (Kelly et al. 1982).

The strong negative geotactic response observed for *P. gigas* decreased in older larvae and it may be that the primary function of the geotactic response is to induce upward migration from the deepwater site of release to the prey-rich surface layers. An ontogenic change in geotactic behavior between instars has also been reported for shallow water species *Leptodius floridanus* and *Panopeus herbstii* (Sulkin 1973), *Callinectes sapidus* (Sulkin et al. 1980), and *Ebalia tuberosa* (Schembri 1982). However, the changes in geotaxis observed in *P. gigas* differ from these reports as there was a decline in geotactic response within stage 1, rather than between instars.

Although the pattern of geotactic response up to 20 hours appears clear, the results of trials from 2 to 13 days are more difficult to interpret and they may be confounded by at least two factors. Diel cycles have been shown to persist in the laboratory which may have influenced results from these trials (Cronin and Forward 1986). Attempts were made to only test healthy larvae by selecting active larvae; however, less fit larvae may have been selected for testing and may have compromised results.

Phototaxis

The spectral sensitivity of larvae in this study was essentially the same as that described for several other species in more detail by Forward (1987), and Forward and Cronin (1979). Larvae were more sensitive to shorter blue wavelengths, which have better penetration, than red wavelengths.

Light adapted larvae were not induced to descend in response to overhead white light of any intensity tested. The experimental design used in this study was intended to demonstrate the approximate field conditions where sinking may have been induced by light. Consequently, the testing chamber was oriented vertically so that negative phototaxis would be required to counter negative geotaxis in order to produce net downward movement (light-induced positive geotaxis). Comparisons between other studies where phototactic response was examined with horizontally oriented columns should be made cautiously.

Where phototaxis has been examined independently of geotaxis by the use of horizontal testing columns, larvae tend to exhibit negative geotaxis at low intensities and positive phototaxis at high intensities. This pattern has been observed in: *Rhithropanopeus harrisii* (Forward et al. 1984); *Cancer gracilis, Lophopanopeus bellus bellus, Hemigrapsus oregonensis* (Forward 1987); and *Paralithodes camtschaticus* (Shirley and Shirley 1988). Forward (1987) attributed this pattern to predator avoidance.

Avoidance behavior, or negative phototaxis at low light intensity, is not clearly demonstrated in vertically oriented columns where the natural behavior of negative geotaxis is incorporated. Both Schembri (1982, *Ebalia tuberosa*) and Jacoby (1982, *Cancer magister*) tested the response of crab larvae to different light intensities in vertical columns and observed only upward movement. It is tempting to infer that the positive phototactic response of *P. gigas* (Figure 7) indicates that the larvae congregate at the surface during the day. However, Forward (1985 and 1988) considers the absence of negative phototaxis in vertically oriented columns to be a laboratory artifact in most studies. For example, Stearns and Forward (1984) found that the copepod *Acartia tonsa* was positively phototactic to all light intensities although the natural migration pattern is nocturnal. Simulated natural underwater lighting distribution is difficult to achieve, so the observed response of *P. gigas* may be nothing more than a laboratory artifact despite attempted simulation of natural light distribution.

Larvae exposed to change in intensity at low light levels responded by downward movement. Conversely, larvae exposed to change in intensity at higher light levels were unaffected. This response was more pronounced at slower rates of change in intensity (in the vertical column only) but was not affected by the sign of intensity change (increasing or decreasing).

Light-induced downward movement in response to change in light intensity, regardless of whether intensity is increasing or decreasing, has not been previously reported. This response may be a variation of the predator avoidance or shadow response proposed by Forward (1986) where negative phototaxis was induced by a rapid decrease in intensity. The shadow response proposed by Forward (1986) was only initiated by rapid decreases in intensity and not increases as was observed in this study. Forward (1986) noted that the change in intensities which resulted in negative phototaxis were too rapid to simulate dusk or dawn. Because of this, he believed that the larval responses did not represent a typical behavior relevant to diel vertical migration. The simulated rates of intensity changes in this study were also greater than that at dawn or dusk (Table 1), suggesting the response in *P. gigas* was a predator avoidance, shadow response. The response of stage 1 *P. gigas* zoeae to change in light intensity, only at low light levels, suggests that the larvae are adapted to respond to low levels; this supports the dismissal of the results of fixed light intensity trials as a laboratory artifact.

There was significantly greater ($P < 0.05$) upward movement of larvae in the vertically oriented column exposed to fixed intensity of light, compared to the column angled directly toward the light source (45°). This suggests that geotaxis is the orienting cue while photokinesis controls locomotory activity. Forward (1985) observed this same interaction in larvae of the xanthid crab *Rhithropanopeus harrisii*. Geotaxis appeared to be less important in the larval response to changes in light intensity at low light levels. When downward movement occurred in response to rapidly changing intensity, the larval distribution was farther from the origin in the angled column. This suggests that larvae were actively swimming from the light, rather than passively sinking. In this case, the response is a true negative geotaxis rather than light-induced, positive geotaxis.

Barokinesis

Larval detection and response to small changes in pressure have been used to explain vertical migration patterns, as it is considered that pressure response provides a negative feedback on vertical movement

(Knight-Jones and Morgan 1966). Stage 1 zoeae of *P. gigas* did not appear to respond to small pressure changes; this has been reported elsewhere for species where the larvae occupy water of considerable depth: *Callinectes sapidus* (Sulkin et al. 1980); *Geryon quinquedens* (Kelly et al. 1982); and *Hemigrapsus oregonensis* (Arana and Sulkin 1993). Barokinesis has been shown to change dramatically with ontogeny (Bentley and Sulkin 1977; Wheeler and Epifanio 1978) so older larvae of *P. gigas* may possess greater pressure sensitivity.

Rheotaxis

Stage 1 zoeae of *P. gigas* were able to detect currents and actively swam against them. Larvae appeared to be unable to detect slight currents below 1.12 cm/s and they were swept along by currents slower than their maximum swimming speed (1.4 and 1.61 cm/s respectively). The combination of the ability of larvae to detect currents, and then to swim against them, resulted in a narrow window within which larvae could maintain position. This suggests that rheotaxis may not be important in larval dispersal. Rheotaxis has also been observed in estuarine species such as the megalopae of *Cancer magister* (Fernandez et al. 1994) and is thought to assist in movement to and from the estuary. With open ocean species, the function of rheotaxis is less obvious as the environment is more homogenous. Shirley and Shirley (1988) also observed rheotaxis in an oceanic species, *Paralithodes camtschaticus,* and suggested that the function of rheotaxis in the oceanic environment may be important for zoeal feeding and predator avoidance.

Conclusions

Based on observed negative geotaxis, first stage zoeae of giant crab probably ascend to the surface waters after hatching. This initial upward migration is probably the main function of the initially strong geotactic response of larvae. As the gravity-initiated strong upward swimming declines with age, the role of geotaxis may be to orient larvae rather than to induce migration. This would produce vertical movement in response to angled light stimuli as appeared to occur in this study. The observed negative phototaxis of larvae to increases and decreases in low light intensities has not been observed in estuarine species and may be a variation of the previously reported shadow response. However, assigning function to this unusual response is speculative and further research is required if the function is to be clarified. Sensitivity of larvae to intensity changes at only low light levels suggests that larvae are adapted for low light conditions. The presence of a rheotactic response is surprising in an oceanic species and may affect the dispersion of larvae by currents. Although rheotaxis may affect dispersal, the biological function of the response is likely to be otherwise in an oceanic environment, perhaps predator avoidance or prey capture.

Behavioral responses of oceanic, deepwater species have been investigated in only a few studies. Understanding the nature of these responses to oceanic conditions may assist in understanding other mechanisms such as survival and dispersal.

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High Latitude Crabs: Biology, Management, and Economics
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Application of Kriging Trawl Survey Data to Estimate Red King Crab Distribution and Abundance in Bristol Bay, Alaska

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Abstract

Annual abundance of legally harvestable male red king crabs (*Paralithodes camtschaticus)* in Bristol Bay, Alaska, has historically been estimated using an "area-swept" technique applied to catch data from annual National Marine Fisheries Service (NMFS) eastern Bering Sea trawl surveys. The area-swept estimation method does not fully utilize the spatial nature of the survey data in estimation of either abundance or the variance of the abundance estimate. "Kriging" is a geostatistical technique for prediction when spatial dependencies are present in data. We investigated the utility of kriging in estimating Bristol Bay legal red king crab abundance and density from the NMFS trawl survey data, and compare abundance estimates based on kriging to those based on the area-swept technique. Problems encountered in applying kriging to the red king crab data include the non-Gaussian statistical distribution of catch numbers in the trawl survey, the wide spacing (20 nautical miles) of tow locations in the NMFS trawl survey grid relative to the highly aggregated spatial distribution of red king crabs; and large-scale spatial trends in the data that are indicative of non-stationarity. A closer look is given by investigating a pot survey and comparing the results of the spatial variability to those found in the trawl survey.

Introduction

The National Marine Fisheries Service (NMFS) has conducted demersal trawl surveys of the eastern Bering Sea (EBS), excluding 1962-1965, an-

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Contribution PP-128 of the Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, Juneau.

nually since 1955 (Figure 1a). The purpose of these trawl surveys was to estimate stock abundance of commercially important fish and crab. Abundance estimates were calculated using the area-swept method, in which average catch-per-unit-effort (CPUE) from individual survey tows is expanded for a prespecified strata of the Bering Sea (Bakkala et al. 1985, Wakabayashi et al. 1985). This methodology, however, does not account for possible spatial correlation that may exist between the CPUE of different tows, in which case the population estimate variances would be overestimated, if autocorrelation existed.

Geostatistics, specifically kriging (a linear estimator which accounts for autocorrelation), were developed within the mining discipline to estimate ore-grade distributions (Matheron 1963). Geostatistic techniques have now been employed in several fields not directly related to mining, such as agriculture (Vieira et al. 1982), entomology (Kemp et al. 1989), soil deposition (Haas 1990), fish stock abundance (Petitgas and Poulard 1989), and shellfish stock abundance (Simard et al. 1992). However, due to the theory and assumptions associated with kriging, the results of these studies have sometimes yielded estimates without increased accuracy. Thus, kriging has not always provided significant benefits to the researcher or manager. This paper will investigate the use of kriging in assessing legal male red king crab (*Paralithodes camtschaticus)* stock distribution and abundance in Bristol Bay.

Methods

Data collection and conversion

Trawl survey data were collected by NMFS during annual EBS trawl surveys. The stratified systematic survey was designed to assess a large portion of the EBS (Figure 1a). In this paper, only trawl data from 1979, 1983, 1993, 1994, and 1995 surveys within Area T, the Bristol Bay King Crab Registration Area (ADF&G 1994), were used in the analysis. The 1979 trawl survey data was used because it had the largest catch of legal red king crab in the years available for study, whereas the 1983 trawl survey had the lowest catch. The 1993, 1994, and 1995 trawl surveys were used because they were the most recent surveys, and data from these years were most comparable to the 1994 ADF&G pot survey. A more detailed analysis of a subarea within Area T (Figure 1b) was conducted using 1993, 1994, and 1995 data sets. Selection of the subarea was based on the highest commercial production of legal crabs from 1990 to 1993 commercial fisheries, as documented in the ADF&G fisher sales (fish ticket) database.

For each tow, trawl location, distance towed, width of net opening, abundance, and catch composition were recorded. Estimated area fished by the trawl, recorded in square nautical miles (nmi^2), was calculated by multiplying the distance towed by the width of the net opening. From

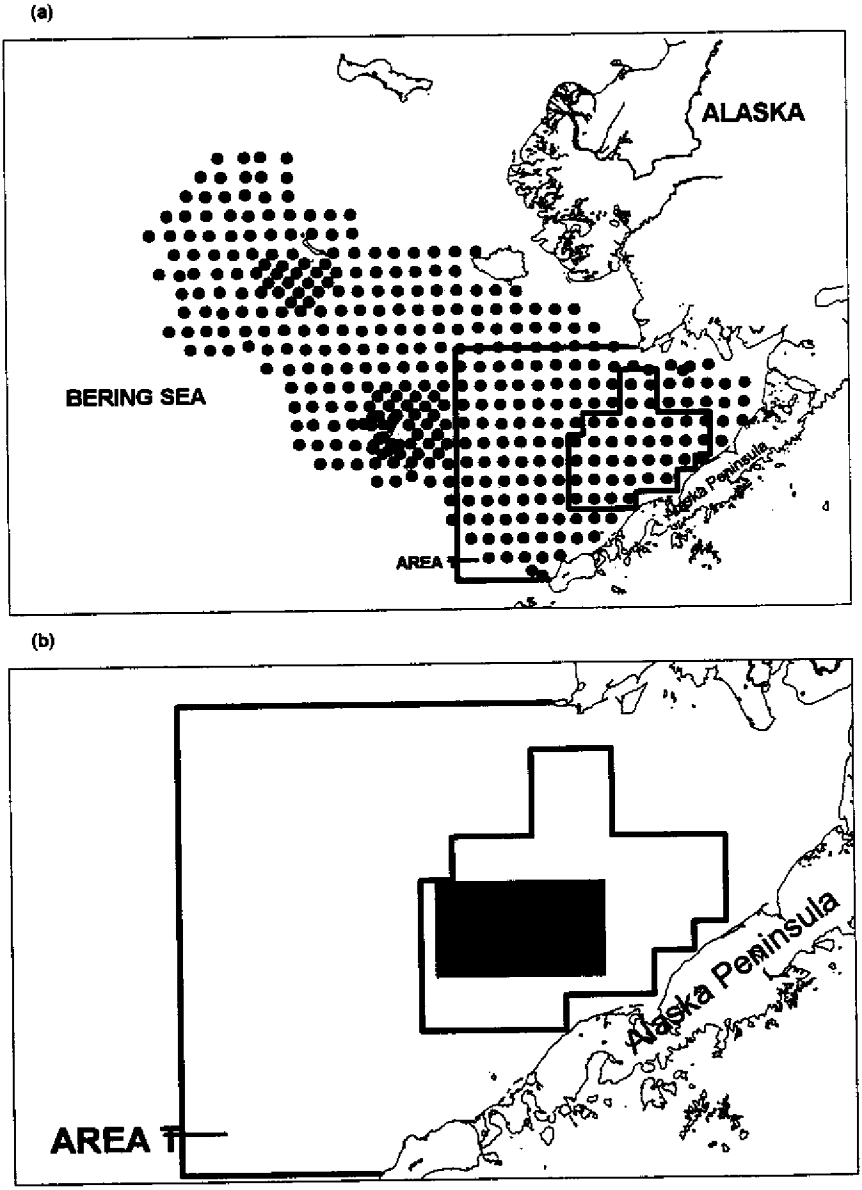

Figure 1. Location of the 1993 EBS trawl survey (a), and location of the 1994 ADF&G pot survey (b). The subarea shown within the Bristol Bay king crab Registration Area T denotes the area of highest harvest and the source for analysis of the 1993-1995 data sets.

catch composition sampling, the number of legal red king crabs caught per tow was recorded. CPUE was calculated and recorded at each location in number of legal red king crabs per hectare (ha). Estimates of population size were based on Area T and the subarea (high-harvest area), with no further stratification.

Tow locations were recorded in degrees longitude and latitude but were converted to a Cartesian coordinate system, distance between points being measured in kilometers (km), because distance between locations was needed for the statistical analysis. A projection equation was used to accomplish the conversion (Snyder 1983).

In addition to the trawl survey, a pot survey was performed within a limited portion of Area T in fall 1994 (Figure 1b). Four pots were deployed at each of 20 sites within a systematic grid. CPUE was calculated by dividing the total number of legal red king crabs caught at a station by the number of pots fished at that station (usually 4). Longitude and latitude locations were converted to a Cartesian coordinate system as described above.

Statistical analysis

Assumptions of spatial stationarity and distribution of the variable are necessary when performing certain geostatistic techniques, i.e., kriging. Statistical stationarity, as used in this paper, describes the variability between points as a function of distance, not location. To address these assumptions, a histogram for each year was made, along with a plot of CPUE at sample locations. Departures from spatial stationarity and the variables distribution can lead to bias, mostly in the variance estimation.

To visualize and estimate the spatial autocorrelation, sample semivariograms were calculated for each data set. Semivariograms are a measure of variability between points and can be used to estimate covariances between different points. Sample semivariograms were calculated using both the "standard" estimator (Matheron 1963) and the "robust" estimator (Cressie 1994). The robust estimator for the sample semivariogram is not influenced by outliers to the degree that the standard estimator is. Sample semivariograms were also calculated when data sets were sufficiently large to consider anisotropy, i.e., different spatial autocorrelation depending on the direction. The 1993-1995 sample semivariograms were fit to an exponential semivariogram model using weighted least squares.

Ordinary kriging (which we will refer to as simply "kriging") was performed on the 1993, 1994, and 1995 trawl survey data within a subarea of Area T. Point estimates using kriging and associated variances were calculated at regular intervals within the area. A global estimate of the mean number of legal red king crab per hectare (ha) and its variance was also calculated for the subarea using kriging methodology (e.g. Isaaks and Srivastava 1989, Journel and Huijbregts 1989, Cressie 1994).

All statistical analyses were performed using Splus (Statsci 1994). Preprogrammed functions were used when available. Many of the calculations, such as the sample semivariogram estimates, were performed from functions written by the authors. All maps were created in MapInfo (MapInfo 1994).

Results

Trawl survey in Area T

1979 data set

In 1979, three survey vessels were used to conduct additional tows within Area T (Figure 2a); however, due to differences in average catch per tow in similar areas, data from one vessel was not used in the analysis (Figure 2b). The histograms for the CPUE and the log of CPUE in 1979 indicated that the distribution of CPUE was neither Gaussian nor lognormal (Figure 3). There seems to be greater variability in the midsection of Area T than in the borders (Figure 2b), indicating a lack of stationarity.

The difference in the isotropic sample semivariograms and the associated model (Figure 4a), especially the sills (the upper limit of the variogram or semivariogram model), indicates a strong influence by outliers. The anisotropic sample semivariogram (robust estimator only) reveals a shorter range (distance between points where 90%-100% of sill is reached) in the north-south direction than the east-west direction (Figure 4b). No kriging estimates were made for 1979 as the CPUE distribution was highly skewed and the CPUE lacked stationarity.

1983 data set

No extra samples were taken in 1983 (Figure 5), and the CPUE distribution was neither Gaussian nor lognormal (Figure 6). Furthermore, with so few legal red king crabs caught, it is hard to tell whether CPUE was stationary. There was little variability in the north but virtually no variability in the southwest sections, indicating a lack of stationarity (Figure 5).

The isotropic sample semivariograms (Figure 7a) indicate outliers; however this is more an artifact of the large number of zero values than true outliers. There was little difference between the north-south direction and the east-west sample semivariograms (Figure 7b). No kriging estimates were made for 1983 because the CPUE distribution was highly skewed and the CPUE lacked stationarity.

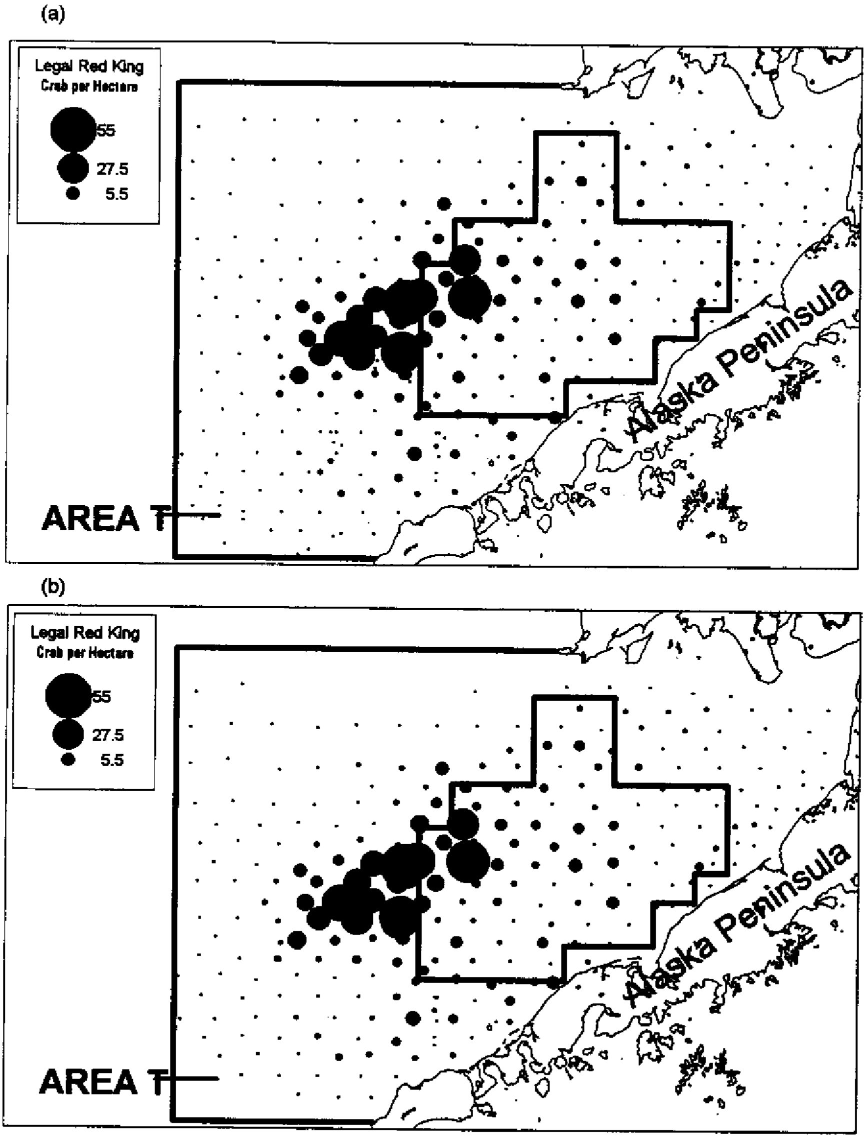

Figure 2. Catch of legal male red king crabs per hectare in the 1979 EBS trawl survey at all tow locations (a) and at tow locations used in the statistical analysis (b).

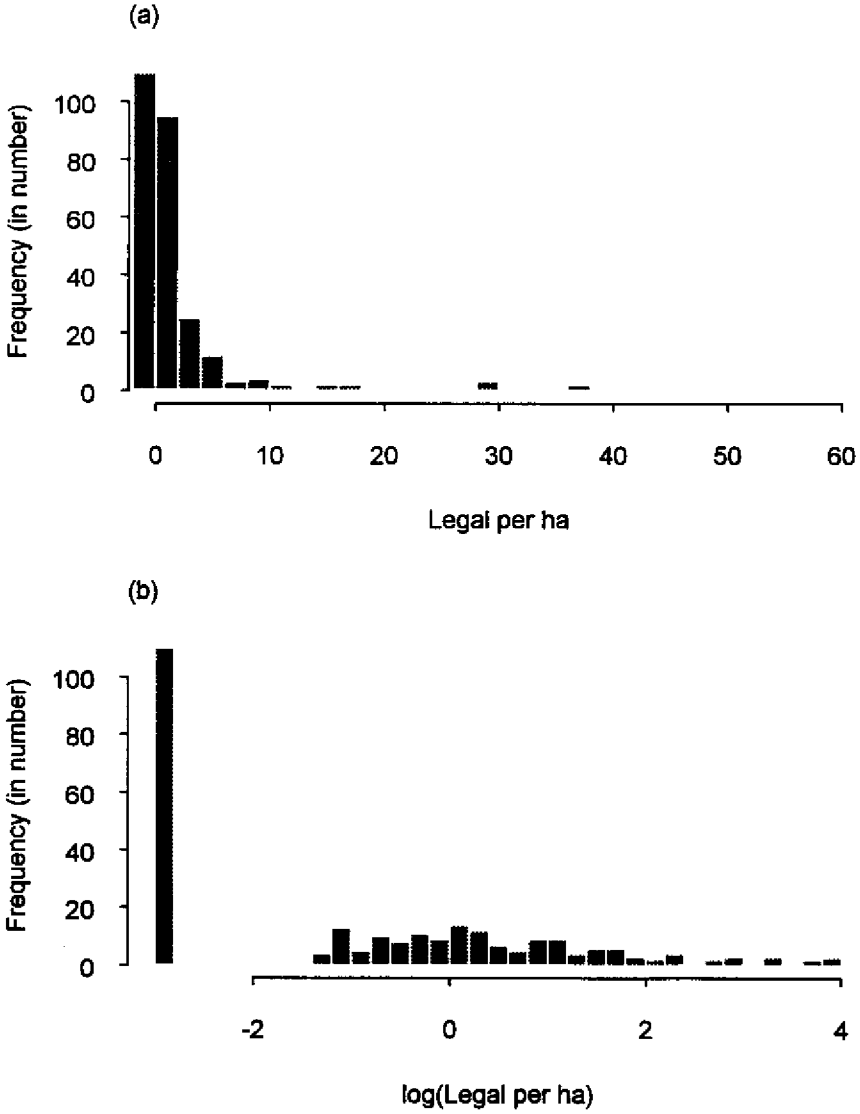

Figure 3. Histograms of legal red king crabs per hectare (a) and log of legal red king crabs per hectare (b) caught in the 1979 EBS trawl survey.

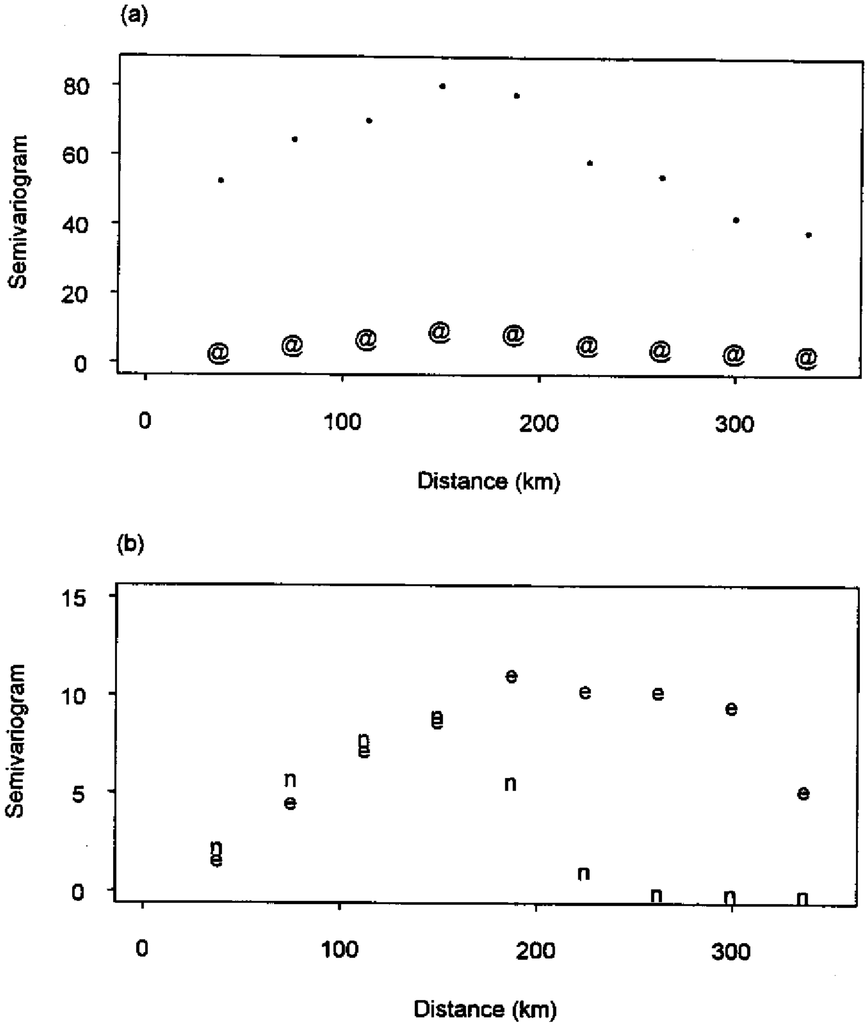

Figure 4. Sample semivariograms of legal red king crab per hectare caught in the 1979 EBS trawl survey. Semivariograms were estimated using the standard method (.) and the robust method (@) and assuming isotropy (a); semivariograms in (b) were estimated using the robust method in the east-west direction (e), and in the north-south direction (n).

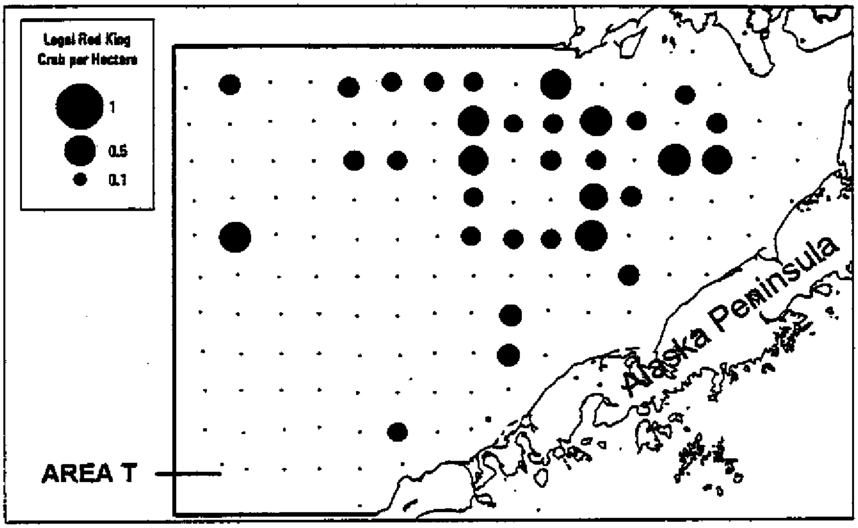

Figure 5. Catch of legal red king crab per hectare from the 1983 EBS trawl survey at all tow locations in Area T.

1993-1995 data sets

The reason we investigated a subarea of Area T was to lower the number of CPUE values equal to zero, and to increase the chance of spatial stationarity. The subarea of Area T chosen encompasses approximately 50,355 km^2 (Figure 1b).

Extra samples were rarely taken in 1993 or 1994 (Figure 8), and though extra samples were taken within a select area in 1995 (Figure 9), they were not incorporated in this study (even those within the subarea), because of a significantly higher CPUE between the two ships employed in the 1995 survey. As can be seen by the histograms for each year (Figure 10), none of the CPUE distributions are Gaussian or lognormal. However, the distributions of the CPUE within the subarea were not nearly as positively skewed (Figures 10d, 10e and 10f). Although the 1993 and 1995 data sets each had one value much higher than the rest, overall there was no strong evidence to suggest a lack of stationarity (Figures 8 and 9).

Trawl survey in subarea of Area T

1993 data set

Due to a single high value, the two sample semivariograms are different (Figure 11a). An exponential model was fit to the robust sample semivariogram values, with an estimated nugget (the vertical jump from the

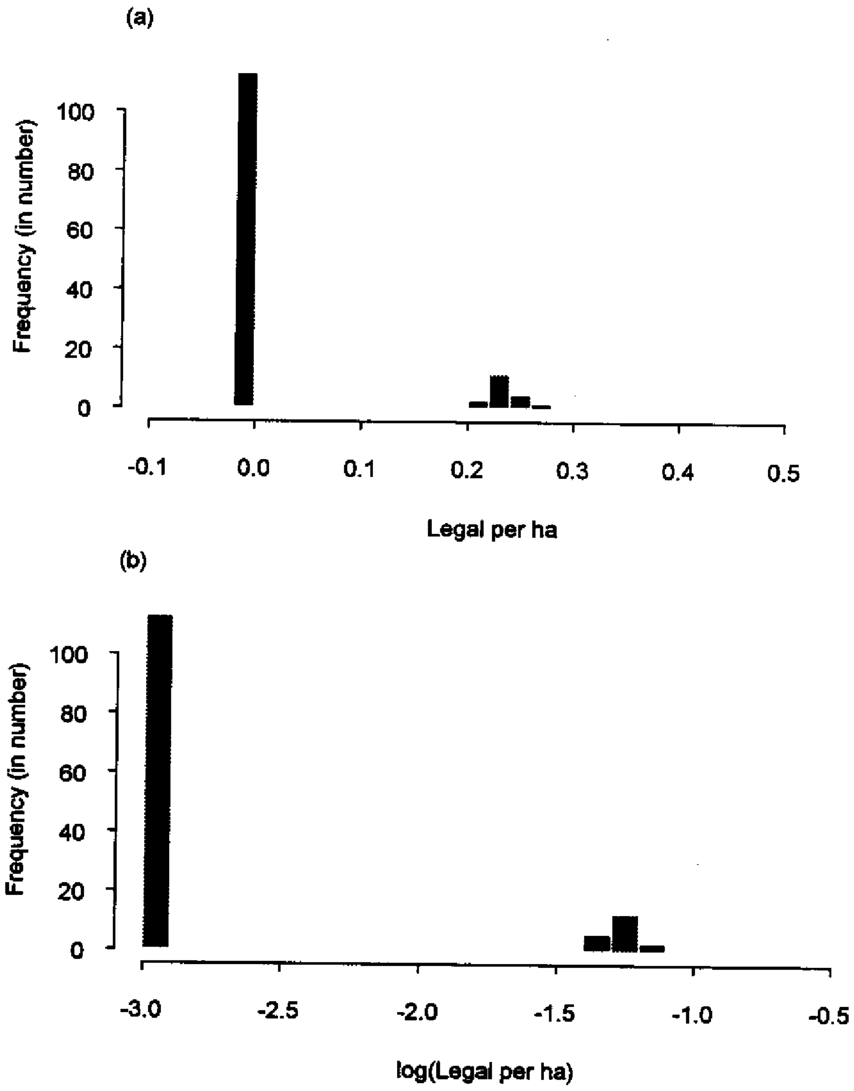

Figure 6. Histograms of legal red king crab per hectare (a) and log of legal red king crab per hectare (b) caught in the 1983 EBS trawl survey.

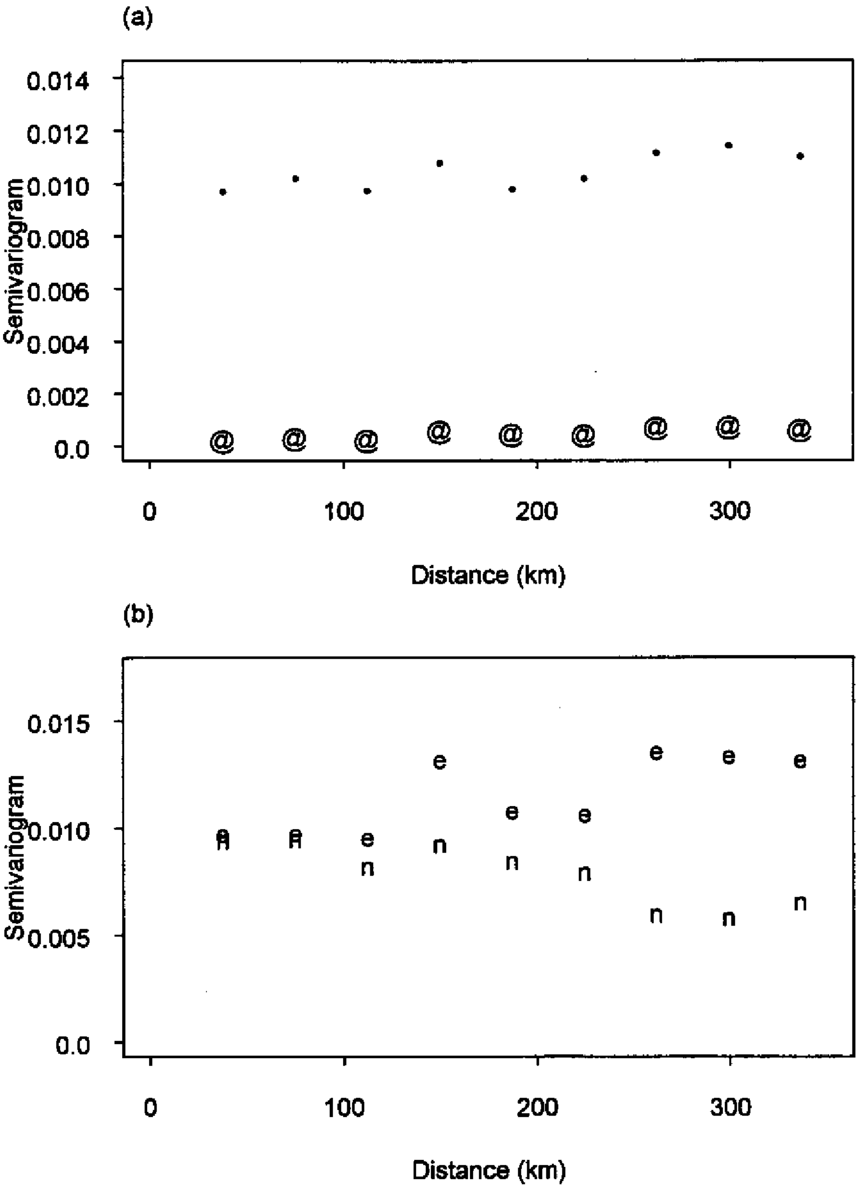

Figure 7. Sample semivariograms of legal red king crab per hectare caught in the 1983 EBS trawl survey. Semivariograms were estimated using the standard method (.) and the robust method (@) and assuming isotropy (a); semivariograms in (b) were estimated using the robust method in the east-west direction (e), and in the north-south direction (n).

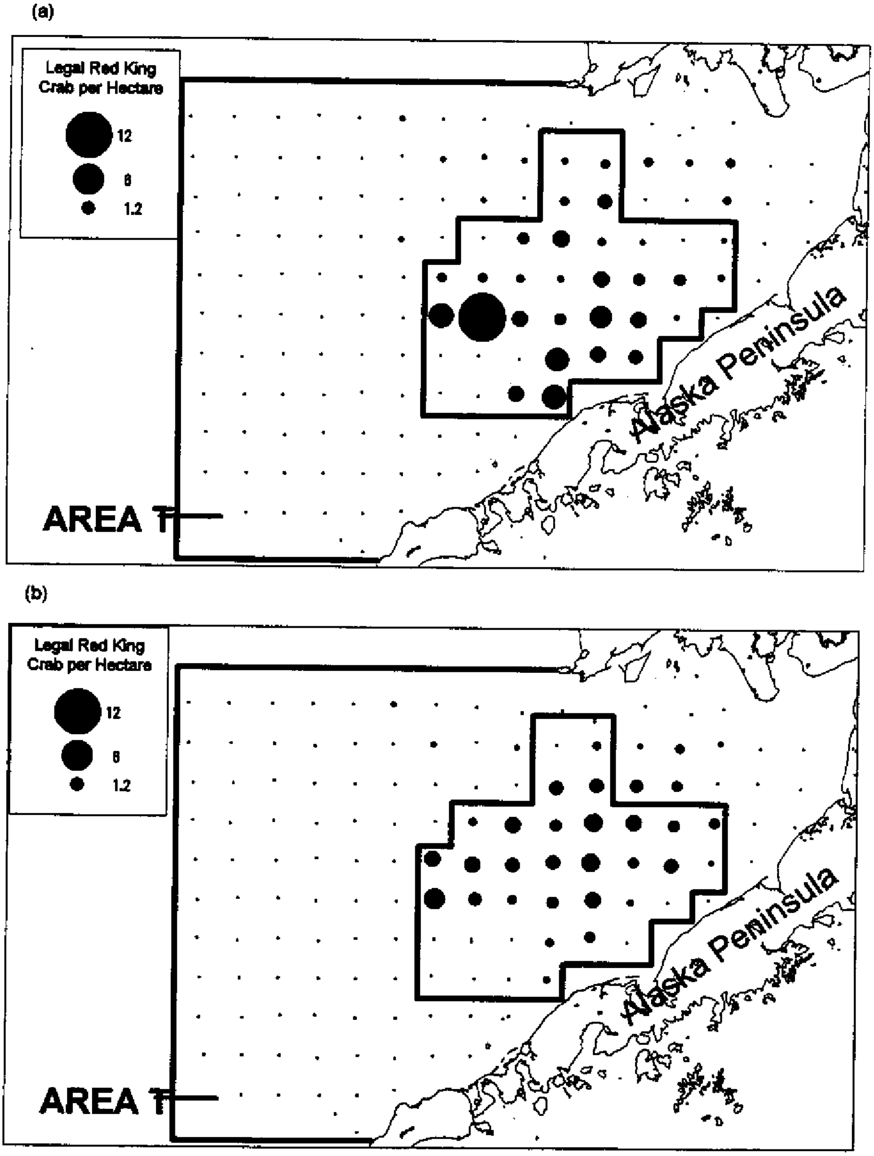

Figure 8. Catch of legal red king crab per hectare from the 1993 (a) and 1994 (b) EBS trawl surveys at all tow locations in Area T.

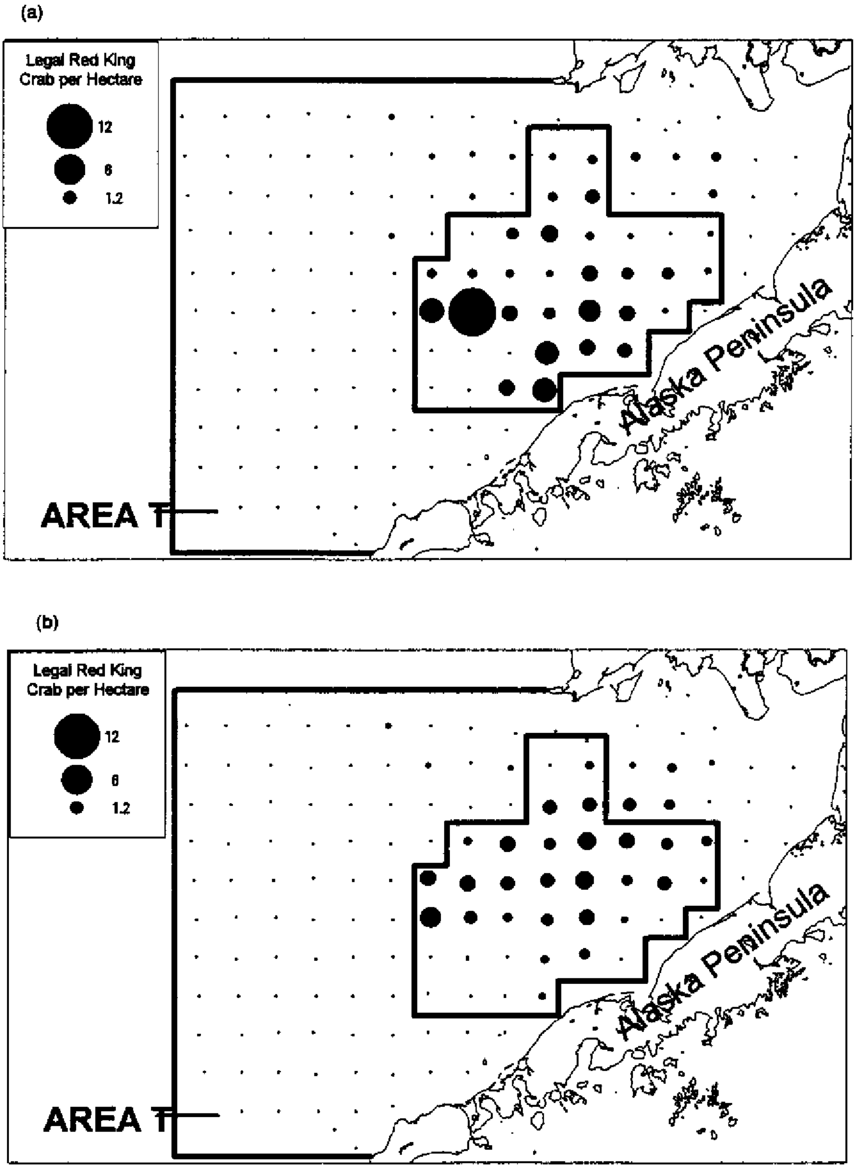

Figure 9. Catch of legal red king crab per hectare from the 1995 EBS trawl surveys at all tow locations (a) and the standard tow locations (b) in Area T.

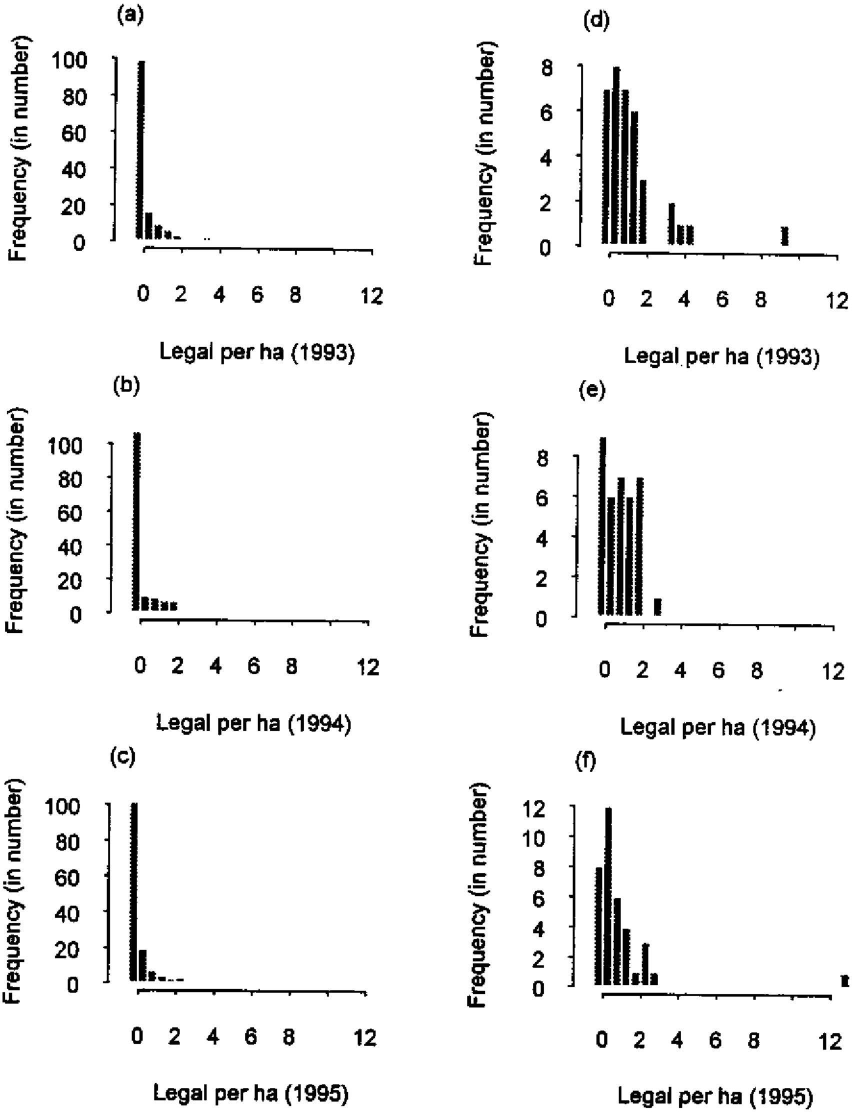

Figure 10. Histograms of legal red king crab per hectare from the EBS trawl survey in Area T in 1993 (a), 1994 (b), and 1995 (c) and in the subarea of Area T in 1993 (d), 1994 (e), and 1995 (f).

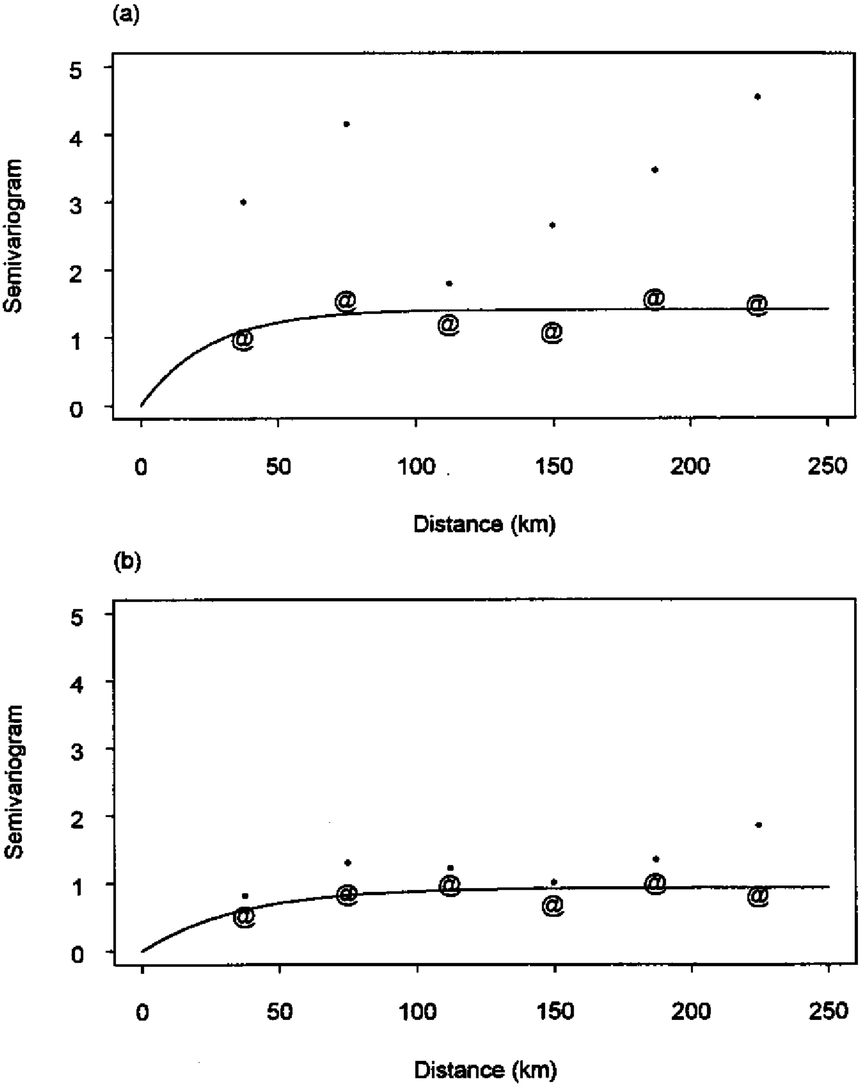

Figure 11. Sample semivariograms of legal red king crab per hectare caught in the 1993 EBS trawl survey within the subarea of Area T (a) and in the subarea of Area T excluding the highest value (b). Semivariograms were estimated using the standard method (.) and the robust method (@) and assuming isotropy. An exponential model was fit to the robust sample semivariogram (—) in each case (a and b).

value of 0 at the origin to the value of the variogram at extremely small separation distances) of approximately zero, a sill of 1.4131, and a range of 24.9977 km (Figure 11a). Removing the high value from the calculations, two more sample semivariograms were estimated; this time there was little difference between the two semivariograms (Figure 11b). This exponential model fit resulted in a nugget of approximately zero, a sill of 0.9361, and a range of 35.5008 km (Figure 11b). Point estimates using kriging were calculated on a regular grid within the subarea using both models. A surface plot of the estimates using the first semivariogram model was constructed (Figure 12a), along with a surface plot of the associated variance (Figure 12b). A plot of points estimated by kriging using the other semivariogram model would be very similar, the variance plot being slightly lower. In addition to the point estimates, an overall average and variance was estimated for each of the two models (Table 1). The two kriging estimates of abundance and area-swept estimate of abundance are all similar; the variances are different, however.

1994 data set

Only two sample semivariogram were estimated in 1994 (Figure 13). The robust sample semivariogram and the standard sample semivariogram are similar due to a lack of outliers. Because there was little difference between the two sample semivariograms, an exponential semivariogram model was fit to the standard sample semivariogram resulting in a nugget of 0.0002, a sill of 0.6527, and a range of 49.5788 km (Figure 13). Point estimates using kriging were calculated on the same regular grid used for the 1993 data. Surface plots of the estimates (Figure 14a) and the associated variances (Figure 14b) were constructed. An overall average, including the variance was estimated (Table 1). The kriging estimate of abundance and the area-swept estimate of abundance are similar, as are the variances.

1995 data set

As in the 1993 data analysis, a single high value in the 1995 data resulted in different sample semivariograms (Figure 15a); however, neither indicate autocorrelation. Using the robust sample semivariogram values and ignoring the lowest sample semivariogram value, the exponential model had an estimated nugget of approximately zero, a sill of 0.9556, and a range of only 5.1884 km. Removing the high value from the calculations improves the autocorrelation only slightly. The two additional sample semivariograms were estimated and produced quite different results (Figure 15b). Ignoring the lowest sample semivariogram value, the exponential model resulted in a nugget of approximately zero, a sill of 0.5012, and a range of 21.0265 km (Figure 15b).

Using the two semivariogram models, point estimates using kriging were calculated on a regular grid. Using the first semivariogram model,

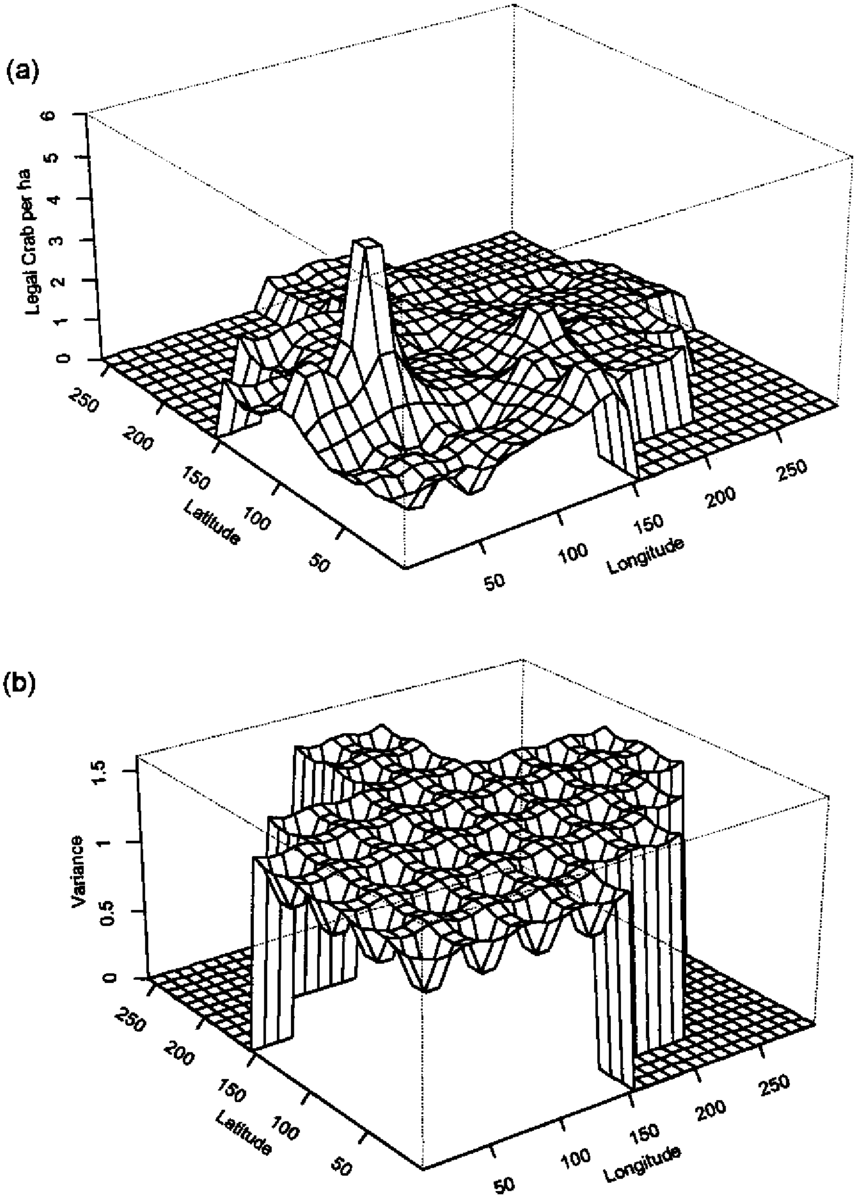

Figure 12. .Kriging estimates of legal red king crab per hectare (a) and the associated variances (b) from the 1993 EBS trawl survey in the subarea of Area T. Longitude and latitude are in kilometers.

Table 1. Kriging and NMFS area-swept estimates of average number and associated variance of legal red king crab per hectare, and abundance estimates and standard error of legal red king crab in the subarea of Area T, for 1993, 1994, and 1995.

	Average (number/ha)	Average variance (number/ha)^2	Abundance (in millions)	Abundance standard error (in millions)
1993 kriging 1st[a] variogram model	1.2966	0.0309	6.5291	0.8853
1993 kriging 2nd[b] variogram model	1.2882	0.0164	6.4868	0.6457
1993 NMFS, area swept	1.2509	0.0864	6.2988	1.4797
1993 NMFS, area swept minus highest value	1.0199	0.0349	5.1357	0.9407
1994 kriging	0.8954	0.0090	4.5088	0.4780
1994 NMFS, area swept	0.8686	0.0151	4.3741	0.6183
1995 kriging 1st[a] variogram model	1.1240	0.0292	5.6601	0.8610
1995 kriging 2nd[b] variogram model	1.1128	0.0119	5.6038	0.5496
1995 NMFS, area swept	1.0629	0.1324	5.3523	1.8325
1995 NMFS, area swept minus highest value	0.7227	0.01765	3.6390	0.6691

[a] Semivariogram using all data to estimate the model semivariogram.

[b] Semivariogram using all data, excluding the highest value, to estimate the model semivariogram.

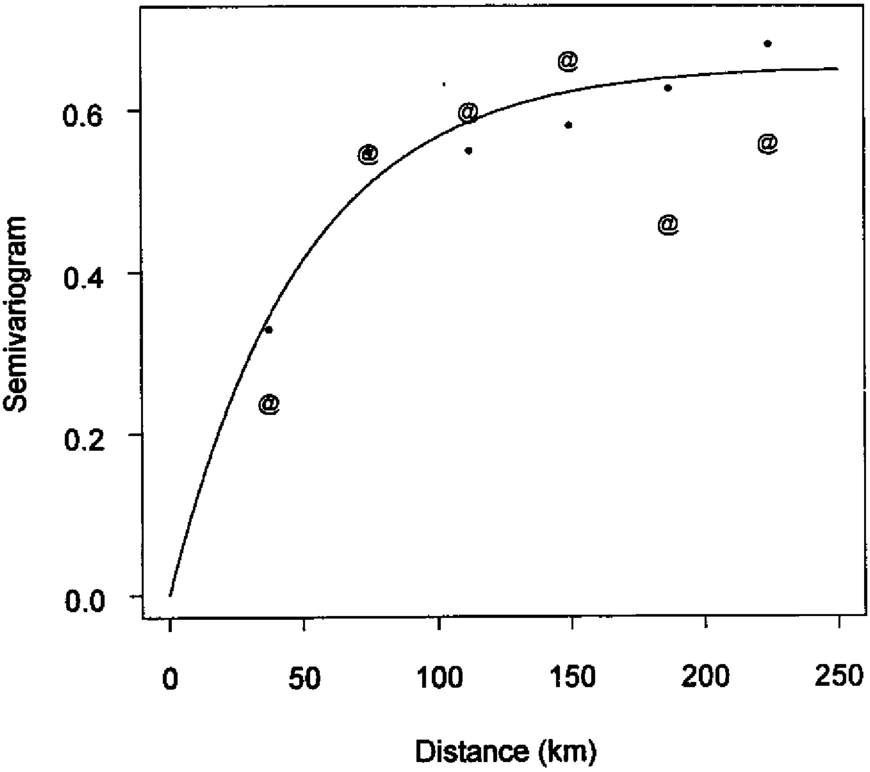

Figure 13. Sample semivariograms of legal red king crab per hectare caught in the 1994 EBS trawl survey within the subarea of Area T. The sample semivariogram was estimated using the standard method (.) and the robust method (@) and assuming isotropy. An exponential model was fit to the standard sample semivariogram (—).

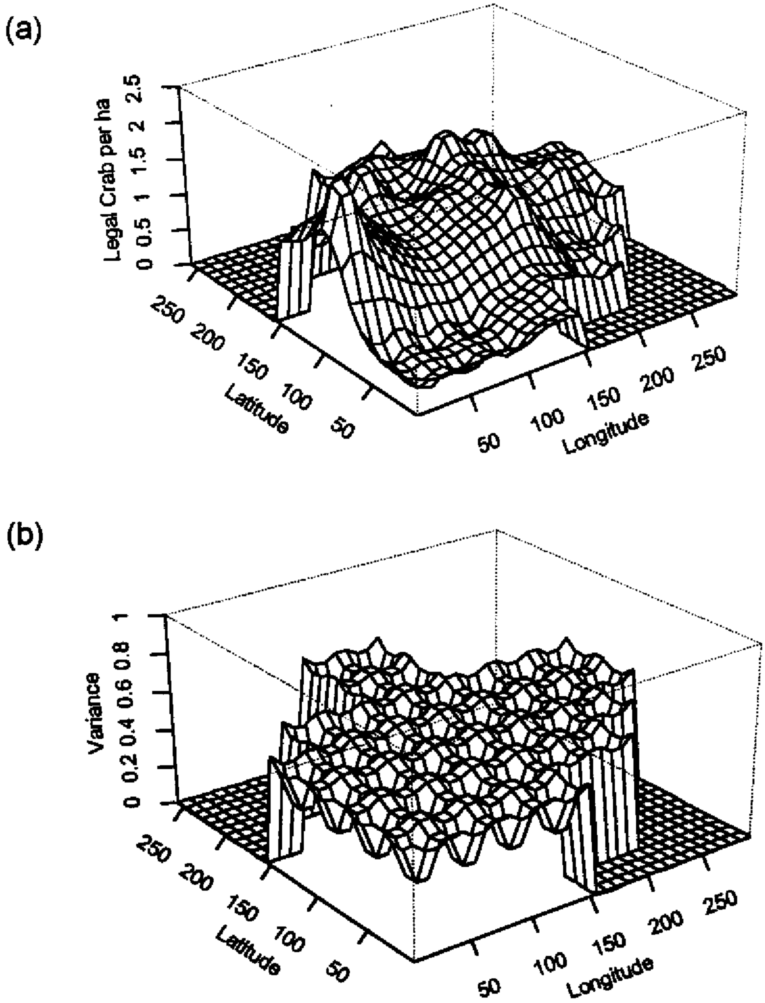

Figure 14. Kriging estimates of legal red king crab per hectare (a) and the associated variances (b) from the 1994 EBS trawl survey in the subarea of Area T. Longitude and latitude are in kilometers.

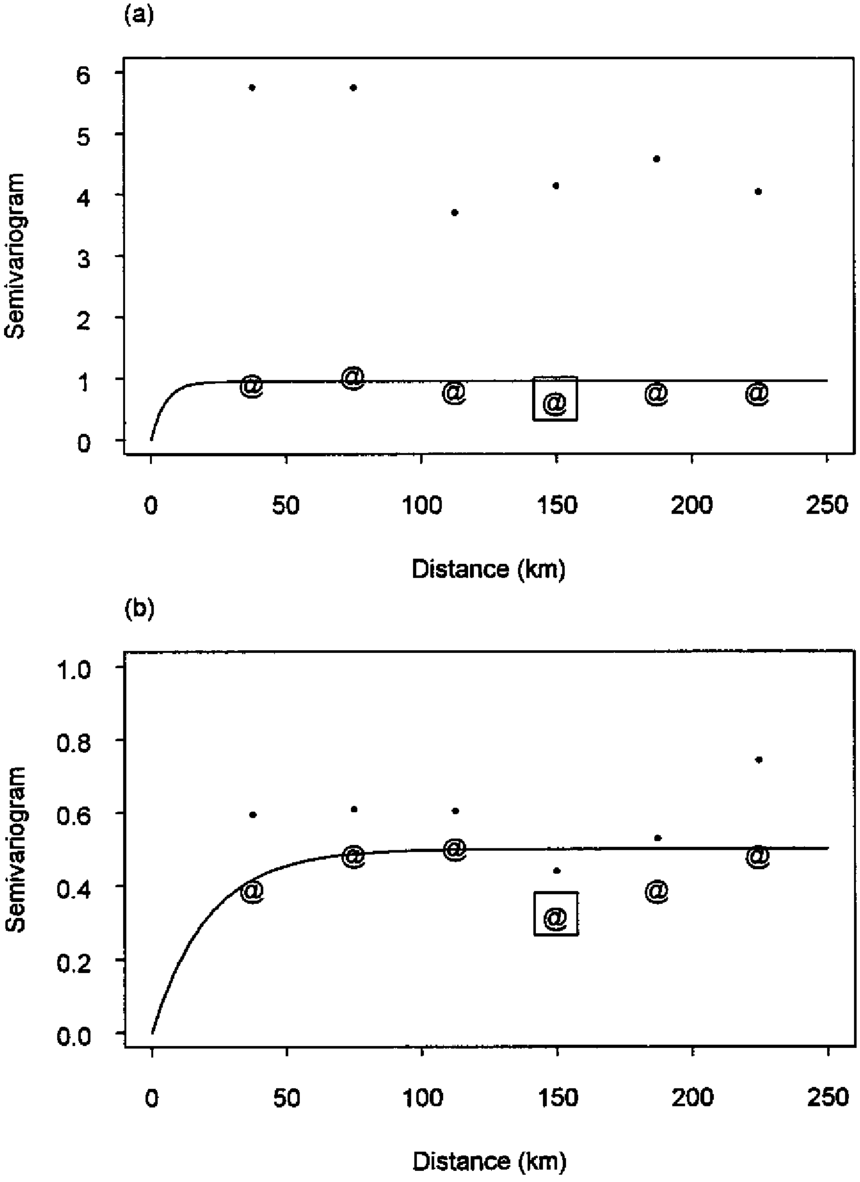

Figure 15. Sample semivariograms of legal red king crab per hectare caught in the 1995 EBS trawl survey within the subarea of Area T (a) and in the subarea of Area T excluding the highest value (b). Semivariograms were estimated using the standard method (.) and the robust method (@) and assuming isotropy. An exponential model was fit to the robust sample semivariogram (—) in each case (a and b) but did not include the point marked by a square.

surface plots of the estimates (Figures 16a), and the associated variance (Figure 16b) were constructed. A plot of points estimated by kriging using the other semivariogram model was different because of large difference in the two ranges (Figures 16c and 16d). An overall average and its variance for the two models were also estimated (Table 1). The two kriging estimates of abundance, and the area-swept estimate of abundance were all similar, as was the case in 1993 and 1994. However, the variances are quite different, as noted in the 1993 analysis.

1994 pot survey

The histograms of the number of legal red king crabs per pot and the log of the number of legal red king crabs per pot indicate that the pot survey CPUE distribution reflected both Gaussian and lognormal distribution patterns (Figure 17). A surface plot of the catch per pot at each station and the catch per station contains some high values; however, the high values were distributed throughout much of the area (Figure 18). The isotropic sample semivariogram for the pot survey had a similar shape to the 1994 trawl survey sample semivariogram (Figures 13). The robust sample semivariogram and the standard sample semivariogram are very similar due to a lack of outliers (Figure 19a). An exponential semivariogram model was fit to the robust sample semivariogram and standard semivariogram, the robust exponential model having a nugget of approximately zero, a sill of 67.8343, and a range of 21.2260 km; the standard exponential model had a nugget of approximately zero, a sill of 68.9963, and a range of 16.0745 km. No kriging estimates were generated from this data.

Discussion

A few important points can be made from this analysis. Estimates of abundance using kriging for legal male red king crabs in Area T were not calculated from the trawl survey because of the large number of zero values affecting the distribution, and the lack of stationarity. In all cases, the histograms indicate a highly and positively skewed distribution that is neither Gaussian nor lognormal (Figures 3, 6, and 10). Even if the bias associated with the distributions was estimated, the lack of stationarity (i.e., the large differences in variability between regions), would bias the results.

The kriging-estimated density and abundance variances were always less than the area-swept variances. The lower variance is in part an artifact of the robust sample semivariogram estimator, which is less affected by outliers than is the standard method (Cressie 1994). The variance of the NMFS area-swept abundance estimator decreases considerably if the highest value is not used when calculating the variance (Table 1). However, when the assumptions are met and there are no large outliers

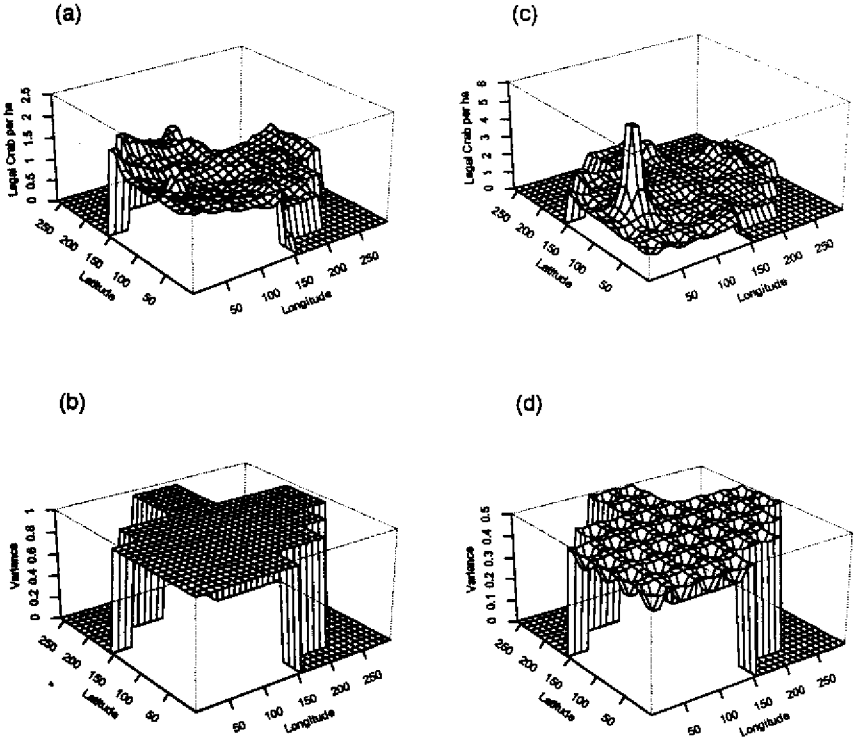

Figure 16. Kriging estimates of legal red king crab per hectare, using the robust semivariogram, in the subarea of Area T from the 1995 EBS trawl survey. Estimate (a) and associated variances (b) depict the semivariogram that included the highest value of legal red king crab; estimate (c) and associated variances (d) depict the semivariogram that excluded the highest value of legal red king crab. Latitude and longitude are in kilometers.

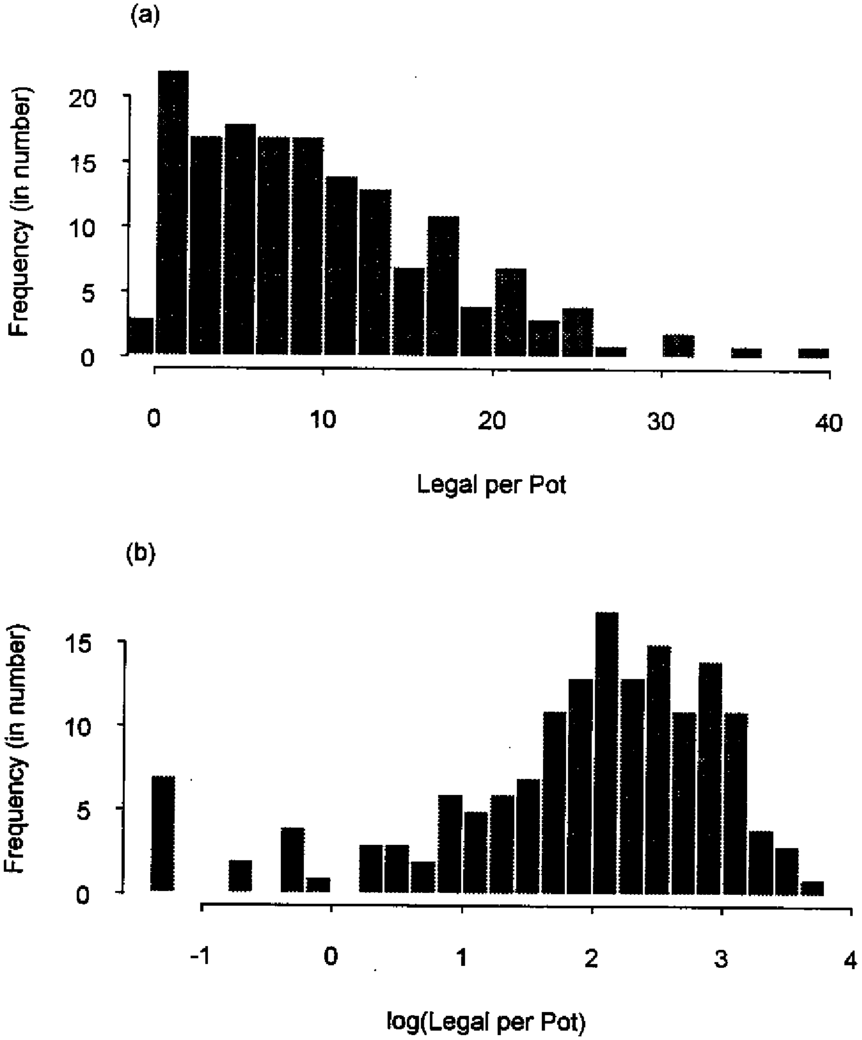

Figure 17. Histograms of legal red king crab per pot (a) and log of legal red king crab per pot (b) caught in the 1994 ADF&G pot survey in a portion of Area T.

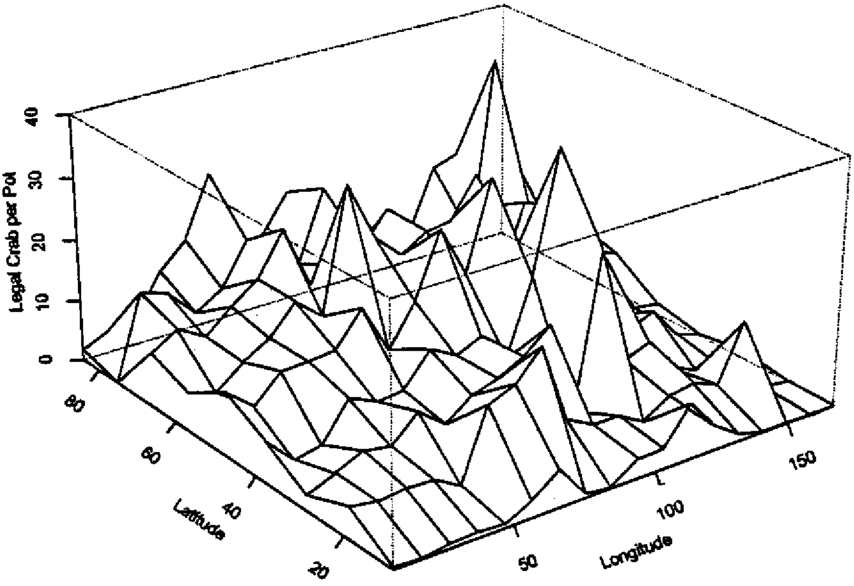

Figure 18. Surface plot of legal red king crab per pot caught in the 1994 ADF&G pot survey in a portion of Area T. Longitude and latitude are in kilometers.

(as in the 1994 trawl survey), kriging is a more precise estimator (lower variance) than the area-swept method. When there are outliers, caution should be taken in evaluating the estimates and their variances.

Though it is possible to use kriging as an estimator, even when there is little autocorrelation, it can give misleading results. In the analysis of the 1995 data, the first sample semivariogram indicated a random process with little or no autocorrelation. This is indicated by the short range (< 6 km) of the sample semivariogram (Figure 15a). We note that point kriging estimates smoothed the surface and obscured the high values within the area. This indicates that kriging should not be used blindly as a "black-box" for making surface plots.

Finally, the distance between trawl stations seems too great to capture the true autocorrelation within Area T or the subarea. Only in the kriging analysis of the 1994 trawl survey was the range greater than the shortest distance between trawls, 37.4 km, and the range in 1994 (approximately 50 km) was less than the next grid point (74.8 km). In contrast, the pot survey has a maximum range of 22 km, which is much less than 37.4 km. Also, from both the 1994 pot survey and the 1979 trawl survey analysis (Figures 4b and 19b), the autocorrelation in the north-

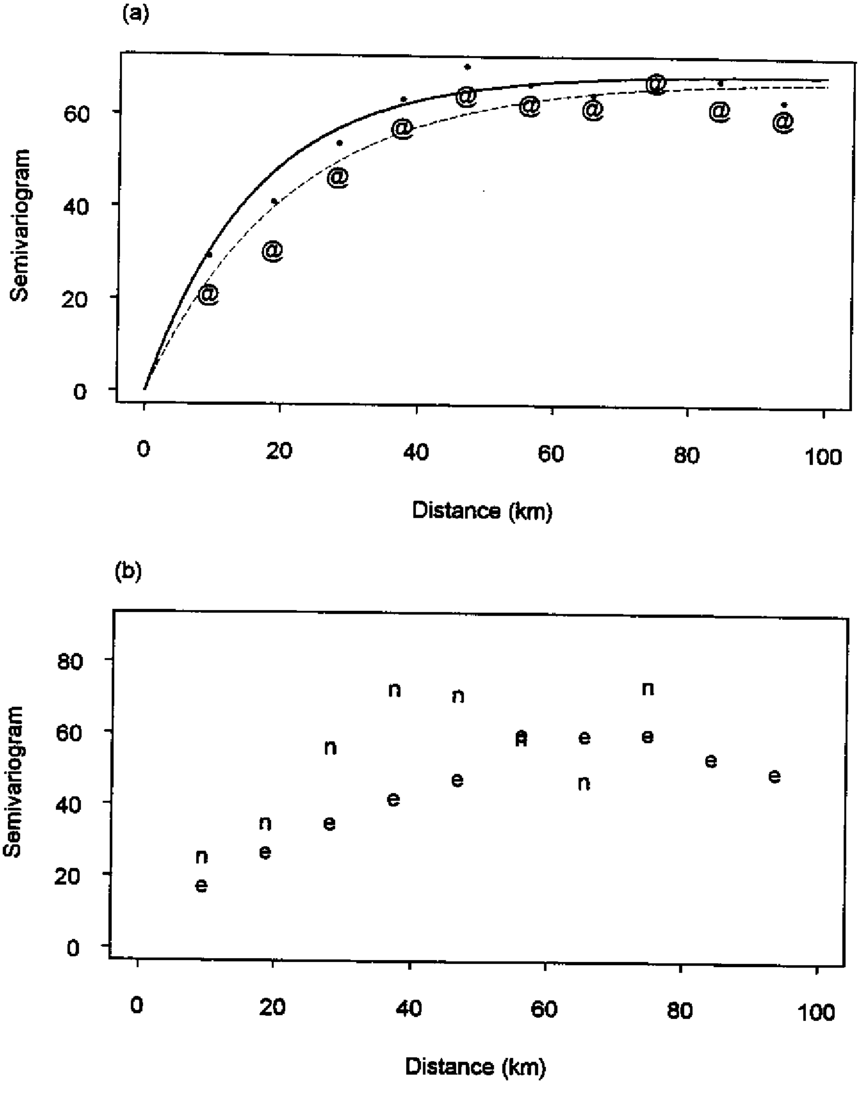

Figure 19. Sample semivariograms of legal red king crab per pot caught in the 1994 ADF&G pot survey in a portion of Area T. Semivariograms were estimated using the standard method (.) and the robust method (@) and assuming isotropy (a); semivariograms in (b) were estimated using the robust method in the east-west direction (e) and in the north-south direction (n).

south direction may have a shorter range than the autocorrelation in the east-west direction. At best, the trawl survey encompasses the basic area in which legal male red king crabs are located but does not identify any spatial correlation between tows. Appropriate evaluation of future pot survey data may be useful in identifying red king crab spatial distribution in Bristol Bay and help to provide more accurate abundance estimates.

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Comparisons of Abundance Estimation Methods for Red King Crabs in Bristol Bay and Kodiak

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Abstract

We compared legal male abundances of red king crabs, *Paralithodes camtschaticus*, in Bristol Bay and off Kodiak Island. For Bristol Bay, we compared estimates from area-swept analyses of annual trawl surveys, catch-survey analysis (CSA), length-based analysis (LBA), and catch-length analysis (CLA). For the Kodiak area, we compared estimates obtained from annual pot surveys, CSA, and CLA. Abundances estimated within each area were similar among methods. The LBA, CSA, and CLA were able to filter out measurement error and produced a smoother time series of abundance estimates than did those obtained directly from the survey. The survey data were generally fitted better by the LBA than by the CSA, which outperformed the CLA. For a given population, the choice of abundance estimation methods depends on data availability, level of desired precision, and intended use of the results. Each method has its own data requirements and output that result in a unique set of advantages, disadvantages, and potential applications.

Introduction

Many crab stocks in Alaska have been assessed by trawl or pot surveys for over two decades. Population abundances can be directly estimated by these surveys, but year-to-year estimates fluctuate greatly with measurement error, confusing actual changes in stock abundances. In addition, several commercial crab stocks in Alaska remain unsurveyed. To address those problems, several methods that fit data from multiple

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years of survey or fishery data have been developed to estimate crab abundances in Alaska. A catch-survey analysis (CSA) utilizing catch and survey data was used to smooth out measurement error in abundance estimates of legal male crabs comprised of two groups: recruits and post-recruits (Collie and Kruse in press). The expanded version of the CSA is a length-based population analysis (LBA) that incorporates variable growth and gradual recruitment over length and estimates abundances of mature crabs of both sexes (Zheng et al. 1995a, 1995b). In cases where no surveys are conducted, the LBA can be modified as a catch-length analysis (CLA) to use only catch-at-length and fishery effort data to assess stock abundances (Zheng et al. 1996).

In this study we applied the above four methods (direct survey, CSA, LBA, and CLA) to red king crabs (RKC) in Bristol Bay and three methods (direct survey, CSA, and CLA) to RKC off Kodiak Island and compared the abundance estimates. For comparisons, only abundance estimates for legal male crabs > 134 mm carapace length (CL) for Bristol Bay and > 146 mm CL for Kodiak are presented. The advantages and disadvantages of each method are summarized and discussed.

Abundance Estimation Methods

Direct survey

Annual trawl surveys have been conducted for Bristol Bay RKC since 1968. The survey employed a systematic design in which a grid, 20 × 20 nautical miles, was overlaid on Bristol Bay, and one trawl tow was typically made per 400 square miles. Occasionally, multiple trawl tows were made within a grid. Crab abundances were calculated by the National Marine Fisheries Service (NMFS) using an area-swept method from the number of crabs caught, the width of the trawl opening, and the distance towed (Stevens et al. 1994).

Pot surveys were conducted for Kodiak RKC by Alaska Department of Fish and Game from 1973 to 1986. Standardized catch per unit effort (CPUE) from pot surveys and tag and recovery data for legal male crabs were provided by Peterson et al. (1986). Mean catchability of the Kodiak pot survey was estimated using the Petersen mark-recapture equation and annual commercial catch, tag, and recovery data from 1973 to 1979 (Zheng et al. 1996), from which annual legal male abundances were estimated by dividing relative abundance (standardized survey CPUE) by the catchability.

Catch-survey analysis

Collie and Kruse (in press) constructed a CSA for crab populations and used it to estimate legal male RKC abundances in Bristol Bay and Kodiak. The model consists of two components: recruits to the legal male population and post-recruits. Post-recruits in year $t + 1$ are the sum of recruits and post-recruits in year *t* adjusted by natural mortality minus the commercial catch. Relative abundances are assumed proportional to absolute abundance with a constant survey catchability coefficient. Observed abundances are assumed equal to the true abundances multiplied by a lognormally distributed measurement error. Measurement error is minimized through a non-linear least squares approach to estimate model parameters.

Data required for the CSA include annual survey abundance estimates for recruits and post-recruits, annual commercial catch, and natural mortality (Table 1). For Bristol Bay RKC, recruits are newshell crabs > 134 mm CL and < 150 mm CL; the area-swept method was used to calculate relative abundance estimates from the survey data. For Kodiak RKC, recruits are newshell crabs > 144 mm CL and < 165 mm CL; pot survey CPUE data were used as relative abundances. Note that the minimum CL for legal male crabs defined by Collie and Kruse (in press) is 2 mm smaller than that defined in the other two abundance estimation methods. This small difference has a negligible effect on abundance estimates. For both stocks, post-recruits are legal crabs minus recruits, and natural mortality was set equal to 0.36.

The CSA estimates the survey catchability coefficient, annual measurement errors, and recruits (except for the last year), and post-recruits (Table 1). Legal crab abundances are derived from the model parameters. Collie and Kruse (in press) included Pribilof RKC in their Bristol Bay RKC abundances. Abundances of Pribilof RKC are very low compared to Bristol Bay RKC except in recent years. For our comparison with other methods, Bristol Bay RKC abundances estimated by Collie and Kruse (in press) with the CSA were reduced by 25.5% in 1993 and 26.7% in 1994. These percentages were estimated from the survey data.

Length-based analysis

Zheng et al. (1995a) developed a LBA for Bristol Bay RKC, and Zheng et al. (1995b) revised and updated the model with new data. The LBA is an expanded version of the CSA. Instead of grouping crabs into recruit and post-recruit components, the LBA models male and female crab abundances by 5 mm CL intervals and two shell conditions: newshell and oldshell. The annual abundance of crabs in a length group is the combined result of growth, molting probability, catch, natural mortality, and recruitment. Each year a length group of newshell crabs is formed from (1) new recruits to the model, (2) addition of some smaller crabs through growth, and (3) the loss of crabs that molt to larger-size length groups. There is a proportion of crabs that do not molt in a given year, and these non-molting crabs will move into oldshell crab groups of the same CL. Natural mortality takes away some crabs from each length group independent of shell condition, and fishing mortality subtracts crabs from legal-size length groups.

Table 1. Summary of data requirements, assumptions, output, advantages, disadvantages, and potential applications of the catch-survey analysis.

Data requirement
1. Relative abundances of recruits and post-recruits estimated from survey data.
2. Total annual catch.
3. Natural mortality.

Assumptions
1. A lognormal distribution of measurement error for recruits and post-recruits.
2. Relative abundance is linearly proportional to absolute abundance.
3. Legal crabs can be approximately separated as recruits and post-recruits; shell condition data are reliable.

Output
1. Abundances of recruits and post-recruits.
2. Catchability of survey gear.

Advantages
1. Simple to implement.
2. Small data requirements.

Disadvantages
1. Limited output.
2. Cannot estimate female and sublegal male abundance.

Potential applications
1. Modeling error structures.
2. Estimating unknown survey catchability coefficients.
3. For stocks without catch by length data.
4. For small stocks or limited sampling effort.

Growth of RKC is modeled by mean growth increment per molt described by a linear function of pre-molt CL and variation in growth increment per molt as described by a gamma distribution. The molting probability for a given length group and time is modeled by an inverse logistic function. Three logistic functions were used to describe the molting probability of Bristol Bay male RKC during different periods: a very high period (1972-1979), low periods (1980-1984 and 1992-1993), and a high period (1985-1991).

Natural mortality was assumed constant over length and two levels over time: low periods (1972-1979 and 1985-1993) and a high period (1980-1984) for Bristol Bay RKC. Recruitment into the modeled population is a function of two parameters: the number of recruits entering the modeled population for a given year and the proportion of recruits belonging to each length group, as described by a gamma distribution.

Required data and parameters for the LBA include mean growth increment over length and annual catch and survey abundance by length and shell condition (Table 2). Survey abundances were estimated using the area-swept method. A non-linear least squares approach was used to estimate parameters which include recruits to the modeled population for each year except the first year, total abundance in the first year, two parameters for growth and recruitment distribution over length, two natural mortality parameters, and six molting probability parameters (Table 2). Legal crab abundances are derived from these parameters and input data.

Catch-length analysis

Zheng et al. (1996) developed a CLA for crab populations and applied the CLA to Bristol Bay and Kodiak RKC. The CLA is similar to the LBA except that no survey data are input, and it can only be applied to legal male crabs. A catchability coefficient for pots is used in the CLA to expand the relative abundance to absolute abundance, and both observations of catches by length and shell condition and fishing efforts are equally weighted.

Annual length-frequencies from commercial catches by shell condition, total annual fishing effort, the mean and variance in growth increment per molt, and natural mortality are required for the CLA (Table 3). The catch-length frequencies were summarized by 5-mm intervals; the largest length groups were ≥ 165 mm CL for Bristol Bay and ≥ 182 mm CL for Kodiak. Zheng et al. (1996) defined fishing effort as total annual pot lifts in the commercial fishery. The mean and variation in growth increment per molt were estimated from tagging data for Bristol Bay and Kodiak stocks, and natural mortality was assumed as 0.4 for both stocks.

Like the CSA and LBA, the CLA employs a non-linear least squares approach to estimate parameters. The following model parameters were

Table 2. Summary of data requirements, assumptions, output, advantages, disadvantages, and potential applications of the length-based analysis.

Data requirement
1. Survey abundance by length, shell, sex, and year.
2. Catch by length, shell, and year.
3. Mean growth increment per molt.
4. Catchability of survey gear.

Assumptions
1. A lognormal distribution of measurement error for survey abundances by length, shell, sex, and year.
2. Shell condition data are reliable.
3. Distribution of growth increment per molt is constant over time for a given length.

Output
1. Abundance of mature crabs by length, shell, sex, and year.
2. Stock-recruitment data.
3. Molting probability.
4. Natural mortality.

Advantages
1. Most complete output.
2. More precise abundance estimates.
3. Can estimate both males and females.

Disadvantages
1. Large data requirements.
2. Difficult to implement.

Potential applications
1. For stocks meeting the data requirement.
2. Studying stock-recruitment relationships.
3. Evaluating harvest strategies.

Table 3. Summary of data requirements, assumptions, output, advantages, disadvantages, and potential applications of the catch-length analysis.

Data requirement

1. Time series of fishery catches by length and shell.
2. Time series of fishing efforts.
3. Mean and variance of growth increment per molt.
4. Natural mortality.

Assumptions

1. A lognormal distribution of measurement error for catches by length and shell condition.
2. Shell condition data are reliable.
3. Distribution of growth increment per molt is constant over time for a given length.

Output

1. Time series of legal male abundances by length and shell.
2. Time series of recruitment to legal male abundances.
3. Catchability of fishing gear.
4. Molting probability for legal male crabs.

Advantages

1. Reduced data requirements.

Disadvantages

1. Estimates may not be as accurate as those by the catch-survey analysis and length-based analysis, especially during the recent years.
2. Cannot estimate female and sublegal male abundance.

Potential applications

1. For stocks without survey data.

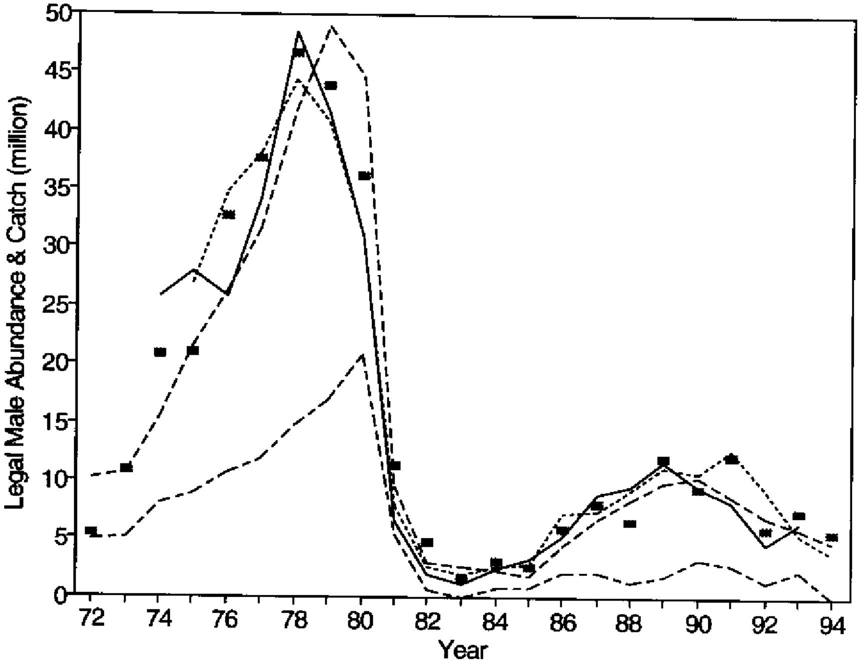

Figure 1. Comparison of estimated legal male red king crab abundances in Bristol Bay by the direct survey by NMFS (boxes), catch-survey analysis by Collie and Kruse (in press) (dotted line), length-based analysis by Zheng et al. (1995b) (dashed line), and catch-length analysis by Zheng et al. (1996) (solid line). The centered line is the total annual catch.

estimated for each stock: recruits for each year except the first year, total abundance in the first year, two recruitment parameters, four molting probability parameters, four selectivity parameters, and the catchability coefficient of fishing gear (Table 3).

Results

Legal male abundances of Bristol Bay RKC were estimated by the four methods (Figure 1). The direct survey estimate of legal crab abundance by NMFS in 1972 was close to the total catch and apparently was significantly underestimated. The survey abundance was fitted very well by both the LBA and CSA from 1975 to 1994. The crab abundance estimated by the CLA was similar to the estimates by the other three methods. The LBA estimates were lower than the other methods in the mid-1970s and very close to the direct survey estimates from 1978 to 1994. Both

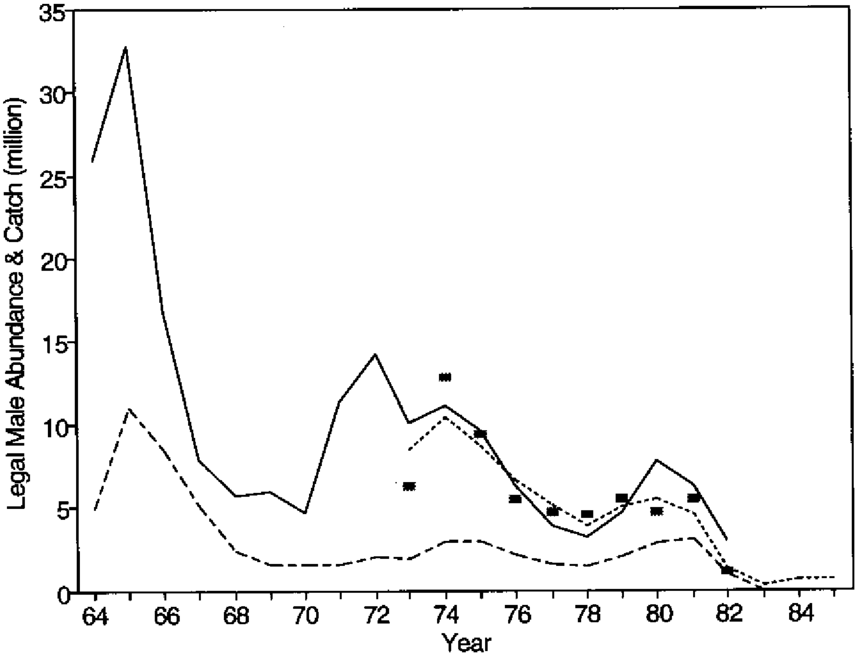

Figure 2. Comparison of estimated legal male red king crab abundances in Kodiak by the direct survey by Zheng et al. (1996) (boxes), catch-survey analysis by Collie and Kruse (in press) (dotted line), and catch-length analysis by Zheng et al. (1996) (solid line). The centered line is the total annual catch.

the CSA and CLA estimates were lower than the direct survey estimates in the late 1970s and early 1980s. This is partially due to the use of a constant natural mortality for these two methods. The direct survey estimates fluctuated much more than the other three estimates on a year-by-year basis.

Overall, all four estimates have the same trend and indicate that the legal male abundance of Bristol Bay RKC increased dramatically in the mid- and late 1970s and decreased precipitously in the early 1980s (Figure 1). After a moderate recovery occurred in the late 1980s and early 1990s, the legal crab abundance reversed the upward trend and declined again in recent years. The catch followed the general trend of the legal crab abundance (Figure 1).

Survey data were not available for Kodiak RKC until 1973 (Peterson et al. 1986), and the LBA has not been conducted. Thus, we compared the legal male abundances estimated by the direct survey, CSA, and CLA after 1972 (Figure 2). The CSA estimates were closer to the direct survey estimates than the CLA estimates because the CSA was fitted to the survey data, whereas the CLA estimated abundance independent of survey data. Overall, the three estimates have a similar trend, but the direct survey abundances were not as smooth as the CSA and CLA estimates.

Using catch and fishing effort data in the CLA, we estimated the legal male abundance of Kodiak RKC back to 1964. The estimated abundances peaked in 1965 and fell to low levels in the late 1960s (Figure 2). The population recovered moderately in the early and mid-1970s; however, it declined again in the late 1970s and completely collapsed after 1982. The high estimated abundances in the early 1960s may partly reflect expansion of the fleet to new fishing grounds (Spalinger 1994). The catch was very high in the 1960s and fairly stable in the 1970s (Figure 2). No fishery has been allowed for Kodiak RKC since 1982 due to low population abundances.

Discussion

The four methods applied to Bristol Bay RKC and the three methods applied to Kodiak RKC produced close estimates of legal male abundances. The LBA, CSA, and CLA filtered out measurement error and resulted in smoother time series of estimates than the direct survey abundances. The survey data were generally fitted better by the LBA than by the CSA, which outperformed the CLA. For a given population, the choice of abundance estimation method depends on data availability, level of desired precision, and intended use of the results. Each method has its own data requirements and output, giving each advantages, disadvantages, and potential applications (Tables 1, 2, and 3).

The CSA requires limited data and produces relatively consistent estimates of time series of legal male abundances (Table 1). One difficulty in applying the CSA is its required estimate of natural mortality, which is not available for many crab populations. If the catchability of the survey gear is known or if it can be assumed to be approximately one, natural mortality can be estimated by the CSA. The main disadvantage of the CSA is that the results are limited to abundance estimates of recruit and post-recruit males. Because fishery data are required to scale the survey relative abundance, female crab abundance cannot be estimated. Future CSA should include sublegal crabs as a third component. Such an extension not only expands the output results, but also increases the robustness of abundance estimates because of an increase in the amount of data used to filter out measurement error. The CSA is very useful for modeling error structures in the survey data because it is easily implemented (Table 1). The CSA can also be used to estimate unknown survey catchability coefficients. Another potential application is to estimate legal crab abundances for stocks without catch-by-length data and for stocks with limited sampling effort such that not enough crabs are caught to satisfy the more data-intensive LBA method.

The LBA must be used when female abundances are needed and when it is necessary to study stock-recruitment relationships and to evaluate harvest strategies. The LBA produces the most complete results among the three model approaches, but it also requires more data than either the CSA or CLA. Because of its large data requirements (Table 2), application of the LBA is limited to only some crab stocks for which extensive data have been collected. In addition to providing abundance estimates by sex, length and shell condition, natural mortality, and molting probability, another main advantage of the LBA is its capability to filter out measurement error to produce consistent time series of abundance estimates owing to its large number of length groups (Table 2).

The CLA is a simplified version of the LBA applicable to crab populations with no survey effort. The CLA incorporated with fishing effort data generally provides accurate estimates of trends in relative population abundance. In cases where natural mortality can be approximated, reasonable estimates of absolute abundance can be obtained (Zheng et al. 1996). Like the CSA, a drawback of using a CLA for crab stocks is the lack of natural mortality estimates. The main disadvantage of the CLA is that its abundance estimates are generally not as robust as CSA and LBA estimates, especially in the terminal year (Table 3). The accuracy of estimated absolute abundance in the terminal year depends on how accurately we can estimate fishing mortality. However, by incorporating fishing effort data, relative abundance trends of legal male RKC can be estimated rather well in the most recent years for Bristol Bay and Kodiak (Zheng et al. 1996).

Besides direct survey, CSA, LBA, and CLA, at least three other analytical methods have been applied to the Bristol Bay RKC trawl survey data: kriging (Vining and Watson 1996), delta distribution (Jerry Reeves, pers. comm.), and recursive age-structured model (Matulich et al. 1988, Greenberg et al. 1991). The kriging and delta distribution approaches have the same disadvantages as the direct survey estimates: they do not link multiple-year data together to smooth out measurement error. However, they may be able to partially filter out measurement error caused by outliers, and it may be useful to treat the raw survey data with either of these methods prior to conducting a LBA or CSA. The recursive age-structured model takes advantage of the age-structured approach, but it assumes a one-to-one relationship between age and length that is not true for RKC, for which size groups are broadly overlapping mixtures of ages. However, in the situation where shell condition data are unavailable and a one-to-one relationship between age and length is an acceptable assumption, then only the age-structured model can be applied to track crab cohorts over time.

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Were Alaskan Red King Crabs Overfished?

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Extended Abstract

Alaskan red king crabs, *Paralithodes camtschaticus,* provide a striking example of collapse of one of the world's most valuable crustacean fisheries. During 1960-1994, domestic landings averaged 27,736 t annually. Conservation concerns were raised when landings from Gulf of Alaska fisheries declined sharply in the late 1960s. Concurrently, mean crab size and commercial catch per unit effort decreased on established fishing grounds and fleets shifted to new areas striving to maintain catches (Royce 1969). Statewide landings peaked at 86,555 t in 1980 composed largely of a record harvest from Bristol Bay in the eastern Bering Sea, but by 1983 virtually all red king crab fisheries crashed decisively. Many have been closed ever since because the depressed stocks have not recovered. In 1994, landings were the lowest (1,019 t) since the fishery began, and only a few small commercial fisheries were conducted in remote areas.

To examine whether red king crabs were overfished we calculated biological reference points for three red king crab stocks and estimated sustainable harvest rates and overfishing levels based on stock productivity. Biological reference points are fishing mortality rates *(F)* that provide useful stock-specific benchmarks for considering appropriate harvest rates. Although rarely calculated for Alaskan crab species, they have been applied to many groundfish fisheries for decades (e.g., Gulland and Boerema 1973). Here, we summarize some of our preliminary findings (complete and final results will appear in a forthcoming journal publication).

We examined biological reference points for three stocks—Norton Sound, Bristol Bay, and Kodiak—because they cover most of the geo-

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graphic range of red king crabs in Alaska and because growth data are available. Because Alaskan fisheries retain only male king crabs, we analyzed exploitation rates only for the male proportion of the population. We developed a length-based cohort model of male crabs to estimate abundance and size distributions over 5-mm size intervals. For each stock we specified an initial abundance and size distribution of the cohort. Initial mean size was set at approximately two molt increments below legal size, and the standard deviation was set to give a dispersion of cohort size consistent with field observations. Because this quasi cohort was composed of crabs of multiple ages (McCaughran and Powell 1977, Stevens 1990), we kept track of relative, not absolute, cohort age starting with relative age 0. As with our other recent work (e.g., Zheng et al. 1995a, 1995b), we separated growth of male red king crabs into two components: molting probability and growth increment. We modeled growth increment as a linear function (Weber and Miyahara 1962) of premolt size and molting probability as a reverse logistic function of premolt size (Balsiger 1974). To model cohort abundance, we set instantaneous natural mortality (M) at 0.3 (Zheng 1995a, 1995b), and we applied M, F, and handling mortality (H) annually. We applied F to legal-sized crabs and H to sublegal-sized crabs. The exact level of H experienced during the history of the fishery is unknown, but we set H at 10% annually for purposes of our analysis.

We calculated two biological reference points with commonly used procedures (Gabriel et al. 1989): $F_{30\%}$ and $F_{40\%}$, which reduce spawning stock biomass per recruit (SSB/R) to 30% (Clark 1991) and 40% of the unfished level (Clark 1993, Mace 1994), respectively. We considered $F_{30\%}$ as a proxy measure of recruitment overfishing based on Sissenwine and Shepherd's (1987) redefinition of recruitment overfishing, Clark's (1991) findings, and precedence by the North Pacific Fishery Management Council for some groundfish stocks. We considered $F_{40\%}$ as a potential target exploitation rate based on advice of Clark (1993) and Mace (1994). Because crab harvests are managed in terms of exploitation rate (E) rather than instantaneous fishing mortality rate (F), we calculated the exploitation rate equivalent of each reference point as: $E = 1 - e^{-F}$ (Ricker 1975). Our estimates are as follows:

Stock	$E_{30\%}$	$E_{40\%}$
Norton Sound	23.6	20.7
Bristol Bay	42.2	34.7
Kodiak	41.1	33.8

So, were red king crab stocks overfished? It appears they were. Comparison of benchmark rates to the harvest history of red king crabs in these three fisheries reveals a periodic history of overfishing. Harvest rates for the Norton Sound fishery exceeded 21% during 1978-1981 with rates in excess of 50% during 1978 and 1979. For the Kodiak fishery, harvest rates exceeded 41% during 1966-1968 and 1980-1982 and harvest rate peaked at 80% in 1982. In Bristol Bay, harvest rates exceeded 42% in 1972-1974, 1980-1981, and 1985-1986 and peaked at 56% in 1981.

Population declines are associated with most of these periods of overfishing. In Norton Sound, the legal crab abundance declined precipitously from 1976 through 1982 while overfishing occurred. Since then, harvest rates have averaged about 12%, and the population has increased through 1991, the year of the last survey. In Kodiak, legal abundance declined coincident with overfishing from about 30 million crabs in 1964-1965 to 6 million in the late 1960s. Harvest rates were held to 14-33% annually during 1969-1972, and the legal population rebounded to 14 million in 1972. However, the stock fell to < 1 million in 1983 after severe overfishing in the early 1980s. This pattern was not mirrored in Bristol Bay where the population increased after a period of higher harvest rates from 1972 through 1974, which was due to the extremely strong 1968-1972 year classes being recruited to the fishery. Overfishing during 1980-1981 did coincide with a crash of this fishery and subsequent closure in 1983, but overfishing during 1985-1986 was followed by modest increases in legal abundance through 1990. The lower correspondence between overfishing periods and stock declines for Bristol Bay may, in part, be attributed to more modest rates of overfishing than occurred in Kodiak and Norton Sound where peak harvest rates were double the $F_{30\%}$ overfishing criterion.

Though we have identified periods of overfishing, red king crab population dynamics are complex and cannot be explained by fishing mortality alone. Population changes are due to gains from recruitment and growth and losses from natural and fishing mortalities. It is still not clear what factors were primarily responsible for the collapse of red king crab stocks. In a comprehensive analysis, Zheng et al. (1995a, 1995b) found evidence for large shifts in mortality and recruitment. High apparent natural mortality rates were coincident with high harvest rates during the period of sharp decline in the early 1980s. More important, strong recruitment in the late 1960s and early 1970s increased the stock from moderate to high levels, and subsequent recruitment failures led to its decline. Two alternative stock-recruit relationships were consistent with the historical record: (1) strong dependence of recruitment on spawning stock density, or (2) recruitment is driven by highly autocorrelated environmental factors. Although stock-recruit relationships have not yet been developed for Kodiak and Norton Sound stocks, it is very clear that depressed king crab stocks generally produce poor year classes. For this reason, regardless of the relative roles of stock and environment on recruitment, recruitment overfishing must be avoided to maintain healthy stocks.

We recommend more conservative harvest rates than have been applied at times in the past. Our analysis of $F_{40\%}$ suggests that prudent legal harvest rates may be 21% for Norton Sound and 34% for Bristol Bay and Kodiak. Based on $F_{30\%}$, past harvest rates in excess of 24% for Norton Sound and 42% for Bristol Bay and Kodiak are too high and should be avoided. Coincidentally, current regulations specify that Norton Sound red king crabs are to be harvested at one-half the rate applied to the rest of the Bering Sea (ADF&G 1994). Ideally, when sufficient information exists, population dynamic models, such as Zheng et al. (1996a, 1996b), should be used to prescribe harvest strategy. However, because recruitment relationships with stock and environment are not available for most stocks, biological reference points such as $F_{40\%}$ and $F_{30\%}$ are useful to extend results from well-studied populations to others for which data are limited.

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Evaluating an Index of Snow Crab *(Chionoecetes opilio)* Biomass from Trapping Surveys

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Abstract

In this study data were analyzed from 13-16 year time series of research trapping surveys in each of three Newfoundland crab management areas toward developing indices of commercial crab biomass. Data were collected using both commercially used (large-meshed) traps and special research (small-meshed) traps. Survey timing varied, from spring to fall, among the three areas. For all areas, however, the survey catch rate of legal-sized crabs, including soft crabs not yet recruited to the fishery, provided a significant predictor of commercial CPUE in the following year. The catch rate index based on small-meshed traps represented a more reliable predictor than that based on large-meshed traps. Survey catch rates of size-specific groupings of sub-legal sized crabs (prerecruits) may indicate future recruitment trends but it is uncertain whether baited traps adequately sample inter-molt prerecruit crabs.

Introduction

The purpose of this study was to examine time series of research survey data toward developing prospective biomass indices based on survey catch rates of legally harvestable crabs as well as crabs not yet recruited to the fishery. Few crustacean resources are managed on the basis of such predictive models (Caputi and Brown 1986, Phillips 1986) because suitable data are seldom collected over a sufficiently long time period.

Biological variables which affect crab recruitment are initially reviewed to provide the basis of the analysis. Then, data series from trapping surveys in each of three fishery areas are analyzed toward developing a model which provides an index of commercial biomass for predicting fishery performance.

Methods

Research surveys

Surveys were first conducted in two crab management areas (Figure 1) in 1979 and in a third area beginning in 1981 (Table 1). Initial surveys used only baited commercial Japanese-style conical crab traps. Special small-meshed traps were first used in one area, Conception Bay, in 1981 and in the other areas in 1982. Small-meshed traps are similar to commercially used large-meshed traps except that the netting is of 2.5 cm stretched mesh, rather than the 13.3 cm stretched mesh of commercial traps. Small-meshed traps were usually deployed 1-2 per fleet within each fleet of 8 or 12 traps (mostly large-meshed). Traps were separated by 45 m within each fleet and were baited using squid and/or mackerel. Soak time was usually about one day, depending on weather conditions. Within each crab management area surveyed, the depth range and actual area sampled corresponded approximately to the commercial fishing area. Minimum depth for sampling was 170 m for all survey areas.

Surveys were carried out annually since 1980 in all three areas, with the exception of Conception Bay, for which there were no surveys in three of the years (Table 1). The timing of surveys varied annually both in the absolute sense, as well as in relation to the time of the fisheries.

Data collected

All crabs from each trap catch were enumerated by sex. For each male, or for representative subsamples, carapace width (CW) was determined to the nearest whole mm, using vernier calipers. Carapace condition was assigned one of four categories (Miller and O'Keefe 1981) with respect to relative age and hardness, to reflect time since molting;

1. Claw easily bent with thumb pressure, claw iridescent on the outer edge, shell without calcareous growths and brightly colored.
2. Claw not easily bent by thumb pressure, claw iridescent on the outer edge, shell brightly colored, and shell usually with calcareous growths.
3. As in (2) but shell less brightly colored and claw edge not iridescent.
4. Shell black and soft from decay at some joints, shell colors dull.

Beginning in 1988, individual catches were further subsampled for determination of chela allometry. Height of the right chela (CH), if present and not deformed, was estimated (0.1 mm) using dial calipers. The ratio of chela height to carapace width was subsequently used to assign crabs to one of two distinct groups with respect to chela allometry; small-clawed or large-clawed.

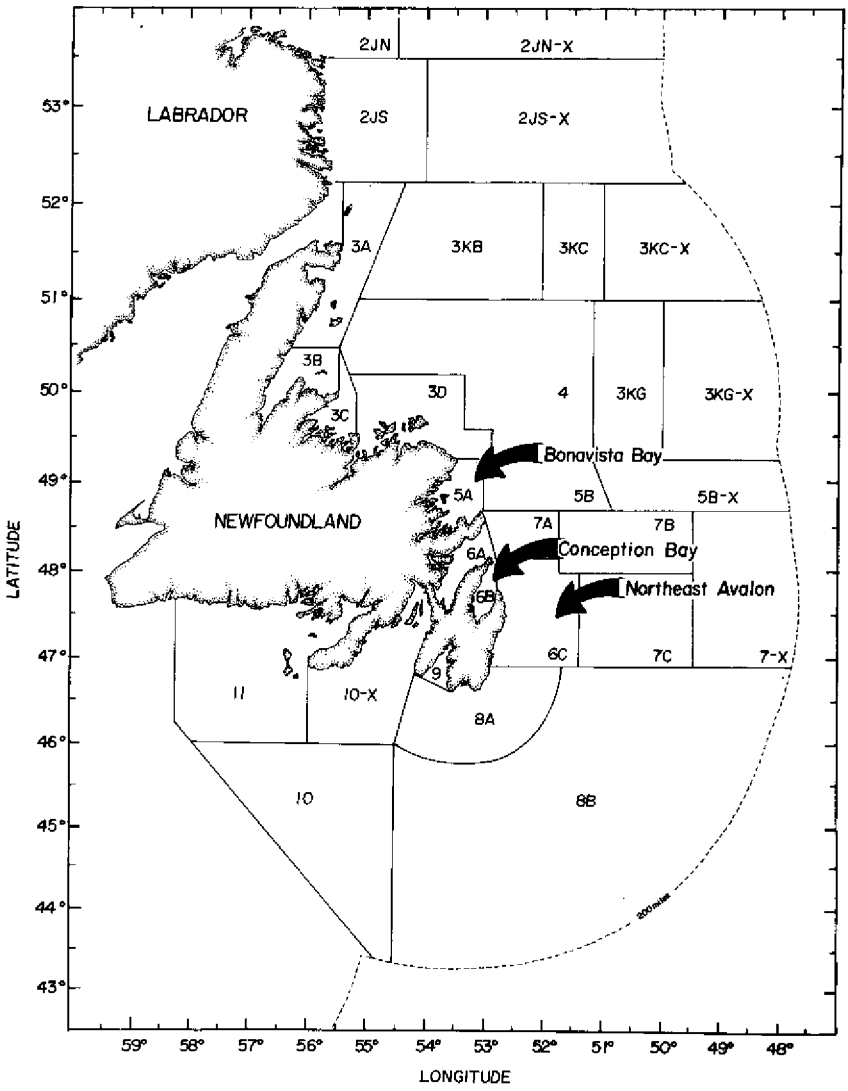

Figure 1. Snow crab management areas; those three which represent the survey areas are identified by dark arrows.

Table 1. Details pertaining to research surveys and fisheries, by year and survey area.

			No. of trap hauls		Fishery	
Year	Period	No. stations	Large meshed	Small meshed	Period	Catch (t)
Conception Bay						
1979						
1980						
1981	Sept. 25-30	13	143	24	Feb. 22-Nov. 28	502
1982	Nov. 4-17	16	170	24	Mar. 22-July 17	694
1983	NO SURVEY				Jan. 3-Dec. 3	564
1984	Oct. 2-11	32	375	12	Jan. 22-Nov. 17	333
1985	Nov. 5-14	23	235	44	Apr. 21-Oct. 26	139
1986	Oct. 31-Nov. 6	24	264	20	Apr. 20-Dec. 6	193
1987	NO SURVEY				May 3-June 13	227
1988	Oct. 3-14	25	249	45	Apr. 24-May 21	499
1989	Oct. 9-13	9	85	18	Sept. 3-Oct. 14*	*476
1990	NO SURVEY				Sept. 9-Oct. 6*	*314
1991	Nov. 2-13	35	382	42	May 19-June 22/	
					Aug. 18-Sept. 14*	*383
1992	Nov. 2-16	23	247	24	May 17-June 27/	
					Sept. 1-Oct. 3*	*304
1993	Oct. 11-22	25	271	24	June 5-8/	
					Aug. 1-13*	*309
1994	Sept. 27-Oct. 7	31	266	103	May 30-June 3/	
					Sept. 6-9*	*416
Bonavista Bay						
1979	June 15-July 4	41	327	0	May 7-Nov. 24	1586
1980	Mar. 24-Apr. 15	16	188	0	Apr. 7-Nov. 30	1905
1981	May 5-18	27	325	0	Mar. 2-Dec. 5	1376
1982	May 3-14	25	253	48	Apr. 5-Nov. 20	905
1983	Aug. 10-26	25	264	44	Apr. 24-Dec. 3	1101
1984	Aug. 6-20	33	361	37	May 13-Dec. 15	1327
1985	Aug. 5-18	31	316	51	May 5-Nov. 9	728
1986	Aug. 4-14	22	249	15	Apr. 27-Aug. 2	648
1987	Aug. 4-19	30	329	25	May 3-June 20	602
1988	Aug. 8-24	22	277	30	May 2-June 5	735
						*109
1989	Aug. 1-15	29	317	34	May 14-June 10	639
						*320
1990	Aug. 2-14	24	260	26	Apr. 15-May 12	656
					Sept. 9-25*	*416

Table 1. (Continued.)

			No. of trap hauls		Fishery	
Year	Period	No. stations	Large meshed	Small meshed	Period	Catch (t)
1991	Aug. 5-16	30	329	32	May 12-June 1	623
					Aug. 11-24*	*479
1992	Aug. 3-15	30	332	28	May 17-June 6	692
					Sept. 1-10*	*468
1993	Aug. 2-25	27	291	34	May 15-June 25	905
					Aug. 1-6*	*526
1994	Aug. 8-19	29	234	112	Apr. 25-May 3	566
					May 30-June/ Sept. 6-9*	*984
Northeast Avalon						
1979	Apr. 9-May 9	32	260	0	Apr. 2-Dec. 24	7632
1980	Mar. 24-Apr. 15	14	162	0	Apr. 7-Dec. 13	5065
1981	Mar. 23-Apr. 15	12	142	0	Mar. 2-Dec. 19	7607
1982	Mar. 31-Apr. 20	20	187	47	Apr. 1-Dec. 11	3368
1983	May 4-12	13	144	10	May 1-Dec. 10	801
1984	May 26-31	12	129	20	May 22-Nov. 17	312
1985	June 11-15	10	103	17	May 26-Oct. 5	113
1986	May 29-June 12	13	129	20	Aug. 10-Oct. 25	144
1987	July 15-24	23	256	16	May 3-Aug. 8	172
1988	June 2-22	26	203	60	May 1-July 16	751
1989	May 1-10	20	211	22	May 7-July 1	661
1990	June 7-18	27	266	63	Apr. 1-June 30	619
					Sept. 16-Nov. 10*	*231
1991	June 3-17	24	259	26	May 12-July 6	699
					May 12-June15/ Sept. 1-21*	*391
1992	June 1-12	26	278	29	May 17-June 6	650
					May 17-June 6/ Sept. 1-26*	*428
1993	May 4-14	12	126	15	May 22-July 1/ Aug. 1-20	702
					June 5-18/ Aug. 1-20*	*839
1994	May 11-20	16	119	70	Apr. 25-May 11	633
					Apr. 25-May 1/ May 30-June 2/ Sept. 6-9*	*566

* Indicates period of, and landings from, supplementary as opposed to full-time fisheries.

Treatment of data

A schematic model of snow crab recruitment was followed in assigning individuals to population components for subsequent analysis (Figure 2). Based on this model, data were grouped into classes for each of three biological variables:

(i) Carapace Width (CW): Based on growth per molt data (Moriyasu et al. 1987, Taylor and Hoenig 1990, and Hoenig et al. 1994) groups were established for crabs which would achieve legal size (95 mm CW) after one molt (76-94 mm CW) and after two molts (60-75 mm CW).

(ii) Chela Allometry: Males develop enlarged chelae when they undergo a final or "terminal" molt, which may occur at any size larger than 50 mm CW. Therefore only males with small chelae will continue to molt and subsequently recruit to the fishery. A model which separates two "clouds" of chela height on carapace width data ($CH = 0.0806\ CW^{1.1999}$) was applied to classify each individual as either large-clawed or small-clawed. Data on chela height were available only since 1988.

(iii) Shell Hardness: Males that undergo their terminal molt in the spring will remain soft-shelled throughout the fishery season of that year and will not be fully hardened and retained by the fishery until the following year. It is assumed that all males with small chelae remain soft-shelled between molts (Figure 2). In reality, however, an annually variable proportion of small-clawed males will not molt in any given year ("skip molters") and so will attain hard-shelled condition between molts. For each year that a crab skips a molt, its eventual recruitment is delayed by a year.

The schematic model (Figure 2) depicts the progression of a molt class of small crabs (60-75 mm CW), with small claws, to eventual recruitment. This component is predominated by a group termed R-3 because they may recruit to the fishery, at 95-114 mm CW, in three years (i.e., after two molts and an additional year to harden). However a more minor group (R-4) is also represented in this category. This group will remain small-clawed and soft-shelled after two molts and so will molt a third time, recruiting to the fishery, in four years, as very large crabs (115-140 mm). Of course, these simplified recruitment processes and numbers of years involved do not take "skip-molting" into account, which as previously noted will further delay recruitment.

Commercial catch per unit of effort (CPUE; kg/trap haul) was used as the index of commercial biomass and the dependent variable in linear regression analysis. CPUE data were subsampled and summarized from vessels' logbooks, maintained by captains as a condition of access to the fishery. Soak time was variable and unstandardized. Where both full-time and supplementary fleet sectors prosecuted the fishery within

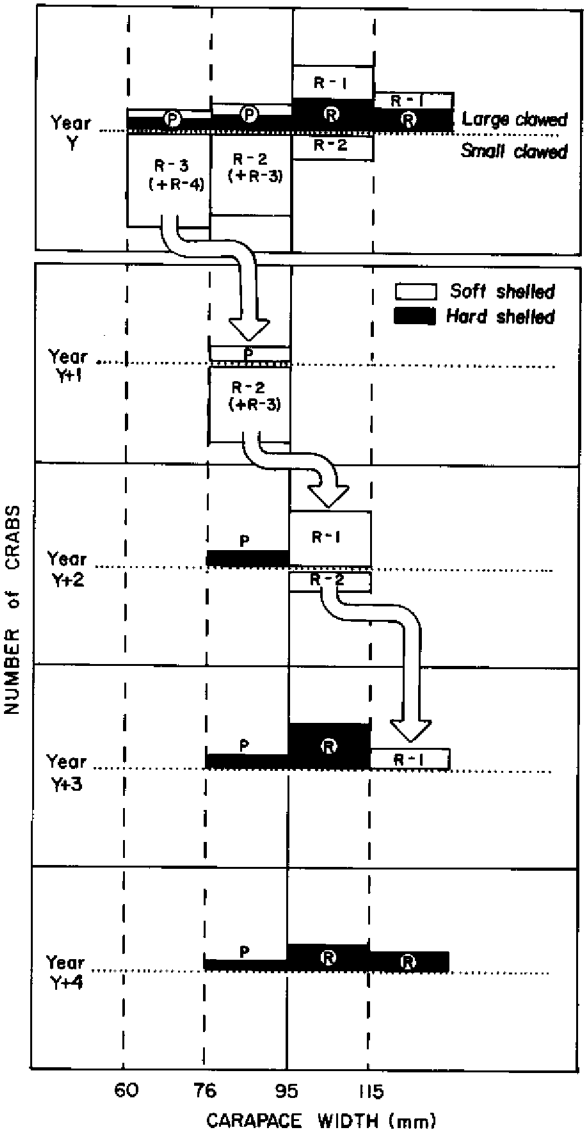

Figure 2. Schematic representation of snow crab population components relevant to recruitment for males ≥ 60 mm CW (top panel) and depiction of the recruitment process for the molt class of smallest (60-74 mm CW) crabs with small claws (all panels). Arrows represent molting. "P" represents "Pygmy" crabs—males which have attained large-clawed status at sub-legal size (< 95 mm CW) and are assumed to have molted for the last time. R represents hard-shelled males which have recruited to the fishery. This model does not include skip-molters.

a management area (i.e., Bonavista Bay and Northeast Avalon, Table 1) only data from the full-time fleet were used to estimate CPUE.

The independent variable in the linear model was the survey catch rate of all legal-sized crabs in the previous year. The survey catch rate in kg/trap was calculated from the number of crabs per trap, the mean carapace width, and a body weight–carapace width relationship for crabs of carapace condition 2 (Taylor and Warren 1991). This survey catch rate included "soft-shelled" and "hard-shelled" crabs, both of which would provide commercially acceptable meat yield and so be fully recruited and reflected in the CPUE of the next year's fishery. A survey catch rate index was developed separately for each of the data sets from large-meshed and small-meshed traps.

Results and Discussion

For all three survey areas positive relationships were found using the large-meshed trap data (Figure 3), but the linear model explained only 46-49% of the variation. In contrast, the model, when applied to the small-meshed trap data sets, accounted for 70-80% of the variation (Figure 4). In both cases, the unexplained variation would likely be due to various sources, including annual variation in methodological factors (e.g., sampling intensity, fishing patterns) or biological variables (e.g., changes in molting season, proportions molting and other factors which affect catchability).

It is surprising that the survey catch rate index based on small-meshed trap data represents a more reliable predictor of commercial CPUE than that based on large-meshed trap data. It is recognized that large-meshed traps are size selective and are biased samples even for legal-sized crabs but, because they are used in the commercial fishery it has been assumed that they would provide the best predictor of fishery performance (Xu et al. 1992). Furthermore, most of the sampling at each station has historically utilized large-meshed traps (Table 1) so catch rate has probably been more precisely estimated by those traps.

This model, based on each trap type, was first applied to predict fishery performance for 1995 (Figures 3-4). For both gear types, the survey catch rate index generally predicted that 1995 catch rates would be comparable to the high catch rates observed during the most recent three years. The more reliable index based on small-meshed trap data predicted record high 1995 catch rates for two of the three areas, Bonavista Bay and Northeast Avalon (Figure 4).

Future refinement of this model will focus on standardizing commercial CPUE for effects of annually variable fishing effort. In a refined model some standardized early-season CPUE would be used as the dependent variable. Also, survey timing in relation to the fishery has varied considerably within and among areas (Table 1). Therefore survey

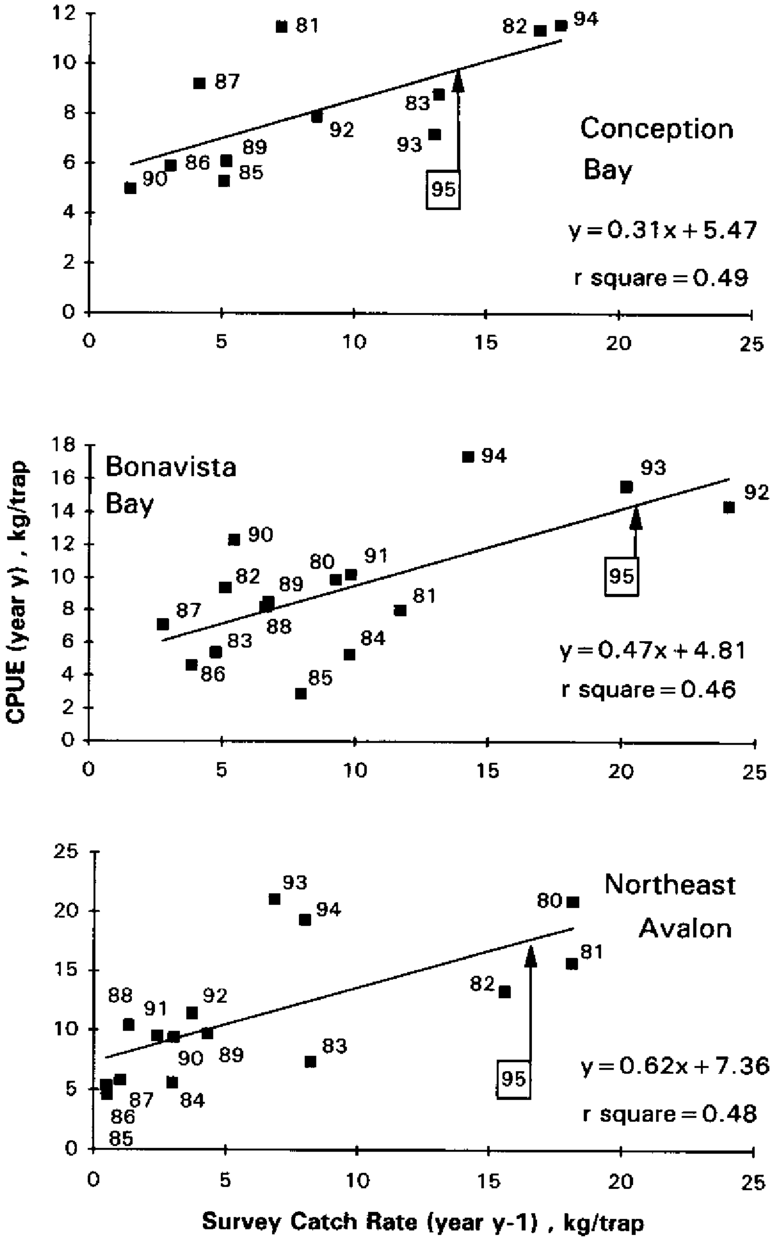

Figure 3. Relationship of commercial CPUE in any year to the survey catch rate of legal-sized crabs from large-meshed traps in the previous year, by survey area. Arrows show projected CPUEs for 1995.

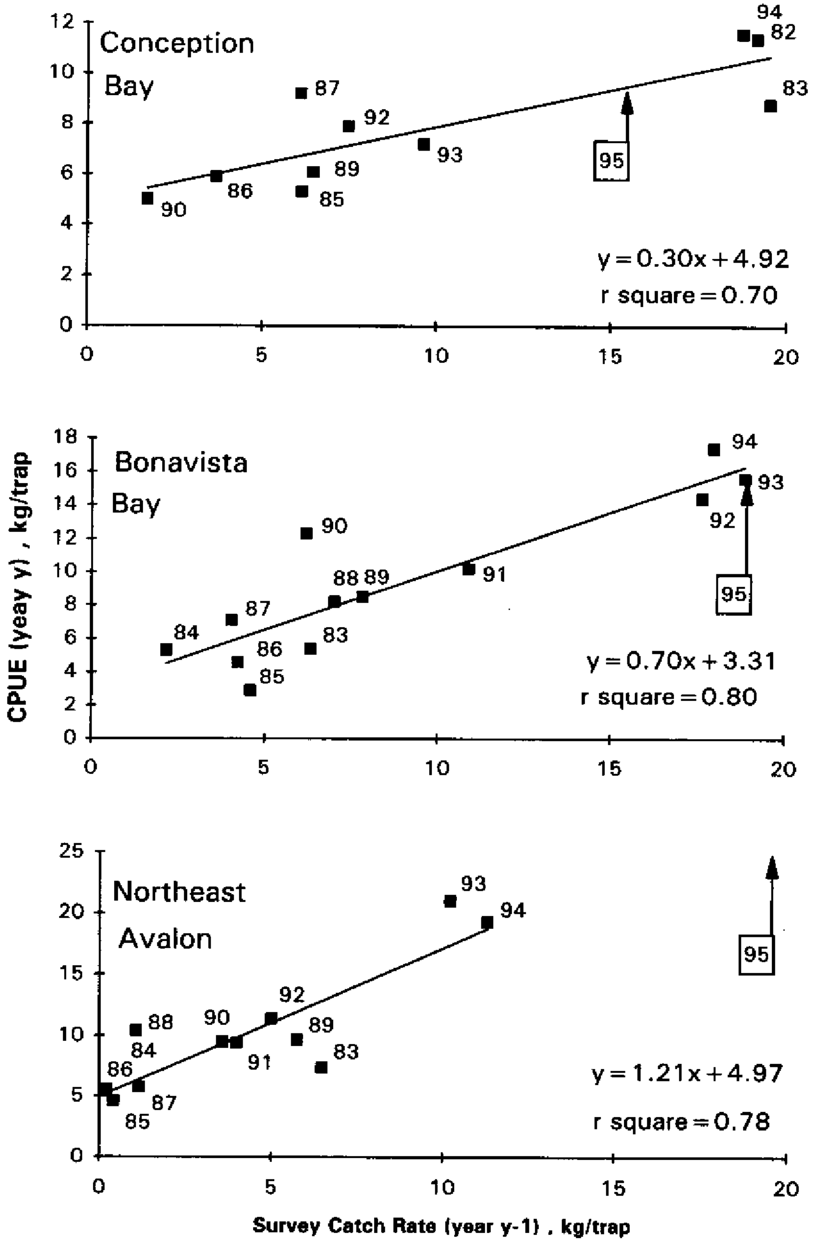

Figure 4. Relationship of commercial CPUE in any year to the survey catch rate of legal-sized crabs from small-meshed traps in the previous year, by survey area. Arrows show projected CPUEs for 1995.

catch rates will have to be adjusted for effects of fishery removals within the same year.

The survey catch rate of the immediate prerecruit size group (Prerecruit 1; 76-94 mm) peaked in either 1991 (Bonavista Bay) or 1992 (Conception Bay and Northeast Avalon) and has been generally declining since (Figure 5). Although 1994 catch rates for this size group remain higher than any prior to 1987, the catch rate of the small-clawed component of this group declined especially sharply since 1991 or 1992. Since only the small-clawed component of this Prerecruit 1 size group will actually molt and subsequently recruit to the fishery (in as little as two years) this suggests that recruitment has been declining recently (since 1993 or 1994).

The small-clawed component of a size group of smaller crabs (Prerecruit 2; 60-74 mm CW) has also declined regularly in recent years, achieving very low catch rates in 1994 (Figure 6). Since this component requires three years before it begins to recruit to the fishery (as hard-shelled crabs) it suggests that relatively poor recruitment will persist for several years.

This interpretation of future recruitment should be considered with caution, however, because baited traps may not represent good samplers for small-clawed crabs. In comparative sampling, for a given body size group, large-clawed crabs predominated in trap catches whereas small-clawed crabs predominated in bottom trawl catches (Hoenig and Dawe 1991). Small-clawed males do not feed or enter traps for a rather extended time period including their molt. Annually molting small-clawed males are assumed to not harden fully between molts. Therefore it is possible that the predominantly hard-shelled small-clawed males sampled in trap surveys may represent the annually variable proportion which did not molt during the most recent spring (i.e., skip-molters). It is not known whether the catch rate of skip-molters provides an indicator of the abundance of all small-clawed crabs for any size group. Therefore, data should also be collected by bottom trawl to provide an independent abundance index for sub-legal sized crabs with small claws.

If catch rates of small-clawed prerecruit crabs do represent declining recruitment for the future then it is unclear when this would first be reflected in declining commercial CPUE. Such effects of low recruitment would not be expected to become evident until the currently high harvestable biomass becomes depleted. The rate of such depletion will probably differ among crab management areas due to variation in spatial distribution of fishing effort.

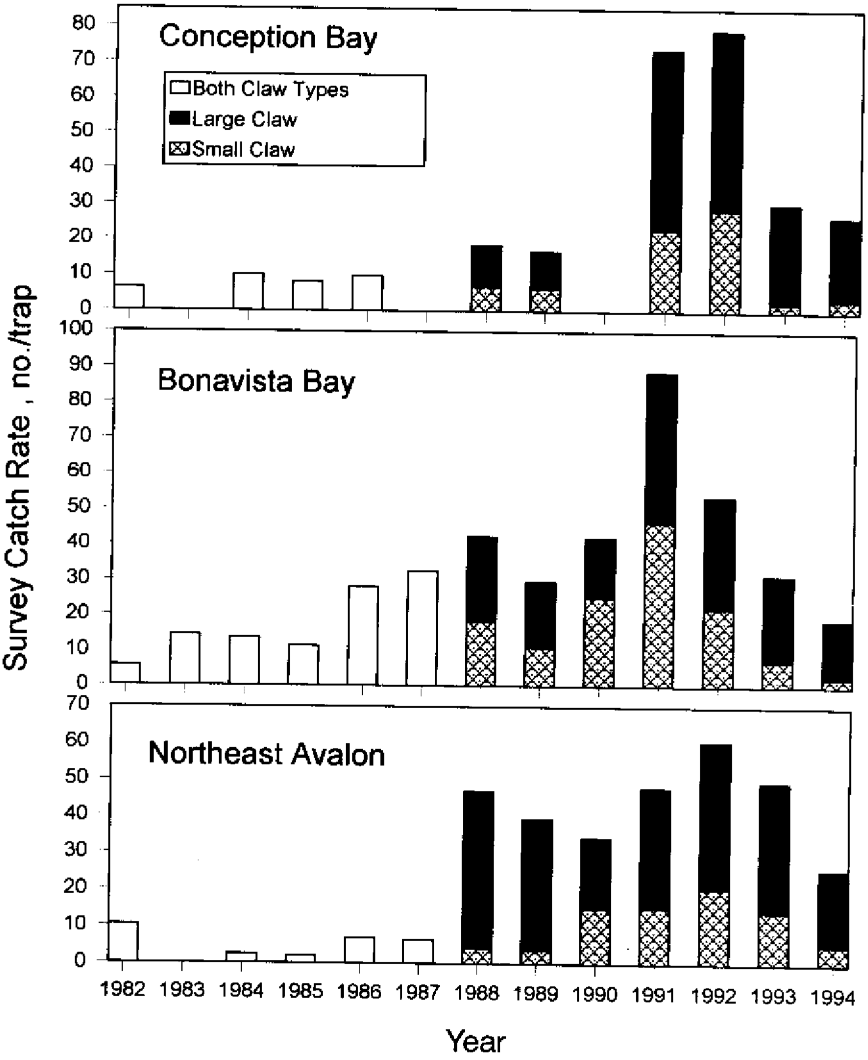

Figure 5. Yearly trends in survey catch rate of Prerecruit 1 crabs (76-94 mm CW) from small-meshed traps, by survey area. Catch rates are partitioned by chela morphometry since 1987.

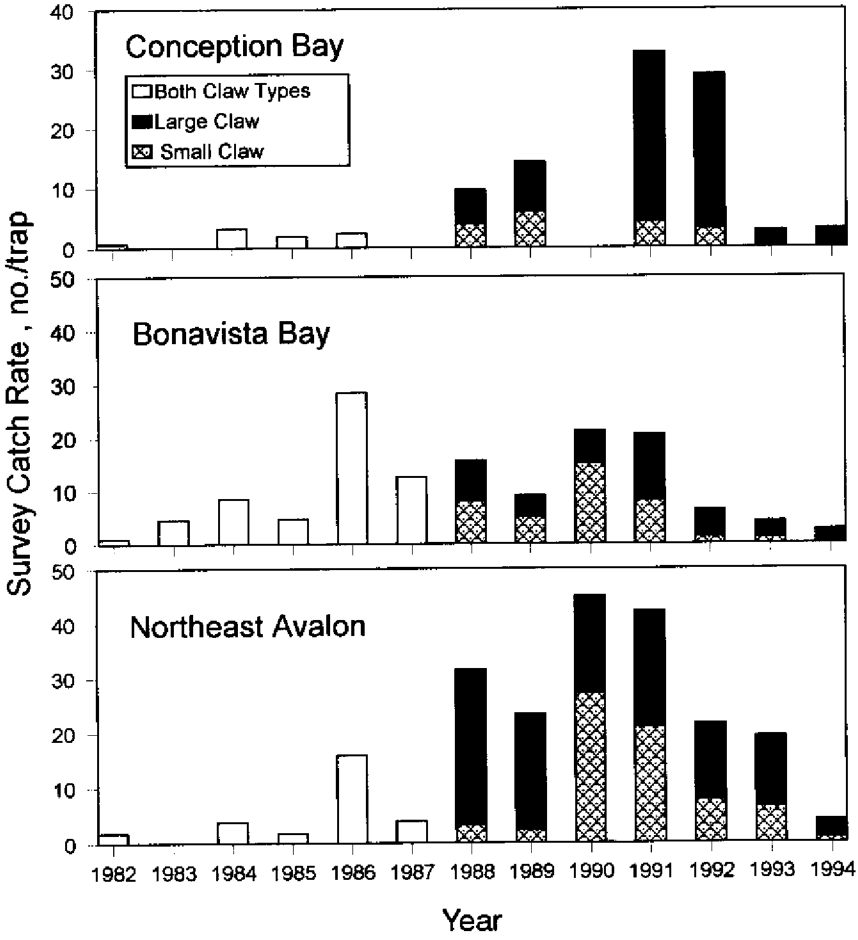

Figure 6. Yearly trends in survey catch rate of Prerecruit 2 crabs (60-75 mm CW) from small-meshed traps, by survey area. Catch rates are partitioned by chela morphometry since 1987.

Acknowledgments

We thank Geoff Evans for comments which were quite helpful in the development of predictive models and Paul Collins and Pat Veitch for developing computer programs. Thanks also go to Paul Beck, Joe Drew, and Paul O'Keefe for summarizing and illustrating the data. The efforts of numerous technicians as well as the captains and crew of several research vessels in collecting the historical data are gratefully acknowledged.

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Spawning Cycle of Horsehair Crab (*Erimacrus isenbeckii*) in Funka Bay, Southern Hokkaido, Japan

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Abstract

To clarify the spawning cycle of the horsehair crab (*Erimacrus isenbeckii* [Brandt]) in Funka Bay, southern Hokkaido, Japan, seasonal changes of ovarian maturity and the gonadosomatic index (GSI) were investigated, based on the anatomical and histological observations for 43 females collected from August 1993 to October 1994. The ovary had H-shape, and changed both in volume and color with maturity. Ovarian maturity was divided into 5 periods: recovery, yolk granule, primary yolk platelet, secondary yolk platelet, and a ripe period. The spawning cycle, including the incubation of eggs on the abdominal appendages, consisted of 3 phases: the pre-vitellogenesis, vitellogenesis, and incubation phase. The pre-vitellogenesis phase lasted for about 7 months after the hatching season (March to April), and during this phase the ovary is in the yolk granule period (GSI = 2-4). Vitellogenesis starts after post molting copulation. The vitellogenesis phase includes the primary yolk platelet, secondary yolk platelet, and ripe period (GSI = 2-28), and its completion requires about 15 months before spawning (January to March). The incubation phase lasted for about 14 months, and ovary is in the recovery and yolk granule period. The females incubate an egg clutch on their abdominal appendages (GSI < 2). These results suggest it takes about 3 years for the female *E. isenbeckii* in Funka Bay to complete one spawning cycle.

Introduction

The horsehair crab (*Erimacrus isenbeckii* [Brandt]), is distributed from Cook Inlet in Alaska and the Pribilof Islands, to Kamchatka and Sakhalin, the Kurile Islands, northern Japan and the Korean Peninsula (Rathbun 1930). The crab inhabits sandy and silty bottoms at depths of 30 to 200 m. *E. isenbeckii* is one of the most important fishery resources in northern Japan. However, its population was severely damaged because of overharvesting. As a result, effective fisheries management is now needed to preserve this resource.

Biological studies of *E. isenbeckii*, such as the larval morphology (Marukawa and Yasunari 1931, Marukawa and Zen 1933), the anatomy (Kawakami 1934a) and the reproductive ecology (Kawakami 1934b, Hirano 1935, 1941, Yoshida 1940, 1951), were initiated in the 1930s. Recently, the spawning season (Domon et al. 1956, Abe 1984), growth of larvae and juveniles (Omi 1971, Omi and Yamashita 1979, Mizushima and Yamashita 1988), mating behavior (Sasaki 1991), and mating pair sizes (Sasaki and Ueda 1992) have been clarified.

Research into the spawning cycle has also been carried out to help with the management of the crab resource. *E. isenbeckii* in the Okhotsk Sea requires 3 years to complete a single spawning cycle, based on the recapture of a tagged crab (Yamamoto and Maruyama 1978). From field research, Abe (1984) considered that most crabs in the Pacific Ocean off eastern Hokkaido took 3 years to complete a spawning cycle, and that a few required 2 years. Sasaki (1990) also suggested that the spawning cycle in that same area took about 3 years, based on seasonal changes of the gonadosomatic index. Omi and Yamashita (1982) observed that a young female laid eggs again 25 months after spawning under laboratory conditions.

Field research by Hirano (1935) suggested that females in Funka Bay, southern Hokkaido, Japan, spawn in spring, release their larvae during the next spring, and then copulate during the winter. Reliable information on the spawning cycle of *E. isenbeckii* was lacking because of uncertainties about the ovarian maturation cycle. This study was undertaken to clarify the spawning cycle of *E. isenbeckii* in Funka Bay from the histological observations of ovaries and seasonal changes of the gonadosomatic index.

Materials and Methods

The 43 female specimens used in this study were collected during 8 sampling trips from August 1993 to November 1994 by trapping at depths of 79 to 88 m in Funka Bay. The sampling locations are shown in Figure 1. Specimens were transported to the Usujiri Fisheries Laboratory, Hokkaido University, and kept in a one-ton tank until they were sacrificed for measurement. Seawater flowing in the tank was kept in the

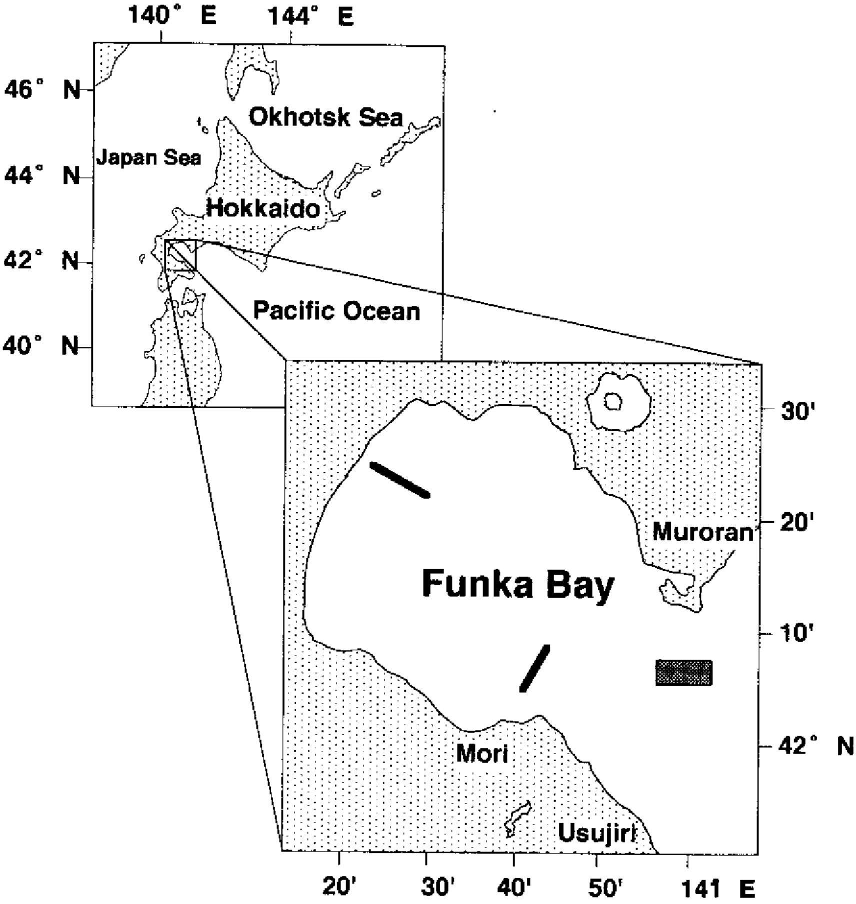

Figure 1. Sampling locations (two lines and a square) in Funka Bay.

range of 4-10°C. The crabs were fed frozen squid (*Todarodes pacificus*) or fish (*Cololabis saira*) once or twice a week. Within 2 weeks after collection, 22 crabs were killed for samples. The remaining 21 crabs were kept as supplemental specimens, to be used in months when crabs from the sea were caught in low number.

Carapace length (CL) and body weight (BW) were measured after the removal of all thoracopods and incubating eggs. After removal of the ovary and the spermatheca, the ovary weight and color were recorded according to Nippon Shikisai Kenkyujyo Jigyo Inc. 1984. To estimate the number and the mean diameter of oocytes in an ovary, a 0.02-0.03 g piece of the ovary was cut from 31 specimens, excluding specimens with extremely immature ovaries. Each measurement was repeated 3 times for accuracy. The remaining part of the ovaries and spermathecae were fixed in Bouin's solution, dehydrated in ethanol, embedded in paraffin, sectioned into 4-8 μm slices, and then stained with Harris's hematoxylin and eosin, or periodic acid-Schiff. The gonadosomatic index (GSI) was calculated as the ratio of ovary weight × 100/BW.

Results

General morphology of the female genital tract

The genital tract of female *E. isenbeckii* consists of the ovary, a pair of oviducts, spermathecae, vaginas, and gonopores (Figure 2A, C). The ovary is surrounded with fibrous connective tissue, and is situated on the dorsal side of the midgut gland and beneath the heart, whose shape forms the letter H. The anterior lobes of the ovary extended to both lateral sides of the cephalic region alongside the gastric mill. The posterior lobes extended to the abdominal segment alongside the intestine. The oviduct is located on the ventral side of the posterior lobes and is connected with the spermatheca. The sac-like spermathecae are located between the oviduct and cuticular vagina, which opens into the gonopore near the lateral margin of the sixth sternal plastron where each third pleopod is articulated. Seven females had copulatory plugs in their gonopores (Figure 2B). The copulatory plug is hard, proteinaceus, and extends into the vagina and some spermatheca.

Histology of spermatheca

Sperm cells were observed in the spermathecae of all females examined in this study (Figure 3), indicating that the crabs had copulated at least once. In most specimens, the spermatophores had already dehisced, and were not observed in the spermatheca. In the other specimens, a few spermatophores were observed in the spermatheca near the vagina. These findings suggest that spermatophores of these crabs are immediately dehisced after copulating, and that some dehiscent sperm cells remain in the spermatheca after spawning.

Oogenesis and ovarian maturation

For describing the criterion of germ cells in oogenesis, histological observations for *Pacygrapsus crassipes* by Chiba and Honma (1972) and for *Ranina ranina* by Minagawa et al. (1993) were applied. Oogonia are nearly circular, measure 8 to 15 μm in diameter, and increase in number by mitotic division. The heterochromatin in the nucleus is uniformly distributed like a net during the resting stage, and the cytoplasm is very thin. Oogonia and young oocytes form germinal zones, which lie scattered in the ovary throughout the year (Figure 4A). Young oocytes including the germinal zone are in the chromatine nucleolus stage and the

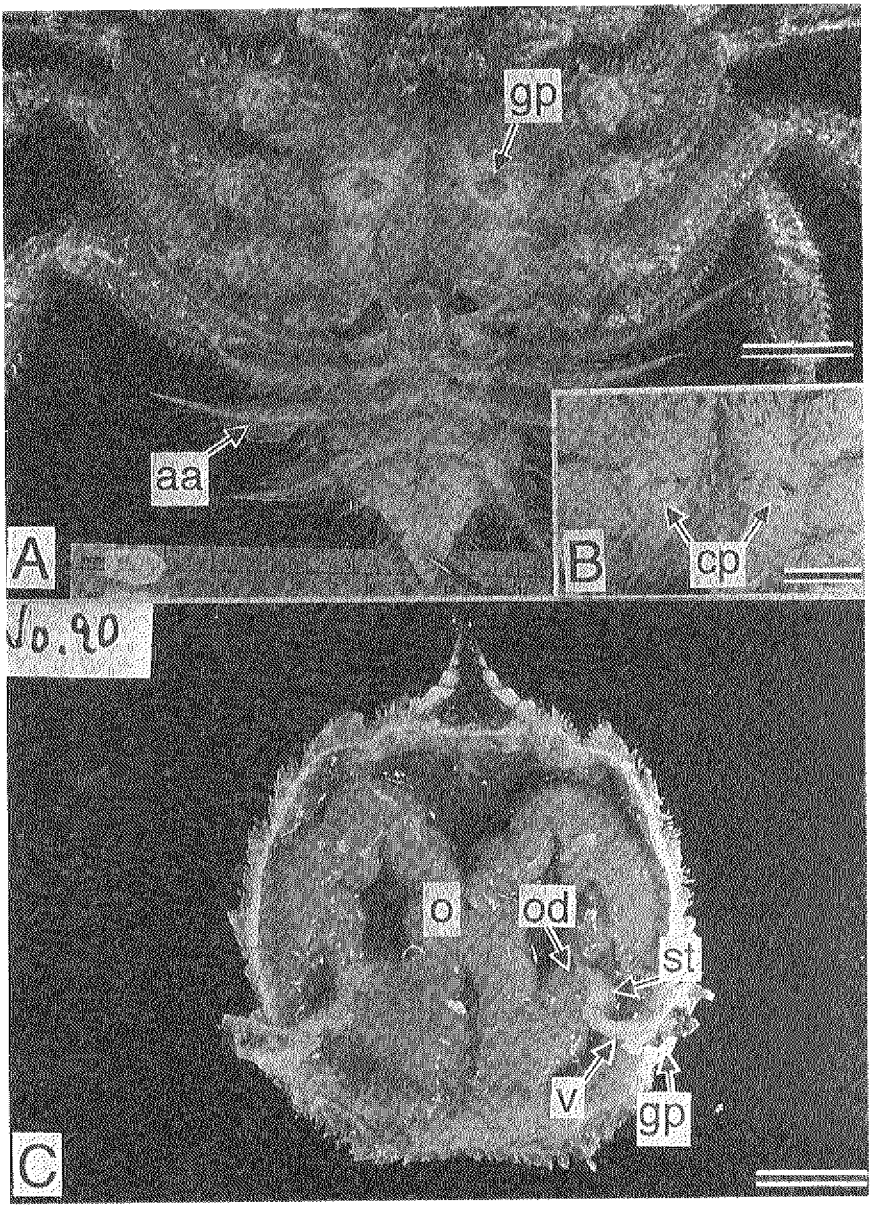

Figure 2. Reproductive system of female Erimacrus isenbeckii. (A) Female, ventral view. (B) Copulatory plugs in gonopores on the third thoracic sternite (C) Interior genital tract. Bar indicates (A and C) 3 cm; (B) 1 cm. aa: abdominal appendage; cp: copulatory plug; gp: gonopore; o: ovary; od oviduct; st: spermatheca; v: vagina.

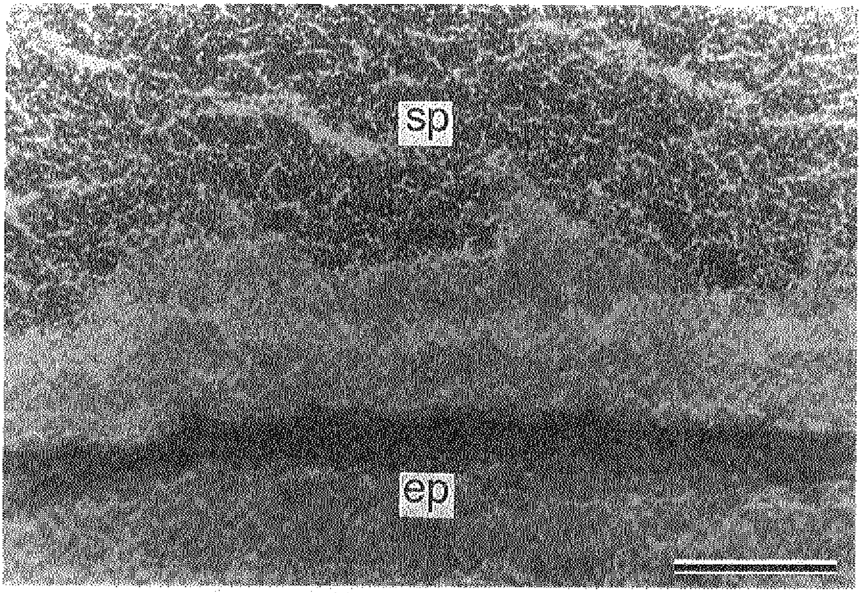

Figure 3. Cross section of spermatheca. Bar indicates 200 μm. ep: epithelium; sp: sperm.

oil globule stage. Oocytes in the chromatine nucleolus stage have a strongly basophilic chromatin nucleolus near the center of the nucleus. The oocytes are 15 to 20 μm in diameter and its cytoplasm is still thin. Oocytes in the oil globule stage measured 20 to 80 μm in diameter and the cytoplasm could be weakly dyed blue with hematoxylin. Oil globules are observed in the cytoplasm as vesicles, the center of which was dyed irregularly by PAS. Oocytes during this stage are also found outside of the germinal zone throughout the year (Figure 4B). After the oil globule stage, oocytes separated from germinal zones and developed synchronously to the yolk granule stage, the primary yolk platelet stage, the secondary yolk platelet stage, and the premature stage. Oocytes during the yolk granule stage have many small yolk granules in the cytoplasm, resembling a honeycomb. The oil globules increased in number and diameter, and moved to the periphery. The oocytes measured 80 to 350 μm in diameter (Figure 4C). Oocytes during the primary yolk platelet stage have eosinophilic yolk platelets, which are stained red-purple with PAS (Figure 4D, E). The platelets increased in number in the periphery of the cytoplasm. The oocytes measured 300 to 450 μm in diameter. Just before the end of the stage, the karyoplasm can be stained with eosin. The yolk platelets continued to grow, the oogenesis stage be-

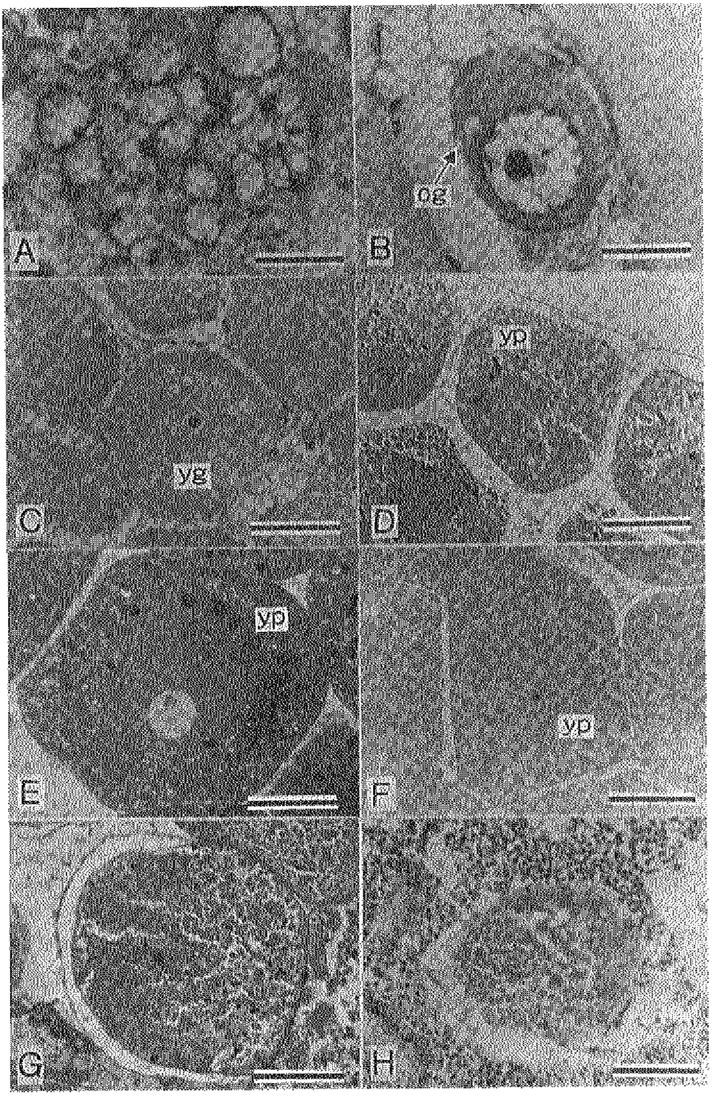

Figure 4. Oogenesis of *Erimacrus isenbeckii*. (A) Oogonia and oocytes of chromatine nucleolus stage and oil globule stage in the germinal zone. (B) Oil globule stage. (C) Yolk granule stage. (D) Primary yolk platelet stage. Harris's hematoxylin and eosin. (E) primary yolk platelet stage. Periodic acid-Schiff. (F) Secondary yolk platelet stage. (G) Premature stage. (H) Atretic oocytes. Bar indicates (A and B) 20 μm; (C and E) 100 μm; (D and F-H) 200 μm. og: oil globule; yg: yolk granule; yp: yolk platelet.

comes the secondary yolk platelet stage. The nucleus was still found at the center of the oocytes and the nuclear membrane was distinct, but only a little cytoplasm was observed around the nucleus. The oocytes measure 400 to 750 μm in diameter (Figure 4E). Oocytes during the premature stage measure to 750 μm in diameter. The fusion of yolk platelets is not seen and the nucleus was not observed (Figure 4F). We could not observe more developed oocytes than these during the premature stage.

Ovarian maturity was divided into 5 stages, based on the oogenesis stage of the most abundant oocytes in the ovary, and the presence of follicle cells after ovulation.

Recovery period (Figure 5A)

Most parts of an ovary are occupied by follicle cells after ovulation, and some atretic oocytes are present (Figure 4G). The most oocytes are in the oil globule stages, and these oocytes were observed both outside and inside of the germinal zones. GSI values are under 2 (n = 7). The ovaries in this period are ivory in color. Most crabs in this period were incubating eggs on the ciliae of their abdominal appendages.

Yolk granule period (Figure 5B)

Oocytes in the yolk granule stage are the most prominent oocytes within the ovary during this period. The ovaries contain follicle cells after ovulation but no atretic oocytes. In comparison with the recovery period, the ovaries do not change in color. The values of GSI range from 2 to 4 (n = 6). Crabs in this period were collected throughout the year. Some individuals were incubating the eggs, and others had copulatory plugs.

Primary yolk platelet period (Figure 5C)

Most oocytes are in the primary yolk platelet stage. The ovary color became maize or nepled yellow. The values of GSI range from 2 to 7 (n = 12). Most crabs in this period had copulatory plugs, and none were incubating eggs.

Secondary yolk platelet period (Figure 5D)

Most of the oocytes in this period are in the secondary yolk platelet stage. Each oocyte becomes deformed, due to compaction. The ovaries increase in volume so that they nearly filled the inside of the carapace. The color changed to orange or sunlight yellow. The GSI values ranged from 4 to 28 (n = 17). Crabs in this period were observed throughout the year.

Ripe period (Figure 5E)

The oogenesis of most oocytes was in the premature period. Only one female recorded in March reached this stage. The color and shape of the

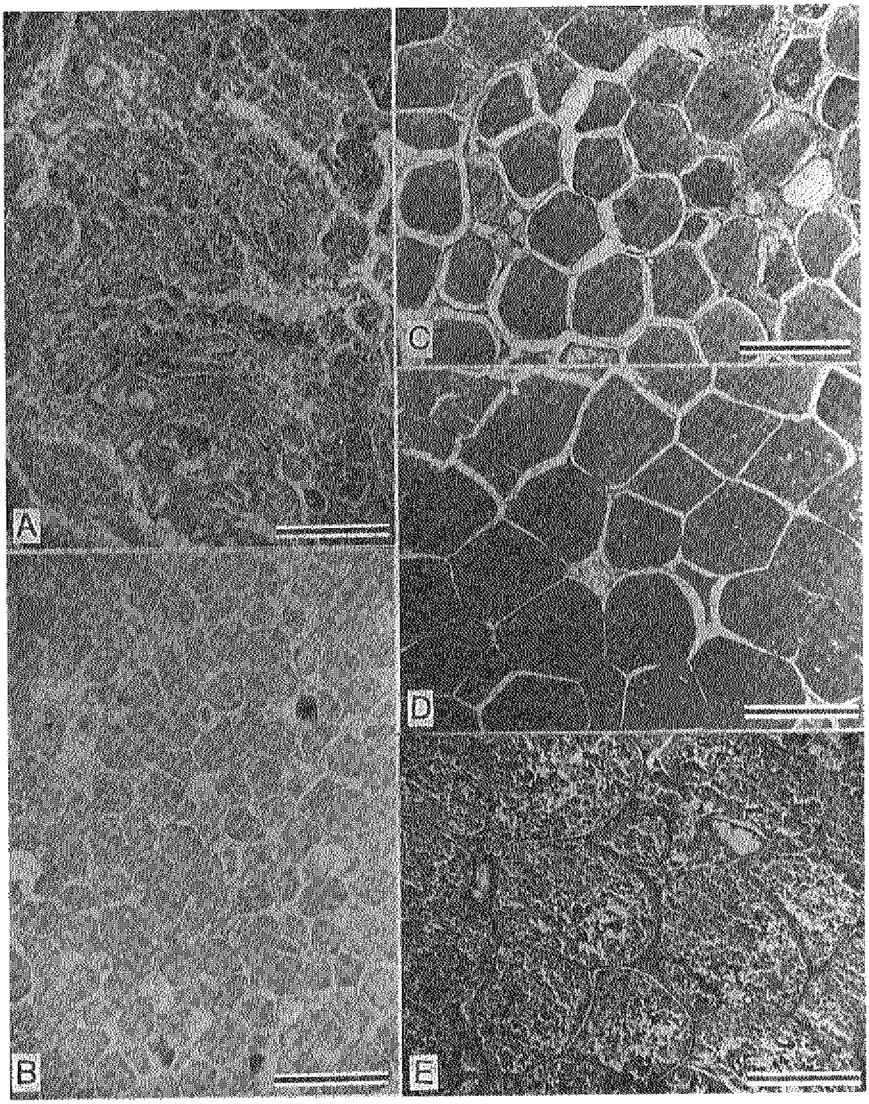

Figure 5. Ovarian maturity of *Erimacrus isenbeckii*. (A) Recovery period. (B) Yolk granule period. (C) Primary yolk platelet period. (D) Secondary yolk platelet period. (E) Ripe period. Bar indicates 1 mm.

ovary was the same as the secondary yolk platelet period. The GSI value equals 27 (n = 1). No females with ovaries including prominent oocytes of more advanced oogenetic stages could be observed.

Spawning cycle

The spawning cycle of *E. isenbeckii* in Funka Bay was investigated based on seasonal changes of ovarian maturity and the GSI value (Figure 6). Two females collected in December were in the secondary yolk platelet period, and their GSI values exceeded 22. One female observed in March was in the ripe period. Three females spawned in January in the laboratory, and 2 females of the crabs collected in February had the eggs in the blastula stage. These observations indicate that the spawning season of *E. isenbeckii* in Funka Bay occurs during January to March.

The GSI values of all females incubating eggs were less than 2, and their maturity was in the recovery period or the yolk granule period. In addition, hatching of the larvae occurred in March or April in the laboratory, and incubating females were collected over a wide time period (January-July). It was, therefore, inferred that more than 1 year is required for incubation.

One female (in the yolk granule period) in September, 5 females (in the primary yolk platelet period) from October to April, and 1 female (the secondary yolk platelet period) in February had copulation plugs in their gonopores. These females had likely copulated 6 to 12 months after the hatching of larvae. GSI values began to increase with vitellogenesis, reaching 22 to 24 in December. Overall, a female *E. isenbeckii* takes about 3 years for the completion of a single spawning cycle.

The number of oocytes

The number of oocytes in an ovary ranged from 33,000 to 297,000 (n = 31). The number was correlated with carapace length (r = 0.907), but not with GSI value (r = –0.012) (Figure 7). The oocytes measured 0.25 to 0.75 mm (n = 31) in diameter, and increased with the value of GSI (r = 0.936) (Figure 8). Female with GSI values less than or equal to 4 had 117,000 (± 80,000) oocytes. These findings suggest that the changes of GSI were due not to an increase in oocyte number, but to the growth of oocytes, and that the number of oocytes would not be established until the start of vitellogenesis.

Discussion

The anatomical characters of the ovary and the process of oogenesis of *E. isenbeckii* are similar with other crab species, including *Potamon dehaani* (Ootsu 1963), *Chionoecetes opilio* (Kon and Honma 1970), *Pacygrapsus crassipes* (Chiba and Honma 1972), *Geryon quinquedens* (Haefner 1977), *Ovalipes punctatus* (Du Preeze and Mclachlan 1984),

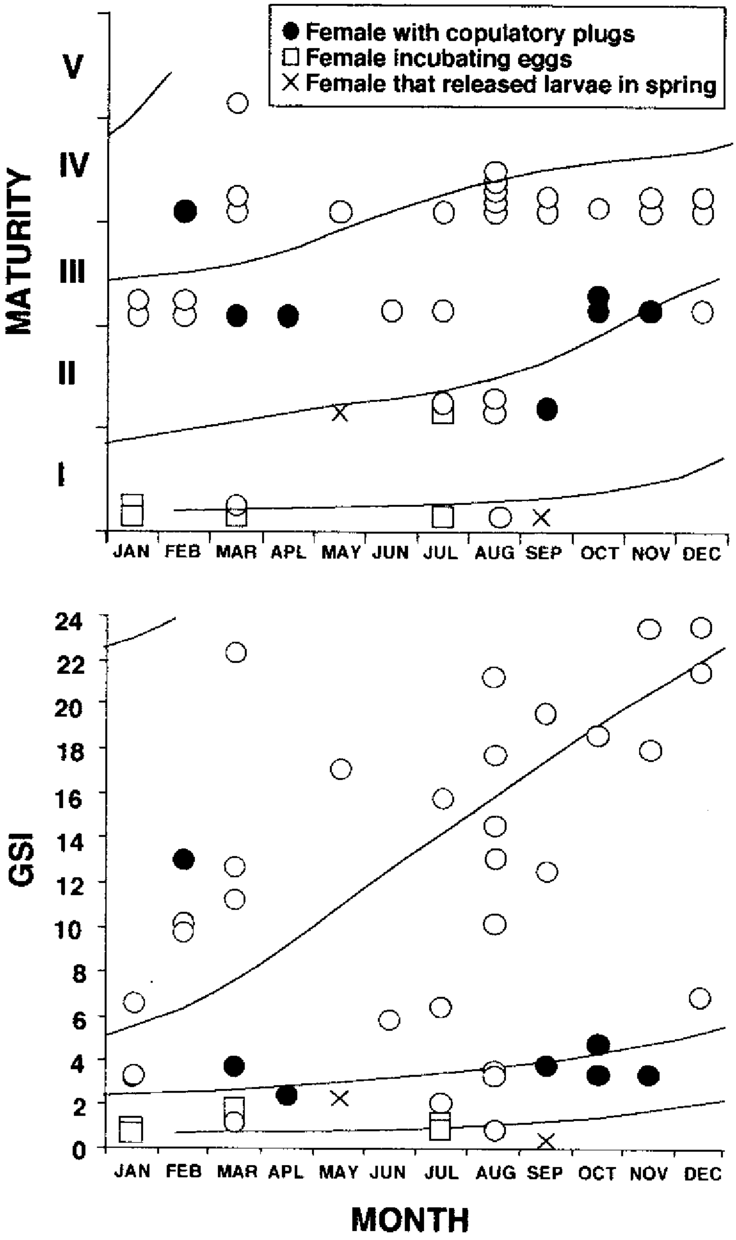

Figure 6. Seasonal changes of ovarian maturity and GSI value of Erimacrus isenbeckii in Funka Bay. I: recovery period, II: yolk granule period, III: primary yolk platelet period, IV: secondary yolk platelet period, V: ripe stage.

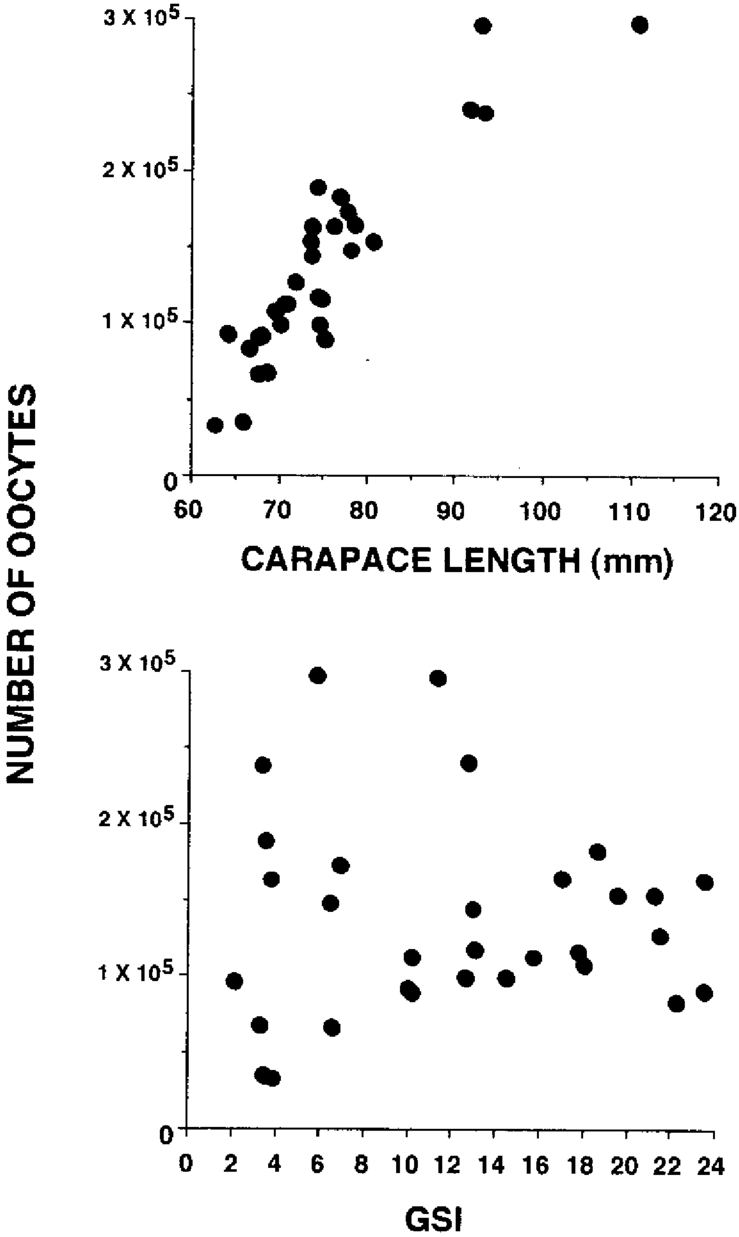

Figure 7. Scattergrams for the number of oocytes in an ovary of Erimacrus isenbeckii on the carapace length, and on the GSI value.

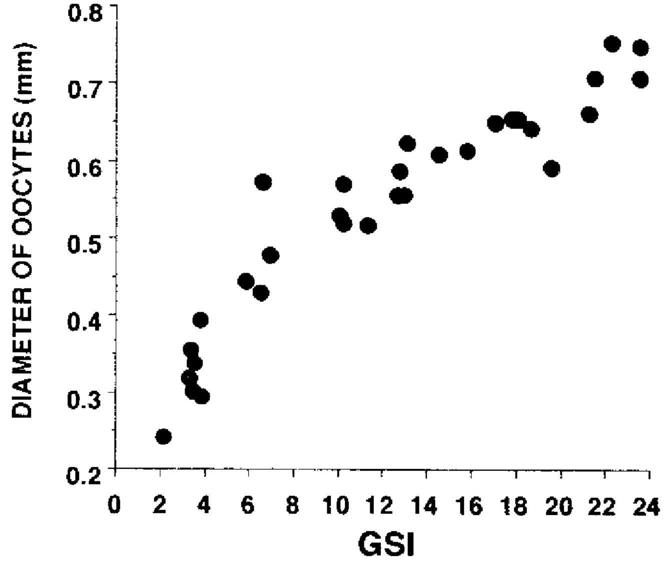

Figure 8. The relationship between the GSI value and diameter of oocytes for female Erimacrus isenbeckii.

Geryon maritae (Melville-Smith 1987), and *Ranina ranina* (Minagawa et al. 1993). However, the distribution of developing oocytes in the ovary varies by crab species according to the spawning frequency during a breeding period and the interval between spawning. Following the oil globule stage in *E. isenbeckii*, oocytes separated from the germinal zones and developed synchronously, demonstrating that *E. isenbeckii* produce one clutch in a spawning cycle. In other crab species, oocytes move from the germinal zone in the center of the ovary toward the periphery of the ovary with the growth (Kon and Honma 1970, Chiba and Honma 1972, Minagawa et al. 1993).

Hirano (1935) suggested that *E. isenbeckii* in Funka Bay may spawn during March to April, based on the occurrence of the eggs in early developing stages on the abdominal appendages. However, we observed that 5 females (reared for 3-5 months) spawned in January. In addition, this finding was supported by the seasonal changes of the GSI value. Hirano might have overestimated the developing rate of eggs in the early stages.

Based on the occurrence of larvae, Omi and Yamashita (1981) suggested that the hatching season of *E. isenbeckii* in Funka Bay begins in the middle of March. Captive females released their larvae during March to April. Considering the spawning season, crabs require more than 1

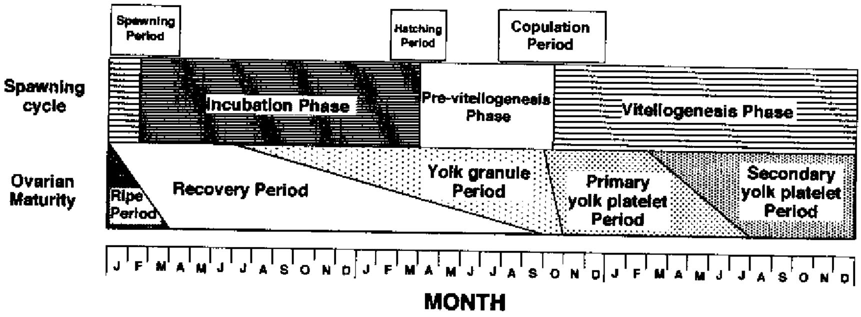

Figure 9. Spawning cycle of Erimacrus isenbeckii in Funka Bay, southern Hokkaido.

year to incubate their eggs, based on observations of artificially incubated eggs removed from abdominal appendages (unpubl. data).

Hirano (1935) reported that copulating pairs of crabs were caught from January to February in Funka Bay. Because female *E. isenbeckii* had copulatory plugs in their gonopores deposited by male crabs while copulating (Hirano 1941, Sasaki 1991), the occurrence of females with plugs provides information on the maturity status of copulated females. Most of the females that had copulatory plugs were in the primary yolk platelet period. They were collected from August to February. All females, except for one, in the secondary yolk platelet period had lost their plugs, so the plugs may fall off several months after copulation.

The spawning cycle of *E. isenbeckii* was divided into 3 phases: a pre-vitellogenesis phase, vitellogenesis phase, and incubating phase (Figure 9). The pre-vitellogenesis phase corresponds to the yolk granule period, and lasts for about 7 months from the hatching season (March to April) until the beginning of vitellogenesis. Molting and subsequent copulation occurred between this phase and the vitellogenesis phase. The vitellogenesis phase consisted of the primary yolk platelet period, the secondary yolk platelet period, and the ripe period. This phase lasted for about 15 months and was followed by spawning (January to March). The incubating phase lasted for about 14 months and included the recovery period and the yolk granule period. Thus, *E. isenbeckii* needs 3 years for the completion of one spawning cycle.

For crabs distributed in high latitude habitats, such as *Chionoecetes opilio, Paralithodes camtschaticus,* and *E. isenbeckii,* a incubating period of not less than one year is common (Kon 1976, Nakanishi, 1987), but the spawning cycle is very different between species. Female *C. opilio* undergoes terminal molting before the first spawning. In the following spawning, they copulate without molting after releasing larvae, so they can spawn every year without molting (Yoshida 1941). *P. camtschaticus* molts between the release of larvae and spawning, and most females produce one clutch in a year (Kurata 1952, Matsuura et al. 1971). The short spawning intervals in these crabs, unlike *E. isenbeckii*, are possible because ovarian maturation occurs simultaneously with egg incubation. In *E. isenbeckii*, ovarian maturation begins after the release of larvae, and the molting occurs before spawning (Sasaki 1991). Such an alternating switch from reproduction to growth allows the crabs to invest all of their energy into either growth or reproduction. The reproductive strategy of *E. isenbeckii* may require the female to invest greater energy for one reproduction or for long-term growth.

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Reproductive Strategies of Two Lithodids in the Beagle Channel, Argentina: A Complementary Management Tool in a Changing Fishery

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Abstract

Two sympatric species occur simultaneously in the Argentinean fishery of the Beagle Channel: *Lithodes santolla* and *Paralomis granulosa*. The species differ markedly in their reproductive potential. The rate of replacement of new individuals to the population is higher in *Lithodes santolla* than in *P. granulosa* because the former grows to maturity faster and its fecundity is greater. Moreover, in male *P. granulosa* recruitment to the fishery is additionally delayed because males probably molt biennially before they enter the fishery. In the last 3 years, the scenario of the fishery changed. Currently, two types of fishers coexist in the area: "industrial" fishers, who have larger boats, more mobility, more traps to fish, and thus develop heavier fishing effort than "artisan" fishers. Moreover, conclusive data from the fishery are very difficult to obtain. Therefore, we suggest a complementary management tool for king crabs in the Beagle Channel based on the reproductive potential of each species, and on the fishing effort that each fraction of the fleet can develop. Industrial fishers should be encouraged to fish *L. santolla*, while artisan fishers should fish the less productive *P. granulosa*.

Introduction

In the Beagle Channel, southern South America, two sympatric species of lithodids occur in coastal waters: *Lithodes santolla* (Molina 1782) and *Paralomis granulosa* (Jacquinot 1847). They are known as southern king crab or "centolla" and false southern king crab or "centollón," respectively. They are markedly different in their morphology. Maximum size of *L. santolla* is 190 mm carapace length (CL), and it has a maximum weight of 8-9 kg. By contrast, *P. granulosa* maximum size and weight are 110 mm CL and 1.5 kg respectively. Therefore, *L. santolla* has been commercially preferred because of its greater meat yield and higher quality. Consequently, its market value is three times that of *P. granulosa*.

Since the 1930s, the Argentinean fishery for king crabs has occurred almost exclusively in an area of the Beagle Channel near the city of Ushuaia. This is a mixed fishery, since frequently both species appear simultaneously in traps used for fishing. Until the late 1970s, the fishing was concentrated on *L. santolla* while *P. granulosa* was considered as bycatch and discarded. In the early 1980s, landings of *P. granulosa* began to increase as a response to declining captures of *L. santolla*. This is a modest fishery: so far, less than 10 small boats (10-15 m length) have fished jointly in the area. This scenario changed in the last 3 years: in 1992, smaller boats (5 m length) began to fish for king crabs and in 1994, attained 17% of the total landings of *L. santolla*. Landings of *L. santolla* and of *P. granulosa* have varied around 250 mt/yr and 150 mt/yr, respectively. Maximum landings of about 350 mt were attained in 1974 for *L. santolla* and in 1995 for *P. granulosa*.

In 1994, the area that had been fished for more than 6 decades was closed because of symptoms of over-exploitation of the stock. The density of *L. santolla* had decreased 80% since 1981, average sizes of males and females decreased significantly, and the proportion of ovigerous females was 35% (Wyngaard and Iorio 1996). Thus, the fishery has developed eastward, about 70 km away from Ushuaia. Unfortunately, fishery data are difficult to obtain, scarce for *L. santolla* and null for *P. granulosa*. Thus, it is difficult to predict when the fishery will recover, or to state precise rules to protect the stock. In this paper we suggest an alternative and complementary management tool for the fishery, strictly based on the reproductive strategies of both lithodid species and on the fishing effort of each fraction of the fleet.

Biology of Lithodids in the Beagle Channel

Biology of Lithodes santolla

In late November–early December, the reproductive cycle of *L. santolla* begins with female molting. The precopulatory embrace and mating occur between an oldshell male and a smaller female recently molted. In the population, mating pairs can be found during approximately one month. As in other lithodids, fertilization is external and occurs immediately after female oviposition. Eggs are carried by females and embryogenesis lasts approximately 9-10 months. Fecundity (number of eggs per brood) varies with female size, between 5,500 and 60,000 eggs

(Table 1). In some areas intensively harvested, females carry fewer eggs and total fecundity is reduced. Larval hatching occurs between mid-September and October, without significant annual variation. However, in other areas of the distribution of *L. santolla*, larval hatching is dependent on seawater temperature and varies considerably (Hernández 1985, Vinuesa 1985). Larvae pass through three zoeal and one glaucothoe stage, and metamorphose to the first benthic crab stage, which is about 3 mm CL.

During the first year, crab molt 6-7 times, during the second year, 4-5 times, and during the third year, 3 times. Crabs of 3 years old are about 50 mm CL. Thereafter, males molt twice a year until they reach morphometric maturity (defined as the change in the allometric relationship between carapace and claw size), i.e., at 5 years old, at 90-99 mm CL. In the fourth year, females begin ovary maturation and thus, to molt annually. Gonadal maturity (defined in males as the presence of spermatozoa in the testicles, and in females as the presence of embryos in the incubation chamber) is reached at 60-75 mm CL in males, and at 66-87 mm CL in females. In females, oogenesis lasts 24 months (Vinuesa and Labal, unpublished results). After gonadal maturity and after morphometric maturity, respectively, females and males continue to molt annually. Males enter the fishery at 110 mm CL and it is suspected that males > 150 mm CL molt biennially (Geaghan 1973).

Biology of *Paralomis granulosa*

During November, the reproductive cycle begins with courtship and mating, supposedly between an oldshell male and a recently molted female. Fertilization is external and the female keeps the embryos in her incubation chamber between 18 and 22 months (Table 1). Fecundity varies between 800 and 10,000 eggs, depending on female size. However, about 50% of the females > 80 mm CL do not carry eggs though their ovaries are well developed (Hoggarth 1993, Lovrich and Vinuesa 1993). Larval hatching occurs mainly during winter (June to August), almost two years after mating. For each individual, larval development (through zoeal and one megalopa stages) lasts approximately 40 days (Campodónico and Guzmán 1982). However, there is no information about larval duration in the natural environment. There is also no information on growth from the first crab stage (of about 3 mm CL) to the stage of about 10 mm CL. During the immature phase, growth is slow. The smaller crabs (< 40 mm CL) molt twice a year, in winter and summer, while crabs > 40 mm CL molt only in summer. During the immature phase, percentage of growth per molt is constant and of 12.4%. At this rate of growth, we suspect that gonadal maturity would be reached at about 10 yrs old.

Males attain gonadal maturity at 50.2 mm CL, and females at 60.6 mm CL (Table 1). Morphometric maturity is reached at 57 mm CL in males and at 66.5 mm CL in females. By molting once after gonadal maturity, males attain morphometric maturity. Males enter the fishery attaining a commercial size of 80 mm CL. Male molting is assumed to be annual, and biennial when males are older (Hoggarth 1993, Lovrich personal observations). However, there is no information about growth rates in mature crabs; the time required to attain legal size remains unknown. Moreover, at mating, crab size and maturity condition is unknown; thus it is difficult to evaluate the role of each category of crabs (gonadal or morphometric maturity, commercial size) in the reproductive process and recruitment.

Discussion

For other crustaceans, the reproductive potential has been previously quantified in terms of fecundity, age at maturity, fishing mortality, proportion of females in each size class, and growth of individuals in a population (Campbell and Robinson 1983, Shields 1991). Evidently, both sympatric species of the Beagle Channel markedly differ in their reproductive potential, thus in the time of replacement of the final "product": crabs of commercial size. Data at hand provide evidence that reproductive potential of *P. granulosa* is constrained morphometrically. As in brachyurans, female body size of anomurans is the determinant of the reproductive output (Hines 1982, Jensen and Armstrong 1989, Lovrich 1991). For the two species, the volumes of developing oocytes in the ovary and extruded eggs are similar (Table 1). Hence, the body size constrains the volume of the ovary, and thus the number of eggs that a female can carry. Size range of mature females in *P. granulosa* is between 60 and 90 mm CL, and in *L. santolla* between 75 and 160 mm CL. This difference in size determines the number of eggs per brood. For example, female *L. santolla* and *P. granulosa* carry similar quantities of eggs, 5,300, at 78 mm CL (Vinuesa 1982, Lovrich and Vinuesa 1993).

Except for the number of zoeal stages, the other larval features are very similar in both species (Table 1). Larvae of both species are lecithotrophic with ability to feed at some time during development (Comoglio and Vinuesa 1991). Therefore, we assume that larval survival in the natural environment is similar in the two species, and does not cause major variations in recruitment to the benthic fraction of each population.

Due to very slow growth of the immature phase, the age at gonadal maturity, and thus the generational time of *P. granulosa*, duplicate those of *L. santolla*. Therefore, two generations of *L. santolla* pass through the fishery while only one of *P. granulosa* does. Slow growth of *P. granulosa* is evidenced also in mature phases. Females molt biennially and their gonadic development lasts about 3 years. Male *P. granulosa* begin to skip the annual molt before reaching commercial size at 75-80 mm CL, while male *L. santolla* smaller than legal size molt annually (Boschi et al.

Table 1. Life-history traits of sympatric species *Lithodes santolla* and *Paralomis granulosa* in the Beagle Channel, Argentina.

Trait	*Lithodes santolla*	*Paralomis granulosa*
Mating frequency	Annual, December[1]	Biennial, November[2]
Fecundity (eggs/female)	5,500-60,000[3,4]	800-10,000[2]
Embryogenesis	9-10 mo.[5]	18-22 mo.[2]
Maximum egg size (diameter)	2.1 mm[5]	1.9 mm[2]
Zoeal size at hatching	2.0 mm CL[6]	2.1 mm CL[7]
Number of zoeal stages	3[6]	2[7]
Larval development	23-26 d[8]	17-22 d[9]
Larval hatching	September-October[1]	June-August[2]
Age at gonadal maturity	5 yrs[10, 11]	9-10 yrs (?)[12]
Size at gonadal maturity	75 mm CL[1]	50-60 mm CL[2]
Duration of gametogenesis, female	2 yrs[1]	> 3 yrs. (?)[13]
Duration of gametogenesis, male	60-90 d[1]	various/year (?)[13]
Legal size	110 mm CL	80 mm CL

1. Vinuesa 1984; 2. Lovrich and Vinuesa 1993; 3. Vinuesa 1982; 4. Lovrich unpublished data; 5. Vinuesa 1987; 6. Campodónico 1971; 7. Campodónico and Guzmán 1981; 8-11. Vinuesa et al. 1985, 1989, 1991, 1990, respectively; 12. Lovrich and Vinuesa 1995; 13. Lovrich 1991. (?) indicates uncertain information. CL: carapace length.

1984, Lovrich unpublished data). This implies that in *P. granulosa*, recruitment to the fishery may be retarded by the molting frequency of adult males. Hence, in fishery terms, *P. granulosa* is much less productive than *L. santolla*. *Lithodes santolla* grows faster and has half the generational time of *P. granulosa*. Female *Lithodes santolla* reach a larger size and spawn annually. Therefore, overall fecundity of *L. santolla*, and thus the rate of replacement of new individuals to the population (if larval survival is similar) is higher than in *P. granulosa*.

Regulations to the fishery were put in place based on the biology of *L. santolla*. They were designed to preserve the reproductive potential of the species. These are: (1) exclusively male landing. (2) Minimum size limit of 110 mm CL for *L. santolla* and 80 mm CL for *P. granulosa* (the latter in force since 1993). (3) Fishing season between January and October (this effectively preserves the mating season of *L. santolla*). (4) Maximum of 1,000 traps in the zone near the city of Ushuaia. The fishery was characterized by frequent violations of the regulations. Moreover, violations of the first two rules made the fishery for *L. santolla* collapse because of overfishing of the reproductive stock (Wyngaard and Iorio 1996). Consequently, in 1994 the area near Ushuaia was closed to fishing for both king crab species. However, for this area, there is no data which support that *P. granulosa* stock is overexploited. Detailed fishing logs have never been required, and will be difficult to obtain because of fishers' reluctance. Scientific surveys are scarce, discontinuous, and exclusive for *L. santolla* (Boschi et al. 1984, Bertuche et al. 1990). Therefore, the fishery does not have data that allow prediction of its evolution.

The scenario of the fishery in the Beagle Channel has changed in the last 3 years. Formerly, only medium-size boats (12-15 m length; crew of 3) fished in the area. They can manage about 120-150 traps/day and navigate 100 km off Ushuaia. Thus, they easily move out of the closed fishing area. Their owners are the fishing companies who also own the factories that process crab landings. This part of the fleet is called "industrial." In 1995, they concentrated their fishing effort on *P. granulosa* and reached a record of 350 mt landings. Three years ago, artisan fishers began to appear in the area near Ushuaia. They have smaller boats (5 m length; crew of 1) which can manage only 20-30 traps/day. Their movements are restricted to near the port, i.e., the closed fishing area, and thus their fishing is impeded.

Given the difficulty of obtaining conclusive data from the fishery, the difficulty of effectively controlling the regulations of the fishery, and the reproductive biology of the species we suggest a new, preventive and complementary tool of management for the fishery of the Beagle Channel. We suggest ruling the fishing based on the productivity of each species and to the fishing effort that each fraction of the fleet can develop. Industrial fishers, who can apply heavy fishing efforts and are more able to expand geographically, should be encouraged to fish for *L. santolla*, preferably in areas never exploited. As occurred so far, *Lithodes santolla* will probably support a heavier, but still modest, rate of fishing than *P. granulosa*. Artisan fishers, who are restricted to operate near the city, are less capable of managing several gear types, and thus less capable of applying a heavy fishing effort, should be encouraged to exploit *P. granulosa* at very low rates.

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Timing and Duration of the Mating and Molting Season for Shallow Water Tanner Crab (*Chionoecetes bairdi*)

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Abstract

We monitored abundance of various categories of Tanner crabs (*Chionoecetes bairdi*) through three breeding seasons (1993-1995) to define timing and duration of the mating season in a shallow water habitat. Divers estimated abundance along measured transects at 4 depths (2, 5, 10, and 15 m) at a site in Womens Bay, Kodiak Island, Alaska. Crab categories included males ≥ 75 mm carapace width (CW), pubescent females ≥ 75 mm CW, primiparous females, multiparous females, and primiparous and multiparous grasping pairs. Exoskeletons of the first two categories were also tabulated. Primiparous pairs were encountered from mid- January through mid-July. Multiparous pairs, however, were seen only during May. A majority of males molted during the fall with lesser amounts through winter and spring. Females molted primarily during winter and spring. The primiparous mating for female Tanner crabs occurs over a period of 6 months, whereas mating activity for multiparous females is limited to a brief period in the spring.

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A Note on Mortality and Injury Rates of Male *Chionoecetes bairdi* (Decapoda, Majidae) Competing for Multiparous Mates

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Abstract

Carapace damage, limb loss, and frequency of death in mature male *Chionoecetes bairdi* incurred while competing for multiparous mates was examined in laboratory tanks. Males, whose carapace width was > 140 mm, commonly crushed their opponents' limbs and perforated carapaces during combat. Many of the wounded males died. These observations may reflect laboratory conditions, but do show that big male Tanner crabs have the power to mortally wound their rivals when competing for mates.

Introduction

In the genus *Chionoecetes*, females reach a terminal size with their maturity molt. They first copulate while their carapace is soft and again as hardshell individuals in following years. Females producing their second and subsequent egg clutches are called multiparous crabs. During the breeding period males compete for females using their chela to grasp the female and to ward off competing males. This note provides information on the extent of damage competing legal-size males (> 140 mm) incur during fights over multiparous mates.

Materials and Methods

Multiparous female and adult male Tanner crabs were captured near Homer, Alaska, and held at the University of Alaska Seward Marine Center Laboratory. The males used in the experiment were legal size, carapace width (CW) ≥ 140 mm and chela height (CH) ≥ 31 mm. None of the males used in the study had apparent carapace injuries such as broken limbs or perforations that went all the way through the shell.

After capture the females were held together without any males in 1,000 L tanks. This was the standard tank size for all observations in this report. These running seawater tanks had a water exchange rate ≥ 100% per hour. During the experiments the water temperature ranged from 3.0° to 5.0°C. The salinity ranged between 32 and 34 ppt. All crabs were fed a surplus of Pacific herring tissue every Monday and Thursday.

While larvae were hatching, males were put in with the females. The sex ratio in all the mixed sex groups was either 5 or 3 females to one male (Table 1). The number of males, plus male size data (CW and CH) occur in Table 1. All the male parents had a hard carapace with oldshell status.

The experimental animals were held in their mixed sex groups from 1 April until 15 July. During that time rates of mortality and limb damage resulting from fights between males were noted. In the summary table the term perforated carapace is used. That term refers to a condition where body tissues were exposed because the punctures incurred while fighting went completely through the carapace.

Two groups, each containing 5 males, were held under the same conditions as the mixed sex test groups, and for the same duration, but without any females present. These two groups acted as controls to show mortality levels not associated with male fights for mates.

Results

In all the mixed sex groups of *C. bairdi* there was almost continual fighting among the males for possession of females. Usually when a male grasping a female was challenged he would hold her as far away from his body as possible on one side and grasp the attacking male with the other claw. The attacking male would try to maneuver toward the female while counterattacking with his chela. Not enough observations were made to tell if the original male or the attacker consistently won these battles. Both day and night observation would have been required and nearly continual observation or filming to quantify the behavioral aspects of fights. This effort was a preliminary low budget study. Several copulations were observed. During copulation the male would move about with the female underneath him. She used her legs to maintain position while he avoided other males and used his chela to fight if necessary. Very few fights were seen once copulation started since the male in possession of the female usually retreated when any crab approached him. During these retreats the female remained in the copulatory position.

The grappling by competing males commonly resulted in perforations of the carapace on the legs and even the chela of fighting males (Table 1, Figure 1). Between 60 and 100% of the males held with females

Table 1. Deaths and injuries to male *Chionoecetes bairdi* > 140 mm carapace width (CW) competing for multiparous mates in comparison to males held without any females.

No. of males/ females	Mean CW mm males	CW range mm males	Mean CH mm males	CH range mm males	% with perforated limbs	% dropping limbs	% dying
10/50	159	142-171	38	34-42	100	30	100
5/25	160	150-168	39	37-42	100	60	100
5/25	157	150-165	37	34-39	100	25	100
4/12	145	141-149	34	31-37	75	0	50
3/9	154	149-170	34	31-34	100	0	0
5/0	145	140-149	33	31-34	100	20	0
5/0	152	145-165	36	31-41	60	0	20

CH = chela height.

had fighting injures that broke through the carapace. The carapace breaks soon took on a black color. These may have been colonies of chitin-dissolving bacteria which are fatal to *C. bairdi* when introduced to internal systems (Grischkowsky and Follett 1982). In the groups with 5 females per male, all the males died. In one group with a 3:1 sex ratio 50% of the males died while in another group no males died. However, some of those males still alive had deteriorating blackened carapace around the fighting wounds that might cause death at a later date. Deaths happened between 1 May and 5 July. In the groups with 5:1 sex ratios, limb loss was common for the males. When there were fewer females to fight over (3:1 sex ratio) no limb loss was seen (Table 1).

Males were commonly seen fighting in the control groups without females, with 100% of the males in one group and 60% in the other having crushed limbs with carapace breaks. One male with severe fighting injuries died. This experiment quantified a phenomenon we have seen often; captive Tanner crab males frequently fight even when females are not present.

Discussion

Only one study provides the in situ sex ratio of Tanner crabs during the mating period. That report showed that multiparous females formed dense aggregations and there was only one male for every 10 females (Stevens et al. 1994). Perhaps with such low sex ratios males seldom fight for mates and mortal combat wounds are avoided. If males commonly fight with each other, even when females are absent, perhaps they avoid each other as a survival strategy.

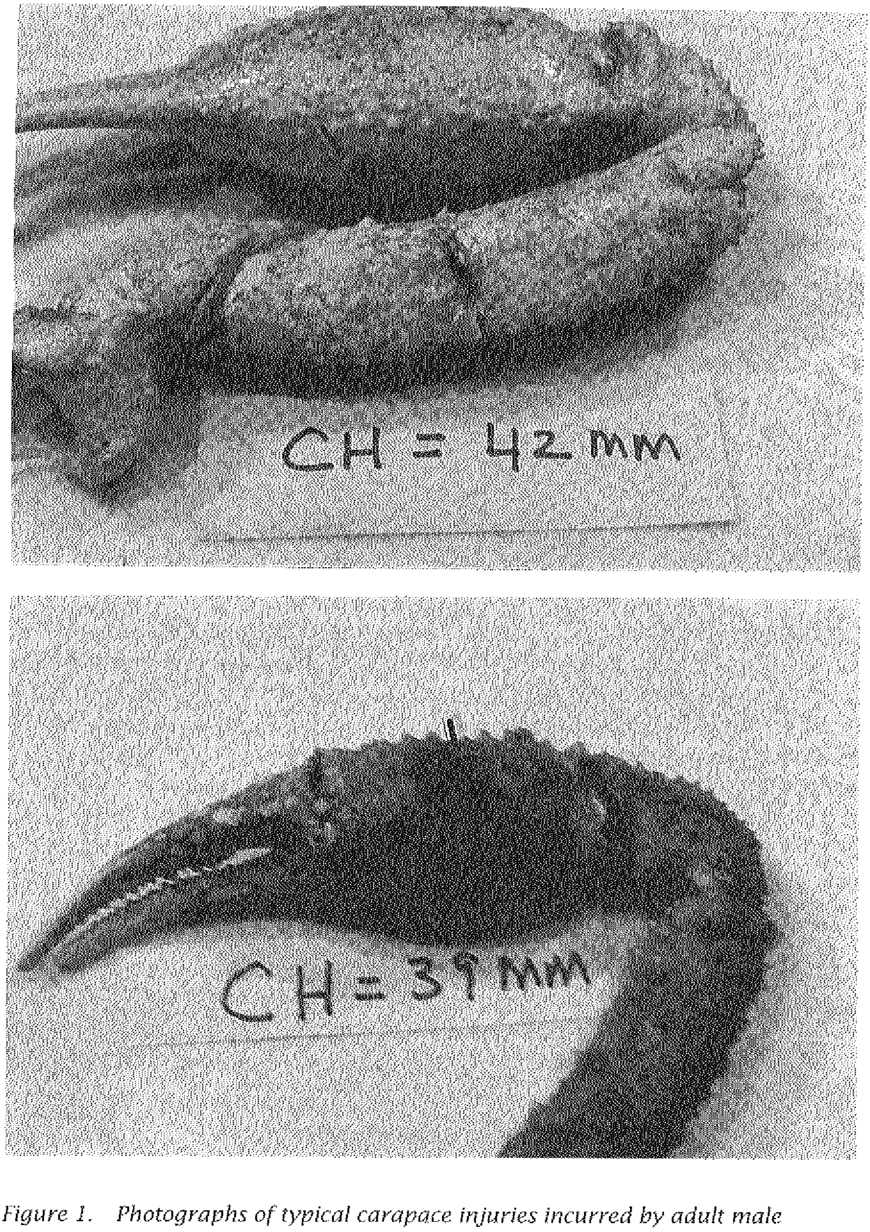

Figure 1. Photographs of typical carapace injuries incurred by adult male Chionoecetes bairdi when two males > 140 mm carapace width fight over which male will copulate with a ripe multiparous female. The injuries are marked by arrows.

Our females that were fought over by males often received severe carapace wounds from being grasped. Perhaps female aggregation prior to egg extrusion alters the sex ratio so there are several females for every local male (Stevens et al. 1993). This might reduce the likelihood of a female being injured by competing males. Also, some females have stored sperm and don't need to breed, and minimizing the likelihood of grasping injuries might increase the chances for survival and successful reproduction.

This is the first time that mortalities have been reported for male *C. bairdi* due to injuries incurred while fighting for mates. Male Tanner crabs seen grasping multiparous females in nature range in size from 110 to 170 mm CW and have an average of 134 mm CW (Stevens et al. 1993). Thus, the males we included in the experiments were the larger sizes that are involved in mating. Experiments with smaller males need to be done. Because these observations were done in the laboratory they cannot be directly extrapolated to in situ conditions. However, they do prove that legal size *C. bairdi* are capable of crushing the carapace of other males and competing for a mate is potentially fatal. Obviously in situ studies need to be carried out to determine if fights for mates commonly result in limb loss or death. These surveys should be done just after the breeding season since our male combatants often died shortly after injury. Trawling or submarine surveys, rather than pot samples, would be the best method to sample since damaged males might not go into pots.

Acknowledgments

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Reproductive Conditions of Prespawning Multiparous Female Tanner Crabs (*Chionoecetes bairdi*) from Chiniak and Womens Bays, Kodiak Island, Alaska

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Abstract

A total of 406 multiparous female Tanner crabs *(Chionoecetes bairdi)* were collected from shallow (< 20 m) or deep (> 150 m) sites in Kodiak, Alaska, by submersible, scuba, and trawl, in spring of 1994, fall-winter of 1994, and spring of 1995. Pre-spawning females collected from deep water in spring had large ovaries and egg clutches, and empty stomachs. Egg clutch volumes were highest just prior to spawning, and lower in fall. Spermathecal contents were extremely low in all three seasons. Stomach contents indicate that females cease feeding several weeks prior to spawning. Females collected from deep water in fall, or shallow water in winter, had smaller clutches, developing gonads, and full stomachs.

Introduction

A mating aggregation of thousands of multiparous female Tanner crabs, *Chionoecetes bairdi* was discovered in 1991 (Stevens et al. 1994) at

150 m depth in Chiniak Bay, Kodiak, Alaska, and observed at the same site annually through 1995. Other females have been observed mating as isolated pairs in the shallow (< 20 m) water of Womens Bay, Kodiak (Stevens et al. 1993, includes map of sites; Munk et al. 1996). This study was undertaken to compare the reproductive status of pre-spawning multiparous females between shallow and deep water.

Methods

Crabs were collected from the deep waters of Chiniak Bay in spring 1994 (April 21-27; coded as Spring94; n = 108 crabs) and again from 23 April to 2 May, 1995 (Spring95; n = 158), using the 2-person submersible Delta. These samples were collected approximately 2 weeks before hatching in each year. A random sample of multiparous females (n = 131) was also collected from Chiniak Bay on 4 October 1994 (Fall94) by trawling. Seven multiparous females were collected from shallow water in Womens Bay by scuba on 10 November and 1 December 1995, and two in April 1995; all are combined as sample WomBay.

Carapace width (CW), and width of the 6th abdominal segment were measured to the nearest mm. Females were categorized as multiparous if they had large abdomens and old shells. Crabs were frozen until dissection, usually within two weeks of capture. After slow thawing, volume of the egg clutch (attached to pleopods) was measured by immersion in tap water in a graduated cylinder. Ovaries were removed and placed in pre-weighed pans for drying. Spermathecae were removed with the vagina and the sternal opening intact, and preserved in 10% buffered formalin; within a week, they were opened, and their contents rinsed into a pre-weighed pan for drying. Stomachs were cut open and contents rinsed into a pre-weighed pan. Pans containing ovaries, spermathecal or stomach contents were dried to constant weight at 60-70°C (dw = dry weight), and re-weighed to the nearest 0.1 mg on an electronic balance. Comparisons of width or dry weight between groups were conducted with a one-way ANOVA, and individual comparisons between pairs of groups were made by Tukeys HSD method (Zar 1984). Differences were considered significant if p was < 0.05.

Results

There was no significant difference in width between multiparous females from Chiniak Bay in Spring94 and Fall94, or WomBay females (Figure 1). However, Spring95 females (97.8 mm CW) were significantly larger than WomBay females (91.2 mm CW). Mean clutch volume for multiparous females in Spring94 (45.4 ml; Figure 1) was not significantly different from that in Spring95 (44.5 ml). Mean clutch volume in Fall94 females (30.5 ml) was not significantly larger than that of WomBay females (21.9 ml), and both were significantly lower than Spring94 or

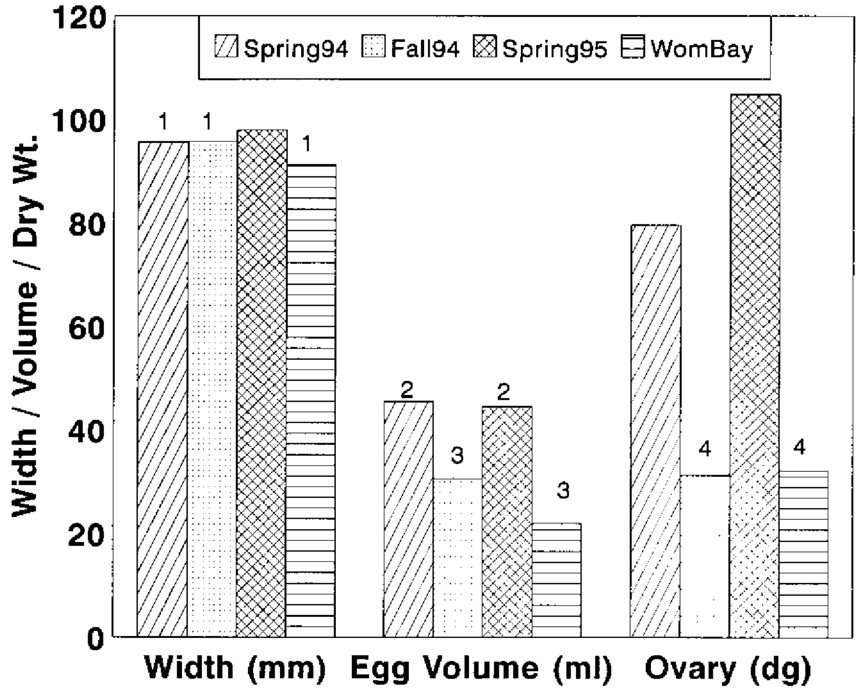

Figure 1. Mean values of carapace width (mm), external egg clutch volume (ml), and ovary dry weight (in dg, for convenience of scale) for multiparous female C. bairdi. Spring94, Fall94 and Spring95 crabs were collected from Chiniak Bay. WomBay crabs were collected from Womens Bay. See text for dates. Numbers (1-4) identify samples which are not significantly different.

Spring95 females. Mean ovary dw of multiparous females from Spring94 (7.95g) was significantly less than that of Spring95 (10.48 g). Mean dw of developing ovaries in Fall94 females (3.12 g), approximately 5 months post-spawning, was not significantly different from that of WomBay females (3.21 g), but both were significantly less than mean dw in Spring94 or Spring95. Dry weight of spermathecal contents (ejaculate) was extremely low, and there was no significant difference between samples (Figure 2). Mean weight of all samples was 0.054 g. The largest was 1.5 g, but 99% weighed less than 0.15 g. Mean dw of stomach contents of Fall94 females (175 mg) and WomBay females (186 mg) were not significantly different, but both were significantly greater than stomach contents of Spring95 crab (52 mg). Contents of Spring94 crab were only liquid and considered empty, so were not weighed. These data suggest that female crabs do not feed for several weeks prior to spawning.

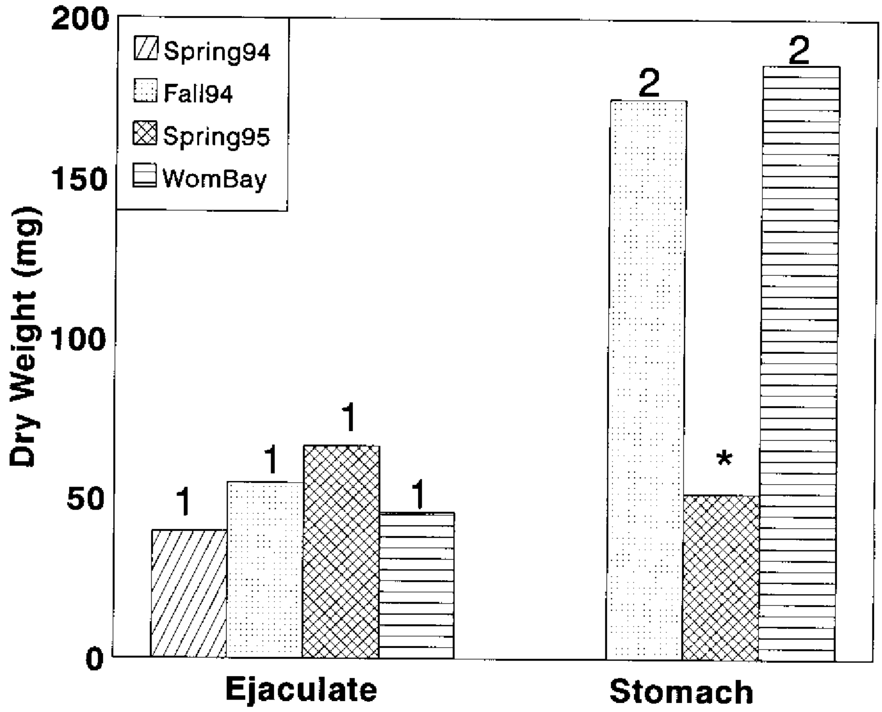

*Figure 2. Mean values for dry weight of spermathecal contents (ejaculate) and stomach contents, in mg, for multiparous female C. bairdi. Sample names as in Figure 1. Numbers (1-2) identify samples which are not significantly different. * is significantly different from adjacent samples.*

Discussion

Multiparous females collected from Chiniak bay in Spring94 and Spring95 were essentially identical in mean CW, egg volume, spermathecal contents, and (presumably) stomach contents, as both groups consisted of ovigerous females collected just prior to mating and hatching, during a time period when they were not feeding. By fall, 5 months after spawning, ovaries were only about 50% of full size, and egg clutches about 67% of fully developed size. Fall94 crab and WomBay multiparous crab were essentially identical in mean CW, egg volume, ovary dry weight, spermathecal contents, and stomach contents, probably because 7 of the 9 WomBay crab were collected in winter. These two samples represent multiparous crabs during mid-winter feeding and non-breeding periods, and no differences were apparent due to location or depth.

Mean ejaculate weight in Kodiak females was low, compared to values of 1-2 g for recently mated *C. bairdi* in the Bering Sea (J. Orensanz, Univ. of Washington, Sept. 1995, pers. comm.). Ejaculate weights decrease over time in *C. opilio* (Sainte-Marie 1993), but whether this would account for the observed values is unknown. Perhaps Kodiak females are not being provided with large quantities of sperm, or are not being inseminated after the maturity molt, due to low numbers of males. Male:female ratios at the Chiniak Bay site range from 0.1 to 0.01 (Stevens et al. 1993, 1994). Commercial fishing in this area has been closed since 1994 due to low male abundance. Paul (1984) reported that the proportion of eggs fertilized declines with age of stored sperm, and Paul and Paul (1992) suggested that "a single insemination at the maturity molt typically did not provide sufficient stored sperm to fertilize subsequent egg clutches in *C. bairdi*." If multiparous females are relying on stored sperm to fertilize their egg clutches, it could result in a decreased reproductive capacity for this population.

Acknowledgments

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A Note on Energy Costs of Molting and Egg Production for Female Red King Crab *(Paralithodes camtschaticus)*

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Abstract

Measurements of the energy costs of molting and egg production for mature female red king crab, *Paralithodes camtschaticus,* were made. Increases in carapace length at molting, exuvia dry weights, and their energy content were all described by linear equations. The number of eggs, clutch dry weight, and clutch energy content tended to increase with corresponding growth in carapace length (CL) until females reached 130-140 mm. However, there was considerable variation in the number of eggs extruded by the females relative to their CL. Whole body energy content increased linearly with CL. Exuvia, newly extruded egg clutches, and postmolt whole body samples had average energy contents of 180 kcal (sd = 25.8), 256 kcal (sd = 106), and 508 kcal (sd = 278) per individual, respectively.

At 110 mm CL the energy allocated to exuvia and egg production by female red king crab was about 108 kcal for a 100 mm exuvia and 184 kcal for the eggs. Females 150 mm CL allocated 203 and 252 kcal to the corresponding tissues.

Introduction

The red king crab *(Paralithodes camtschaticus* Tilesius) is an important commercial species in Alaska. Stocks of this species are in low abundance and there is considerable interest in understanding the various aspects of their basic biology. Previously, the authors studied red king crab reproductive biology (Paul and Paul 1990). That endeavor provided the opportunity to determine whole body energy content and energy costs of molting and ovulation for females of this species. Crabs are most subject to predation when they are softshell and this data could be used to model energy flow to predators. The energetic measures provide the ability to compare the costs of molting and ovulation in king crabs to other species.

Materials and Methods

Multiparous female king crab captured in late winter were held in 1,000 L seawater tanks at the Seward Marine Center Laboratory. During the three months that the females were held the water temperature was 4° to 6°C and salinity 31-32 ppt. There were 84 females from which premolt and postmolt carapace length (CL) was measured from eye notch to the middle of the dorsal carapace. The postmolt CL for all females averaged 136 mm (sd = 13) with a range of 110 to 161 mm. The smallest premolt CL was 100 mm.

Females were held with males and after molting the exuvia were collected immediately and dried in a convection oven to a constant weight at 60°C and weighed to the nearest 0.1 g. Only exuvia and females with all the appendages were included in the sample. Dried exuvia were powdered with a mortar and pestle, followed by a grinding mill. All the powdered material from each molted carapace was stirred vigorously and about 1 g sample taken with a scoop. The 84 1 g samples were pooled and mixed, and eight subsamples were combusted in a Parr adiabatic calorimeter. Estimates of the energy content of the exuvia from all 84 females were determined by multiplying their individual dry weights by the average caloric content of the pooled exuvia. To plot the data individual values were used, and in addition values were grouped together based on CL. Ten mm intervals of CL were selected for the grouping of weight and energy values. Data is plotted using the mean CL for individuals falling within the 10 mm increment.

About one week after egg extrusion, the eggs were removed from the pleopods of the females (n = 115) and dried at 60°C as above. The number of eggs per clutch was determined by dividing clutch weight by the average weight of one dried egg. The dried weight of an egg was determined by weighing 20 dried eggs from each of the pleopods from the separate clutches with an electrobalance.

The caloric content of clutches was determined by pooling about 1 g of dried and powdered eggs (using a mortar and pestle) from each female, mixing the material, and combusting triplicate subsamples in the calorimeter. Estimates of the energy content of the eggs of all the females were determined by multiplying their egg clutch dry weight by the average caloric content of the eggs. The egg clutch weight and energy content information was also organized in 10 mm CL groups for plotting.

The body energy content of newly molted females was measured for 20 individuals. The eggs were removed from the pleopods, the carapace length measured to the nearest mm, each individual dried for 24 h in a freeze dryer, and then dried to a constant weight in a convection oven at 60°C. Dried crab were weighed to the nearest gram, powdered in a blender, the material mixed, and 20 g samples from each of the 20 individuals were then combined. Six subsamples of pooled whole body tissues were combusted in the calorimeter. Estimates of individual body energy content were determined by multiplying individual dry body weights by the average energy content of body tissue.

The energy content of eggs, carapace, and body is derived by multiplying the dry weight of each component by a pooled energetic constant for that component. Thus, the variance associated with the energetic constants is not considered.

Most of the size and energy relationships were fitted to log, power, exponential, and linear models and the relationship with the highest coefficient of determination (r^2) adopted. A polynomial least squares program was used to fit mean estimates for egg energy and abundance data.

Results

Females with postmolt carapace lengths of 110 to 161 mm had an average energy expenditure of 180.2 kcal per individual (sd = 25.8) allocated to the exuvia (Figures 1 and 2, Table 1). The exuvia from female red king crabs had an average moisture content of 54% (sd = 2) and contained an average of 1.6 kcal per g dry wt.

The increase in female carapace length associated with the annual molt was about 4% (Table 1). The energy content of recently molted female king crab bodies averaged 472 kcal per individual. The relationships of CL (mm) to body dry weight based on the mean values for females put into 10 mm cohorts (Table 1), and energy content (Figure 2), were linear (r^2 = 0.88). Mean whole body energy content increased linearly with CL; a 110 mm body had 388 kcal vs. 862 kcal for a 150 mm newly molted female. The average energy content of dried crab was 3.5 kcal per g. Moisture accounted for an average of 89% (sd = 1%) of the live weight of these females.

The number of eggs in newly extruded clutches ranged from 20,000 to 348,000 eggs per individual (Figure 3) with an average of 179,000 (sd = 97,000). There were large variations in the number of eggs that females carried (Figure 3), relative to CL, as would be expected with a population of various ages and nutritional history. The average energy content of an egg clutch was 256 kcal. The relationship of carapace length (mm) to clutch caloric content, using mean values for females grouped in 10 mm intervals, is illustrated in Figure 2 (see Table 1 for polynomial equation). The energy content of newly extruded dried eggs averaged 6.3 kcal per g.

If a female molted to 110 mm (body energy = 388 kcal), the 100 mm exuvium (equation 1 in Table 1) would contain 108 kcal and at 110 mm

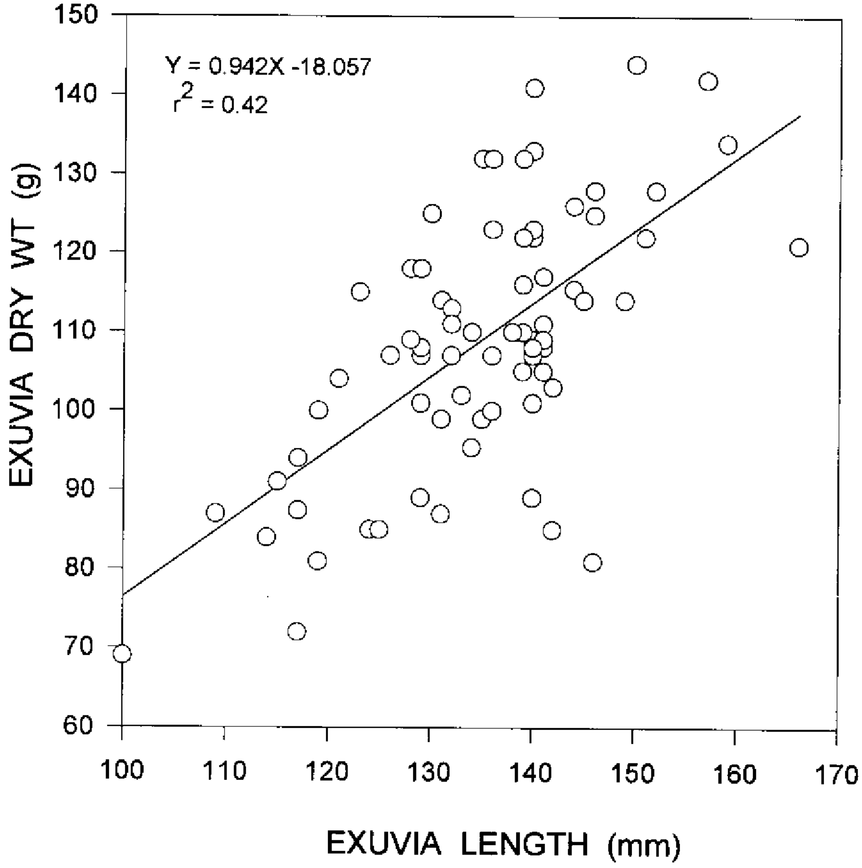

Figure 1. Exuvia dry weight (g) relative to carapace length for newly molted female red king crab, Paralithodes camtschaticus.

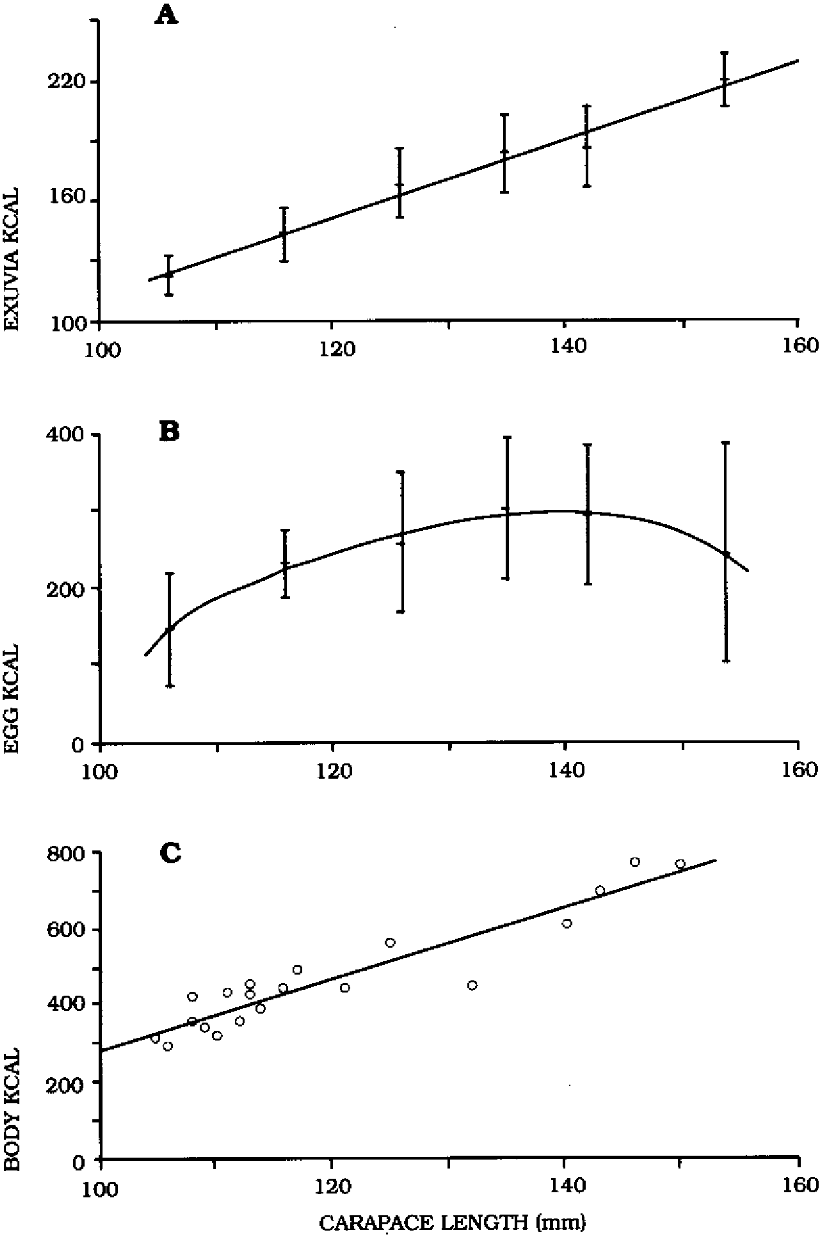

Figure 2. Energy content for: exuvia (mean, sd; A), egg clutches (mean, sd; B), and whole bodies (C) of newly molted female red king crab, Paralithodes camtschaticus. (See Table 1 for equations). Note standard deviations reflect variations in weight, not energy content.

Table 1. Growth, size-weight, and energy relationships for newly molted mature female king crab, *Paralithodes camtschaticus*, and their egg clutches relative to carapace length (CL) in mm.

Growth carapace length (mm)

Postmolt CL = 0.863 (premolt CL) + 23.6; $r^2 = 0.96$.

Size-weight relations

Exuvium dry wt. (g per indiv) = 1.187 (CL) – 50.1; $r^2 = 0.98$ (based on mean values)

Body wet wt. (g per indiv) = 27.889(CL) – 2148; $r^2 = 0.90$

Body dry wt. (g per indiv) = 2.666(CL) – 187.4; $r^2 = 0.88$

No. eggs (per clutch) = –4.3267940393E+07 + 1346581.7960 (CL) + –15699.780826 (CL^2) + 81.516180746 (CL^3) + –0.1587688886 (CL^4) standard deviation of Y = ± 6360 (based on mean values)

Energy content measurements

Exuvia energy (kcal per crab) = 1.9 (CL) – 81.8; $r^2 = 0.98$ (Figure 2)

Egg clutch energy (kcal per clutch) = –28586.529482 + 886.91517294 (CL) + –10.367831426 (CL^2) + 0.05444590809 (CL^3) + -0.0001079623077 (CL^4) standard deviation of Y = ± 5.4 (Figure 2)

Body energy (kcal per crab) = 9.486 (CL) – 655.5; $r^2 = 0.88$

the egg clutch energy content would be 184 kcal. Thus, these three components would account for 57%, 16%, and 27% of their summed energy, respectively. In an old female of 150 mm CL, increase in length would only be 3 mm, the somatic tissue would have 796 kcal (64%), exuvium 203 kcal (16%), and eggs 252 kcal (20%).

Discussion

For red king crab estimates of energy content of dried exuvia (1.65 kcal per g) and eggs (6.28 kcal per g) are similar to those of other large decapods. Other published values for dried exuvia energy content (kcal per g) include: *Chionoecetes bairdi* 1.3 (Paul and Fuji 1989); *Hyas araneus* 1.2 (Anger 1984); and *Homarus americanus* 1.2 (Logan and Epifanio 1978). Examples of decapod egg energy content (kcal per g) include: *C. bairdi* eggs 6.4 (Paul and Fuji 1989); *Crangon crangon* 5.5 (Pandian 1967); and *Pandalus borealis* 5.5 (Clarke 1987).

The body energy content of newly molted dried king crab (3.5 kcal per g) is comparable to that of other large decapods. For primiparous *C.*

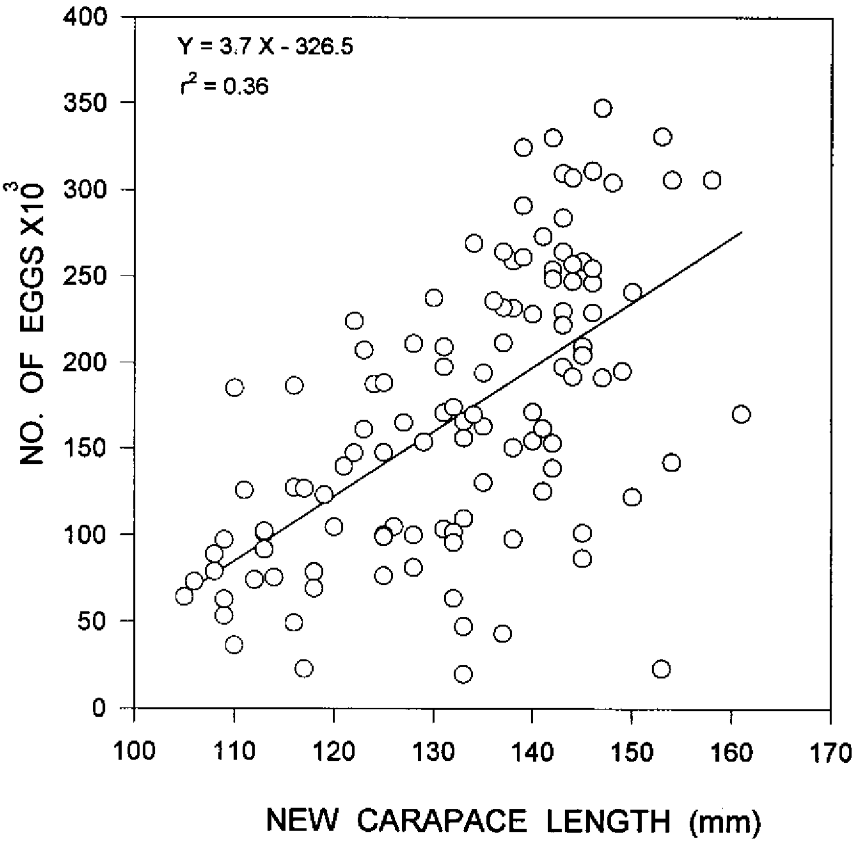

Figure 3. The number of eggs in clutches of newly molted female red king crab, Paralithodes camtschaticus, in relation to carapace length (mm).

bairdi postmolt dried body energy content is on the order of 3.7 kcal per g (Paul and Fuji 1989). Newly molted *Carcinus maenas* have energy contents of 4.3 kcal per g (Klein Breteler 1975). In decapods body energy content changes throughout the molt cycle (Anger 1984). Body energy measurements of red king crab will have to be made during other molt stages, and for males and immature crabs, to fully describe the somatic energy cycle.

No other studies concerning the relative energy expenditures for molting and egg clutches in the North Pacific's large anomurans were located by the authors. However, this information is available for *C. bairdi*, the brachyuran Tanner crab. The reproductive strategy of Tanner and king crab are quite different. In Tanner crab the females' maturity molt is their final molt (Paul 1984). Thereafter, consumed energy is directed to metabolic needs and the annual egg clutch. In mature female king crab molting occurs annually in the spring. While in the softshell state eggs are extruded. Generally female body size increases with the molt, so this pattern of reproduction calls for the annual expenditure of energy incorporated in the exuvia and new body tissue.

Mature king crab are larger than Tanner crab so relative energy allocation herein is expressed as a percentage of energy in body tissue, exuvia, and eggs. In primiparous Tanner crab (CW = 90 mm), egg clutch, body tissue and exuvia account for 32%, 48%, and 18% of the combined energy of these components respectively (Paul and Fuji 1989) vs. 48% for eggs and 28% for body of recently matured red king crabs. For non-molting multiparous Tanner crab nearly all available energy could be allocated to egg production since there are no exuvium or increase in body size (Paul and Fuji 1989), although some seasonal somatic energy changes undoubtedly occur.

Cast exuvia are degraded and used as energy sources by bacteria and king crab exuvia are consumed by *Tealia crassicornis*, a large sea anemone (Powell 1976). With an energy content of 1.6 kcal per g for dried exuvia it would not appear to be a high energy food. Also, most metazoans do not have the capability of digesting chitin. Comparative values for whole copepods which an anemone might consume would be 5.2 kcal per g dry wt (Laurence 1976) and small fishes like pollock (*Theragra chalcogramma*) 4.6 kcal per g dry wt (Harris et al. 1986). While exuvia are low in energy they are locally abundant during the molting period (Powell 1976) and may represent concentrations of salt and minerals.

Reproduction is only one aspect of the bioenergetic budget for king crab and considerably more work will need to be done before a reasonable energy flow model involving this species can be constructed.

Acknowledgments

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Causes of Reduction in Crab Brood Abundance and Role in Reproductive Strategy

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Introduction

Conservation and rational exploitation of bioresources are impossible without knowing the nature of reproductive processes, reproductive potential of populations, and the factors limiting abundance. Scientific research of this kind should be aimed at:

- Identifying a general mechanism that determines reproductive strategy for species groups.
- Working out criteria to estimate biological status of the species groups.
- Finding a way to use this system for long-term forecasting.

The studies in these directions are essential to plan further research into biological features of the far-eastern commercial crab species and improving the reliability and accuracy of the yield forecasts (Fedoseev and Rodin 1986; Fedoseev and Slizkin 1986, 1988; Fedoseev et. al. 1988). Enough information has been collected on biological features of crabs to identify common trends of their reproductive strategy. This information enabled us to analyze the main stages of the reproductive process in far-eastern crabs and put forward a hypothesis describing the critical stages of brood formation. We think the hypothesis can be taken as a basis for further research. To shed more light upon this problem of critical stages investigations are required on cellular, individual, and population levels, using laboratory experiments and modern procedures. We emphasize that our paper doesn't offer solutions to the problem; its goal is to propose concrete research tasks.

Reproductive Features of Crab Species

Abundance fluctuations affecting populations are associated mainly with alternation of abundant and non-abundant broods and the rate at which they are harvested by fishing fleets. Abundance of broods or generations is determined by the impact of limiting factors in the process of their formation. Impacts on developing broods vary at different reproductive stages and are not the same even for populations belonging to the same species. This is probably a distinctive feature of reproductive strategy of closely related species, singular species, and even individual populations. Fedoseev and Rodin (1986) listed the following reproductive stages in crab: gametogenesis, embryo development, post-embryo development as larvae, and development of the juveniles into mature individuals. We thought it reasonable to add an adult stage, starting at maturation of crab individuals and lasting to the end of their life to characterize the whole life cycle of a brood. We also considered identifying a senile substage within the adult one. This substage would be characterized by the period during which individuals lose their reproductive functions. But as we don't have convincing evidence in favor of existence of the aging substage, we excluded it from our discussion.

The foundations of brood abundance are laid down at the gametogenesis stage, thus forming initial reproductive stock of a population. This stock represents a sum of oocytes to be carried by all the mature females, i.e., maximum number of potential mature individuals. But in the process of brood development a gradual abundance reduction occurs, therefore actual recruitment is provided by individuals that survive.

Stage of Abundance Reduction

Process of abundance reduction is in a close relationship with reproductive strategy developed by a given species. Ignoring some details, one can identify common abundance reduction trends in closely related species. In our paper we examine this phenomenon based on crabs inhabiting the seas of the Far East of Russia. Two abundant species groups are found there, represented by Lithodidae (*Lithodes, Paralithodes, Paralomis*) and Majidae (*Chionoecetes*). In our opinion of all these crabs reproductive strategy is most fully studied for lithodids. Therefore in examining a nature of abundance reduction we took lithodid crabs as an example. Then we compared a nature of abundance reduction in Lithodidae with that in Tanner crabs.

The first considerable decrease in reproductive potential may occur at the end of the gametogenesis stage due to the impact of abnormal environmental conditions (Nizyaev and Fedoseev 1990). Some females may temporarily lose an ability to molt and become nonbreeding because of resorption of oocytes. This phenomenon was found to be significant in *Paralithodes platypus, Paralithodes camtschaticus,* and *Lithodes aequispina.* Mature females having an old unmolted (unshed) carapace and whitish gonads (or whitish spots) are nonbreeding. These features are indicators of oocyte resorption. The number of whitish spots is an indicator of a specific resorption stage. While the nonbreeding phenomenon was observed frequently enough, the mechanism causing appearance of nonbreeding females is still unknown. The portion of nonbreeding females in catches was observed to be very small in most cases. It appears that the nonbreeding phenomenon in crab females is abnormal. We think that disorders making females nonbreeding affect specific individuals, and there is no protection mechanism at the population level. Nonbreeding females are unable to participate in reproductive processes until their gonads get clear of the remnants of resorbed oocytes. Large numbers of nonbreeding females in a crab population may cause a long-term abundance decrease. The duration of the period for which females stay nonbreeding is not known. According to expert estimates based on trawl surveys data for the western Kamchatka shelf, in 1988 nonbreeding *P. platypus* females constituted up to 10% with no such females observed in 1989. It seems possible that disorders in the organs of females, influenced by their nonbreeding state, might lead to their death. It appears that first females become unable to lay eggs, probably due to disorders in spawning-molting processes, and then pathological transformations in their reproductive systems occur.

It is necessary to note that decreases in population abundance may take place throughout each of the reproductive stages discussed, and during transitional phases between the stages (spawning, larvae settling). Decrease in abundance occurring at the spawning stage, during which a transition from gametogenesis to embryo development occurs, may have two causes. One is the appearance of the so-called pseudo-nonbreeding females whose eggs were not fertilized and fell off females because no males were around (Nizyaev and Fedoseev 1990). Pseudo-nonbreeding females may have a new carapace (i.e., undergo molting) and normal oocytes; such females may have either no outside eggs on their pleopods, or a very small number that fall off easily when touched. Abundance of such females depends largely on specific spawning conditions and the structure of the spawning centers. A sharp increase in the pseudo-nonbreeding female portion in the catches of *P. camtschaticus* (up to 32.8%), recorded off western Kamchatka in 1987, was observed for those western Kamchatka shelf areas where mass-scale male molting was observed during spawning. In the years to follow, when no such abnormality was observed, numbers of pseudo-nonbreeding females were low. Appearance of pseudo-nonbreeding females in the above-mentioned case was caused, in our opinion, by intensive harvesting of males during spawning, when first spawning centers had already been formed and finding new male partners became impossible for females. According to Paul and Paul (1990) *P. camtschaticus* males with carapace length less than 140 mm could successfully fertilize an average of 2-3 females (maximum 6) under lab conditions. According to our experimental data, obtained in 1989-1992 at the Popov Island biological station (Peter the Great Bay), one male with carapace 140 mm in length could fertilize from 1 to 4 females under lab conditions. According to Fedoseev and Rodin (1986), males do not excrete all the reproductive products during spawning—a portion is stored until the next year. This portion of reproductive products probably serves as a reserve for spawning males. When the sex ratio deviates from optimum, males may use at least a portion, if not all, of non-excreted reproductive products, thus significantly reducing the number of pseudo-nonbreeding females. With 30% of commercial *P. camtschaticus* crab being harvested during spawning on the western Kamchatka shelf, an abundance of pseudo-nonbreeding females was found to be stable and amounted to 4% on the average, with annual fluctuations ranging from 3 to 5% of the total mature female abundance. It is interesting to note that pseudo-nonbreeding females were seldom observed in regions where no intensive crab fisheries were conducted. According to 1989 trawl survey data, pseudo-nonbreeding females of deepwater lithodid crabs were observed in extremely low quantity in the Okhotsk Sea bathial zone. We consider an appearance of pseudo-nonbreeding females as a natural reaction to disorders in the spawning processes. It seems that females probably learned to lay eggs even with no males around to prevent over-ripening and resorption of oocytes. In addition, there appear to exist the strong population-level mechanisms that protects females from becoming pseudo-nonbreeding. These protective mechanisms are represented mainly by spawning migrations during which the spawning centers with an optimum sex structure may form. Furthermore, as was mentioned earlier, males probably use part of reproductive products, stored previously, whenever a sex-ratio in spawning centers is changed beyond normal. It should be mentioned that spawning migrations in deepwater lithodid crabs are probably of somewhat different nature as compared with lithodids living at shallower depths. Population groups of deepwater lithodids in most cases live within the areas of stationery gyre, and because of it their reproduction and growth occur in the same territory (Nizyaev 1990). Therefore contrary to spawning migrations in shelf-zone lithodids, which may cover great distances, deepwater lithodids probably form nuclei of spawning centers. This suggestion is supported by the observed increased schooling of females soon after laying their eggs (Nizyaev 1990).

Females that became pseudo-nonbreeding are excluded from the reproductive process for only one year and may reduce the abundance in only one year class. We have already mentioned that in one of the fishery regions a portion of pseudo-nonbreeding females reached up to 10% when there was an abnormal spawning situation (Nizyaev et al. 1990). The next year, however, the situation with spawning normalized and the fraction of nonbreeding females dropped to the usual 3%.

The second reason for brood abundance reduction during spawning time may be that females lose a portion of oocytes when mating. This was supported by experiments on multiple mating of males and females under laboratory conditions (Paul and Paul 1990). The authors observed that with every repeated contact between males and females the percentage of fertilized oocytes tended to be less. We admit the possibility that a portion of oocytes is lost during mating judging from the variation in individual fecundity in crabs of the same size (Agafonkin 1982). Here an important role is played by the probability of spermatozoa and oocytes getting into contact.

Spawning in crabs is followed by a prolonged period of embryo carrying by females during which they migrate for considerable distances (Rodin 1985). In the course of such migrations females may also lose a portion of embryos due to such factors as:

- Abdomen rubbing against the sea bottom.
- Predation.
- Parasites or some other reasons.

It was observed that for crabs of the same size the number of eggs with developed embryos on the average is considerably lower than that of newly laid eggs (Jewett et al. 1985). Because of that not all the excreted and fertilized oocytes develop into larvae. The postembryonal development stage is characterized by the progeny leaving their parents. Hatched larvae began to be transported by currents. At postembryonal stage, strong differences emerge in groups of lithodids. These differences influence abundance reduction throughout the postembryonal development period up to juvenile stage. Lithodids found in the seas of the Far East can be easily divided into two subgroups in terms of fecundity and egg size. Females of the first subgroup (*P. camtschaticus, P. platypus*) have high fecundity and small egg size (Table 1). Females of the second group (*Lithodes couesi, L. aequispina, Paralithodes brevipes*) are characterized by an order of magnitude lower fecundity, but at the same time greater egg size than in the former group. The same can be said about *Paralomis verrilli* and *P. multispina* (both species live in the far-eastern seas) even through visual inspection. With the exception of *P. brevipes*, all species with low fecundity and large eggs inhabit great water depths. Size of the hatched crab larvae is similar to that of eggs (Table 2). Somerton (1981), based on more developed yolk-sac in larvae of *L. couesi* as compared with those of *P. camtschaticus*, doubted that the former should migrate into the photic zone.

Table 1. Fecundity and egg size in some Lithodidae crab species of the North Pacific.

Species (depth range)*	Fecundity, thou. ind.	Length of eggs, mm
P. brevipes	2.2-68.6	No data
(2-100 m)	(Agafonkin 1982)	
P. camtshaticus	60-220	1.0
(5-200 m)	(Rodin 1985)	(Haynes 1968)
P. platypus	120	1.2
(50-200 m)	(Sasakawa 1975)	
L. aequispina	10.6-27.0	2.1-2.4
(200-800 m)	(Somerton and Otto 1985; Jewett et al. 1985)	
L. couesi	2.6-5.5	2.1-2.4
(600-1,200 m)	(Somerton 1981)	

* Depth range information was taken from Vinogradov (1950).

A few years later, Somerton, in a paper written with Otto (1986), suggested a hypothesis (apparently to develop further the above-mentioned presumption) that larger size of *L. aequispina* larvae compared with that of *P. camtschaticus* would enable the former to endure prolonged starvation and feed on relatively large food organisms. Therefore it is possible that after hatching these larvae continue to stay at great depth. Pears (1969), having reviewed literature on the development of marine bottom invertebrates at larva stage, came to a conclusion that for the species living in high latitude seas and at bathial-abyssal levels pelagic development (or demersal development by his terminology) would be more common. According to Ochelman (1965), with depth, the percentage of species with lecithotrophic development increases and that of species with planktotrophic development decreases. Data by Thorson (1950) indicate that direct development type, vivipary, reduced the duration of the pelagic stage, and development via lecithotrophic larvae are characterized by higher fecundity than that found in planktotrophic larvae, noted for a long plankton stage. These observations support a possibility that larvae of deepwater lithodids enjoy lecithotrophic feeding and demersal development type throughout their life as a larvae, while larvae of shelf lithodids are characterized by planktotrophic development. It seems that with depletion of yolk sac, lecithotrophic feeding of larvae of deepwater crabs is replaced with planktotrophic, with larvae getting food from "plankton rain." The fact that larvae of deepwater lithodids have not been observed in nature so

Table 2. Larva size of some Lithodidae crabs of the North Pacific at different development stages.

		Development stage				
Species		Zoea I	Zoea II	Zoea III	Zoea IV	Glaucotoe
P. brevipes	Lc	1.4	1.5	1.7	–	1.6
				(Kurata 1956)		
	Lb	5.7	6.1	5.9	–	3.6
				(derived from H. Kurata drawings, 1956)		
P. camtschaticus	Lc	1.2	1.4	1.5	1.5	1.8
				(Sato 1958)		
P. platypus	Lc	1.2	1.3	1.6	2.0	1.8
	Lb	4.9	5.2	5.5	6.8	–
				(Hoffman 1968)		
L. aequispina	Lc	2.3	–	2.9	2.9	2.2
				(derived from E.B. Haynes drawings, 1982)		
	Lb	7.3	8.0	7.6	6.8	5.9
				(Haynes 1982)		

Hyphen (–) means either no data available, or absence of that stage in the development cycle of the larvae; Lc = carapace length; Lb = body length. Measurements in mm.

far, while larvae of *P. camtschaticus* and *P. platypus* are known to be distributed in the surface layers and were often observed there (Marukawa 1933, Takeuchi 1962, Kurata 1964, Hoffman 1968), may serve as indirect evidence in favor of Somerset and Otto's hypothesis. Transport of deepwater lithodid larvae to the settling areas is performed apparently by bottom currents, rather than surface currents.

Predation by plankton-eaters is the main cause of brood abundance reduction at the larvae stage. However this type of predation seems to be an abundance reducing factor only for the larvae distributed in the surface layers. The number of plankton eaters sharply drops with depth. Predation appears to be factor number one for *P. camtschaticus* and *P. platypus* larvae, for which mass-scale hatching occurs simultaneously with a peak of plankton bloom. Higher fecundity of these species enables them to sacrifice a portion of their broods to provide the remaining part with guaranteed food—phytoplankton; also, the small size of the larvae in these species enables them to remain unrecognized by predators. According to Somerton and Otto, predation on larvae of deepwater crabs is less severe than on larvae of shelf zone crabs; otherwise these larvae would be exterminated by plankton-eaters when they move up to the photic zone, due to their low fecundity and comparatively large larva size. One of the other abundance limiting factors at that stage of development is probably availability of food. Paul et al. 1989 conducted research on *P. camtschaticus* and established the relationship between success of transition of crab larvae to zoea II and phytoplankton species composition. Mass-scale hatching and bloom peak occurring at different times may result in limited growth and even death of a portion of the broods. For the larvae of the deepwater species, the lack of phytoplankton, at least for some period, is compensated by a large yolk sac. However, at subsequent development stages in these larvae, availability of food appears to play a more important role in their survival.

Transport of crab larvae by currents is also an important abundance reducing factor, along with predation and availability of food. According to Thorson (1950), being carried by currents out to open sea causes death to many larvae. Lithodid crab larvae thrive when they are transported by currents to areas with abundant epifauna which protect them from predation and at the same time serve as food (Rodin 1985). Rodin and Lavrentiev (1974) suggested that mortality of some *P. camtschaticus* larvae from western Kamchatka was caused by current transport into regions with adverse environmental conditions. The system of currents off western Kamchatka divides the reproductive area into a number of bathymetric zones with different intensity of larvae scattering or dispersal. That's why the larva mortality rate may depend on the hatching areas. This suggests a relationship between larva abundance and spawning migrations in mature individuals (Nizyaev et al. 1990). The situation is somewhat different for lithodid crabs. Population groups of these species concentrate within the stationary gyres which prevent the larvae from being carried away to other areas. Long-distance dispersal of deepwater lithodid crab larvae has not been properly studied so far, but it might be possible only in cases of deviations of marine gyres from traditional gyre routes and movement of the larvae outside the marine circulation zones.

After settling, crab larvae grow rapidly. According to Marukawa (1933), during the first year of life *P. camtschaticus* juveniles may molt 11-12 times, with 6-7 molts during the second year. Small body size and frequent molts make the crab at this development stage extremely vulnerable to predation. Therefore *P. camtschaticus* juveniles tend to hide among epifauna and inside rock crevices and carcasses of dead animals, such as sponge, Bryozoa, and polychaetes (Feder et al. 1980). That's why lithodid crab juveniles are found in higher numbers on rocky and pebble substrates with diverse epifauna (Bukin et al. 1988, Rodin 1990). As larvae cannot resist currents, location of substrates onto which they might settle is determined by the direction and velocity of currents. Larvae that settle onto a substrate that provides no shelter usually don't survive. This is supported by the absence of larvae on sand and silt substrates. In addition to using various shelters, juvenile lithodid crabs protect themselves with their hard carapace with lots of spines. This feature is characteristic of nearly all lithodid species. When carapace width reaches 5 cm and more, the number of molts drops to 2-3 per year, predation reduces, and juveniles leave their shelter. With maturation of juveniles toward the senile stage, the abundance of broods stabilizes. Abundance reduction in this period is considered to be caused by fisheries mortality (if it is a commercially harvestable population) and predation on small-size individuals during molting.

Therefore, reduction of brood abundance in lithodid crabs may have several stages, determined by concrete biological processes, and is related to abiotic environmental conditions. Most important in regulating abundance of a new generation are factors that reduce abundance at initial stages of the reproductive process. These factors may take effect during spawning migrations. These factors determine spawning conditions that are characterized by larvae dispersal and exclusion of some mature females from reproduction. Abundance reductions due to these causes are in direct relationship with the functioning of the parental part of a population. Mortality caused by spawning area conditions may be great and comparable with predation-related abundance reduction at the larva stage. High mortality level in lithodid crabs at the initial stages of reproduction, up to formation of juvenile stock, can be explained, in our opinion, by exterior fertilization common to them (Fedoseev and Rodin 1986). This suggests a need in spawning migrations and high level of dependence upon abiotic environmental conditions.

Features of Formation of Tanner Crab Broods

The features of reproductive biology in Tanner crabs are similar (Slizkin 1982). The features of the reproductive system in females (internal seminal receptacles, internal fertilization) and the nature of its functioning enable them not to be dependent on males. This makes it possible to avoid high mortality rates at initial stages of reproduction. We don't know of cases of Tanner crab females being nonbreeding and although we occasionally observed females without eggs and mature oocytes, we think that the number of larvae produced by females is practically equal to the number of eggs. Small abundance decrease at this stage may be caused by loss of eggs due to the abdomen rubbing against the substrate and natural mortality. Therefore it seems that even with equal initial reproductive potential, abundance of Tanner crab larvae will exceed that of lithodid crabs. Abundance decrease at the larva stage has the same causes in Tanner and lithodid crabs. Decrease at larvae stage is caused by their floating up to the photic zone (Pereira 1967, Takeuti 1972, Fedoseev and Slizkin 1988), where they are exposed to predation by plankton eaters.

In contrast to juveniles of lithodid crabs, forming assemblages on rocky-pebble substrates among epifauna, aggregations of Tanner crab juveniles are found on fine-grain sediments (Fedoseev and Slizkin 1988) with scarce or no epifauna shelter. Most Tanner crab juveniles form assemblages within areas of stationary gyres, although single juveniles can be found throughout the species range (Slizkin 1982, Nizyaev 1992). Taking this into account we inferred that dispersal is not a mortality factor for Tanner crab larvae. Survival of these larvae is apparently determined by the abundance of benthic fauna predators at larva-settling locations and probably by availability of fine-grain substrates, into which they dig to avoid predation. However, high predator-related mortality observed in Tanner crab juveniles suggests that this kind of shelter is not reliable. Moreover, wide occurrence of fine-grain substrates within shelf areas and continental slopes of far-eastern seas (Leonov 1962) significantly reduces the probability of Tanner crab larvae getting into regions with other substrate types.

Therefore abundance decrease in Tanner crab broods prior to juvenile assemblage formation is limited to mortality at larvae stage, while in lithodid crabs significant abundance reduction may take place even preceding reproductive stages. While preserving abundance at initial stages of the reproductive process, Tanner crabs lose a large portion of their broods at the juvenile stage. Since Tanner crab juveniles are covered by a relatively fragile carapace with few spines, they are easy prey for predator fishes like cod, halibut, scate, Macruridae, sculpins, etc. According to preliminary data by Zgurovsky et al. (1990) for the western Bering Sea, predator-related mortality in *Chionoecetes opilio* juveniles may be as high as 300,000 t during summer. Due to the fragile carapace, Tanner crab juveniles suffer from pressure by benthos eaters for a longer period than lithodid juveniles. After several molts, Tanner crab females stop growing (Fedoseev and Slizkin 1982) and they remain potential prey throughout their lives because they are small.

Comparison of Reproductive Strategies in Lithodidae and Tanner Crabs

Simply put, reproductive strategy is a complex of adaptive reactions, worked out in the course of evolutionary process to attain optimum conformity between reproductive processes and environmental conditions where any negative impact is compensated with proper alternative protective response. That's why when speaking about weak survival-related links in reproductive strategy, attention should be paid to positive traits acquired by broods through making forced concessions to nature. Let us take spawning migrations in lithodid crabs as an example. On one hand, migrations in these crabs increase dependence of parental stock on environmental conditions and may cause mortality of a significant portion of the broods during early reproductive stages. On the other hand, however, they enable low abundance populations to function normally.

Appearance of a new brood in the crabs is guaranteed by instinctive obligation to produce spawning centers, which is inherent in reproductive strategy of parental stock. It means that a probability of severe abundance declines in this case is compensated by high stability of reproductive process of a population. The absence of pronounced spawning migrations in Tanner crab, on the contrary, suggests that there should be some critical abundance level below which it becomes impossible for males and females to have enough mating sessions. But the ability of Tanner crab females to produce larvae for a number of years without male assistance, coupled with no significant brood mortality at early reproductive stages, make spawning migrations practically unnecessary for this crab species.

The dynamics of abundance decrease in crab broods is determined by the type of habitat conditions for juveniles. In lithodid crabs reproductive strategy is based on selecting only those habitats that provide good opportunities for juvenile rearing. Such strategy determines local nature of juvenile rearing areas and sets limits for abundance (amount) of juvenile stock. Major abundance reductions here occur prior to juvenile stock formation. Therefore, survival of lithodid crab individuals sharply increases upon reaching the juvenile stage. In Tanner crab significant abundance reduction is observed at the juvenile stage, due to a great number of individuals attaining the juvenile stage and their high vulnerability. But despite severe predation, initial high abundance of newly hatched broods enables a relatively high number of Tanner crab individuals to reach maturation stage and participate in the reproductive process. Preliminary data suggest that there is a relationship between the rate of predation on juvenile Tanner crabs and the size of first-matured females; the higher predation rate is, the smaller the size of first-spawning females.

In our opinion, the reproductive strategy of Tanner crabs is more suitable for individual settling than that of lithodids because this strategy is based on such features as:

- Dispersal of larvae over great distances.
- High abundance of larvae.
- High tolerance of juveniles to rearing habitat conditions.
- Lack of need in spawning migrations which suggests unavailability of local reproductive centers.

Tanner crabs may join the reproductive process at any new marine areas they have been transported to. This phenomenon contributes to permanent distribution of these crabs throughout the northern Pacific, and makes it impossible to identify clearly the boundaries of the areas occupied by different populations or population groups (Slizkin 1982). Lithodid crabs in contrast form several clearly differentiated populations or population groups, which is due to their attachment to local juvenile rearing areas. Local nature and limited size of the rearing areas act as a brake preventing rapid abundance increase in lithodid crab populations and probably determining the upper abundance limit. Under favorable conditions, abundance of some populations may exceed this limit and cause the range to expand. Expansion of the range of specific lithodid populations occurs by means of their settling or distribution over adjacent areas where migrating groups form, similar to the Ozernoy group of the western Kamchatka population (Rodin 1990). Due to the remoteness of such groups from juvenile rearing areas individuals of the groups become functionally barren, i.e., lose the opportunity to mate, etc., and are considered pseudopopulations according to Beklemishev (1960). We believe that availability and abundance of such groups may serve as indicators of abundance level and status of a whole population.

A System of Monitoring Crab Population Abundance

It was demonstrated that reproductive strategies in lithodid and Tanner crab species considerably differ. While lithodid crabs perform recruitment by means of generating the more protected and viable but comparatively fewer juvenile stocks, Tanner crabs reproduce well due to high abundance. There are vulnerable stages in the reproductive process in both crab species that determine brood abundance. For rational fishery management of these two groups, the fishery should be taken under control. We think that monitoring the fisheries for harvested crab populations should have two parts.

First of all monitoring of the current population status should be carried out. In this case one should take into account abundance of the fishery portion of the population and possible recruitment rate for the two nearest years. The importance of these two criteria for lithodid and Tanner crabs is obvious. However, using only these criteria as a basis for either short- or long-term harvest forecasts are considered to be not enough.

Second, biological status of the harvested population should also be taken into account as an important component of general monitoring. This would enable to detect and prevent possible abundance declines by introducing partial or overall moratoriums on the fisheries. Because reproductive strategies in lithodid and Tanner crabs are different, monitoring should take into account vulnerable reproductive stages. That's why for each of the crab species in question specific criteria for biological status estimation should be worked out.

Below, we propose some monitoring criteria that we consider important. These criteria can be estimated after procedures which are either already in use, or can be worked out based on the data available.

Monitoring criteria for lithodid crab species

1. Juvenile rearing habitat conditions

Normal functioning of lithodid crab populations depends on habitat conditions within the juvenile rearing localities. These localities should possess appropriate environmental parameters; their change may cause death to the population. We propose to include monitoring of such factors as:

- Epifauna composition within juvenile rearing localities.
- Area of the juvenile rearing localities.
- The type of bottom scraping and other operations that are conducted within the localities or in their vicinity which might adversely change the bottom habitat conditions.

2. Spawning conditions

The abundance of new broods depends greatly on mortality losses in early reproductive stages. Furthermore, for lithodid crabs mortality rate at these stages is highly variable due to their reproductive strategy, and appears to be a reason for severe fluctuations in brood abundance. To perform an estimation of a spawning situation, one should possess data on initial reproductive potential, parental stock abundance, and the ratio of nonbreeding and pseudo-nonbreeding females. Also, larvae dispersal rate is an essential component of successful spawning. Unfortunately, the latter can be estimated only by indirect data, i.e., by hatching area. Yet for populations with stable abundance level spawning, monitoring may be conducted based on only such parameters as the ratio of nonbreeding and pseudo-nonbreeding females and larva dispersal rate.

3. Recruitment

This estimation criteria is intended for additional monitoring and forecasting of a parental stock abundance for a spawning season. Monitoring of this kind consists of:

- Taking account of recruitment of the mature portion of the population for several year classes.
- Comparing recruitment data with spawning conditions giving rise to a specific recruitment.

Monitoring criteria for Tanner crab species groups

1. Initial reproductive potential

Reproductive strategy in Tanner crabs is characterized by a nearly direct relationship between brood strength at the late stages of their formation and abundance of mature females in a population, or to be more precise—the initial reproductive *potential* of this population. That's why the abundance of mature females of Tanner crab, in our opinion, should be a main biological estimation criterion for the Tanner crab species.

2. Predation rate

While there is a general relationship between brood abundance and abundance of females, the nature of the relationship might be broken by predation. That's why predation rate should be monitored as one of the most vulnerable links in the reproductive process in Tanner crabs.

3. Recruitment

This third estimation criterion is practically identical to that for lithodid crabs. However, for Tanner crabs, species recruitment monitoring is more difficult than for the lithodids, due to features of spatial structure in Tanner crabs, which do not form well-defined local population groups.

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High Latitude Crabs: Biology, Management, and Economics
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Hormone and Reproductive Strategies in Spider Crabs with Emphasis on Commercially Important Species

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Knowledge of the reproductive cycle and its hormonal control is imperative for the development of successful management strategies for majid crab populations important to the fisheries.

Libinia emarginata, a Western Atlantic spider crab, serves as our model system for investigating majid reproduction and development. *Libinia* has several distinct advantages as an experimental model, because it is relatively abundant on the North Atlantic coast of the United States and is easy to maintain under laboratory conditions. Since this species is from temperate waters, females produce a brood of eggs every 20 days from spring to fall, while cold-water species of *Chionoecetes* produce a clutch of eggs once a year or every second year. *Libinia* also appears to display many of the same reproductive behavioral characteristics reported for *Chionoecetes*, such as aggregation and podding, mate carrying by males, display of male aggression toward other males, etc.

We have found what we believe to be a reproductive hormone, methyl farnesoate (MF), in Crustacea (Laufer et al. 1987). MF is synthesized by the mandibular organs (MOs), and has been found in the hemolymph of more than 25 species, including *Chionoecetes opilio* and *C. bairdi*. In female *L. emarginata*, the levels of MF in the hemolymph and the rates of synthesis in vitro by the MOs are correlated with the ovarian cycle (Laufer et al. 1986, 1987). Indeed, we believe the relationship to be causal since MF can be fed to shrimp to increase nauplius production (Laufer et al. 1996). Also, Hinsch (1980) implanted MOs from large males into juvenile females and observed ovarian growth. We have found that MO activity is lowest in prematurational-molt juvenile females and previtellogenic adult females. The MO is most active during vitellogenesis, and its synthesis of MF declines prior to oviposition. In male *L. emarginata* elevated levels of MF in the hemolymph are found only in those crabs that exhibit reproductive behavior and have large gonad indexes (2-6% body wt). These males typically have old (abraded) shells, and can be large-bodied with enlarged and elongated claws, or they can be small-bodied with small claws. The MF concentrations in old (abraded) shell males are 2-3 times higher than males with new (unabraded) shells, which have small reproductive indices and are non-reproductive (Homola et al. 1991; Sagi et al. 1993, 1994).

We have found a long interval of 8-12 months, following the last molt before new (unabraded) shell males lose the velvety epicuticle (become abraded) covering the exoskeleton, and are then recognized as being old shell (abraded) males. During the abrading process, males have low concentrations of MF in their blood, and their reproductive indices are quite small (< 1% body wt) (Ahl et al. 1994). These males are considered to be in a state of reproductive diapause as they do not exhibit mating behavior (Sagi et al. 1994).

Mature reproductively active males can be distinguished by being abraded (old shell), that is, their epicuticle is worn. They have undergone a differentiational molt to a large-clawed form, and such males subsequently become the dominant primary reproductives. They aggressively compete with other males for females, and carry and guard these females with which they also mate. These males have high concentrations of MF in their blood. Surprisingly, smaller, less differentiated males with smaller carapaces and smaller claws, if abraded, also have high MF concentrations in their blood. However, these smaller males only attempt mating with females in isolation, and do not compete with the large-clawed larger-bodied abraded males (Sagi et al. 1994). They will, however, attempt "sneak mating" with a receptive female when the primary reproductives are distracted.

In addition to describing the relationship of MF to reproduction, we have also found specific binding proteins for MF in the blood, the hepatopancreas, and the reproductive tissues. One of these proteins is an inducible esterase that binds and degrades MF (Takac et al. 1996).

We have examined MF levels in the blood, and reproductive indices of 156 *C. bairdi*, which included six coupling pairs, during the breeding season of 1994-1995, and the data are summarized in Table 1. Reproductively active females had significantly ($p \leq 0.05$) elevated levels of MF in the hemolymph (mean = 6.073 ng/ml) compared to females that were not mating (mean = 0.140 ng/ml). However, the reproductive indices of these females were similar. The active females had indices that averaged 8.77% of the body weight, while those of inactive females were

Table 1. Comparison of hemolymph levels of methyl farnesoate (MF) and reproductive indices (RI) in coupling compared to non-coupling males and females of *Chionoecetes bairdi*.

	(N)	MF (ng/ml) (mean ± SE)	(N)	RI (% body wt) (mean ± SE)
Coupled				
females	(6)	6.073 ± 5.104	(3)	8.77 ± 0.21
males	(6)	1.080 ± 0.681	(3)	0.89 ± 0.21
Non-coupled				
females	(46)	0.140 ± 0.043	(46)	7.86 ± 0.14
males	(21)	0.184 ± 0.033	(19)	1.02 ± 0.08

7.86%. This trend was repeated in the males. Active males had significantly ($p \leq 0.05$) elevated levels of MF in the hemolymph (mean = 1.08 ng/ml) compared to the inactive males (ave. = 0.184 ng/ml), which were nearly five-fold less. The reproductive indices of both groups were similar with an average of 0.89% for the active males and 1.02% for the inactive ones.

It is possible that the RIs of active and inactive old shell females are similar because the latter may still become reproductively active in the near future. Further, development of large gonads in both males and females, especially in cold water, is a long-term process, some parts of which may be MF independent without subsequent regression. Then, it is possible to have part of the process of gonadal growth be MF dependent resulting in stimulated gonads.

As in *Libinia*, MF blood levels and the reproductive indices of *C. bairdi* appeared to differ according to the condition of the carapace (Table 2). Newshell animals had lower average levels of MF (0.163 ng/ml in females and 0.223 ng/ml in males) compared to oldshell animals (0.227 ng/ml in females and 0.415 ng/ml in males). The reproductive indices in new shell females were significantly smaller ($p \leq 0.05$), averaging 1.68% of the body weight, compared to 7.95% in oldshell females. Newshell males also had significantly smaller reproductive indices ($p \leq 0.05$), averaging 0.31% of the body weight, compared to those of oldshell males, which averaged 1.08%.

The major advantage of comparative endocrine studies in Crustacea is that many of the conclusions reached in an easily studied species such as *Libinia emarginata* may be applicable to species that are more difficult to study. While direct experiments will always be needed to confirm understanding gained from our model species, the results on new species may conform to an already known and understood pattern. Thus, in such cases, fewer samples will have to be obtained and assayed

Table 2. Comparison of hemolymph levels of methyl farnesoate (MF) and reproductive indices (RI) of *Chionoecetes bairdi* with new shells and old shells.

	(N)	MF (ng/ml) (mean ± SE)	(N)	RI (% body wt) (mean ± SE)
Newshells				
females	(20)	0.163 ± 0.043	(14)	1.68 ± 0.34
males	(32)	0.228 ± 0.083	(27)	0.31 ± 0.07
Oldshells				
females	(67)	0.227 ± 0.46	(64)	7.89 ± 0.18
males	(28)	0.412 ± 0.168	(23)	1.08 ± 0.09

to draw conclusions. Furthermore, such studies are needed to gain new insights in order to devise rational management strategies for our major crab resources.

Since we find similar patterns in the MF levels and relative increases in the size of the gonad in reproductively active individuals within a population when investigating other species, such as *C. bairdi*, we are assured that *Libinia emarginata* is a useful model for reproductive studies of crustaceans. Furthermore, confirmation of our findings in *Libinia* with other species, such as *C. bairdi*, supports the accumulating evidence that MF is indeed a reproductive hormone in Crustacea.

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Radiometric Estimation of Shell Age in *Chionoecetes* spp. from the Eastern Bering Sea, and Its Use to Interpret Shell Condition Indices: Preliminary Results

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Abstract

Shell Condition Indices (SCIs) are routinely collected in Alaska for Tanner and snow crab in the course of surveys, and as part of observer programs. These data are important in stock assessment and, if interpretable in terms of shell age, could be used to model growth. Assumptions about correspondence between SCIs and shell age remain untested. Here we present preliminary results on the use of radiometric techniques to estimate shell age (time since last molt) in Tanner and snow crab from the eastern Bering Sea. Uncertainty about shell age is greatest for "very old" shells (SCI 4 and 5 in-the scale utilized by the National Marine Fisheries Service). Our results for three specimens in SCI category 4 indicate shell ages ranging from 4 to 7 years. The method appears promising for the interpretation of large amounts of information on SCI collected over more than two decades of surveys.

Introduction

Crabs, as other crustaceans, grow by molting; as a consequence they do not have hard structures that could be used for absolute age determination. In the absence of such structures, time-since-last-molt ("shell age"), combined with other data (for example sequential size frequency distributions), could possibly provide the information needed to assess growth and production.

The only correlates of shell age that can be practically recorded for large samples of crab (trawl surveys, commercial landings) are subjective shell condition indices, SCIs, which incorporate observations of hardness, fouling, and deterioration. In Alaska, SCIs have been regularly recorded in surveys of Tanner and snow crabs (*Chionoecetes* spp.) conducted by the National Marine Fisheries Service (NMFS) and the Alaska Department of Fish and Game (ADF&G) over the past two decades (Beers 1991, NMFS 1993). Assumptions about the correspondence between shell age and SCI are largely untested, so there is no valid basis for the use of existing SCI data in the assessment and modeling of Tanner and snow crab stock dynamics.

Two techniques have been suggested in the past to calibrate SCIs: tagging, and aging of epibionts. To calibrate SCI by means of tagging it would be necessary to tag and release a large number of recently molted crabs, and recover them over a period of several years. Such an approach would be expensive and requires a long-term study with highly uncertain chances of success, particularly for high (old) SCI categories. The epibiont method is based on the use of epibiotic barnacles as "living tags," since growth marks (corresponding to growth seasons) can be counted in barnacle shells (Paul and Paul 1986). This technique can provide only a *minimum* shell age, because the time of barnacle settlement after the crab molted cannot be determined.

A third approach is to use radiometric techniques, which have been employed before in several studies of age and growth in mollusks (Turekian et al. 1979, 1983; Turekian and Cochran 1981), fish (Bennett et al. 1982; Campana et al. 1990, 1993; Fenton et al. 1990; Kastelle et al. 1994), and crab (Bennett and Turekian 1984, Le Foll et al. 1989). Here we report measurements of concentration of naturally occurring radionuclides, and discuss the estimation of Tanner and snow crab shell age by means of radiometric techniques.

Radiometric Technique

The measurements are based on the determination of naturally occurring $^{228}Th/^{228}Ra$ and other isotopic ratios. The basic assumptions for radiometric age determination are that (1) during molting virtually all the calcium and associated nuclides are lost by the animal; (2) the new carapace is calcified rapidly enough after molting, so that (3) addition or removal of radionuclides during the intermolt period is negligible. When the new carapace is formed, radium is incorporated with calcium into the exoskeleton, and with time decays to thorium:

$$^{228}\text{Ra} \xrightarrow[5.76\,\text{yr}]{\beta} {}^{228}\text{Ac} \xrightarrow[6.13\,\text{h}]{\beta} {}^{228}\text{Th} \xrightarrow[1.91\,\text{yr}]{\alpha} {}^{224}\text{Ra} \qquad (1)$$

^{228}Th accumulates with time and the activity ratio of ^{228}Th to ^{228}Ra will lead to an age estimate according to the equation

$$\frac{A_{^{228}\text{Th}}}{A_{^{228}\text{Ra}}} = 1.4925(1 - e^{(-0.2444t)}) \qquad (2)$$

where t is time expressed in years.

The measurement of thorium and radium activities can be conducted by two different methods: radiochemical separation and α-spectroscopy (which is a slow process), and γ-spectroscopy (which is a relatively fast process).

In the measurement of ^{228}Th and ^{228}Ra by radiochemical separation and α-spectroscopy, when ^{228}Ra activity is too low it can be measured indirectly from the ingrowth of ^{228}Th in purified radium fraction. This requires storing the sample from six months to one year to allow ^{228}Th to grow toward equilibrium. This approach was used by Bennett and Turekian (1984) for aging the shells of crabs from hydrothermal vents, and by us in the present study.

Measurement of ^{228}Ra activity by γ-spectroscopy can be deduced from a combination of the count rates at 338.7, 911.2 and 968.8 KeV peaks due to the short half-life ($t_{1/2}$ = 6.13 h) of ^{228}Ac. This method requires the use of a large, 140 cm^3, well-type germanium detector with low background (less than 10% of the sample activity). Le Foll et al. (1989) used this approach and counted each sample for 3-4 days to measure ^{228}Ra activity; ^{228}Th activity was measured by α-spectroscopy.

Recently, Talidec and Reyss (1993) reported measurements of both ^{228}Th and ^{228}Ra by γ-spectroscopy using a much larger germanium crystal, 440 cm^3. They reported an accuracy of the thorium/radium ratio of about 15% for a 24-hour counting of a one-gram sample. It should be noted that this type of γ-spectroscopy requires elaborate and expensive instruments and special laboratory facilities to reduce cosmic ray background (e.g. built deeply underground), which were not available for this study.

Materials and Methods

A preliminary sample of adult males was collected during the 1992 crab and groundfish survey in the eastern Bering Sea conducted by the NMFS

(Stevens et al. 1992), onboard the FRV *Alaska*. A more comprehensive collection, consisting of 105 adult male specimens, was obtained during the 1993 survey (Stevens et al. 1993) onboard the FV *Arcturus*. In both cases the samples included specimens of *Chionoecetes bairdi* (Tanner crab) and *C. opilio* (snow crab) representative (in each case) of the five SCI categories routinely utilized by the NMFS (1993):

1. "Softshell" (NMFS) or "new/soft shell" (ADF&G). Carapace soft and pliable.
2. "New hardshell" (NMFS) or "new shell" (ADF&G). Carapace firm to hard, clean, brick red to yellow brown on topside.
3. "Old shell." Carapace hard; topside usually yellowish brown; thoracic sternum and underside of legs yellow with numerous scratches; pterygostomial and branchial spines worn and polished; dactyli on meri and metabranchial region rounded; epifauna (barnacles and leech cases) usually (but not always) present.
4. Carapace hard, topside yellowish-brown to dark brown; thoracic sternum and undersides of legs yellow with many scratches and dark stains; pterygostomial and branchial spines rounded with tips sometimes worn off; dactyli very worn, sometimes flattened on tips; spines on meri and metabranchial region worn smooth, sometimes completely gone; epifauna most always present (large barnacles and bryozoans).
5. Conditions observed in (4) above much advanced; large epifauna almost completely covers crab; carapace is worn through in metabranchial regions, along pterygostomial branchial spines, or on meri; dactyli flattened, sometimes worn through, mouth parts and eyes sometimes immobilized by barnacles.

Categories (4) and (5) are collectively labeled as "very old shell," and sometimes subsumed under the "oldshell" category for reporting.

Assignment of specimens to each category followed consultation with the NMFS expert on board. In some cases a finer scale was used, splitting each category into – and + subcategories to indicate, respectively, an early or advanced condition. All specimens were placed individually in plastic bags and frozen immediately after the catch was sorted.

Once in the laboratory, specimens were defrosted and photographed individually. Measurements included carapace width, height of the propodus (both claws), durometer readings of different parts of the carapace, and basal diameter of the largest barnacle (whose shell was saved). All epibionts (including the basal plates of barnacles) were then removed, and the external surface of the carapace was carefully cleaned with an electric toothbrush. The shell was opened, all meats removed,

Table 1. Results of radiometric age determination in *Chionoecetes* spp.

Species	SCI	Latitude N/ Longitude W[2]	Station Haul[1]	Radiometric age in years (at time of capture)
opilio	1-	59.355667 171.814333	N-23 135	0.11 ± 0.19
bairdi	2+	56.990000 167.709667	G-01 80	0.85 ± 0.27
opilio	4	57.342167 167.739167	H-01 81	4.43 ± 0.33
opilio	4	58.345833 171.647000	K-23 138	4.89 ± 0.37
bairdi	4	56.990000 167.709667	G-01 80	6.60 ± 0.33

[1] Station and haul numbers correspond to the NMFS survey of 1993 (Stevens et al. 1993). All specimens were obtained onboard FRV *Arcturus*.

[2] Latitudes and longitudes given in decimal degrees.

and the exoskeleton was placed in 15% hydrogen peroxide, dried at 80°C, and stored in airtight plastic bags for radiochemical analyses.

For radiochemical determination, 5 to 10 g of exoskeleton material was digested in hot nitric acid, and the organic mater was decomposed with hydrogen peroxide. The sample was diluted to 500 ml with water, and ^{230}Th tracer and barium carrier were added to the sample. Calcium was partially precipitated (along with thorium) with saturated oxalic acid, and separated by centrifugation. The sample was dissolved in 8 M nitric acid and thorium was purified on ion exchange resin. Thorium was electroplated on stainless steel disc, α-counted, and the activity of ^{228}Th was calculated from the ratio of the counts of ^{228}Th/^{230}Th and the known activity of ^{230}Th added to the sample as tracer.

^{228}Ra was measured via its progeny ^{228}Th. ^{228}Th grows in initially pure ^{228}Ra according to Equation (2). The rate of ingrowth is about 20% in six months, and about 35% one year later. After the first thorium measurement, the sample was stripped from all thorium isotopes and stored for thorium ingrowth for radium. Radium was coprecipitated with barium, dissolved in perchloric acid/aluminum nitrate, and thorium was separated by extraction with aliquat-336. Thorium was electroplated and α-counted as above. From the activity of ^{228}Th and the ingrowth period, the activity of ^{228}Ra was calculated using Equation (2). All the activities and the corresponding ages were calculated for the time that each individual sample was analyzed. Then, the time interval between capture and analysis was subtracted from the calculated ages.

Specimens of *C. bairdi* which molted on known dates were kept alive at the Seward Marine Center (Alaska) and sacrificed at various postmolt times. These were processed as indicated above for samples from the field, and the results will be used for calibration of the technique.

Results

The results of radiometric age determination obtained so far are shown in Table 1. As mentioned above, determination of ^{228}Ra by radiochemical techniques requires a long ingrowth waiting period. Hence, results accumulate slowly. Currently 18 additional specimens are being analyzed by radiometric methods for both ^{228}Th/^{228}Ra and ^{210}Pb/^{226}Ra ratios. Shells from crab which molted at known dates in captivity have been analyzed for ^{228}Th and are currently being stored for ^{228}Ra analysis.

Discussion

Interpretation of survey data and modeling of growth require assumptions about correspondence between SCIs and shell age. Somerton (1982), for example, assumed the following scale for *C. bairdi* from the eastern Bering Sea:

SCI	Shell age
1	less than 2 weeks
2	2 weeks to 1 year
3	1 to 2 years
4-5	more than two years

Yet, such assumed correspondences remain untested. Uncertainty in the shell age inferred from SCIs increases with time since molting: while it is not questionable that crabs in SCI category (1) molted recently, it is nearly impossible to guess the age of "very old shells." Our preliminary results indicate a post-molt time ranging from 4 to 7 years for males in SC category (4).

Estimation of the age of crustacean shells with radiometric techniques (briefly outlined above) was first conducted on four specimens of *Bythograea thermydron* (a brachyuran crab ubiquitous in the Galapagos hydrothermal vents) by Bennett and Turekian (1984). The method was validated by Le Foll et al (1989) using individuals which molted in aquaria at known dates: five specimens of the European lobster, *Hommarus gammarus*, and four specimens of the spider crab, *Maja squinado*. More recently, the use of γ-spectroscopy (a relatively fast technique) has allowed the analysis of larger samples of the Norway lobster, *Nephrops norvegicus* (Talidec and Reyss 1993). Radiometric techniques are rather involved, either in terms of time or facilities. They are most useful in the calibration of age estimates based on less costly observations available for large samples, as is the case of SCIs in crabs (our study) or otolith readings from long-lived fishes (Bennett et al. 1982, Campana et al. 1990, Kastelle et al. 1994).

Problems with radiometric techniques relate to assumptions made in the calculation of shell age. If, for example, there is incorporation of radium into the shells during the intermolt period (as may be the case for lobsters; J.P. Reyss, pers. comm.), then radiometric age would underestimate true age (i.e., radiometric age should be viewed as a lower bound for true age). With more knowledge of nuclide dynamics in calcified animal tissues (which is still poorly understood), the process could be modeled to adjust the estimates.

Overall, the method appears promising in allowing a better interpretation of large amounts of information on SCI collected in Alaska in the course of surveys and observer programs.

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Molting Patterns in Southern British Columbia Dungeness Crab and Implications for Fisheries

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Abstract

Analysis of Dungeness crab data from Clayoquot Sound and the Fraser River delta, British Columbia, over the past decade has suggested that many prerecruit male crabs were dying before molting to a size that would have allowed them to be caught in a commercial fishery (Jamieson and Smith 1997). In part, this was because many mature, prerecruit male crabs appeared to have a two-year intermolt period. These mature, prerecruit male crabs accounted for most of the matings that occurred in the population, but the cost of such behavior may be their shorter life span. Data interpretation suggests that population size frequency analysis of Dungeness crab may be more complex than previously thought, and that existing minimum legal size limits may not be optimal for either fishers or conservation of the species. All male crabs in a year class should be given opportunity to breed at least once. Where fisheries largely remove most recently recruited, newly mature male crabs before the seasonal period of most female molting, and therefore mating, delaying harvest of unmated males until after the female molt is advisable. Implications of alternative exploitation strategies for Dungeness crab allowing this are considered.

Introduction

It is generally accepted that because Dungeness crab *(Cancer magister)* landings have been relatively consistent for most fishing locations over the past century, current management practices, which rely primarily on a minimum legal size limit and seasonal fishery closure to minimize exploitation of softshell crabs, are appropriate, if not optimal. In fisheries for this species where landings have fluctuated significantly, there is little evidence that fishing has been the cause of recruitment variability.

Fisheries management usually has as its primary goal conservation of the species, and where a species ranges over a number of political jurisdictions, conservation of locally exploited stocks within that jurisdiction. The biology of the Dungeness crab is somewhat unique among exploited eastern Pacific invertebrates in that this crab has a particularly long pelagic larval period, estimated to be about 4 months under regional oceanographic conditions. With water current patterns along the northeast Pacific coast during the larval period, larvae may be readily transported distances in the hundreds of kilometers (see Crawford and Jamieson 1996). Given this potential substantial mixing of larvae from different hatching sources, and the subsequent settlement of larvae from unknown sources on any fishing ground, a management approach based on classical stock recruitment models has not been used for Dungeness crab populations. There is little evidence of a lack of larvae, with Dungeness crab megalopae appearing to be one of the more dominant plankton components when seasonally expected in areas that have been investigated (Jamieson et al. 1989, Hobbs et al. 1992, Wing et al. 1995). Where crab settlement has been sporadic, such as off the west coast of Vancouver Island, this has been shown to be primarily the result of meteorological and oceanographic events and not a lack of larvae (Jamieson et al. 1989).

A minimum legal size limit thus seems particularly appropriate as the primary regulation tool for Dungeness crab. This is the approach adopted by managers throughout the species' range, but it should be pointed out that size limits used are not based on optimal yield-per-recruit (YPR) analyses. The optimal size for first exploitation of any species is that which allows the maximum biological yield to be obtained from a year class, while considering species' size-at-maturity to ensure sufficient population reproductive potential. However, existing Dungeness crab size limits are not based on any known scientific determination but were rather established in regulation in the early part of this century on the basis of unknown criteria. The state of Washington based its regulation on a cursory study in 1926-1927, but to what extent this evaluation was based on species' biology, which was then largely undescribed, is uncertain (P. LaRiviere, Dept. of Fish and Wildlife, Montesano, WA, pers. comm.).

In this paper, I challenge the assumption that existing accepted size limits (159 mm carapace width [CW], notch-to-notch in the United States and 165 mm CW, spine-to-spine [= 155 mm CW, notch-to-notch] in Canada) may be most appropriate (all subsequent reference to CW will be notch-to-notch). Given the manner in which fisheries are conducted, with substantial legal male harvest in the time interval between male and female molting periods, I argue this point on data suggesting:

1. The fastest growing, largest male crabs have a disproportionately small mating opportunity relative to slower growing male crabs, with possible long-term selection implications.
2. Fisheries may be foregoing a substantial potential harvest from each year class because many male crabs in a year class may never molt to a size larger than the current legal size limit, and hence become available to a fishery.

Data in support of the above are provided by Jamieson and Smith (1997). Their data, based on Clayoquot Sound (Tofino: 1985-1994) and Fraser River delta (1989-1994) Dungeness crab populations, supports the contention of Smith and Jamieson (1991a) that mature, prerecruit crabs have a high intermolt natural mortality, with relatively few of these crabs molting to legal size. Postmolt male crabs of the size mature prerecruit crabs would be expected to molt to are disproportionately low in abundance in both the commercial catch and the wild population. They also show that mature, prerecruit male crabs, in contrast to legal-size crabs, are most likely to have mating marks, and that many prerecruit crabs appear to retain their mating marks through the next spring male molting period. This indicates that these crabs did not molt that spring, since most mating (which creates mating marks) in this population occurs in the summer when mature female crabs molt and the previous year's mating marks were retained through the expected male molting period. Together, these data argue that in intensively exploited populations at least, many mature, prerecruit crabs do not molt again, there is a two-year intermolt period for those crabs which do molt, and that mature, prerecruit male crabs predominate in mating activity.

Here, then, I discuss management implications and options arising from these observations. Understanding the dynamics of exploited Dungeness crab populations is essential if long-term fishery sustainability and maximal short-term harvest levels are to be achieved. This assumes particular importance with the Dungeness crab, since all known significant populations are fully exploited.

It should be noted that because females are not exploited, I am not arguing here that total population fecundity is negatively affected. Smith and Jamieson (1991b) have previously considered this possibility because of a suggested relative lack of particularly large females in heavily exploited Dungeness crab populations.

Crab Versus Other Crustacean Fisheries

Jamieson and Smith (1997) discussed implications of size and sex selection in invertebrates, and note that many crab fisheries are unique in that only males are exploited. This is in contrast to fisheries for other crustaceans, where either both sexes are equally exploited, although there may be some seasonal preference for males when females are carrying eggs, or in the case of pandalid shrimp, which are protandric hermaphrodites, females tend to be selected because of their larger size. This exploitation pattern may explain the general abundance of Dungeness crab larvae, since population fecundity would seem little affected if most females were mated on first reaching sexual maturity (about 80 mm CW [Smith and Jamieson 1991b]). However, since no significant unexploited populations of Dungeness crab appear to exist, apparent complete removal of most legal-size, and therefore the largest males, would nevertheless intuitively seem likely to be having some effect on species' population dynamics.

Benthic Crustacean Yield-per-Recruit Models

Breen (1994) recently reviewed population dynamics and stock assessment considerations for lobsters, noting that YPR and egg-per-recruit (EPR) analyses have become a major assessment technique for these crustaceans in the past decade. However, he points out that while these models may be adequate for demonstrating that fishing intensity is far too high, they generally fail to incorporate important considerations from our current general understanding of crustacean population dynamics. Such consideration is essential if optimal harvest advice is to be provided to managers. Problems arising from discontinuous growth, density-dependent growth and maturity, reproductive interaction with growth, and size-related differences in reproductive effectiveness all need to be addressed. To date, analyses have only specifically addressed discontinuous growth, although authors may note other concerns. There is no systematic evaluation of consequences of oversimplifying reality in YPR and EPR models with crustaceans.

There are relatively few published YPR analyses on crabs, with the most detailed analysis being by Ehrhardt and Restrepo (1989) for stone crab *(Menippe mercenaria)* in Florida. They addressed discontinuous growth but not the other issues identified above, including a likely change in molting characteristics arising from the declawing aspect of this particular fishery. Only claws are landed, while live, clawless crabs are released in the hope that these crabs will regenerate new claws for future harvest.

Male Dungeness Crab Reproduction

The size at which male Dungeness crabs first mate has been determined from gonad examination (MacKay 1942) and both from observation of males in mating embraces and, after mating, from exoskeleton abrasions on their chelae (Smith and Jamieson 1991b), referred to as mating marks. These marks are obtained when a male carries a female around

Table 1. Estimated means (μ_i) and SDs (σ_i) for carapace widths (notch-to-notch CW, mm) of successive instars of Tofino Dungeness crabs > 80 mm CW.

Instar	Males			Females		
(i)	μ_i	σ_i	% (σ_i/μ_i)	μ_i	σ_i	% (σ_i/μ_i)
x	80.5	9.3	11.6	81.7	12.5	15.3
x+1	104.1	10.5	10.1	102.9	11.0	10.7
x+2	129.4	11.7	9.0	121.3	9.7	8.0
x+3	156.3	12.9	8.3	137.1	8.5	6.2
x+4	185.2	14.2	7.7	150.8	7.6	5.0

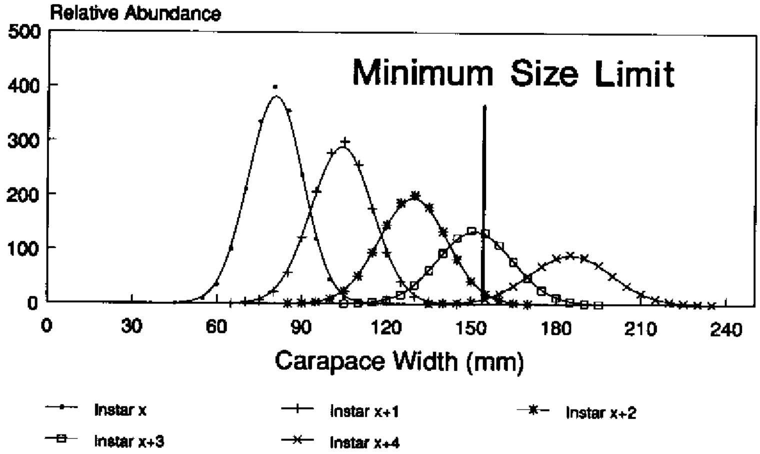
Source: Smith and Jamieson 1989a.

in a premating embrace (Butler 1960). Premolt female brachyuran crabs ready to molt and mate typically require a larger hardshell male mating partner (Butler 1960, Snow and Neilsen 1966, Hartnoll 1969), as only a larger male can hold them in a mating embrace. Although not all male Dungeness crabs that have mated have mating marks, the range of size frequencies of crabs with mating marks is assumed to be representative of the size range of the male population that is capable of mating. Proportion varies by size, though, and in the Tofino, British Columbia, population, about 10% of crabs between 130-135 mm CW and a maximum of ≈40% above 140 mm CW show mating marks (Smith and Jamieson 1991b).

Smith and Jamieson (1991b) gave percentages of male crabs with mating marks by size from the Tofino crab population. Smith and Jamieson (1989a) identified a number of male instars, using maximum likelihood analyses, and using their designations (Table 1), instar x+3 is the first instar in which male crabs are sexually mature. This cannot be stated with absolute certainty, as the smallest instar x+3 crabs overlap in size with the largest instar x+2 crabs, but based on sexual maturity patterns in other crabs (e.g., majids), maturity is probably mostly related to instar stage rather than absolute size or age. It is impossible to determine from wild crabs what exact instar the smallest sexually mature crabs are in, since molting histories of individual crabs from the wild cannot be accurately determined.

Male instar x+3 crabs from Tofino have an estimated mean size of 156 mm CW, with a 95% confidence range of 130-182 mm CW. With a legal size limit in Canada of 155 mm CW, this means that about half of instar x+3 crabs are below the legal size limit and about half are of legal size (Figure 1A).

A. No Fishing



B. Fishing

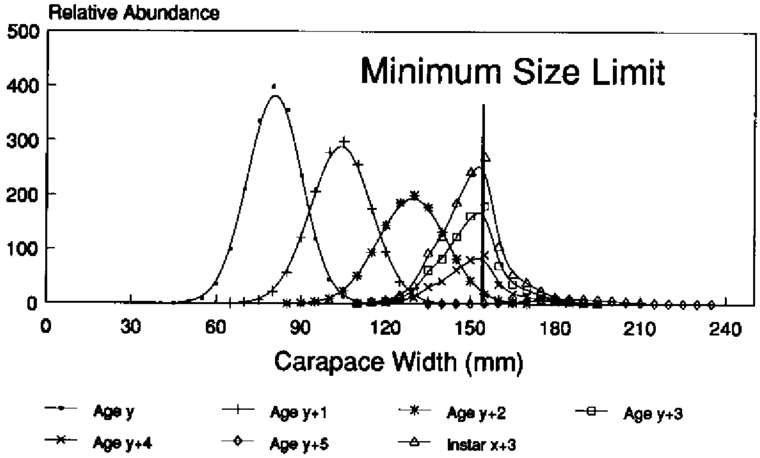


Figure 1. *Estimated Dungeness crab size frequency distributions (mm, notch-to notch CW) by A. instar and B. age for male Dungeness crab. (Note: in-stars match those in Table 1, absolute abundances are arbitrary, and increments in age refer to molts, which may not always be on an annual basis.) Ages y+3 and y+4 (the latter assumed to be 50% of y+3) are summed to give a size frequency distribution for instar x+3, with attenuation of abundance at size above the legal size of 155 mm CW (the vertical bar) because of fishing. Most prerecruit instar x+3 crabs appear to have a 2-year intermolt period, at least when the population is fished, and relatively few (here shown as 10% of age y+4) crabs appear to survive to age y+5 (instar x+4).*

Table 2. Natural mortality (M) estimates by sex and size for Dungeness crab from the published literature.

	M
Hankin et al. (1985, 1989):	
Tagged females > 140 mm CW	2.0-2.5
Tagged females 125-140 mm CW	≈ 0.7
Smith and Jamieson (1991):	
Tagged prerecruit males (920 of 4,038 recovered, 210 (5%) as legal males)	2.5 (2.3-2.8)
Tagged females 135-171 mm CW	1.3

Note: M = 1.0, 1.5, and 2.0 represent annual survival rates of 36.6, 22.3, and 13.5%, respectively.

Smith and Jamieson (1991a) tagged male crabs ($\bar{X}$= 142 mm CW, with 95% between 106 and 162 mm CW) around Tofino, with 920 of the 4,038 crabs tagged (May 1985-June 1986) recovered between May 1985 and February 1987. Average annual natural mortality rate (M) of prerecruit male crabs was estimated (Table 2) to be 2.5 (95% CI of 2.3-2.8). Jamieson and Smith (1997) then showed that many, if not most, prerecruit instar x+3 crabs did not appear to have an annual molt cycle. In their quarterly monitoring of crab size frequency distribution around Tofino, the exceptionally large 1983 year class, responsible for above average landings of instar x+3 crabs in 1986 and 1987 (Smith and Jamieson 1991b), did not show up as instar x+4 crabs until 1988. These instar x+4 crabs represented the molting of only prerecruit instar x+3 crabs because all legal instar x+3 crabs are considered to be harvested by the intense Tofino fishery before they have opportunity to molt.

Even just a few months after a male molt, i.e., when females molt, there are relatively few legal-size, i.e., large, mature male crabs, in the population. The legal crabs that are present are the result of at least some crabs molting to legal size every month. Fishery mortality rate (F) around Tofino was estimated to be 5.1-6.9 (Smith and Jamieson 1989b), and so all legal-size instar x+3 crabs are likely removed by the fishery within a few weeks of their becoming hardshelled. Most mating consequently appears to be done by mature male crabs below the legal size limit (Jamieson and Smith 1997).

Population Size Frequency Structure

The following assessment of male Dungeness crab size frequency structure is primarily based on data obtained from Clayoquot Sound. Recent study of the Fraser River delta population suggests this assessment is relevant there as well, but because of significant, but unquantified, illegal retention of sublegal crabs in that fishery, accurate estimation of natural mortality rate of mature, prerecruit male crabs in the Fraser River delta is proving difficult, with studies still under way. It is assumed the following assessment of size frequency structure applies to other regional Dungeness crab populations that have a similar size frequency distribution to the Tofino crab population.

Because of the suggested 2-year intermolt period for sublegal male instar x+3 crabs, the sublegal male instar x+3 cohort consists of crabs of different ages (Jamieson and Smith 1997). Presuming male crabs molt to instar x+3 at age y+3 (increments in age refer to molts, which for smaller crabs may not always be on a strictly annual basis), this age class would be most abundant within this instar under constant recruitment (Figure 1B). This is because loss to natural mortality is still minimal and relatively little natural mortality of these crabs appears to be disease related. Age y+3 crabs are easily recognizable by their clean shells and lack of epizootic growth.

Crabs one year into the intermolt period, i.e., age y+4, would be the next most abundant age class in instar x+3 (Figure 1B). These crabs show the physical consequences of having a longer-than-one-year intermolt period (crabs this size appear to have at least a 1-year intermolt period). Incidence of old shell (typically shown by epizootic fouling and bacterial infections of the chitinous exoskeleton) is high, claws or legs are often missing, tips of legs are often worn away, and crabs are typically relatively listless and moribund in comparison to age y+3, instar x+3 crabs. In part, this may be the result of numerous captures and releases by the commercial fishery. With the current Canadian minimum escape ring requirement of 100 mm, many sublegal crabs are regularly caught and released a number of times because of high fishing effort levels. It is not known what effect such captures have on crab survival, although it is presumed to be negative.

Although estimated M was high (2.5) for Tofino prerecruit crabs, this was estimated for all prerecruit crabs combined by Smith and Jamieson (1991a). M for mature, sublegal instar x+3 male crabs may not have a linear rate over time, being significantly higher for age y+4, instar x+3 crabs than for age y+3, instar x+3 crabs (Jamieson and Smith 1997).

A few age y+4, instar x+3 crabs survive to age y+5 (Figure 1), and these crabs, two years into the intermolt period, can be identified by extensive epizootic fouling and sometimes, considerable shell deterioration. Some of these crabs are so moribund that they do not appear to have the ability to molt, and it is presumed that these crabs will die in the near future (natural senescence).

The relatively few sublegal instar x+3 crabs in the Tofino population that appear to molt to instar x+4 crabs do so mostly at age y+5. All instar x+4 crabs are of legal size. Most instar x+4 crabs may then be two years older than legal instar x+3 crabs (Figure 1). The unusual situation thus might arise, depending on relative sizes of adjacent year classes and timing of fishing, where average age of mature, sublegal male crabs may exceed that of larger, legal male crabs.

Management Implications

Two issues are raised from the population dynamics described above, both of which will affect YPR calculations:

First, there is the long-term issue of possible selection by the fishery for slower growing crabs. Slower growth could be the result of selection for a smaller molt increment, expressed as a percentage of premolt size, which would increase the probability of an individual being sexually mature at a size below the legal size limit. Alternatively, it could be the result of reduced probability of instar x+3 crabs molting to instar x+4, i.e., selection for a 2-year intermolt period, which would increase the period available for mating. However, the full effect of fishing on mating activity of sublegal male crabs is not clear. Mortality rate may be increased by repeated capture and release of sublegal crabs, thereby decreasing opportunity for mating, but removal of larger competitors may increase mating opportunity.

Evidence for selection will be difficult to compile, as there are few, if any, discrete and modestly large unexploited Dungeness crab populations to compare exploited populations against. Selection may even be the incorrect word to use, as it implies a genetic component. A behavioral change in molting pattern of individuals may simply be a non-genetic response to either a changed crab population structure or a change in community dynamics arising from magnitude of fishery removal. Given the intensity of most existing Dungeness crab fisheries, though, and the decades over which most of the major crab populations on the coast have been exploited, a possible genetic change in species population dynamics over time cannot be ruled out. Butler (1960) noted that sublegal size males also appeared to be doing a disproportionately large amount of mating in exploited populations, so significant selection may have been in effect for upwards of at least 9 generations (assuming a 4-year generation period). Selection has been shown to occur in fish populations (Ricker 1969, Vaughan and Burton 1994) and has been hypothesized for invertebrates (Thouseau et al. 1991; Weinberg and Helser 1996), so appropriate further investigation to determine if fisheries selection is occurring in Dungeness crab would seem warranted.

If the failure of sublegal, mature male crabs to molt to legal size has a genetic basis, i.e., this failure is related to male crabs in a year class which are available to mate, the solution might be to give all male crabs in a year class equal mating opportunity. This can best be done by only allowing fishing of males to occur after females molt, which is typically a few months after recruiting males have molted to legal size. In British Columbia, this would eliminate year-round fishing and delay most fishing until the fall. On the outer coasts of Washington, Oregon, and California, where males first molt to legal size in the late fall and females molt in the spring (P. LaRiviere, Dept. of Fish and Wildlife, Montesano, WA, pers. comm.), this would delay the existing legal male fishery, which currently occurs from about December to May, until late spring-summer.

Second, there is the issue of whether existing size limits are generally appropriate and what an alternative, better minimum legal size limit might be if they are not. As indicated earlier, the best argument for existing size limits is the suggested stability in landings over past decades. Argument for a modified size limit must be supported by clear evidence of change in species population dynamics and/or associated increased benefits to fishers. To date, this evidence is not strong enough to warrant change, as it is based on detailed study of only one, relatively small crab population. However, it is nevertheless possible to speculate on what alternatives would be available to managers if future studies confirm broader hypothesis relevance.

If the size limit were to be increased to allow only instar x+4 crabs to be exploited (operationally difficult because of overlapping instar size ranges), then all instar x+3 crabs would theoretically be given opportunity to mate. However, although this might ensure a whole year class has opportunity to breed, over the short term, this still might not result in most instar x+3 crabs molting to instar x+4. As with the current case with sublegal male instar x+3 crabs which mate, with this scenario, many, if not most, instar x+3 crabs might never molt to instar x+4, as most, if not all, crabs would presumably breed as instar x+3 crabs. What might be achieved would be greater probability of the smallest instar x+3 crabs to molt, assuming these crabs would have the lowest breeding success rate. Continual fishery removal of instar x+4 crabs would prevent establishment of a large cohort of breeding instar x+4 crabs, which is possibly necessary to facilitate a large proportion of instar x+3 crabs to molt. The overall result could then be even fewer legal size crabs in a year class than now occurs.

This assumes that propensity of mated male crabs to molt may in part be determined by the presence and relative abundance of even larger mature male crabs in the population. This seems likely because larger crabs are better competitors than smaller crabs in aggressive interactions among males for females. Butler (1960) noted that invariably larger males were successful in competitions for females about to molt.

Increasing the minimum legal size limit only slightly from the current size would also seem to have little beneficial effect from a fisher's perspective, since again increased molting of breeding, sublegal crabs cannot be assured. In theory, though, it would allow more of a year class to mate and so would be more beneficial from a genetic conservation perspective.

The best management action would probably be to delay fishing until after the seasonal mating period is over, with the benefit described above of allowing the whole year class to mate. Then, if supported by fishers, the size limit could be reduced from the current level to allow capture of more instar x+3 crabs. An alternative to delaying the fishery might be to raise the size limit temporarily at the commencement of the fishery to effectively exclude instar x+3 crabs until after mating occurred, at which time the size limit could be reduced, even if only to existing levels, to allow exploitation of instar x+3 crabs. This would allow instar x+4 crabs to be caught and some fishing to continue during the critical period between male molting and mating. However, unless escape ring size was also adjusted when only instar x+4 crabs were being harvested, this could result in undesirable high levels of capture and release of instar x+3 crabs.

Because it is necessary to allow escape of immature, male instar x+2 crabs, and because instars x+2 and x+3 overlap in size range, it would be advisable to forego exploitation of the smallest instar x+3 crabs in any fishing scenario. Foregoing catch of some instar x+3 males, and assuming these do not molt to legal size, has the additional benefit of leaving a reserve of the current year's mature males to assist the next year class's males, in case the next year class is relatively small, in mating with the population's accumulated year classes of females. Mature females, being unexploited, are generally expected to be more abundant than mature males.

This could allow more of any year class to be harvested as instar x+3 crabs than is now the case, giving a potential greater return to fishers from each year class. However, to minimize capture of instar x+2 crabs (95% of these crabs are within 22 mm [2 SDs] of the mean instar size of 129 mm CW), a maximum size limit reduction after the mating period to only about 150 mm CW would seem desirable.

I appreciate that these management approaches might have market implications that would make some suggestions impractical (e.g., consumer resistance or lower price for smaller crabs). If they are untenable, then simply delaying the fishery, but retaining existing size limits, until after the female molt may be the preferred option. This would also minimize female soft-shell mortality.

From a fisher's perspective, decreasing the size limit has the potential to increase landings, and probably economic return, considerably. Implications arising from changes in timing of fishery openings and possibly price need further investigation to determine both what economic consequences might accrue to fishers and what fishery management approach would be most optimal in meeting specified biological and harvest objectives.

Discussion

The ideas presented above may seem radical, particularly for an exploited species such as Dungeness crab which has seemingly supported viable fisheries in a relatively stable manner for decades. Nevertheless, from a science perspective, we as researchers and managers should always be challenging our understanding of a species' population dynamics to ensure that we understand it fully and correctly. Having a partial understanding of population dynamics can be detrimental and in the worst situation, possibly result in ultimate fishery closure (e.g., western Atlantic groundfish and British Columbia abalone). In this paper, the conventional understanding of Dungeness crab population size frequency structure is challenged, and for the first time, Dungeness crab minimum legal size limits are hypothesized as being possibly not optimal.

A consequence of not challenging conventional paradigms is that we may be unprepared to detect warning signals that all is not right, and even worse, not have required data to then interpret what these warning signals mean. An example is how researchers and managers have dealt with majid crab fisheries over the past decade. Until the mid-1980s, the biology of commercial majid species was thought to be similar to that of commercial cancrid and portunid crabs. Management approaches for majids were thus established along lines traditional to these latter species. However, harvestable abundance in some majid stocks, at least, did not seem to be following expectations, leading Conan and Comeau (1986) to bring forward the idea of a terminal molt and all its ramifications. Previous population monitoring had not always included appropriate parameters to evaluate this new hypothesis, and the result was debate, which continues today, as to what the population dynamics of *Chionoecetes* really is.

If the molting/mating pattern of Dungeness crab proposed here is characteristic of the species, I do not have answers to many questions my hypotheses raise, unlike the majid situation where the biologies of other non-commercial majid species were well known and in support of a terminal molt characteristic for *Chionoecetes*. I do not know why many mature, breeding, sublegal male Dungeness crabs often do not molt again. It is probably not because of a terminal molt as with majid crabs, although the effect may be the same. Jamieson and Smith (1997) have speculated as to some possible explanations. However, explaining an observation is not a prerequisite to mitigation of an effect. Investigation of the molting and mating characteristics of newly mature male Dungeness crabs in additional populations is needed, as such data may significantly influence how we ultimately exploit and manage Dungeness crab on a regional basis in the future. This may give an immediate economic benefit to fishers, but more important are possible conservation benefits which might help ensure long-term sustainable harvest of this important renewable resource.

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Activity and Feeding of Ovigerous Dungeness Crabs in Glacier Bay, Alaska

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Abstract

The activity and feeding behavior of ovigerous Dungeness crabs, *Cancer magister*, were examined as part of a long-term study. Part of this study surveyed Bartlett Cove in Glacier Bay, Alaska, during the spring of 1994 where 50 commercial pots were soaked for 24 hours. Catch per unit effort (CPUE), dispersion, and stomach samples of male, nonovigerous female, and ovigerous female crabs were compared. A laboratory experiment compared feeding rate, foraging response, and survival between starved and fed ovigerous and nonovigerous crabs over a six-month winter period (December 1994–May 1995).

CPUE differed significantly for crabs of different reproductive groups caught in pots during the spring 1994 survey in Bartlett Cove (ANOVA, $P < 0.01$). CPUE averaged 3.7 ± 0.5 (standard error) for males, 1.3 ± 0.3 for nonovigerous females, and 0.4 ± 0.1 for ovigerous females. Male and nonovigerous female Dungeness crabs were homogeneously dispersed throughout the pot transect area; however, ovigerous crabs were aggregated. A significant difference in dry weight of stomach contents and stomach fullness between reproductive groups existed.

Ovigerous females had significantly lower feeding rates than nonovigerous females in the laboratory (two way ANOVA, $P < 0.01$). The foraging responses of ovigerous crabs were significantly lower in comparison to nonovigerous females (Mann-Whitney U test, $P < 0.01$). Seasonal differences were also found for foraging within the two groups over the course of the study period (Kruskal-Wallis one-way ANOVA, $P < 0.01$). No mortality occurred in treatments of fed and starved ovigerous and nonovigerous crabs over the six-month experiment, demonstrating Dungeness crabs can survive overwinter without feeding in laboratory conditions.

Introduction

The Dungeness crab, *Cancer magister*, has long supported an important commercial fishery along the northern Pacific coast. Dungeness crabs inhabit a wide variety of habitats and environmental conditions and have a range extending from Pt. Conception, California, north to Prince William Sound, Alaska, and west to Amchitka Island in the Aleutians (Jensen and Armstrong 1987). Within the northern range of Dungeness crab, life history events occur later in the year (Shirley et al. 1987, Koeneman 1984) and juvenile growth rates are significantly slower (Kondzela and Shirley 1993). In southeastern Alaska, female Dungeness crabs mate with males throughout late fall and early winter (Leder et al. in press, Shirley et al. 1987, Shirley and Shirley 1988). Females extrude eggs beginning in the fall and carry eggs until hatching occurs from April through August, with peak hatching events occurring throughout May and June (Shirley et al. 1987).

Dungeness crab egg and larval mortalities have been investigated with reference to environmental parameters such as temperature and salinity (Shirley et al. 1987, Mayer 1973). After performing a series of laboratory experiments, Mayer (1973) suggested that the "burying" behavior of ovigerous Dungeness crabs in Washington may help prevent egg mortality. By burying, crabs might avoid temperature changes around their egg masses, but as a result minimize their own movements.

A biotelemetry study of Dungeness crabs in Glacier Bay, Alaska, found differences in activity levels, rates of movement, and habitat use by males and females in different reproductive states (O'Clair et al. 1990). Female Dungeness crabs, with and without egg masses, had more restricted movement patterns than males and reduced rates of movement in comparison to males. Also, ovigerous crabs were less active and used less habitat available to the whole population than nonovigerous females and males. These results supported diving observations which indicated that ovigerous crabs aggregate in discrete areas. These discrete areas consisted primarily of coarse sand sediments, perhaps allowing enhanced interstitial water flow and providing a favorable brooding environment. Selection of brooding habitat may result in enhanced oxygenation of the egg clutch when optimal habitat is available (O'Clair et al. 1990). The tendency for ovigerous Dungeness crabs to limit their movements may be related to predator avoidance, greater egg protection (thermal protection, oxygenation, egg predation), avoidance of biofouling, or combinations of these. Whatever the purpose, activity of ovigerous crabs appears to be limited, but no study has directly examined foraging or feeding activities of ovigerous Dungeness crabs.

During the first few years of the Multi-Agency Dungeness Study (MADS) in Glacier Bay, Alaska (1992-1995), few ovigerous female Dungeness crabs were collected in pots and the stomachs of these ovigerous females appeared empty. These observations raised the following questions: (1) do ovigerous crabs have different feeding habits than males and nonovigerous females, (2) can ovigerous crabs overwinter without feeding, and (3) can sampling bias or crab dispersion explain the catch of few ovigerous crabs in pots? Here we present the results of a study of the activity and feeding behavior of Dungeness crabs in Glacier Bay, Alaska, and in the laboratory. Our objectives were to: (1) compare male, nonovigerous female, and ovigerous female stomach contents from individuals collected from pots; (2) compare male, nonovigerous female, and ovigerous female catch per unit effort, CPUE; (3) compare the dispersion of male, nonovigerous female, and ovigerous female crabs collected from pots; (4) determine if starved ovigerous and nonovigerous Dungeness crabs can survive a six-month period in the laboratory; (5) compare the feeding rates and foraging responses of fed ovigerous and nonovigerous Dungeness crabs.

Methods

Field

The study area for this experiment was Bartlett Cove (58°30'N, 135°53'W), which lies in Glacier Bay National Park and Preserve (see Figure 1 in O'Clair et al. 1996).

For this field study only the April 1994 Bartlett Cove data were used. These data were chosen since stomach samples from each reproductive group were available. The data were collected as part of the much larger MADS project. During this project, spring (April) and fall (September) sampling periods were selected to coincide with particular aspects of the reproductive cycles of Dungeness crabs and to avoid sampling conflicts with the commercial fishery, which is closed until June 15 and from August 15 to September 30. During each sampling period 50 commercial pots were baited and allowed to soak for 24 hours; 25 pots were set in shallow water depths (0-9 m) and 25 pots were set in deeper depths (10-25 m). The escape rings of all pots were sealed in order to retain crabs of all sizes.

Dungeness crabs were identified by sex and females were further classified based on reproductive state (ovigerous or nonovigerous). A female was considered ovigerous if she had an egg clutch under her abdominal flap. Carapace width, measured just anterior to the tenth anterolateral spines, was recorded to the nearest millimeter with a vernier caliper. Ten stomach samples were collected from each reproductive group in each bay (10 males, 10 nonovigerous females, 10 ovigerous females).

The number of individual crabs and their reproductive status was determined for each pot fished in Bartlett Cove in April 1994 and CPUE was determined. Analysis of variance was used to examine the catch rate relationship between each reproductive group. The dispersion (pattern of spacing of individuals in a population) of reproductive groups was quantified by determining the number of pots in which each reproductive group was captured and graphically analyzing their spatial relationships.

The stomachs collected from Bartlett Cove during April 1994 were dissected and the contents were examined for food. Dry weight of stomach contents was measured and stomach fullness was estimated (Heinzel et al. 1993). Fullness was determined by visually estimating the percentage of total stomach volume that contained food using the following index: 0 = empty, 1 = trace, 2 = 25% full, 3 = 50% full, 4 = 75% full, 5 = 100% full (Stevens et al. 1982, Norman and Jones 1992, Stehilik 1993). To analyze the dry weights of stomach content the Student's *t*-test and analysis of variance were used to examine differences between reproductive groups. Stomach fullness was analyzed using the nonparametric Kruskal-Wallis one-way ANOVA test.

Laboratory

To determine if ovigerous and nonovigerous Dungeness crabs can survive a brooding season without feeding, a laboratory experiment was performed in which 6 ovigerous and 6 nonovigerous crabs were fed and 6 of each group were starved. The 24 crabs were collected during September 24-25, 1994, and held in seawater tanks until the experiment began. The carapace widths of the crabs used in the experiment ranged from 111 mm to 159 mm. The same size range of crabs was used for each treatment.

Crabs were randomly assigned to separate compartments within each treatment tank. All crabs were held in flow-through tanks of filtered seawater. A substrate of sand and gravel up to 8 mm in diameter was added to mimic the natural habitat. The substrate was collected from a local site, Eagle Beach, where Dungeness crabs are known to inhabit the nearshore area. Water entering the tanks was pumped directly from a depth of 30 m in Auke Bay. The temperature was not controlled; the maximum temperature recorded over the six-month period was

8.9°C and the minimum temperature was 5.1°C. Crabs receiving food were fed squid once a week; food was available to the crabs for two days. At the end of the second day any remaining food was removed to help prevent the tanks from fouling. The feeding rate and foraging response for crabs in the fed treatment were measured every two weeks on 12 study dates from December 6, 1994, through May 6, 1995. The starved crabs received no food throughout the six-month study period.

The feeding rate for each crab in the fed treatment was determined by weighing each portion of squid prior to feeding the crab. The squid was placed in seawater for one hour before weighing to allow it to equilibrate in seawater. Squid was also placed in an isolated section (from which crabs were excluded) of the tank containing fed crabs in order to determine changes in the weight of the squid placed in seawater for 24 hours. The crabs were monitored over 24 hours and given more food if the initial supply had been eaten to ensure that each crab had food continually available when feeding rates were being determined. After 24 hours the remaining squid in each crab compartment was weighed. We tested the difference in feeding rates between the two groups, ovigerous and nonovigerous crabs, over the entire six-month period using two-way analysis of variance.

Foraging response was determined for each crab in the fed treatment by recording when each crab first initiated feeding. Food was placed in each crab compartment as far from the crab as possible so that the crab would have to move in order to feed. The crabs were monitored continually for the first hour of the 24-hour study period. Thereafter, each crab was examined for evidence of feeding activity at six and 24 hours. The foraging response was recorded as follows: 1 = immediate response, 2 = response within the first fifteen minutes of the observation period, 3 = response within the first hour of the observation period, 4 = response within the first six hours of the observation period, 5 = response within 24 hours, 6 = no response within 24 hours. The nonparametric Kruskal-Wallis and Mann-Whitney U tests were used to test the difference in foraging response between the ovigerous females and the nonovigerous females over the course of the study period.

Crabs in the starved treatment were checked periodically for mortality. Starved crabs were disturbed as often as the crabs in the fed treatment. Each time the fed group was given squid or uneaten squid was removed from the tank of fed crabs, tank covers were also removed from the starved treatment tank to ensure that each treatment group was disturbed equally. The survivorship over the six-month period was determined for each treatment.

All data are presented as mean ± standard error of the mean. The Student's *t*-test and two-way analysis of variance were used to compare the means of the different reproductive groups. Values were considered significant when $P < 0.05$.

Table 1. CPUE for Dungeness crabs sampled in Bartlett Cove during the spring of 1994.

Reproductive groups	Total no. crabs	No. pots with crabs	Average no. crabs/pot
Males	179	35	3.7 ± 0.5
Nonovigerous females	63	24	1.3 ± 0.3
Ovigerous females	21	14	0.4 ± 0.1

Average values are reported as mean ± one standard error.

Results

CPUE and dispersion

The CPUE differed between reproductive groups during the spring 1994 survey in Bartlett Cove (ANOVA, $P < 0.01$). Significantly more male Dungeness crabs were captured in pots than nonovigerous and ovigerous females (ANOVA, $P < 0.01$), and significantly more nonovigerous females were captured than ovigerous females (ANOVA, $P < 0.01$). Male crabs averaged 3.7 ± 0.5 crabs per pot and nonovigerous female crabs averaged 1.3 ± 0.3 crabs per pot. The CPUE averaged 0.4 ± 0.1 for ovigerous females. (Table 1).

Crabs were captured in 45 of the 50 crab pots set in Bartlett Cove. Males were captured in a total of 35 pots, nonovigerous females were captured in 24 pots, and ovigerous females were captured in 14 pots. Both male and nonovigerous female crabs appeared to be homogeneously dispersed within the cove; however, the ovigerous females were caught in just a few areas (Figure 1).

Stomach contents

Stomach samples collected from Bartlett Cove in April 1994 had significant differences in dry weight content between males and ovigerous females (Student's t-test, $P < 0.05$); no significant difference existed between ovigerous and nonovigerous females (Student's t-test, $P = 0.4$). Two of the females, one ovigerous female and one nonovigerous female, had eggs in their stomachs. Most likely these eggs were ingested after the crabs were collected from the pot and placed together in a sampling bucket. Stomachs were dissected after the last pot was pulled, so sampled crabs may have been held together for more than an hour. If these two crabs are omitted, significant differences existed between all three reproductive groups (Figure 2).

There was a significant difference in the average stomach fullness index values between each reproductive group, with the ovigerous crabs

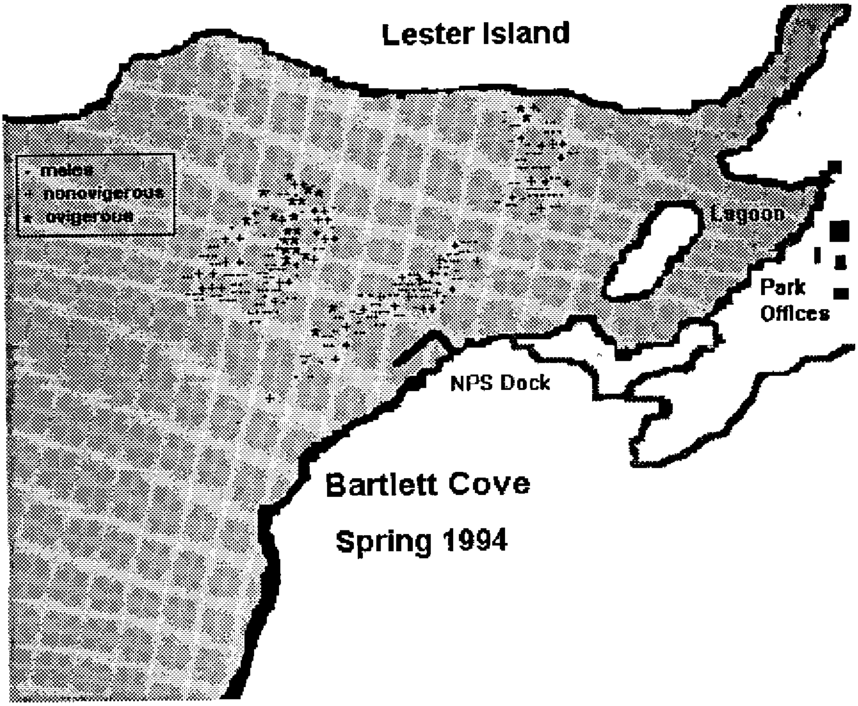

Figure 1. Dispersion of crabs in Bartlett Cove during the spring of 1994. The numbers of crabs in each pot are shown clustered in the site where the pot was pulled; each symbol represents one crab.

having the smallest fullness index value (Kruskal-Wallis test, $P < 0.01$, Figure 3).

Laboratory feeding rates and foraging response

In the laboratory, the average daily feeding rate for ovigerous females was significantly less than nonovigerous females (2 way ANOVA, $P < 0.01$, Figure 4). The average wet weight of food eaten by nonovigerous crabs was 16.8 ± 0.4 grams per day, while ovigerous crabs ate an average of 9.0 ± 1.5 grams per day of squid. Feeding rate did not significantly differ over the six-month period of the experiment within either group.

The foraging response index was significantly different between the two groups (Mann-Whitney U test, $P < 0.01$, Figure 5). There was also significant difference within each group over the course of the study period (Kruskal-Wallis one-way ANOVA, $P < 0.01$). On average an ovigerous

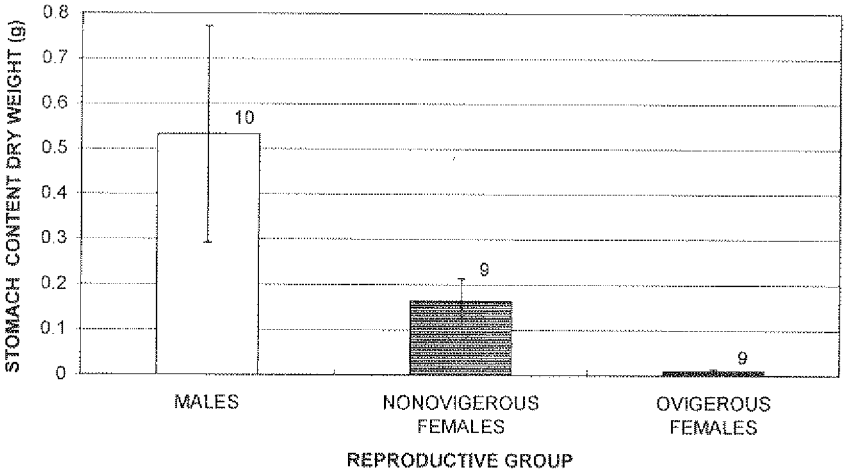

Figure 2. Stomach content dry weights (g) for Dungeness crabs of each reproductive group from Bartlett Cove during the spring of 1994. All values are reported as mean ± one standard error. Number of crabs in each group is shown above each bar.

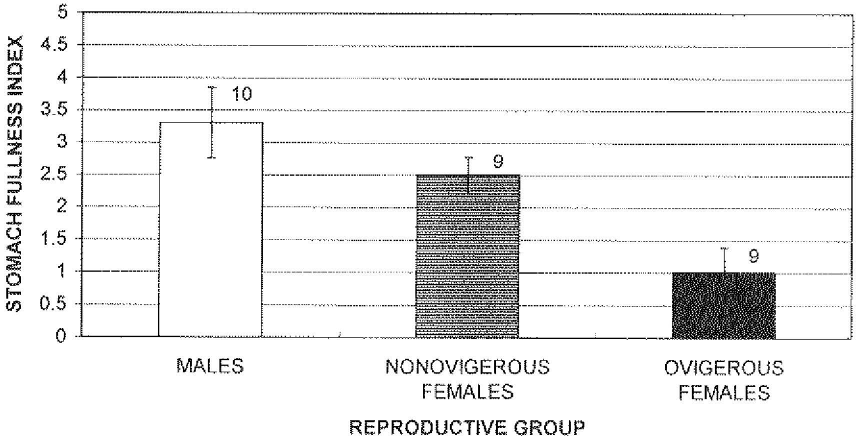

Figure 3. Stomach fullness for each reproductive group of Dungeness crabs in Bartlett Cove during the spring of 1994. All values are reported as mean ± one standard error. 0 represents an empty stomach and 5 represents a full stomach. Number of crabs in each group is shown above each bar.

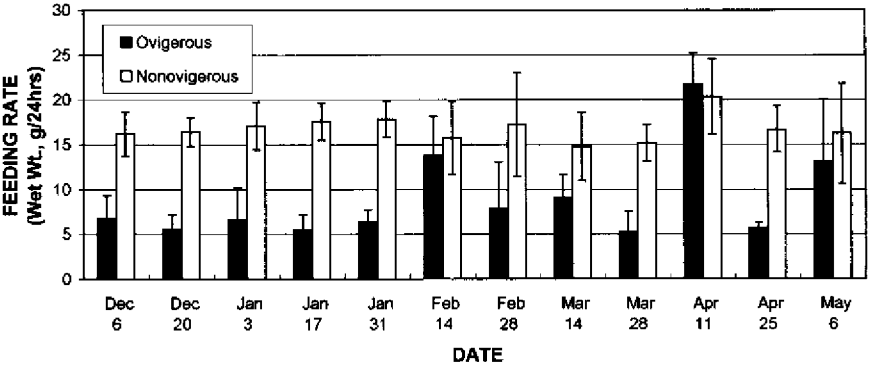

Figure 4. Average daily feeding rates (wet wt. g/d) for ovigerous and nonovigerous female Dungeness crabs kept in the laboratory for six months. All values are reported as mean ± one standard error. N = 6 for each treatment, for all dates.

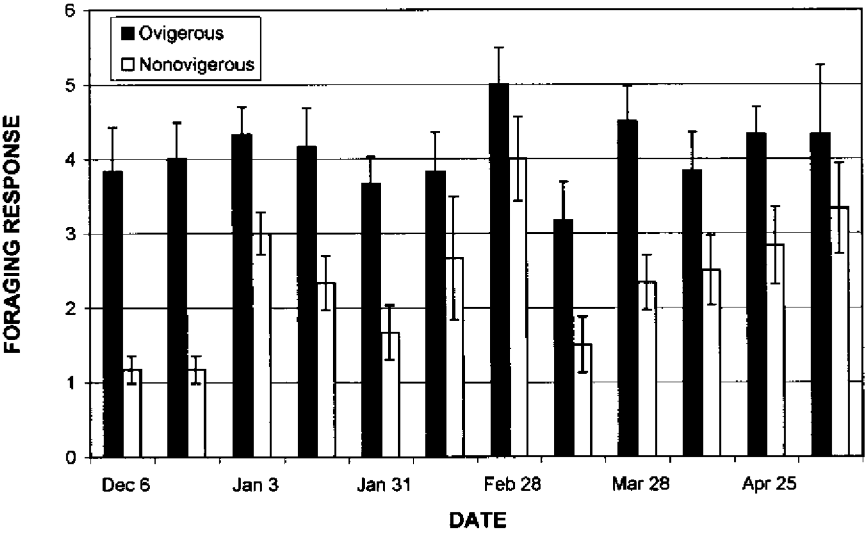

Figure 5. Average daily foraging responses for ovigerous and nonovigerous female Dungeness crabs kept in the laboratory for six months. All values are reported as mean ± one standard error. 1 = immediate response, 2 = 15 min, 3 = 1 hr., 4 = 6 hrs., 5 = > 6 hrs., 6 = no response. N = 6 for each treatment, all dates.

female began feeding 6 hours after food was placed into the tank, while nonovigerous crabs responded earlier, within the first fifteen minutes. No mortality occurred in either fed or starved treatments of ovigerous and nonovigerous crabs during the experiment.

Discussion

From our pot survey in Bartlett Cove, it appears that collections of ovigerous crabs occurred in specific sites, suggesting aggregations. Dive surveys conducted in some of the same areas as our pot locations revealed that the location of one group of pots containing ovigerous females was near an aggregation of buried, ovigerous crabs (C. O'Clair, personal observations). Another group of pots containing ovigerous crabs was below the depths of the diver transects, but may indicate another aggregation. Results of the dive transect study indicated that ovigerous Dungeness crabs were usually more frequently and more strongly aggregated than male and nonovigerous crabs, particularly at spatial scales from 20 to 100 square meters (O'Clair et al. 1996). Recent studies involving other crab species such as *Chionoecetes opilio* and *C. bairdi* (Kon et al. 1996, Stevens and Haaga 1996) have suggested spatial variability in the dispersion of ovigerous females. Because ovigerous crabs are more aggregated than males or nonovigerous females, their spatial heterogeneity may lead to a sampling bias when they are surveyed with pot transects. If the transect does not intersect an ovigerous female aggregation perhaps no ovigerous females will be captured. Stevens and Haaga (1996) have suggested the use of sampling procedures such as kriging to estimate density distributions of these aggregations.

The feeding habits of Dungeness and related crab species have been the subject of many studies (MacKay 1943, Stevens et al. 1982, Asson-Batres 1986, Wolff and Cerda 1992, Stehlik 1993). However, little attention has been given to ovigerous females of the genus *Cancer*, probably because of the difficulty in collecting them and because females are not commercially harvested. Stevens et al. (1982) reported food preferences of Dungeness crabs and feeding habits with reference to the life stage of the crab, but did not examine relationships based on reproductive status. The crab *Carcinus maenas* has an optimum size of prey at which it can maximize the energy content while requiring the least amount of handling time for each crab size; as crab width increased so did the optimum prey size (Elner and Hughes 1978).

Bernard (1979) used a stomach fullness index and found larger Dungeness crabs had a larger mean fullness index. In our field study, the males had an average carapace width of 156 ± 1 mm, the average carapace width for nonovigerous females was 144 ± 2 mm, and the average carapace width of ovigerous females was 150 ± 2 mm. On average, ovigerous females had smaller carapace widths than males but larger carapace widths than nonovigerous females. The ovigerous Dungeness crab stomach samples contained less food than males and nonovigerous females. In many cases the ovigerous crab stomachs were empty, both for ovigerous females of smaller (121 mm) and larger (169 mm) carapace width sizes. These crabs were captured in pots with food available to them, yet they did not appear to have eaten. Perhaps foraging is not the reason the ovigerous female Dungeness crabs entered the pots.

In a laboratory study of the crab *Cancer polydon*, the weight gained relative to the amount of food ingested was lower for females (5.3%) than for males (10.3%) (Wolff and Cerda 1992). Wolff and Cerda (1992) suggested that the different growth values between the sexes can be explained by the fact that females convert a higher percentage of the ingested food into egg production instead of growth. In our laboratory study, ovigerous crabs had significantly lower feeding rates and significantly lower foraging responses than did nonovigerous females. In many cases the ovigerous crabs did not feed at all within the 24-hour observation period. The ovigerous crabs appeared uninterested in the food available to them. Perhaps the ovigerous females conserve energy reserves by reducing their foraging and feeding activities while they are brooding their eggs.

Environmental effects on feeding and foraging were not the focus of this study and the effects of variables such as temperature and photoperiod on feeding rates were not tested. However, in the laboratory, crabs were held at ambient water temperature and photoperiod and a seasonal change in foraging response was found. We do not have continuous measurements of field temperatures; however, water column temperatures in the five bays within Glacier Bay were nearly isothermal within each bay between 6-9°C in September (1993) and were isothermal between 4-6°C in April (1993). Dungeness crabs have five times greater feeding rates at 15°C than at 5°C (Kondzela and Shirley 1993).

The foraging activities of *Cancer novaezelandiae* were influenced by photoperiod and tidal variables in a field study using pots (Chatterton and Williams 1994). The timing of foraging activity of *C. novaezelandiae* was based on a direct responsiveness to tidal stimuli. A parallel laboratory study subjected crabs to various daylight conditions and most of the crab activity was during hours of the dark phase with the greatest activity occurring just after lights were turned off (Chatterton and Williams 1994). Diel activity of Dungeness crabs was examined in an estuarine field study by Stevens et al. (1984). Crabs were found to be more abundant at night in the intertidal site and this was concluded to be a response to the availability of their predominant food, a crangonid shrimp (Stevens et al. 1984). In our laboratory study, the feeding rate was determined for a 24-hour period. Food was first placed into the tank just before dark so that the peak activity time could be monitored. Future feeding studies with *Cancer magister* should examine the effects of environmental variables. For example, foraging and feeding rates of nonovigerous and ovigerous females might converge at lower temperatures, or perhaps the feeding rates of nonovigerous crabs may not be as affected as those of ovigerous crabs as temperature decreases.

A starvation study has been conducted on Dungeness crabs with mixed results (Paul et al. 1994). Paul et al. (1994) reported 20% mortality among continually fed Dungeness crabs and mortality rates up to 80% for the two treatments starved for 30 and 60 days. They suggested Dungeness crabs are sensitive to stresses of capture, handling, and captivity.

Temperature has been found to influence the survival of Dungeness crabs in the laboratory (Shirley et al. 1987, Kondzela and Shirley 1993). Shirley et al. (1987) reported almost 100% survival rates for all adult Dungeness crabs held at temperatures of 5°C and above, with an unexpected 100% mortality of adult crabs held at 1°C. In contrast, Kondzela and Shirley (1993) observed higher survival rates of juvenile Dungeness crabs held at lower temperatures. They had 100% survival of juvenile Dungeness crabs held at 1°C, but no molting occurred and feeding was minimal. In our laboratory experiment both fed and starved ovigerous and nonovigerous female Dungeness crabs survived a six-month overwintering period with no mortality. Diver observations indicate that ovigerous Dungeness crabs are reluctant to leave the sediment (O'Clair et al. 1996). This may minimize exposure of ovigerous females to predation or may protect the egg clutch from other environmental hazards (Mayer 1973, O'Clair et al. 1990, O'Clair et al. 1994). Our results indicate that feeding rates and foraging responses of ovigerous Dungeness crabs are reduced compared to nonovigerous females and that it is possible for an ovigerous female to overwinter without feeding in the laboratory.

Ovigerous female crabs are often left out or grouped together with nonovigerous females in laboratory and field studies. Our research indicates that ovigerous females have different activity and feeding behaviors than both nonovigerous females and males. Future studies should include ovigerous females and treat them separately, because their reproductive condition may impose different physiological and ecological requirements than are imposed on nonovigerous females and males. These requirements can find expression in behaviors that differ in ovigerous crabs from those of nonovigerous female and male crabs.

Acknowledgments

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Preliminary Report on Interannual Variation in Size-specific Molting Probabilities of Adult Female Dungeness Crabs *(Cancer magister)* in Northern California

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Abstract

For adult decapod crustaceans for which molting takes place at most annually, an adequate description of growth requires specification of (a) size-specific molt increments, and (b) size-specific molting probabilities. During 1981, 1982, 1992, 1993, and 1995, we generated molt increment data from 83 to 178 adult female Dungeness crabs annually. These data have shown that postmolt carapace widths are tightly related to premolt carapace widths ($0.88 < R^2 < 0.98$); interannual variation in size-specific molt increments has been relatively small. Using extensive shell condition observations as post molting season indicators of molting history, we used simplified methods of Mohr and Hankin (1989) to assess qualitative patterns in annual size-specific molting probabilities. In their original application to adult female Dungeness crabs in northern California, Mohr and Hankin (1989) found that size-specific molting probabilities were close to one for crabs less than 130 mm carapace width, but then declined rapidly to near zero for crabs with carapace widths exceeding 155 mm. Preliminary analyses of shell condition data collected during 1993, 1994, and 1995 have suggested size-dependent declines in annual molting probabilities that are consistent with these earlier results. During 1992, however, molting probabilities were close to 100% for almost all crabs, irrespective of size. In future work, we intend to collect more data reflective of interannual variation in size-specific molting probabilities and we hope eventually to determine the environmental basis for such interannual variation.

Introduction

Development of fishery dynamics models suitable for management of crustacean fisheries is complicated by the discontinuous nature of crustacean growth. Whereas growth of most finfish takes place in a smooth and relatively continuous fashion, reasonably modeled by continuous growth curves such as the von Bertalanffy, Brody, or Gompertz equations (see Ricker 1975 for a review), crustacean growth consists of two components: size increase at molting (molt increment) and time interval between molts (intermolt interval—a reflection of molting probability). Both of these components appear to be environmentally labile (Aiken 1980, Hartnoll 1982), and both components are known to be size-dependent (i.e., depend on premolt size of crustaceans; e.g., McCaughran and Powell 1977—Alaskan king crab, Campbell 1983—American lobster, Lipcius 1985—review for crustaceans in general, Hankin et al. 1989—Dungeness crab).

On the basis of the above considerations, Caddy (1986, 1987) and Cobb and Caddy (1989) have argued in favor of development of (stochastic) crustacean growth models that incorporate these discrete component events of molting and size increase, and in favor of incorporating such models in crustacean fishery assessment models (e.g., Fogarty and Murawski 1986, pp. 238-40). Because many biologists have asserted (without empirical evidence) that mortality rates of crabs must be high when animals molt and are in a vulnerable soft-shelled condition, Cobb and Caddy have also stressed that "research on the relationship between molt frequency and M [natural mortality] should clearly be a high priority for future work in crustaceans."

Although it has long been recognized that crustacean growth consists of these two distinct components (molt increments and molting probabilities), it has proved difficult to obtain reliable estimates of molting probabilities for crabs. One obvious device used for estimation of molting probabilities and for generation of molt increments has been generation of crab tag and recovery data. Analysis of tag recovery data is, however, fraught with many difficulties including at least (a) commercial fishery size selection biases and (b) tag loss (Diamond and Hankin 1985a); (c) effects of tagging on growth or recovery (Edwards 1965, Hartnoll 1982); and (d) uncertainty in number of molts (or molting opportunities) prior to recovery (Conan and Gunderson 1979). Given these biases and uncertainties, which have often been ignored, it seems unlikely that tag recovery data can provide other than a relative or qualitative picture of size-dependent changes in molting probabilities.

For species of crabs that exhibit a relatively well defined molting season, however, physical appearance or chemical composition of an animal may allow accurate molt classification prior to or shortly after the molting season. Candidate structures or observations that may allow molt stage classification can be generally classified as "premolt indicators" or "postmolt indicators." Premolt indicators allow assessment of ongoing premolt preparation, whereas postmolt indicators allow assessment of whether or not a molt has recently taken place. Integumental structure (Hepper 1965, Aiken 1980), pleopod regenerative state (Aiken 1973, 1980), and serum protein concentration (Ennis 1973, Hepper 1977) have all been considered as possible premolt indicators in *Homarus* spp., but only pleopod regenerative state or histological examination of integumental structure have allowed reliable prediction of molting. Visual inspection of carapace condition shortly after completion of the molting season has led to successful classification of animals into those that have or have not molted for at least Alaskan king crab (Weber and Miyahara 1962), American lobster (Ennis 1977), and Dungeness crab (Mohr and Hankin 1989).

Opportunities to observe interannual variation in molting probabilities are especially good for female Dungeness crabs *(Cancer magister)* for two reasons. First, commercial harvest of females is prohibited so that most large adult females, for which molting probabilities are low when compared to smaller crabs, remain prevalent in the population of adult females. Second, the molting season is relatively well defined. In northern California, molting of female Dungeness crabs and mating of softshell females with hardshell male crabs takes place primarily from mid-February through mid-May, with a usual peak during early April. Male crabs apparently can sense when molting of female crabs is imminent and they grasp females in a "premating embrace" several days prior to female molting (Butler 1960); when females molt, males grasp females in the true mating embrace (Snow and Nielsen 1966). Upon completion of the molting and mating season, postmolt indicator methods may be used to estimate annual size-specific molting probabilities. Alternatively, premolt indicator data may be collected prior to initiation of female molting.

Material and Methods

Size-specific molt increments were generated through recoveries of tagged female Dungeness crabs (1981, 1982), as reported by Hankin et al. (1989), or from laboratory molting of female crabs collected from premating embraces (1981, 1982, 1992, 1993, 1995). Premolt carapace width (CW, excluding posterolateral spines) of female crabs was measured (± 0.1 mm) at time of tagging or collection from premating embraces; postmolt CW was measured at time of recovery or approximately 5 days after laboratory molting. Most female crabs collected from premating embraces molted within 1-4 days of collection.

We used experimental small mesh traps to collect adult female Dungeness crabs in northern California, relying on a contracted commercial crab fisherman to set gear and pull traps, etc. Design of experimental traps was described previously in detail by Diamond and Hankin (1985b). Traps were nonselective for female crabs with CW exceeding 85 mm.

During 1982 and 1983, experimental traps were set in approximately 14 m depth off Clam Beach, 41°00′N, during January-February (1982) and mid-May (1983). Traps were set during two periods (mid-June and again in mid-July) at two locations (off Clam Beach, 41°00′N, and off Big Lagoon, 41°10′N) along depth contour lines at approximately 14 m and 28 m, respectively, during 1992, 1993, and 1995. Traps were set at approximately 14 m depth off Clam Beach only during mid-July 1994. Traps were typically baited with rockfish carcasses and squid and were allowed to soak from 2 to 5 days prior to pulling. Numbers of adult female Dungeness crabs per trap generally ranged from 40 to 90; male crabs made up less than 2% of total catches. Molting history of female crabs with respect to the previous molting season was classified into one of five categories based on visual assessment of shell condition (see Hankin et al. 1989, Mohr and Hankin 1989): 1—definitely molted; 2—probably molted; 2/3—uncertain molting history; 3—probably did not molt; and 4—definitely did not molt.

For the preliminary assessments of interannual variation in molting probabilities that are reported in this paper, we combined all shell condition observations from a given year and we used a simplified version of the methods proposed by Mohr and Hankin (1989). Given an observed sample frequency distribution of molted (categories 1 and 2) and nonmolted (categories 3 and 4) crabs, we projected the premolt size distribution of molted crabs by predicting premolt size from postmolt size using linear regressions based on year-specific molt increment data. We then compared the projected premolt size frequency distributions of molted crabs to the summed size frequencies of these crabs plus those that did not molt so as to produce a qualitative assessment of size-dependent changes in molting probabilities, as illustrated in Figure 1. We omitted the small percentage of crabs classified as of uncertain molting history (category 2/3).

In contrast to the more formal methods developed by Mohr and Hankin (1989), we did not (1) make any adjustments for the possible differential survival of molting as compared to nonmolting crabs, and we did not (2) account for the natural variation in molt increments given premolt size. Point estimates produced by these simplified methods should be essentially the same as those for the methods proposed by Mohr and Hankin for the special case $R^* = 1.0$ (i.e., relative survival through the molting season is the same for molting and nonmolting crabs). Methods used in this paper do not, however, allow any assessment of errors of estimation, an important advantage of the methods developed by Mohr and Hankin (1989).

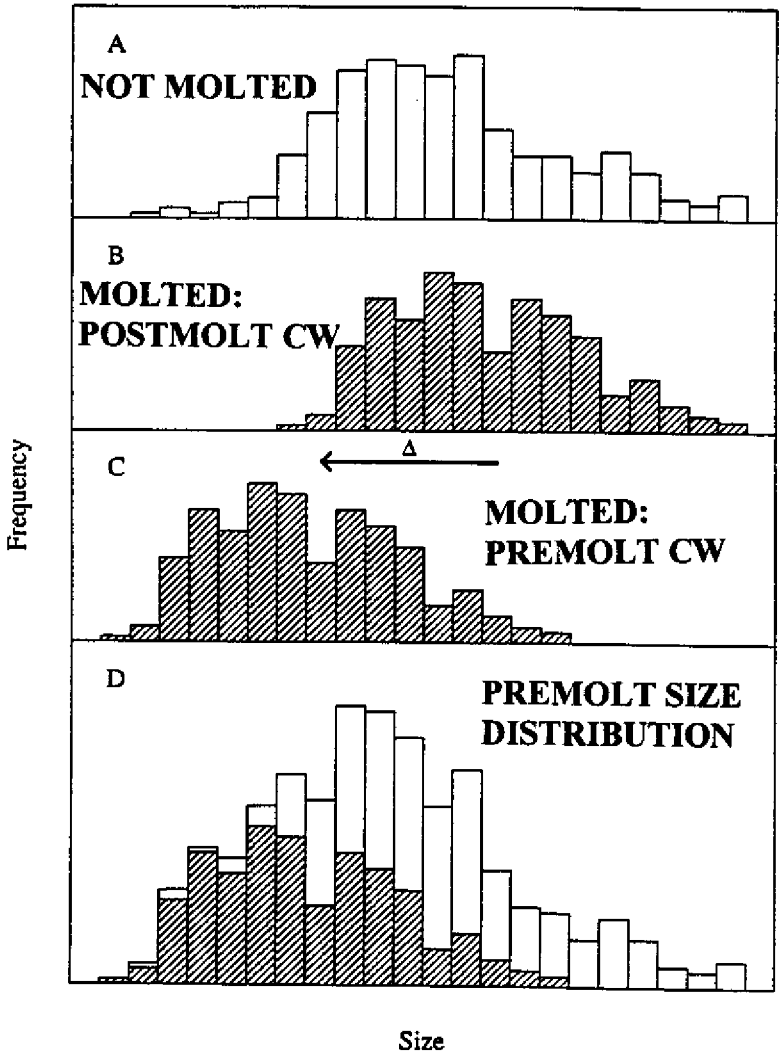

Figure 1. Simplified representation of the process of estimating size-specific molting probabilities from shell condition data, following Mohr and Hankin (1989). Panels A and B show hypothetical size frequency distributions of not molted and molted crabs based on postseason indicator data. If molt increments are assumed constant, then Panel C shows the premolt size distribution of molted crabs, constructed by shifting the molted frequency distribution to the left by a fixed factor, delta. Finally, summed frequencies of not molted crabs and premolt size frequencies of molted crabs allow estimation of interval-specific molting probability as the proportion of an interval that is shaded, as in Panel D.

Results

Observed size frequency distributions of molted and nonmolted adult female Dungeness crabs collected during 1982 and 1983 were similar to one another and provided substantial evidence that molting failure was most prevalent among females with carapace widths in excess of 140 mm (Figures 2 and 3). When 1983 data were used to estimate size-specific molting probabilities using the full methods of Mohr and Hankin (1989), a steep decline in molting probabilities from approximately 100% molting for carapace widths less than 135 mm to effectively 0% molting for carapace widths greater than 155 mm was noted (Figure 4).

Size frequency distributions for molted and nonmolted female crabs collected during 1993, 1994, and 1995 (Figures 5, 6 and 7) were similar to those for 1982 and 1983. Relatively large numbers of nonmolted crabs were observed in each of these years and most of these crabs exceeded 135-140 mm carapace width. Very few nonmolted females were observed during 1992, however, suggesting that most females may have molted during that year (Figure 8).

Projection of premolt size frequencies of female crabs during 1992-1995 required fitting of linear regressions of premolt CW (Y) against postmolt CW (X) based on laboratory-generated records of premolt and postmolt sizes (Table 1). Although estimated intercepts and slopes of regression lines have varied substantially, plots of premolt vs postmolt CW regression lines have been similar and have suggested that interannual variation in size-specific molt increments has been relatively small (Figure 9).

Superimposed size frequency distributions of projected premolt carapace widths of molted crabs compared to total frequencies of molted and nonmolted crabs confirmed that data collected during 1993, 1994, and 1995 conformed to the kind of size-dependent decline in size-specific molting probabilities calculated previously by Mohr and Hankin (1989). In these three years, almost all crabs with carapace widths less than about 130 mm were destined to molt, but then proportions of molting crabs declined rapidly to near zero for crabs with premolt carapace widths exceeding 150 mm (Figure 10, 11, 12). In contrast, almost all crabs molted during 1992 with the minor exception of crabs with premolt carapace widths exceeding about 150 mm (Figure 13).

Discussion

Substantial interannual variation in size-specific molting probabilities has been previously documented in commercially important crustacean populations. For example, Balsiger (1974, Figures 3.13, 3.14, 3.15) constructed graphs suggesting that size-specific molting probabilities of Alaskan red king crab *(Paralithodes camtschaticus)* were substantially less during the period 1966-1969 than during the period 1954-1961.

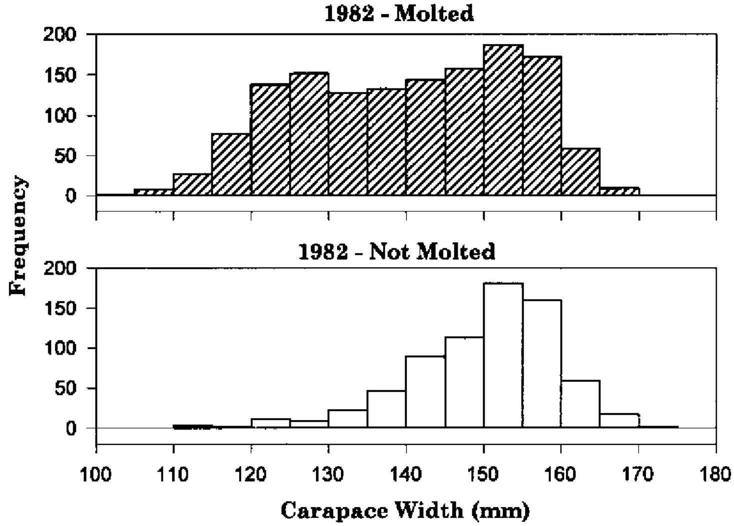

Figure 2. Size frequencies of molted and not molted adult female Dungeness crabs sampled near Trinidad, California, January-March 1982, based on shell condition observations.

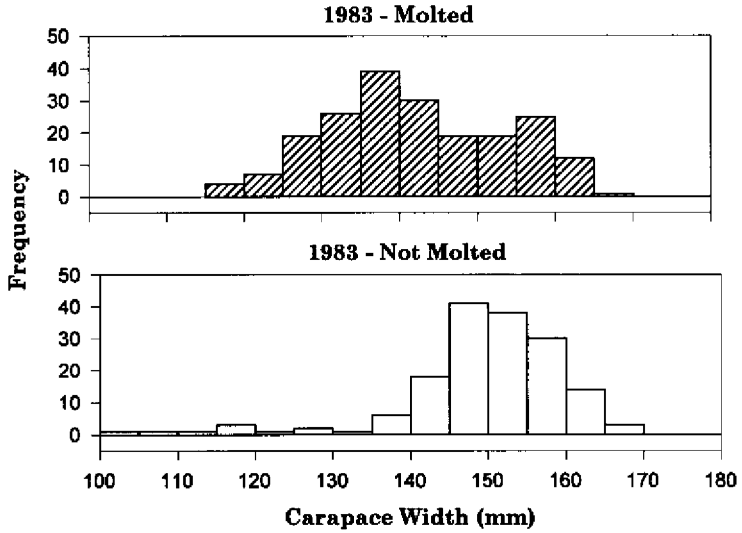

Figure 3. Size frequencies of molted and not molted adult female Dungeness crabs sampled near Trinidad, California, May 1983, based on shell condition observations.

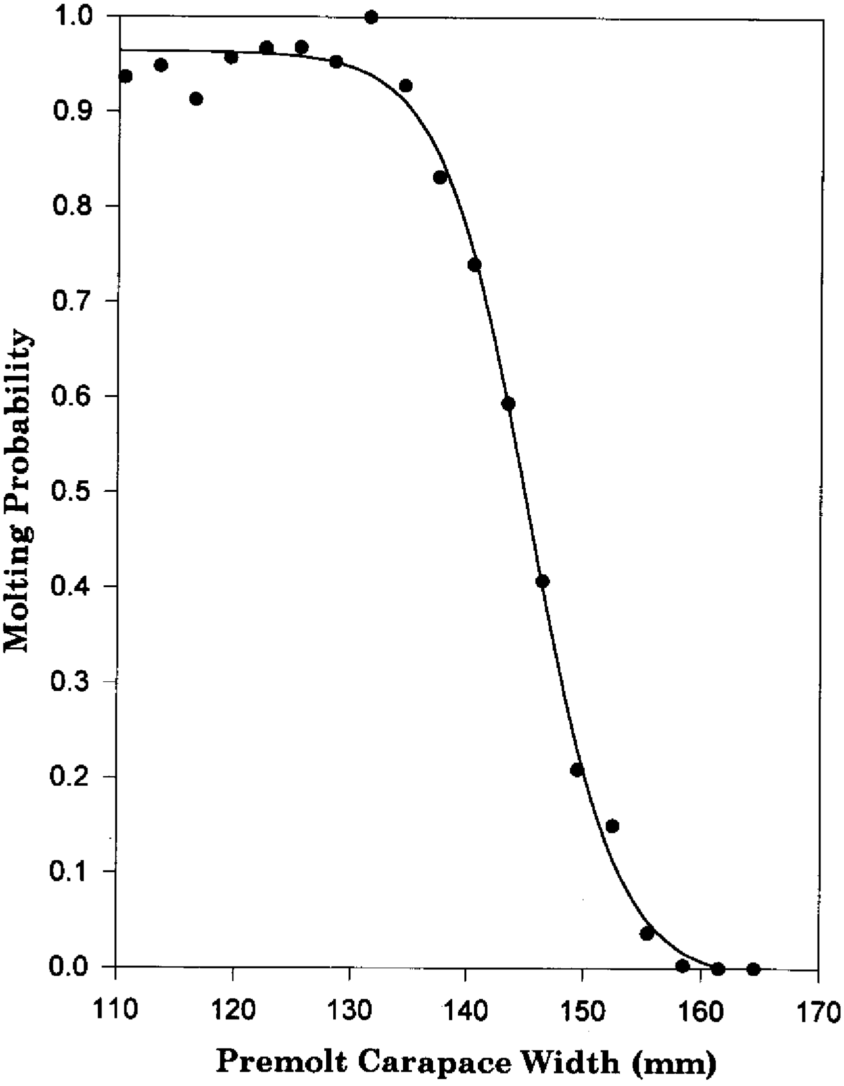

Figure 4. Estimated size-specific molting probabilities of adult female Dungeness crabs in northern California based on application of the complete methods of Mohr and Hankin (1989) to shell condition data displayed in Figure 1. Smooth curve is a fitted logistic model.

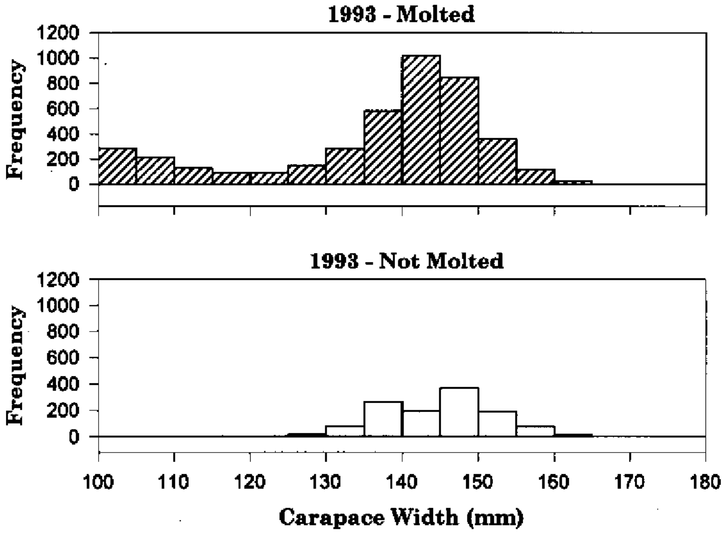

Figure 5. Size frequencies of molted and not molted adult female Dungeness crabs sampled near Trinidad, California, June-July 1993, based on shell condition observations.

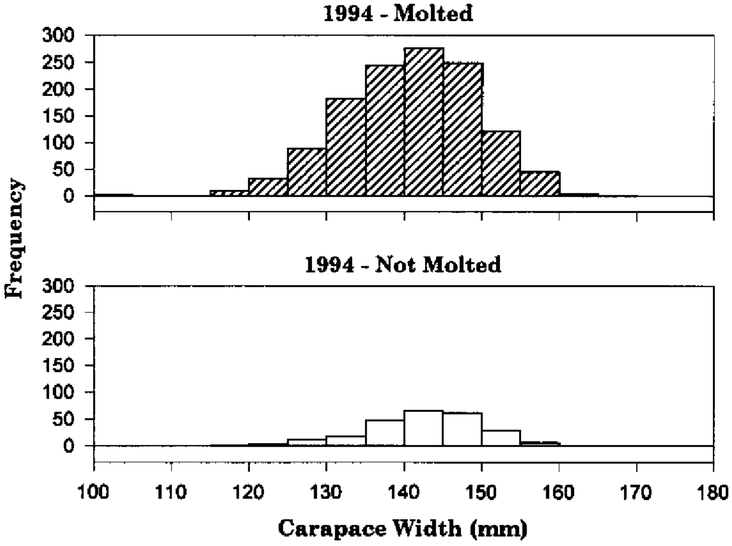

Figure 6. Size frequencies of molted and not molted adult female Dungeness crabs sampled near Trinidad, California, June-July 1994, based on shell condition observations.

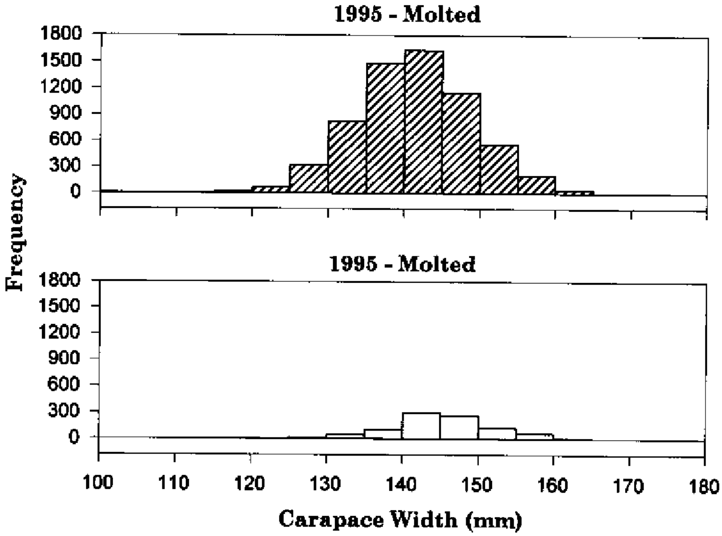

Figure 7. Size frequencies of molted and not molted adult female Dungeness crabs sampled near Trinidad, California, June-July 1995, based on shell condition observations.

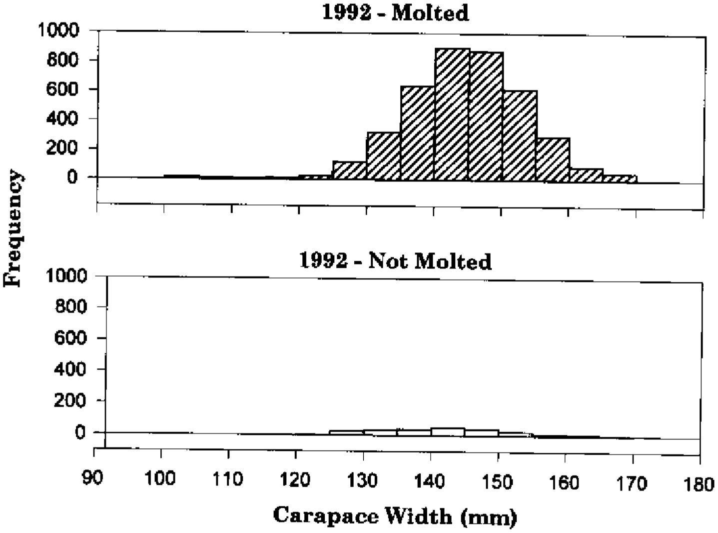

Figure 8. Size frequencies of molted and not molted adult female Dungeness crabs sampled near Trinidad, California, June-July 1992, based on shell condition observations.

Table 1. Summary statistics for fitted linear regressions of premolt carapace widths (Y) against postmolt carapace widths (X) for adult female Dungeness crabs in northern California.

Year	Sample size	Intercept	Slope	R^2
1981	102	–16.4594	1.0178	0.9453
1982	144	–31.1225	1.1111	0.9504
1992	178	–29.0725	1.1023	0.9725
1993	86	–36.5341	1.1635	0.9784
1995	155	–9.8010	0.9620	0.8824

Based on tag recovery data (1981, 1982) and/or laboratory generated molt increments (1981, 1982, 1992, 1993, 1995).

Balsiger (1974) and later McCaughran and Powell (1977) also proposed that size-specific molting probabilities were conditioned on prior molting history: crabs that had previously failed to molt had greater size-specific molting probabilities than those that had molted during the most recent molting season. Fogarty (1986) presented evidence that annual molting probabilities declined with increasing CW of male and female American lobsters and he investigated the possible effects of temperature on fishery yields, in part through alteration of molting probabilities.

For female Dungeness crabs in northern California, it appears that interannual variation in size-specific molting probabilities must make a larger contribution to interannual variation in size at age than does interannual variation in size-specific molt increments. Premolt CW could be accurately predicted from postmolt CW in each of five years, and interannual variation in location of regression lines (and therefore in size-specific molt increments) was relatively small. In contrast, interannual variation in size-specific molting probabilities appears large. Although size-specific molting probabilities of adult female Dungeness crabs appear to "typically" exhibit a strong size-dependent decline from approximately 100% at CW < 130-135 mm to approximately 0% at CW > 155 mm, it is nevertheless apparent that almost all females molted during 1992. This suggests to us that some key environmental variable may have caused unusual levels of molting during that year.

Based on published literature, the single environmental variable that seems most likely responsible for observed variation in size-specific molting probabilities appears to be water temperature (Caddy 1987, Justo et al. 1991). Unfortunately, the number of years for which we have estimates of size-specific molting probabilities is still too short (5 years total) to justify examination of any correlations between size-specific molting probabilities and environmental variates. Until we have a longer

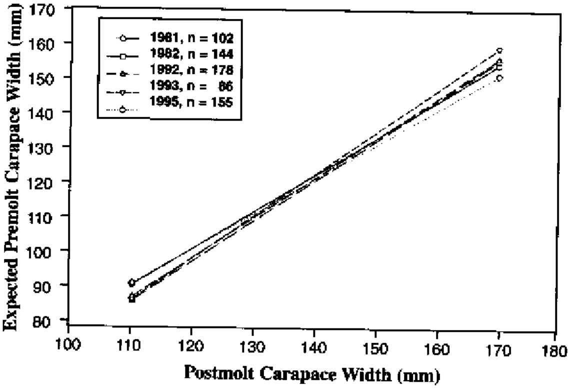

Figure 9. Fitted premolt-postmolt CW regression lines for adult female Dungeness crabs near Trinidad, California, in 1981, 1982, 1992, 1993, and 1995. Sample sizes for regressions are indicated on figure.

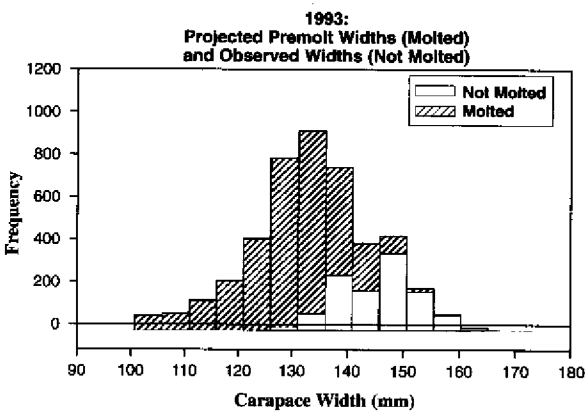

Figure 10. Reconstructed premolt size frequencies of crabs destined to molt superimposed on size frequencies of crabs that were not molted based on postmolt shell condition observations collected near Trinidad, California, June-July 1993. For Figures 10-13, premolt sizes are predicted from a regression of premolt CW against postmolt CW. No adjustments are made for the possibility that survival rates for molting crabs may be less than those for nonmolting crabs.

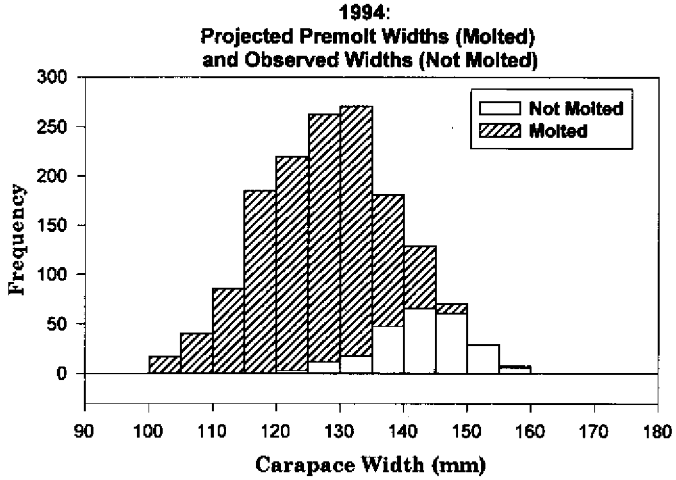

Figure 11. Reconstructed premolt size frequencies of crabs destined to molt superimposed on size frequencies of crabs that were not molted based on postmolt shell condition observations collected near Trinidad, California, June-July 1994.

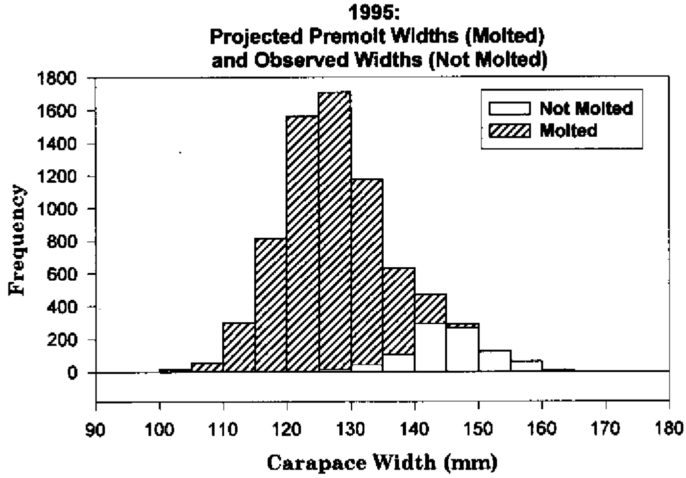

Figure 12. Reconstructed premolt size frequencies of crabs destined to molt superimposed on size frequencies of crabs that were not molted based on postmolt shell condition observations collected near Trinidad, California, June-July 1995.

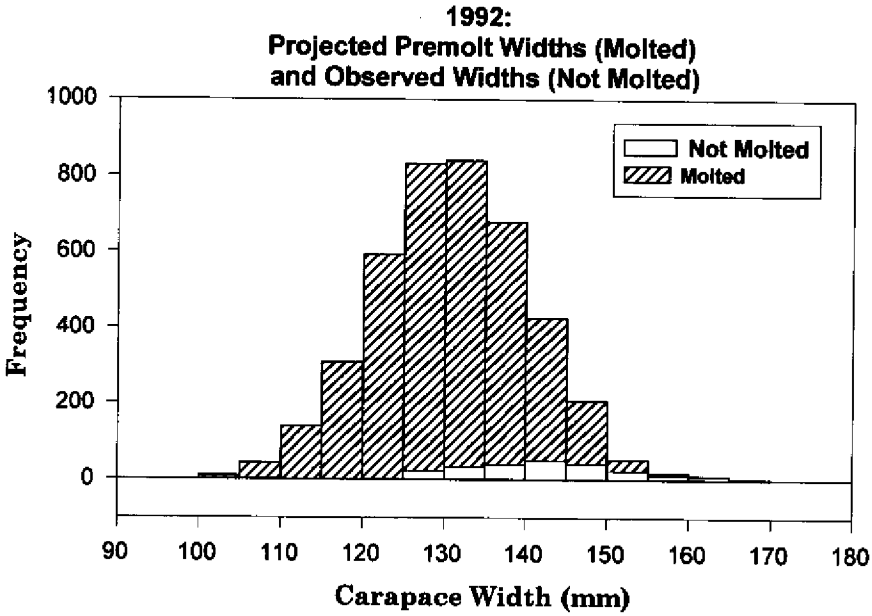

Figure 13. Reconstructed premolt size frequencies of crabs destined to molt superimposed on size frequencies of crabs that were not molted based on postmolt shell condition observations collected near Trinidad, California, June-July 1992.

time series of molting probability estimates, we will resist the temptation to speculate.

Although postseason indicator methods in principle allow estimation of size-specific molting probabilities, the methods of Mohr and Hankin (1989) do require specification of the ratio of survival rates through the molting season for molting as compared to nonmolting crabs. Because softshell crabs are more vulnerable to predation than hardshell crabs, it is reasonable to assume that this ratio has a value less than one. For the very largest adult female Dungeness crabs that may be close to physiological senescence, it is not inconceivable that survival rates through molting are extremely low. If this were the case, then postseason estimates of molting probabilities, based on assumed ratios, could be seriously biased due to the discrepancy between true and assumed survival ratios. In the most extreme situation, for example, if a large fraction of all females > 155 mm CW molted but all such females died while molting, no larger molted crabs would be observed and estimated size-specific molting probabilities would be zero for crabs > 155 mm CW.

In our current research we propose to develop a reliable premolt indicator of molting in female Dungeness crabs. Classical molt staging methods developed by Drach (1939) have been applied previously to various mouth parts of commercially important crustaceans (e.g., Moriyasu and Mallet 1986, O'Halloran and O'Dor 1988—snow crab, *Chionoecetes opilio*), but there are no published accounts of application of such methods to female Dungeness crabs. The most promising structure for use as a premolt indicator in Dungeness crab appears to be the branchial epipod of the first maxilliped (Armand Kuris, Univ. Calif., Santa Barbara, CA, pers. comm.).

If we are successful in our attempt to develop reliable molt staging methods for female Dungeness crabs, then we will estimate size-specific molting probabilities from samples of crabs collected prior to the molting seasons in 1996 and 1997. From such sample data, estimates of size-specific molting probabilities may be easily calculated as the fraction of crabs within a given CW interval exhibiting late premolt molt stages (D_0 or perhaps D_1 through D_4). Comparison of the preseason estimates of size-specific molting probabilities with corresponding postseason estimates in principle allows estimation of the unknown survival ratios of molting as compared to nonmolting crabs (Mohr and Hankin 1989, Appendix B, p. 1830). Finally, in collaboration with E. Chang, Univ. Calif., Davis, CA, we are currently exploring the possible connections between size-dependent declines in molting probabilities and production of molting hormones.

Acknowledgments

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High Latitude Crabs: Biology, Management, and Economics
Alaska Sea Grant College Program • AK-SG-96-02, 1996

Reproductive Conditions, Fecundity, and Size at Maturity for the Arctic Lyre Crab *(Hyas coarctatus)* in the Eastern Bering Sea

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Abstract

The arctic lyre crab *(Hyas coarctatus)* is common throughout the eastern Bering Sea and many shallow water marine habitats, but very little literature exists for this species. Eight hundred ninety-five crabs of both sexes and various maturity conditions were collected during the National Marine Fisheries Service trawl surveys in 1992, with another 132 collected in 1993 for additional fecundity studies. Carapace lengths and shell conditions were recorded on all crabs, and chela heights were recorded for males. Measurements of the fifth abdominal segment, egg condition, and clutch size were recorded for females. Clutches were removed from females with newly extruded, uneyed eggs for fecundity determination. Using a computer program developed by Somerton (1980) the size at 50% maturity for males was estimated to be 49.8 mm. In our sample 53% of the mature individuals above 55 mm had new shells indicating that most of the mature males had recently molted to maturity. Mean size at maturity for females is 39.7 mm. Fecundity ranged from 692 to 44,148 eggs and is strongly correlated with size, but oldshell females exhibit a wider range of fecundity. Oldshell females produce 60% more eggs than newshells of similar size; predicted fecundity for an average-sized female is 8,615 (newshell) or 13,757 (oldshell). Evidence suggests a biennial reproductive cycle for a portion of this population.

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Changes in Carapace and Chela Measurements of Functionally Mature Male *Chionoecetes bairdi* Held in the Laboratory

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Abstract

Laboratory observations with functionally mature male *Chionoecetes bairdi* proved that they can molt. Forty-six males with carapace widths (CW) < 119 mm copulated with primiparous mates in the laboratory and then molted. Seventeen males 110 to 139 mm CW copulated with multiparous females in the laboratory and then molted. This report provides the measurements of initial and postmolt carapace width and chela height so other researchers can have access to the data.

Introduction

The ability of functionally mature males of the genus *Chionoecetes* to molt, and the relationship of chela size to maturity, are topics about which there has been much recent discussion (Paul and Paul, in press). Conan and Comeau (1986) concluded that to be mature, male *C. opilio* required "a special molt, which coincides with the differentiation of the claw for grabbing the female."

Our observations on Tanner crab (Paul and Paul 1995) show males do not have to be in a terminal instar, or reach their maximum claw size, to be functionally mature. Those experiments were designed to determine if functionally mature male *C. bairdi* could molt, to identify the changes in chela height (CH) and CW if growth occurred. This data report provides the measurements of initial and postmolt carapace width and chela height.

Materials and Methods

Males with multiparous mates

Males found grasping multiparous mates in nature are typically > 110 mm CW (Stevens et al. 1993). Males of this size were captured with a small otter trawl, fished at 30 to 60 m depth in Kachemak Bay, lower Cook Inlet. These males were transferred directly to the Seward Marine Center laboratory. Seventeen males with CW 110-139 mm from this area copulated with multiparous mates in the laboratory and later molted. Their CW and CH measurements were taken to the nearest millimeter.

Male crabs were held communally in running seawater tanks (1 m × 4 m × 0.5 m deep) with a water exchange rate > 100% per hour. There were 11 or 12 crabs per tank. The intake for the seawater is at a depth of 80 m, well below the 20 m summer pycnocline in the fjord. Thus, the laboratory had a temperature and salinity regime suitable for holding crabs. Salinity ranged between 31 and 34 ppt and the seawater temperature range was 4-9°C. All captive crabs were fed twice per week, primarily chopped Pacific herring (*Clupea harengus pallasi*) and other fish species.

Males with primiparous mates

In the laboratory, we made 46 observations of growth in CW and CH in male Tanner crab that copulated with primiparous mates. All the crabs in this experiment with primiparous females were trawled near Homer, Alaska, in 30 to 60 m of water. This information was gathered over several years. The thermal and salinity records under which they were held were not available.

Results and Discussion

The premolt and postmolt measurements of CW and CH for the 15 males that molted after copulating with multiparous mates is listed in Table 1. The CW and CH measurements for the small mature males that fertilized primiparous mates is listed in Table 2.

In situ observations noted that most male *C. bairdi* grasping multiparous mates had CH/CW ratios > 0.17 and their CH > 17 mm (Stevens et al. 1993). The researchers concluded that a *C. bairdi* male with measurements equal to or greater than these values was "morphometrically mature" (Stevens et al. 1993). In the laboratory some crabs that copulated with multiparous mates and then molted had initial CH\CW ratios > 0.17 and 100% had CH > 17 mm. Thus, by the criterion set forth by Stevens et al. (1993) which assigns morphometric maturity to males with CH/CW ratios > 0.17, it appears "morphometrically mature" males molt. However, it could be argued that using the ratio of CH/CW is not a valid method to assign morphometric maturity; rather models of CH vs. CW should be used. Data on the relationship between CH and CW for males

Table 1. Changes in carapace width and chela height of male *Chionoecetes bairdi* that had copulated with multiparous mates and later molted (mm).

Initial carapace width	Postmolt carapace width	Initial chela height	Postmolt chela height
110	132	18	25
119	134	21	26
123	143	20	31
125	146	25	35
126	147	30	34
126	147	24	34
129	152	21	33
130	150	30	38
131	149	21	31
132	159	24	40
134	156	28	37
134	155	29	37
134	159	21	35
135	158	27	30
139	162	31	40
123	143	20	31
119	134	21	26

Table 2. **Changes in carapace width and chela height of male *Chionoecetes bairdi* that had copulated with primiparous mates and later molted (mm).**

Initial carapace width	Postmolt carapace width	Initial chela height	Postmolt chela height
54	65	7	8
55	66	7	9
57	68	7	9
59	71	9	10
59	71	9	10
59	70	8	10
59	70	7	9
60	72	9	10
61	73	9	10
62	74	9	10
64	76	9	11
65	77	8	11
70	83	9	12
73	86	10	12
75	89	11	12
82	100	11	14
84	104	11	20
84	102	12	15
86	105	12	19
86	104	12	15
86	105	12	17
88	104	12	16
89	109	12	18
91	119	12	21
92	109	12	16
94	114	14	20
97	118	14	24

Table 2. (Continued.)

Initial carapace width	Postmolt carapace width	Initial chela height	Postmolt chela height
98	112	15	18
98	112	15	18
100	116	15	21
100	115	15	20
100	124	16	23
101	116	15	21
104	127	15	22
104	111	15	20
104	126	16	25
105	125	16	22
105	128	17	27
105	121	15	23
106	122	15	23
109	130	16	22
110	132	18	25
110	132	16	25
112	131	19	25
118	130	18	26
119	134	21	26

from the Cook Inlet study area needs to be gathered prior to making this determination. Currently, only CW measurements are available for males from Cook Inlet. This data report has been prepared so some new CH growth data would be available to researchers interested in studying molting and morphometric maturity.

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High Latitude Crabs: Biology, Management, and Economics
Alaska Sea Grant College Program • AK-SG-96-02, 1996

Recruitment Variability in Snow Crab *(Chionoecetes opilio)*: Pattern, Possible Causes, and Implications for Fishery Management

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Abstract

An exploited, coastal population of *Chionoecetes opilio* in the northwest Gulf of Saint Lawrence has been monitored annually since 1988 to resolve the nature of recruitment variability. The beam trawl used to sample the population retains all benthic growth stages and has provided a clear picture of recruitment patterns. Our time series and prior historical data indicate that the population alternates groups of strong and weak year classes, which recur approximately every 8 years. Each year class impacts the spring fishery about a decade after settlement, which represents the minimum time to grow to the legal size of 95 mm carapace width and harden after molting. Year-class strength is determined soon in ontogeny, suggesting that settlement intensity and/or early survivorship are critical. The cycle is apparently endogenous and may result primarily from negative, density-dependent interactions between a settling age class and age classes established in the preceding 6 years. Cycles cause striking changes in population features, due to the existence of a terminal molt to adulthood for both females and males, to marked intrasexual differences in size/age for recruitment to adulthood, and to limited life expectancy after terminal molt. The size, condition, and maturity composition of both sexes are affected, and marked

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fluctuations occur in adult sex ratio and female spawning biomass. Cycles may be reflected in the fishery by periodic shifts in the maturity and size composition of legal-sized males and in catch rates and landings. The implications of endogenous population cycling for the resource and for fishery management are discussed.

Introduction

The fishery

Snow crab (*Chionoecetes opilio*) has been fished commercially in eastern Canada since the late 1960s (Elner and Bailey 1986, Bailey and Elner 1989). The *C. opilio* fishery has expanded into a major exploitation, with 1995 landings of ≈ 60,000 metric tons valued at ≈ 325 million U.S. dollars (J. Boucher, Division des services économiques, Ministère des Pêches et des Océans, Québec, pers. comm.). Fishery management is based on resource conservation and catch allocation measures (Miller 1976, Elner and Bailey 1986). Important conservation measures that have been enacted over the years are the prohibition to land females, a minimum size of 95 mm carapace width (CW), a provision to close the fishery when the quantity of soft-shelled crabs becomes too high, and total allowable catches (TACs).

Since the fishery's inception, catch rates and landings of *C. opilio* in the Gulf of Saint Lawrence have fluctuated markedly over time, following a pattern described as "boom and bust" (Hare and Dunn 1993). After an initial exploratory phase from 1965 to 1975, the overall trend was one of (1) increasing catch rates and landings until 1982, (2) high catch rates and landings from 1983-1986, (3) a fishery collapse from 1987-1990 in the southwest Gulf and from 1988-1989 in the north Gulf, followed by (4) an increase in catch rates and landings until 1994 (Chiasson et al. 1992, Hare and Dunn 1993, Dufour 1995). The 1976-1982 increase in landings has been attributed to fishery expansion and increased effort and efficiency (Chiasson et al. 1992), while the precipitous decline in catch rates and landings in 1987-1990 has been attributed to overfishing (Jamieson and McKone 1987, Hare and Dunn 1993, Jamieson 1993).

The *C. opilio* fishery collapse prompted major research efforts in the southwest and north Gulf of Saint Lawrence (Science Branch 1995, Camirand in press). In the north Gulf, a multidisciplinary research program entitled GROCRABE (a French acronym for Genetics, Reproduction and Ontogeny of Snow Crab) was initiated at the Maurice Lamontagne Institute in 1989. The program's goal was to improve knowledge of growth, reproduction, and interannual recruitment variability for *C. opilio*, and to develop the tools necessary for short- and long-term forecasts of population trends, in order to implement management strategies which might promote stock recovery plus biological and economic stability.

Growth and reproduction

A deeper appreciation of growth and maturation processes in *C. opilio* has emerged through these research efforts. In males, complete maturation occurs in three successive developmental stages (Comeau and Conan 1992), which we term immature, adolescent, and adult (Sainte-Marie et al. 1995). Immature males are physiologically immature; adolescent males are physiologically mature but have undifferentiated chelae; and adult males have acquired all primary and secondary sexual characters including differentiated chelae. Other investigators have used the terms "small-clawed," "morphometrically immature," or "juvenile" to designate immature and/or adolescent males, and "large-clawed," "morphometrically mature," or "mature" to designate adult males. The passage from the adolescent to the adult stage occurs at a terminal molt (O'Halloran 1985, Conan and Comeau 1986, Yamasaki and Kuwahara 1991, Sainte-Marie and Hazel 1992, Sainte-Marie et al. 1995). Adult males belong to one of six post-settlement instars (IX to XIV) and may vary in size from 40 mm to 162 mm CW (Sainte-Marie et al. 1995, Sainte-Marie unpubl. data). Thus, only a fraction of immature males in a population eventually reaches the legal size of 95 mm CW and recruits to the fishery. Carapace aging by radioisotopes suggests that males do not survive for more than 4 years after terminal molt (Comeau et al. 1991), but an ongoing tag-recapture study of a commercially unexploited population indicates that longevity may reach 5-6 years (Sainte-Marie and Dufour 1994, Sainte-Marie unpubl. data). It has been estimated that the hard-shelled adult males with clean or lightly fouled carapaces which are exploited in spring fisheries are mainly 1-3 years postmolt age; thereafter, the appearance, overall condition, and catchability of males deteriorate rapidly and they may be lost for the fishery or retain little market value (Sainte-Marie and Dufour 1994).

Female *C. opilio* follow a growth-maturation trajectory similar to that of males, and can be separated into immature, maturing, and adult stages (Alunno-Bruscia 1993). Females undergo a terminal molt before becoming reproductively active (Watson 1972). Adult females vary in size from 39 mm to 85 mm (and exceptionally to 95 mm) CW, and according to Alunno-Bruscia (1993) belong to one of three post-settlement instars (IX to XI). For coastal populations, the maturity molt and first mating of females occur in shallow waters from January to April, while multiparous females may re-mate in shallow to deep waters from April to the end of June (Moriyasu et al. 1987, Ennis et al. 1990, Sainte-Marie and Hazel 1992, Lovrich et al. 1995). Recent studies have revealed the intricacies and plasticity of *C. opilio* mating, which involve both adolescent and adult males (Elner and Beninger 1995, Sainte-Marie et al. in press). Ovaries and egg clutches of adult females may develop synchronously over a period of one (Watson 1969) or two (Kanno 1987, Sainte-Marie 1993) years, probably depending on temperature (Mallet et al. 1993). Eggs of primiparous females (first spawning) are ≈ 23% fewer per clutch, but are ≈ 3% larger each, than those of similar-size multiparous females (Sainte-Marie 1993).

Chionoecetes opilio larvae hatch mainly from May to June and develop in the plankton for 3-5 months, settling between late August and the end of October (Robichaud et al. 1989, Conan et al. 1992, Lovrich et al. 1995). Subsequently, the molting frequency of *C. opilio* is approximately semiannual for instars I (≈ 3.2 mm CW) through V (≈ 14 mm CW) and generally annual for larger immature and adolescent males, as well as for larger immature and maturing females (Alunno-Bruscia 1993, Sainte-Marie et al. 1995). The intermolt period for some adolescent males may extend to 2-3 years (Comeau et al. 1991, Sainte-Marie et al. 1995), but the prevalence and causes of this phenomenon remain undetermined. In the north Gulf, males that reach the legal size are at least 8.7 years of post-settlement age, and another year must elapse before they fully recruit to spring fisheries (Sainte-Marie et al. 1995). Adult females are at least 5.7-7.7 years of post-settlement age (Alunno-Bruscia 1993).

Research into recruitment patterns

In 1989, as part of the GROCRABE research program, annual monitoring was initiated for the *C. opilio* population in Baie Sainte-Marguerite, northwest Gulf of Saint Lawrence, to evaluate the magnitude and causes of interannual changes in recruitment. The Baie Sainte-Marguerite population has been exploited continuously since 1977 and in recent years has sustained some of the highest yields per unit area of the north Gulf of Saint Lawrence (Sainte-Marie 1993). Fortuitously, Baie Sainte-Marguerite and surrounding localities were targeted by sporadic but intensive fisheries as early as 1968 and by research surveys as early as 1980 (Lafleur et al. 1984, Brêthes et al. 1987), so prior historical information exists on the fishery and population size structure. In this paper, we describe temporal changes in the abundance, size structure, and maturity composition of *C. opilio* in Baie Sainte-Marguerite and relate these to fishery performance. Recent and historical data suggest that recruitment to population and fishery have followed an ≈ 8-year cycle over the past 25 years. We briefly discuss the possible causes of cyclic recruitment and emphasize its implications for the *C. opilio* resource and fishery.

Materials and Methods

The corpus of data used in this study comes from an annual beam trawl survey of the *C. opilio* population in Baie Sainte-Marguerite (approximately 50°06′N, 66°35′W). Information on the study site, sampling and sorting procedures, measurements, determination of maturity for males and females, and general terminology is provided in Sainte-Marie (1993) and Sainte-Marie et al. (1995). Briefly, in late April or early May of each year since 1989, three or more randomly selected sites were sampled in each of three depth strata, shallow (4-20 m), intermediate (20-80 m), and deep (80-140 m). In 1988 sampling was conducted during late March only in the shallow depth stratum. Sampling was also carried out in October 1991, 1993, and 1994, but it did not follow the regular depth-stratified sampling scheme. Crabs were collected with a 3-m beam trawl fitted with heavy tickler chains to dislodge buried animals and with 15-mm mesh netting in the codend. Crabs < 10-15 mm CW were retained once the mesh became occluded with debris and organisms. Tows lasted 5-20 min at 2.5-3 m/s and positions at start and end of tow were recorded to determine the surface area sampled by the trawl. Size frequency data were also available for *C. opilio* in the Rivière-au-Tonnerre district, neighboring Baie Sainte-Marguerite, from a trawl and a dredge survey conducted in July 1982 (Brêthes et al. 1987) and July 1986 (Réjean Dufour, Institut Maurice-Lamontagne, unpubl. data), respectively.

The quality and quantity of information derived from samples of *C. opilio* changed over time. In all years, individuals were sexed on the basis of abdomen shape, except those < 6-7 mm CW which were recorded of indeterminate sex since they could not be determined by visual examination alone. From 1982 to 1988 the CW of all crabs was measured to the nearest 1 mm using a modified vernier caliper, and chela height was measured for males in 1986. After 1988, the CW of all crabs and the chela height of males were measured to the nearest 0.1 mm using a non-modified vernier caliper. Starting in 1991, exoskeleton condition was scored 1 (clean-soft), 2 (clean-hard), 3 (intermediate), 4 (dirty-hard) or 5 (dirty-soft) according to criteria in Sainte-Marie (1993). These scores reflect progressive change and deterioration of the exoskeleton with time elapsed since the last molt (Sainte-Marie and Dufour 1994). In 1986 and 1989-1995, males > 35 mm CW were classified as adolescent or adult using CH and CW measurements and a site-appropriate discriminant function (Sainte-Marie and Hazel 1992). Similarly, females were classified as immature/maturing or adult on the basis of the relative width of their abdomen. Starting in 1991, adult females were designated primiparous or multiparous based on exoskeleton condition and presence of mating scars. Primiparous females had a clean-soft, clean-hard, or intermediate exoskeleton, usually had no or only faint mating scars, and usually carried eggs. Multiparous females had an intermediate, dirty-hard, or dirty-soft exoskeleton, usually had conspicuous mating scars, and usually carried eggs. The abdomens of adult females were examined for the presence of eggs or egg remains, which we classified either as orange eggs, dark-orange eggs with developing eyespots, purple eggs with well developed eyes (i.e., nearly ready to hatch), degenerating eggs, or egg shells (Sainte-Marie 1993).

Size frequency distributions based on $\log_{10}$ CW were derived for *C. opilio* in each tow sample from the 1989-1995 spring temporal series, standardized to a constant surface area, and then combined by year to produce an overall size frequency distribution that was weighted for sampling effort and total surface for each depth stratum. The resulting histograms represent the number of million crabs per size class of 0.02 log units and are directly comparable across years. Calculation of mean CW and mean exoskeleton condition was based on weighted frequency distributions for CW and exoskeleton condition. Pre-1989 surveys were qualitative and resulting distributions of $\log_{10}$ CW are presented as the smoothed frequency of crabs per size class of 0.02 log units. Analyses usually excluded *C. opilio* of instars I and II ($\leq$ 5.6 mm CW) as trawl samples may misrepresent their abundance.

The operational sex ratio (Emlen and Oring 1977) was calculated as the quotient of abundance of either primiparous or multiparous females on abundance of adult males. Multiparous females were considered only when they carried purple eggs or egg shells, because only those females would be susceptible to mate in a given year after the spring survey. Adult males with clean-soft exoskeletons were excluded from calculation of sex ratio since they reportedly do not participate in mating (Moriyasu and Conan 1988). Separation of the two adult female types for calculation of operational sex ratio is justified by temporal segregation of breeding for each female type (Moriyasu et al. 1987, Sainte-Marie 1993) and hence, lack of direct competition for male mates. However, the resulting operational sex ratios are probably slanted in favor of males because breeding of pubescent-primiparous and multiparous females occurs on separate and distant grounds (Sainte-Marie and Hazel 1992, Lovrich et al. 1995), so in effect not all adult males are available to mate with both types of adult females.

Catch rate and size structure for *C. opilio* in the commercial fishery were obtained from logbooks for Baie Sainte-Marguerite or for a larger management area (zone 16) including our study site. A catch rate was derived for each of the two most widely used traps (small conical and large rectangular) by computing the mean of the quotients of known catch on known effort over the 31 March to 31 July period for soak times of 1, 2, and 3 days. Total fishing effort with each trap type varied among years, but over the 1986-1995 period for which reliable data were available, the two trap types together caught $\approx$ 83.1% of *C. opilio*. Interannual trends in catch rate for individual trap types were similar, but we present below only the average of the mean catch rate for each trap type with missing values in years when both traps were not used.

Results

Population dynamics

Conspicuous modes were apparent in the size frequency distributions of *C. opilio* in all years (Figures 1, 2, and 3). For figures 1 and 2, size frequencies for non-quantitative surveys conducted from 1982 to 1988 and for quantitative surveys conducted from 1989 to 1995 are presented respectively as the relative frequency of crabs and absolute abundance of crabs per size classes of 0.02 units of $\log_{10}$ CW. Numbers beneath modes represent year classes, occasional numbers above modes represent maximum frequency or abundance, and the vertical dashed line represents the minimum legal size of 95 mm carapace width.

Modes were more pronounced at smaller than larger sizes, and for pre-adult than adult individuals (Figures 1 and 2). Adult males occurred in at least 5 modes while adult females were concentrated essentially in 1-3 modes, depending on year. For sublegal *C. opilio* we assigned individual modes to an instar and a year class using the growth model in Sainte-Marie et al. (1995), assuming that the fraction of individuals that does not molt annually is negligible. For *C. opilio* < 20 mm CW, modes to which no year class was assigned may be composed of individuals belonging to either or both of the year classes assigned to flanking modes. Obviously, adults from several consecutive year classes may accumulate in a given size class.

There were marked variations in the strength of successive year classes represented in the population from 1989 to 1995. The 1985-1987 year classes were the weakest, each with at least one order of magnitude fewer individuals than each of the year classes in the 1981-1984 and 1988-1992 periods (Figures 1 and 2). The 1988 partial survey of Baie Sainte-Marguerite also showed the 1985-1986 year classes to be weak. The 1982 and 1986 surveys for grounds neighboring Baie Sainte-Marguerite further revealed that the 1977-1979 year classes were relatively weak (Figures 1 and 2). Successive weak year classes form a "recruitment trough," while the interspersed year classes of moderate to strong importance represent a "recruitment wave" (Sainte-Marie and Dufour 1995).

Upon reaching instar VI (≈ 20 mm CW), year classes in both the 1985-1987 trough and 1988-1992 wave progressed toward larger sizes at a tempo of one molt per year (Figures 1 and 2). The spring time series indicated that the strength of a year class with respect to other year classes was established before the end of the second year of benthic life and was subsequently conserved until recruitment to adulthood was initiated. The 1993 and 1994 fall surveys (Figure 3) showing a paucity of *C.*

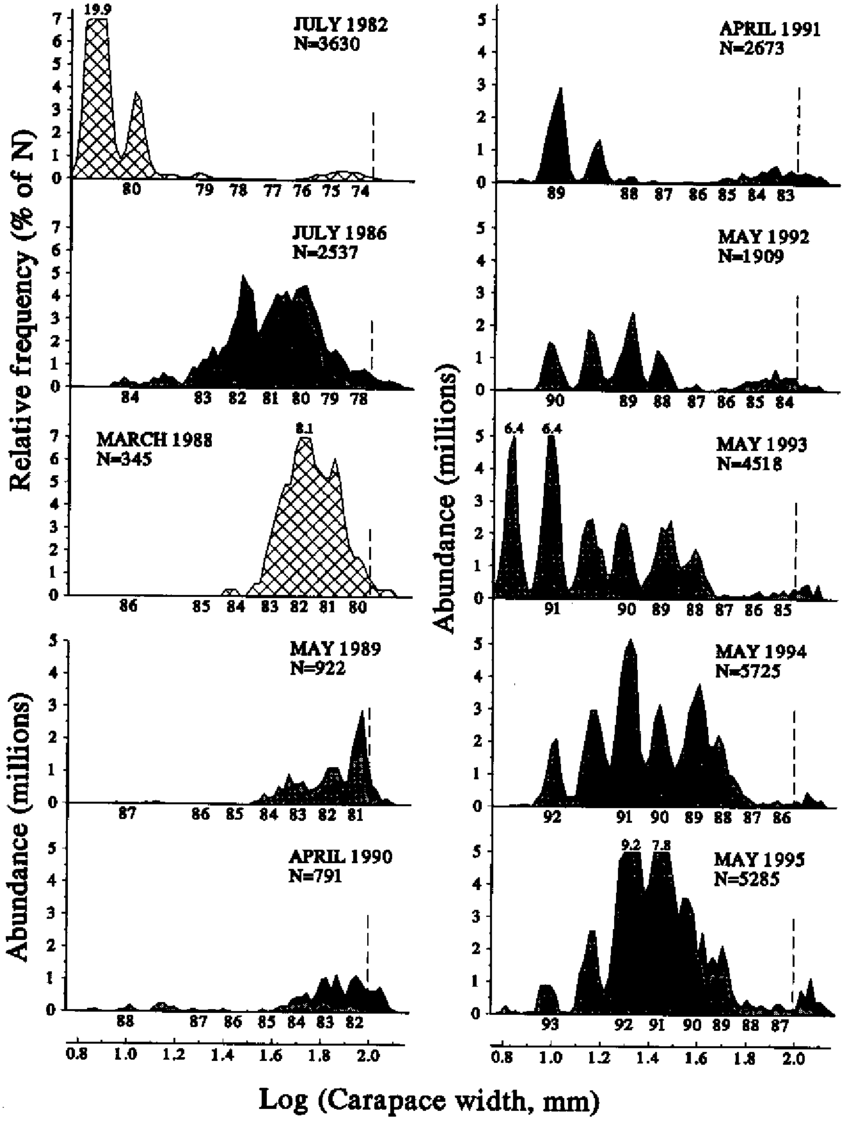


Figure 1. Size structure of male Chionoecetes opilio in the Baie Sainte-Marguerite population from 1988 to 1995 and in the neighboring Rivière-au-Tonnerre population in 1982 (Brêthes et al. 1987) and 1986 (R. Dufour, Institut Maurice-Lamontagne, unpubl. data). Hatched areas represent males of unspecified maturity, gray areas represent immature and adolescent males, and black areas represent adult males. Refer to text for further details.

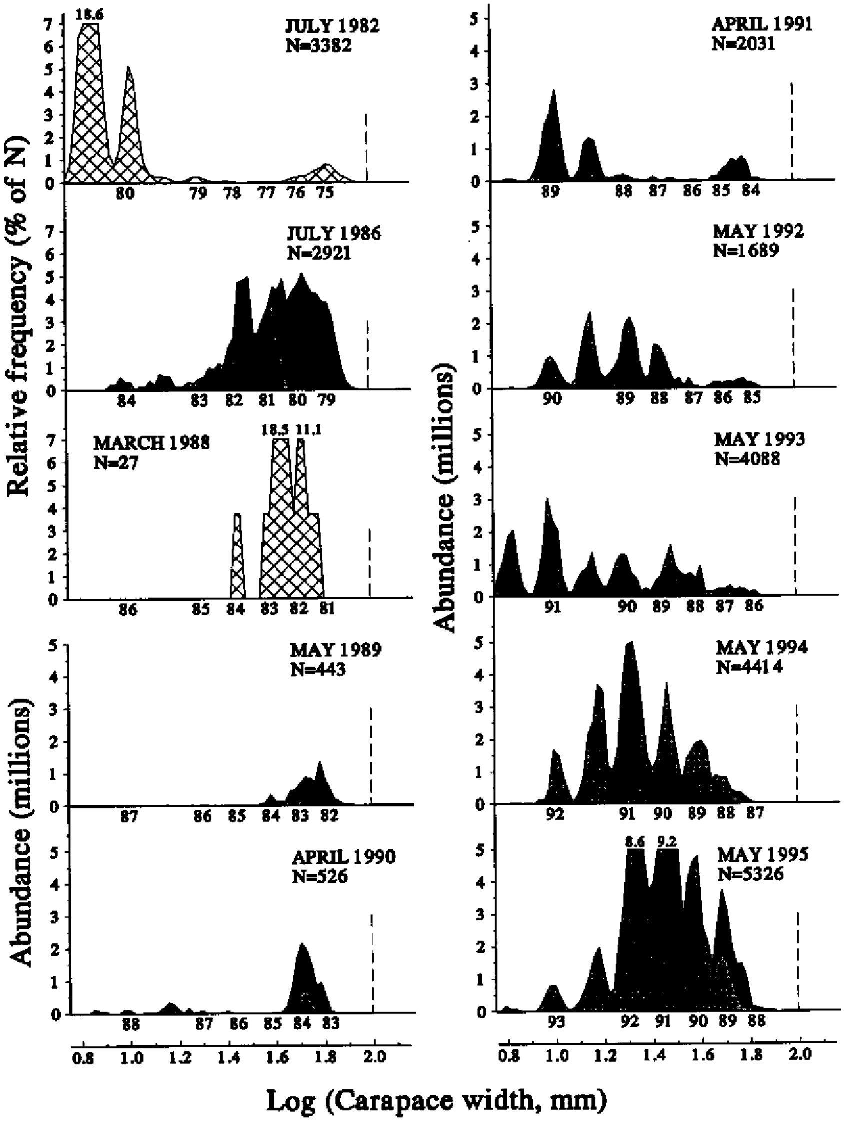


Figure 2. *Size structure of female Chionoecetes opilio in the Baie Sainte-Marguerite population from 1988 to 1995 and in the neighboring Rivière-au-Tonnerre population in 1982 and 1986. Hatched areas represent females of unspecified maturity, gray areas represent immature and maturing females, and black areas represent adult females. Refer to text for further details.*

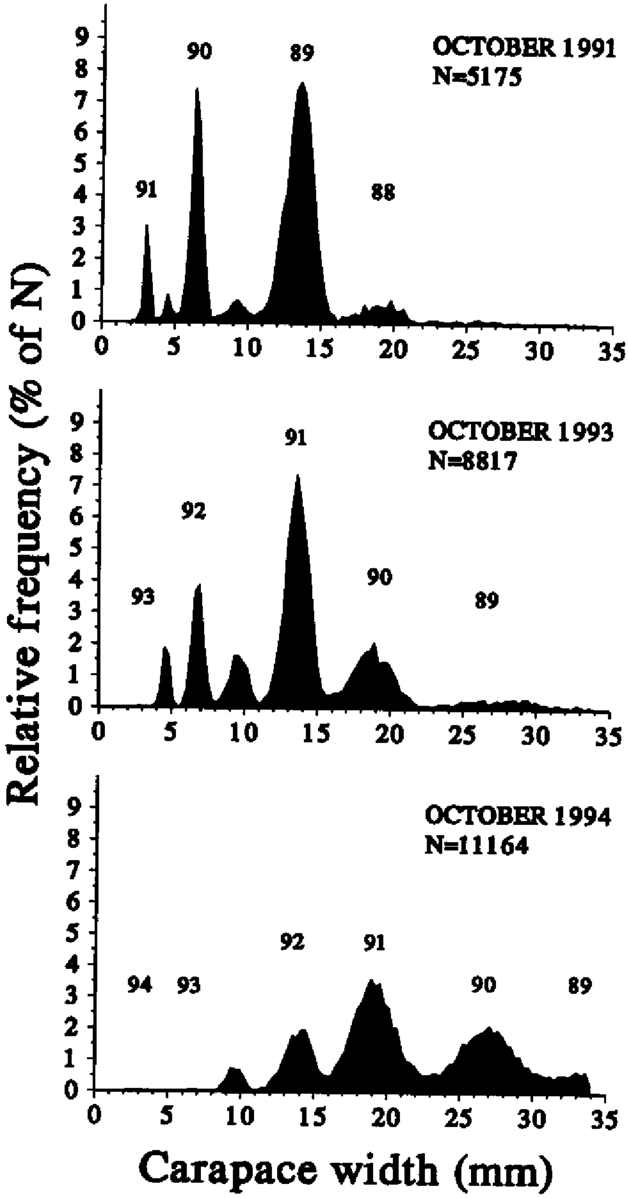


Figure 3. Size structure of combined male and female Chionoecetes opilio ≤ 34 mm carapace width in the Baie Sainte-Marguerite population in October 1991, 1993, and 1994. Size frequencies are presented as the relative frequency of crabs per size class of 0.3 mm carapace width. Numbers above modes represent year classes.

opilio < 4 mm and < 8 mm CW, respectively, suggest that the 1993 and 1994 year classes were also weak and that the relative strength of a year class may be determined before, at, or soon after settlement.

As the 1985-1987 trough progressed toward larger sizes, the composition of the *C. opilio* population changed dramatically with respect to sexual maturity (Figures 1 and 2). Numerical dominance of the population by adult females and adolescent and adult males in 1989-1990 was completely reversed in favor of immature females and males in 1993-1995. The recruitment trough had particularly striking effects on adult females, as their numbers plummeted from 8.3 million in 1990 to 0.9 million in 1994. The decrease in the abundance of adult females can be attributed to die-off from natural mortality, those adult females recruited massively around 1986-1988 (i.e., the strong 1980-1982 year classes) having reached their life expectancy after terminal molt, and to weak recruitment from the 1985-1987 year classes. A reduction in the number of adult males also occurred, from approximately 11.5 million in 1990 to 2.8 million in 1994, but the impact of the 1985-1987 trough was less pronounced due to males recruiting to adulthood over a greater number of instars and over a longer time period than do females. The slight resurgence in adult recruitment that occurred in 1994 was followed by a burst in adult recruitment in 1995, as the first two year classes of the 1988-1992 wave contributed adult females and small adult males.

Recruitment waves and troughs caused the size structure of adult females and males to change over time. The mean CW of multiparous females remained approximately constant from 1991 to 1994, varying between 54.4 mm and 56.1 mm, but decreased to 52.7 mm in 1995 after recruitment of adult females resumed in 1994. The trend was more obvious for primiparous females, whose mean CW decreased from 57.1 mm in 1991 to 50.3 mm in 1995. Mean CW of all adult males was rather constant from 1989 to 1994, but in 1995 it dropped sharply (Figure 4) as recruitment of small adult males resumed. However, over the same time period, there was a regular and significant increase ($r = 0.98$, $P < 0.001$) in the mean CW of legal-sized males (Figure 4).

The condition of populations of adult females and males also changed in response to varying levels of recruitment. The mean exoskeleton condition of adult females deteriorated through the 1991-1993 period of weak recruitment, but ameliorated in 1994 as primiparous females entered the population (Table 1). The process of senescence was most remarkable in multiparous females (Figure 5), many of which were barren or carrying few or degenerating eggs in 1993-1995. Mean exoskeleton condition of adult males < 95 mm CW also changed over the years, decreasing from 1993 to 1995, but variation was more attenuated than that seen in adult females (Table 1). Changes were asynchronous between two arbitrary size classes of sublegal adult males: mean exoskeleton condition peaked at 4.1 in 1992 for those of 40-67.5 mm CW and at 3.6 in 1994 for those of 67.5-95 mm CW. This two-year lag proba-

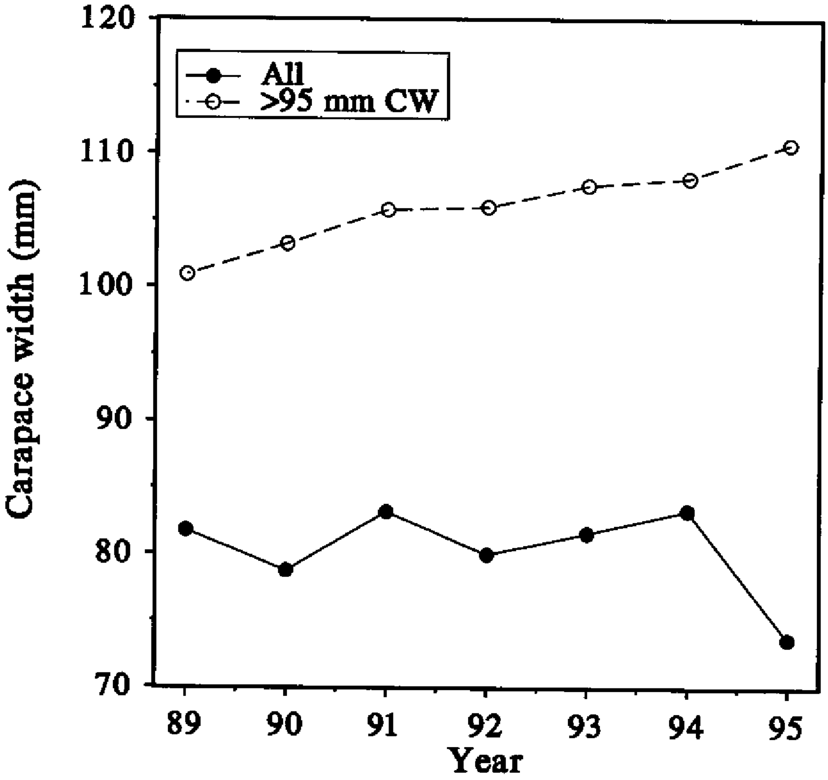


Figure 4. Mean carapace width for adult male Chionoecetes opilio in spring beam trawl surveys conducted in Baie Sainte-Marguerite from 1989 to 1995.

bly reflects the fact that the smaller adult males recruited en masse to the population before the intermediate-sized adult males. The exoskeleton condition of legal-sized adult males was less variable than that of sublegal adult males and adult females, and showed no particular trend, probably due to the fishery removing many terminally molted males before they could age.

Qualitative and quantitative changes in the population of *C. opilio* had at least four effects on reproductive processes. First, the burden of reproduction shifted from young multiparous females in 1991 to primiparous females and senescing multiparous females in 1994-1995 (Table 1, Figure 5). Thus, the conclusion that primiparous females contribute 40% of larvae annually for populations with females having a biannual reproductive cycle (Sainte-Marie 1993), which was implicitly based on

Table 1. Mean exoskeleton condition of adult males and females, ratio of abundance of primiparous to multiparous females, and abundance of adult females hatching larvae for *Chionoecetes opilio* in Baie Sainte-Marguerite from 1991 to 1995.

	Adult males		Adult females		
	Mean exoskeleton condition		Mean exoskeleton condition	Ratio of primiparous to multiparous	Number (millions) producing larvae
Year	< 95 mm	≥ 95 mm			
1991	3.4	3.0	3.2	0.14	1.5
1992	3.5	2.6	3.7	0	0.4
1993	3.4	3.0	3.9	0.03	0.1
1994	2.7	2.8	2.6	2.69	0.2
1995	2.5	2.6	2.3	8.05	0.6

Mean exoskeleton condition: 2 = clean-hard, 3 = intermediate, 4 = dirty-hard.

the assumption that adult female recruitment is constant, must be corrected. It is now clear that the relative contribution to reproduction of both types of adult females cycles over the years, as inferred elsewhere (Sainte-Marie et al. 1995, Elner and Beninger 1995). Second, annual larval production certainly fluctuated extensively and probably was at least one order of magnitude less in 1993-1994 than in 1989-1991, owing mainly to a drastic reduction in the number of adult females contributing to the larval stock (Table 1). The temporal change in the composition of the female breeding stock, from young multiparous (high individual fecundity) in 1991 to primiparous or senescing multiparous (both have lower individual fecundity) in 1993-1994, would also have contributed to reduce larval production even more. In this respect, it is noteworthy that the failure of 1993-1994 year classes coincided with the lowest female spawning stocks recorded over the 1989-1995 period (Table 1, Figure 2). Third, the size composition of males in mating pairs can be inferred to have changed over the years, as has been observed directly in Bonne Bay (Ennis et al. 1990, Comeau et al. 1991, Conan et al. 1992), in relation to the passing of troughs and waves of recruitment. Fourth, marked changes in the operational sex ratio were manifest for both primiparous and multiparous females. However, the pattern of change in the operational sex ratio was dephased for primiparous and multiparous females. For primiparous females the ratio shifted from male- to female-dominated from 1991 to 1995 (Figure 5), while for multiparous females it decreased from 0.85 in 1991 to 0.09 in 1994 and then increased to 0.15 in 1995. Changes in the operational sex ratio and size structure of breeding males imply that the levels of male competition for mates will vary considerably across the years, which may affect

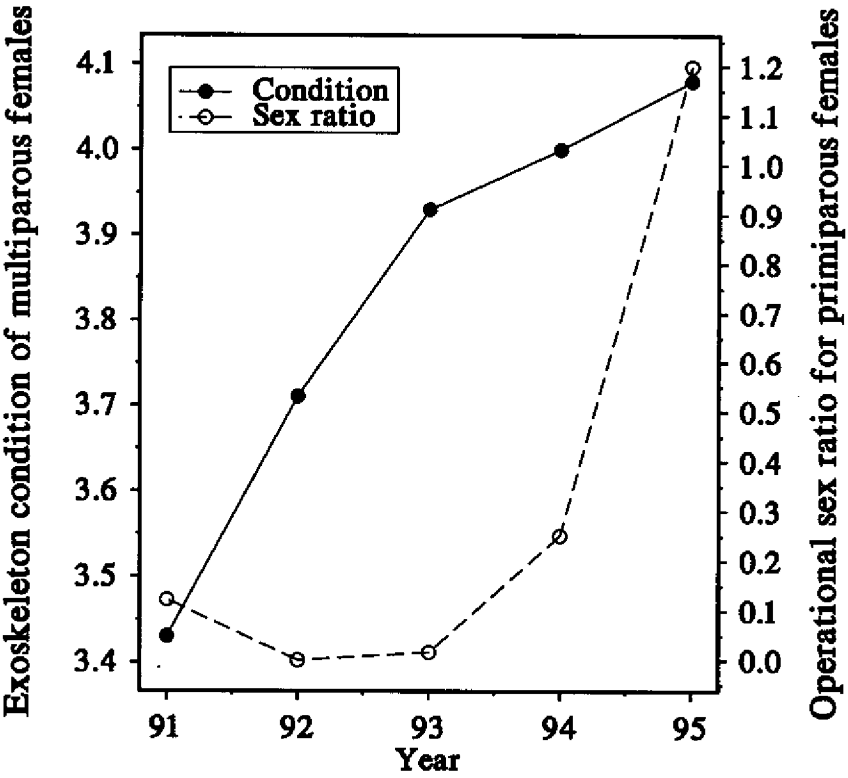


Figure 5. Mean exoskeleton condition (3 = intermediate, 4 = dirty-hard, 5 = dirty-soft) of multiparous females and operational sex ratio for primiparous females (ratio abundance of primiparous females to abundance of adult males excluding those soft-shelled) of Chionoecetes opilio in spring beam trawl surveys conducted in Baie Sainte-Marguerite from 1991 to 1995.

the quantity and quality of sperm that primiparous females can acquire for storage and future use in fertilizing egg clutches (Sainte-Marie and Carrière 1995, Sainte-Marie et al. in press). Over the 1996-1997 period, the predictable rarefication of large adult males, much greater abundance of adolescent and small adult males, and sharply female-biased operational sex ratios, should favor breeding of small adult and adolescent males with primiparous females and increase the proportion of multiparous females relying on stored sperm to fertilize a new clutch of eggs.

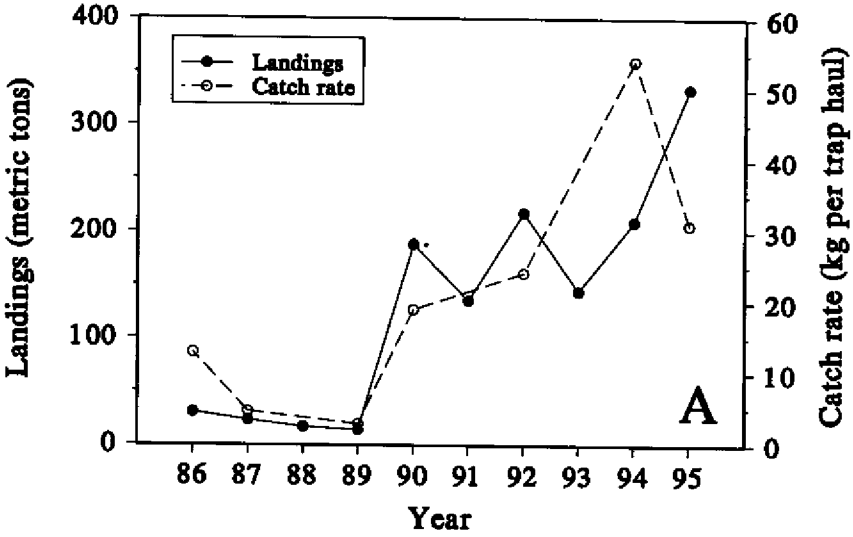
Fishery

Changes in the abundance and size structure of the *C. opilio* population were reflected in the Baie Sainte-Marguerite fishery. The impact of the 1977-1979 recruitment trough on the fishery was record low catch rates, landings, and mean CW from 1987 to 1989 (Figure 6A). On the other hand, the 1980-1984 recruitment wave caused catch rates, landings and mean CW to increase markedly from 1990 to 1994, while the sharp decline in catch rates which occurred as predicted in 1995 (Sainte-Marie and Dufour 1994, 1995) marked the entry to the fishery of the 1985-1987 recruitment trough. The decrease in mean CW from 1986 to 1987 can be attributed to a decline in the abundance of the largest adult males due to the combined effects of reduced recruitment, fishing, and natural mortality. Consequently, from 1987 to 1988, the fishery depended on a trickle of yearly recruitment and in 1989 was closed prematurely owing to a massive entry of soft-shelled crabs that signaled a resumption of fishery recruitment associated with the 1980-1984 wave (Sainte-Marie and Dufour 1994, 1995). The progression in mean CW of adult males from 1990 to 1995 (Figures 4 and 6B) may be explained by growth of adolescents and recruitment of adults to increasingly larger sizes in a context of relatively low exploitation rates and a heeded 1993 recommendation that legal-sized adolescent males be returned to the sea (Sainte-Marie and Dufour 1994). The progression in mean CW resulted in mean individual body weight increasing by 50.2% from 1990 to 1995 (Figure 6B). Over the 1986-1994 period, there was a significant correlation between the mean CW of landed crabs and of crabs in fishery trap samples ($r = 0.74$, $P = 0.022$). Thus, interannual trends in catch rate and landings reflect fluctuations both in the abundance and in the size structure of legal-sized males.

Discussion

Pattern and geographical extent of recruitment variability

The idea that recruitment to the *C. opilio* population and fishery follows a cyclic pattern is not new (Somerton 1981, Coulombe and Nadeau 1985, Comeau et al. 1991). However, hitherto no population had been studied across all body sizes sufficiently long in time to resolve the period for cyclicity and provide insight into the underlying factors. Our present data indicate that the *C. opilio* population in Baie Sainte-Marguerite has been influenced by an ≈ 8-year cycle with recruitment troughs for the 1977-1979, 1985-1987 and 1993-1994 year classes, and by recruitment waves for the 1980-1984 and 1988-1992 year classes (Figures 1, 2, and 3). Moreover, historical data provide evidence of a much longer record of cyclic recruitment in the northwest Gulf of Saint Lawrence (Sainte-



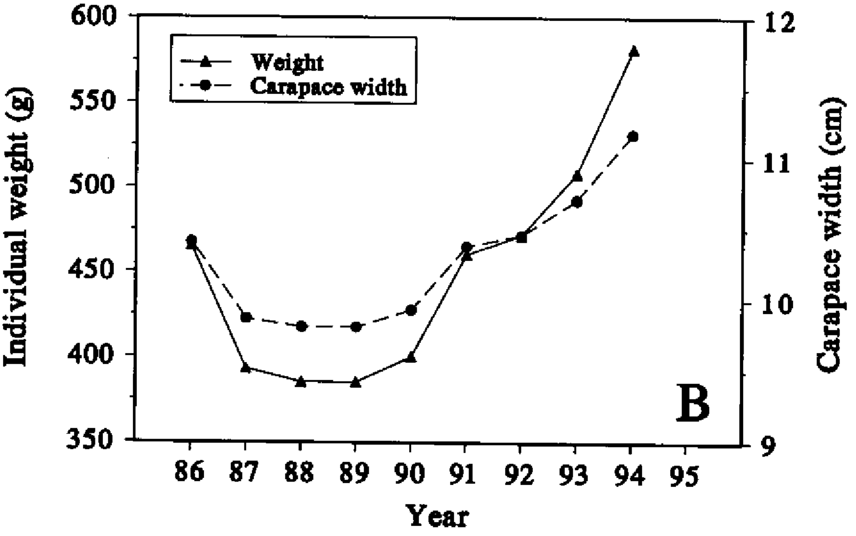


Figure 6. Chionoecetes opilio in management zone 16, which includes Baie Sainte-Marguerite. A. Commercial catch rate and landings from 1986 to 1995. B. Mean carapace width and estimated mean individual weight for males in commercial traps (at-sea sampling) from 1986 to 1994. Individual weight was estimated from the weight-width relationship for males with new-hard shells given by Taylor and Warren (1991).

Marie and Dufour 1995). After a period of intense exploitation in 1969-1970 the fishery collapsed in 1971-1972 and was abandoned, and it was thought that populations of *C. opilio* could not sustain intensive fishing (Lafleur et al. 1984). Exploitation resumed at very modest levels in 1977, but catch rates and landings again slumped in 1981. These observations suggest the existence of two other recruitment troughs (1961-1963 and 1969-1971) which impacted the fishery 10 years later.

There is ample direct evidence to support the view that the alternating pattern of periods of weak and strong year classes is a widespread phenomenon for *C. opilio* populations. In eastern Canada, trawl or trap surveys have shown that coastal populations in Baie des Chaleurs (Coulombe et al. 1985), off northwest Cape Breton (Robichaud et al. 1989), in Bonne Bay (Comeau et al. 1991), in the Estuary and northeast Gulf of the Saint Lawrence (Sainte-Marie and Dufour 1994, 1995, Dufour 1995), and in the Saguenay Fjord (Sainte-Marie unpubl. data) all had none or very few individuals in a size range representing a few specific and consecutive year classes. Troughs in the size distribution of *C. opilio* are also seen in the offshore population of the southwest Gulf of Saint Lawrence (Loch et al. 1995). In the eastern Bering Sea, trawl surveys have shown extended troughs in the CW frequency distributions for both *Chionoecetes bairdi* and *C. opilio* (Somerton 1981).

Indirect evidence for the existence of alternating groups of weak and strong year classes may also come from commercial fishery data. For example, *C. opilio* fisheries in the eastern Bering Sea (Somerton 1981, Otto 1990, Morrisson and Gish 1994, Stevens et al. 1994) and off eastern Cape Breton Island (Tremblay et al. 1994) have long traditions of fluctuating landings which have been related to periodic or sporadic recruitment. Perhaps the most striking example comes from the seine fishery in the Sea of Japan, where landings from 1973 to 1991 have oscillated with a period of about 8 years (Kon et al. 1993). However, without corroborating trawl surveys the connection between variation in catch and year-class strength can only be conjectural. Alternative explanations might exist; for example, Taylor et al. (1994) attributed the 1982-1985 fishery collapse off the Avalon Peninsula of Newfoundland to a reduction in recruitment to legal size due to cold water inhibiting the molting of sublegal males for several consecutive years.

Cycling populations of *C. opilio* appear to be in synchrony over much of the Gulf of Saint Lawrence. In any given year and in most sites where extensive CW frequency distributions are available for comparison with Baie Sainte-Marguerite, a good coincidence is seen in the range of CWs and of presumed year classes for recruitment troughs and waves. This can be inferred from examination of CW frequency distributions for coastal populations along the south and north shore of the Saint Lawrence Estuary and all across the north Gulf (Dufour 1995; J.-C. Brêthes, Département d'océanographie, Université du Québec à Rimouski, Rimouski, Québec, pers. comm.), for the offshore population in the southwest Gulf (Loch et al. 1995), and even for the supposedly isolated Bonne Bay population (Comeau et al. 1991).

Possible causes

Predation and density-dependent processes have been invoked to explain missing size classes and changes in the abundance of *C. opilio* populations. Although none of these hypotheses was developed to account for recruitment failure of early benthic stages, but rather emphasized population control in the late fishery pre-recruit stages, we briefly review them before considering two other hypotheses which could explain recruitment failure early in ontogeny.

Early analyses by Bailey (1982) suggested a negative relationship between abundance of cod (*Gadus morhua)*, a known predator of *C. opilio* (Waiwood and Elner 1982, Robichaud et al. 1991), and recruitment of *C. opilio* to the fishery 3-6 years later. However, as the time series lengthened it became apparent that changes in cod abundance were inconsistent with major fluctuations of the *C. opilio* fishery (Elner and Bailey 1986). The failure of 1993 and 1994 year classes of *C. opilio* reported herein certainly cannot be explained by predation, as cod populations (along with other groundfish) reached historical lows and have remained depressed since the early 1990s (Chouinard and Fréchet 1994). Nevertheless, this does not preclude a regulatory role for groundfish, which in the past may have contributed to dampen fluctuations in fishery recruitment or reduce populations of *C. opilio* by preying selectively on the strongest year classes in a recruitment wave.

Large adult males of *C. opilio* have been suggested to regulate fishery recruitment. Waiwood and Elner (1982) proposed that prior to the fishery populations of *C. opilio* were maintained in a stagnant phase by larger males which monopolized niche space and restricted resources available to pre-recruits. By removing large males, the fishery presumably relaxed competition and allowed greater survival and/or faster growth of pre-recruits, thereby contributing to increase stock productivity (also see Elner and Bailey 1986, Conan et al. 1992, Tremblay et al. 1994). However, although this hypothesis may explain skip-molting (see below), it seems unable to account for the fact that year-class strength is determined close to settlement time because large adult males are spatially segregated from the early benthic stages (Lovrich et al. 1995). Comeau and Conan (1992) suggested that the level of male recruitment into the largest size classes is regulated by the abundance of large hard-shelled adult males, through cannibalism of adolescent males at molting. This hypothesis cannot explain changes in the abundance of instar I and, for coastal populations at least, is inconsistent with the fact that premolt adolescent males segregate from large adult males by moving to marginal grounds presumably for refuge from predation and cannibalism at molting (Comeau et al. 1991, Sainte-Marie and Hazel 1992, Lovrich et al. 1995).

Two nonexclusive density-dependent recruitment processes have been proposed to explain the establishment of recruitment troughs for *C. opilio* (Sainte-Marie and Dufour 1994, 1995, Sainte-Marie et al. 1995). The first emphasizes a role for cannibalism and resource limitation (space and/or food) at or soon after settlement. Lovrich et al. (1995) provided evidence that instars I-V are cryptic and tend to concentrate in a narrow segment of the overall *C. opilio* habitat where, moreover, they may depend on microhabitat offering refuge from predators. According to this hypothesis, the limiting cryptic habitat becomes saturated through successive settlements and subsequent settlers are cannibalized by larger immature crabs or forced to use inhospitable grounds where they are subject to high mortality rates. Successful recruitment to the population would not occur again until the older year classes have at least partially vacated the settlement grounds, through the onset at instars VII-IX of annual migratory behavior and dispersal to deeper grounds. Cannibalism on settlers has been suggested to regulate recruitment in some decapod crustaceans (Botsford and Wickham 1978, Stevens et al. 1982, Kurihara and Okamoto 1987, Zeldis 1989, Fernández et al. 1993).

The second hypothesis is that recruitment troughs result from a marked reduction in the supply of postlarvae, as they appear to be generated in years when female spawning biomass is at a minimum. Incze et al. (1987) found a positive correlation between the abundance of adult females and larvae for *C. opilio* in 2 of 3 sub-areas in the southeast Bering Sea over a period of 4 years. Using CW-fecundity relationships in Sainte-Marie (1993) and assuming local retention of larvae with a conservative 99.9% mortality rate (Sale 1990), we calculated that the 1993-1994 female spawning biomasses would have been largely insufficient to account for any of the strongest year classes which recruited to Baie Sainte-Marguerite. However, in spite of that fact, we surmise that changes in the female spawning biomass are mainly a consequence rather than a cause of population cycles. Nevertheless, it is conceivable that fluctuations in larval abundance reinforce cycling (positive feedback) of major subpopulations, generate cycling in marginal populations dependent on allopatric recruitment, and contribute to the phasing of subpopulations within the Gulf of Saint Lawrence. These two last hypotheses stem from the possibility that the geographic extent and intensity of larval dispersal away from production zones may vary in proportion to larval abundance, as suggested for some fish species (Frank 1992).

The cycling of *C. opilio* populations agrees with predictions of population dynamic theory for iteroparous invertebrates subject to density-dependent recruitment (Botsford and Wickham 1978, McKelvey et al. 1980, Botsford 1995 and references therein). Endogenous cycles can arise in populations if recruitment and/or abundance of one age group declines in response to increasing abundance of older age groups. Populations where this occurs will cycle in abundance with a period of about twice the difference in mean age between the age group being affected and the age groups causing the effect. If the first post-settlement instar (0^+ age group) represents the most vulnerable benthic life stage in *C. opilio* (Lovrich et al. 1995), and cannibalism on instar I is caused by sympatric instars III (1^+ age group) to IX (6^+ age group), as observed by Sainte-Marie and Sévigny (unpubl. data), one would expect the population to cycle with a period of ≈ 7 years. However, in laboratory experiments the mortality rate of first instar scales exponentially to cannibal CW (Sainte-Marie and Sévigny unpubl. data), so the relative contribution of larger cannibals to population cycling could be more important than that of small cannibals, thereby lengthening the cycle's period.

We have discounted the possibility that the environment plays a role in generating cyclicity for *C. opilio* populations. It has been suggested that *C. opilio* year-class strength is related to varying levels of larval survivorship resulting either from interactions between ice cover, intensity of phytoplankton bloom, and success of match between larval release and bloom (Somerton 1982, but see Starr et al. 1994) or from interactions between thickness and stability of the mixed layer and availability of food resources at time of larval release (Incze et al. 1987). In our opinion, none of these effects could explain both the cyclic behavior of *C. opilio* populations and the convergence toward an 8-year period for populations as distant as those of the Gulf of Saint Lawrence and Sea of Japan. However, on the West Coast of the United States, which is rather uniformly subjected to common environmental phenomena (e.g., dominant winds and Davidson current), wind forcing is considered to be one factor contributing to the cyclic fluctuations of *Cancer magister* populations (Johnson et al. 1986, Hobbs et al. 1992, Botsford and Hobbs 1995).

Implications for fishery management

Endogenous population cycling for *C. opilio* causes the number, size, and quality of males to fluctuate over time (Sainte-Marie and Dufour 1994, 1995). The imminence of a recruitment trough may be signaled by a decline in the abundance of sublegal adolescent and adult males in the fishery. As year classes in a trough recruit to legal size and there occurs a depletion of accumulated commercial biomass through exploitation and natural mortality, the fishery becomes increasingly dependent on annual recruitment and this results in a reduction of the number and mean CW of exploitable crabs and an increase in the proportion of soft-shelled crabs at sea. When a recruitment wave approaches the legal size the abundance of sublegal males both adolescent and adult increases markedly, and as consecutive year classes in the wave recruit to legal size there may occur an increase in the abundance and mean CW of legal-sized males. If the exploitation rate is low as a wave fully recruits to legal size, the increase in commercial biomass will be accompanied by an increase in the proportion of legal-sized adult males with aged exoskeletons.

The extent to which symptoms of population cycles become manifest to fishers and managers will depend on the commercial biomass, exploitation rate, and behavior of fishers. Low exploitation rates and fishers' propensity to avoid areas with lesser quality crabs may all contribute to mask the underlying cycles in *C. opilio* abundance and quality. In this context, changes in catch rates and in the mean CW may be more informative of real population trends than total landings and condition of crabs (Tremblay et al. 1994).

Recognition of the cyclic nature of *C. opilio* populations allows a different interpretation of historic fishery events than has been presented so far. Hence, the decrease from 1979 to 1981 of the mean CW for males landed in the southwest Gulf of Saint Lawrence (Bouchard et al. 1986), which was first attributed to intensive exploitation (Lamoureux and Lafleur 1982), probably reflected the impact of the presumed 1969-1971 recruitment trough. The subsequent increase in mean CW from 1982 to 1984 (Coulombe and Nadeau 1985, Bouchard et al. 1986) is consistent with the entry of a recruitment wave to the fishery. Finally, the fishery collapse of 1987-1990 probably resulted mainly from the passing of the 1977-1979 recruitment trough, not from overfishing or mismanagement, and the subsequent increase in commercial biomass primarily reflected recruitment to the fishery of the 1980-1984 recruitment wave. The bottom line is that even in the absence of exploitation the biomass of legal-sized male *C. opilio* will fluctuate extensively due to natural mortality and changes in recruitment intensity and size structure, as is the case for the unexploited adult females.

More important, our recent understanding of population dynamics for *C. opilio* has permitted long-term prediction (≈ 10 years) of overall fishery trends and provided new insight into the ways the resource should be managed. Medium- to long-term prediction has afforded management and industry stakeholders the opportunity to plan investments and develop exploitation strategies. For example, in 1994, while the accumulated commercial biomass was high but rapidly aging, and certainly would be lost if not exploited, the prediction of a decline both in the resource and in market value for 1996-1997 led representatives of the north Gulf industry to request an increase in TACs in order to maximize revenues before market prices and resource decreased. The finding that populations fluctuate cyclically and that adult crabs cannot be "banked" indefinitely, owing to degradation of their condition after terminal molt, has generated new paradigms and guidelines for population assessment and management. First is the recognition that biological and economic stability probably cannot be achieved for the *C. opilio* fishery, at least at moderate to high exploitation rates, so that industry and management must learn to adjust their strategies to the cyclic nature of the resource. Second, in order to protect the resource and optimize its utilization the prediction of short-term fluctuations of commercial biomass is essential, either through direct surveys of biomass where this is possible (Loch et al. 1995) or through the monitoring of catch rates and development of fishery pre-recruit indices using data from commercial fishery or trap surveys (Tremblay et al. 1994) where bottom topography precludes direct assessment by trawl. For the purpose of long-term prediction, which necessarily involves labor-intensive sorting of benthic samples, monitoring of a few judiciously selected subpopulations probably suffices given the apparently phased cyclicity of Gulf of Saint Lawrence subpopulations. Third, post-season estimates of exploitable biomass must take into account exoskeleton condition of standing stocks, as crabs with exoskeleton conditions 4 or 5 either will not be of commercial value or will not survive to the next fishing season (Sainte-Marie and Dufour 1994, 1995). Fourth, the protection of legal-sized adolescent males and the preferential removal of males with older shells over males with younger shells during the last two years that a wave recruits to the fishery would contribute to maximize yield per recruit and, to some extent, might even dampen the impact of a recruitment trough. Indeed, if legal-sized adolescent males from the last year classes of a recruitment wave are allowed to grow, they may undergo their terminal molt shortly before or during the first year of a recruitment trough and contribute by their very large size and high individual biomass to compensate the reduction in the number of legal-sized crabs (Sainte-Marie and Dufour 1994, 1995). Last, managers must keep in mind the fact that exploitable biomass fluctuates as a function of both number and size of males. Hence, for a constant TAC, fishing mortality will increase markedly when a recruitment trough enters the fishery owing to a reduction both in the number and size of exploitable males, while the reverse will occur when a recruitment wave enters the fishery.

Although we have dismissed the fishery as a direct cause of *C. opilio* population cycling, based on pre-fishery evidence for cyclic behavior in currently exploited populations and on recent evidence of cyclic behavior for commercially unexploited populations (see above), it is conceivable that exploitation could perturb cycles. It has been predicted from population dynamic theory that exploitation can destabilize cycles and lead to greater variability in recruitment for *C. magister*, by modifying the size/age structure of one of the population components responsible for population cycles (Berryman 1991, Botsford 1995). However, in the case of *C. opilio*, the fishery probably does not directly impact any of the life stages which may promote population cycling. Therefore, any fishery effect on the cycle would likely be indirect. Conceivable effects of the fishery on population dynamics, which may or may not affect population cycling, are (1) increased survivorship for those small and intermediate-sized crabs which control the abundance of instar I, through a reduction in the competition/cannibalism by legal-sized crabs; (2) a cyclic reduction in female fertility resulting from fishery-exacerbated fluctuations in operational sex ratio; and (3) a reduction in the frequency of skip-molting for adolescent males owing to relaxed competition between legal-sized adult males and fishery pre-recruits (i.e., a derivation of Waiwood and Elner's 1982 hypothesis).

Thus, the next step in the study of *C. opilio* dynamics is to model a population in order to assess the hypothesis that mortality of early benthic instars can explain cyclicity and determine to what extent, if any, the fishery might contribute to modify population cycling. These modeling efforts should also explore the effects of management and exploitation strategies which might promote a reduction in the amplitude of population oscillations, if at all possible. There is also a need for research into (1) the importance of cannibalism and resource limitation for population dynamics; (2) the determinism(s) underlying terminal molt and skip-molting, be they genetic or density-dependent; and (3) the relation between operational sex ratio and female fertility. Finally, we should concentrate on identifying those,subpopulations in eastern Canada which fluctuate in synchrony, through genetic and demographic studies, as these would represent the most relevant units for the application of conservation measures and the assessment of resource status and future trends.

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High Latitude Crabs: Biology, Management, and Economics
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Growth Assays with First-feeding Zoeae of King Crab (*Paralithodes camtschaticus,* Decapoda, Lithodidae) in a Plankton Community of a Deep Fjord

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Abstract

The ability of the plankton community in a deep fjord to support red king crab *(Paralithodes camtschaticus)* larvae was examined. In April 1991 zoeae were reared in water taken from 5, 10, and 15 m depths. During the growth assays total cell counts seldom exceeded 118 cells per ml. In all assays the larvae merely maintained their weight or lost weight. Cohorts of theirs reared with concentrated plankton grew at rates exceeding 5% dry body weight per day, demonstrating that the zoeae were competent. The results indicated that first feeding red king crab larvae were unsuccessful at feeding in the spring plankton community in this deepwater habitat in 1991.

Introduction

The red king crab (*Paralithodes camtschaticus* Tilesius) has supported a major fishery in the North Pacific for many years. Because of the value of the fishery, and drastic population declines (Blau 1986), some research has focused on the role of intraannual variations in primary production on growth of king crab larvae (Paul et al. 1989, 1990). First feeding king crab zoeae are poorly adapted to capturing common crustaceans such as copepods (Paul et al. 1979) and nauplii (Paul et al. 1989) and rely primarily on phytoplankton as their major energy source (Paul et al. 1989). They require relatively high cell counts (near 1,000 cells per ml) of their preferred diatom taxa to grow at maximal rates (Paul et al. 1989, 1990).

Benthic stage red king crab are most abundant on shallow shelf areas of Alaska, and their range extends from southeastern Gulf of Alaska to Norton Sound in the northern Bering Sea (Figure 1). There are major concentrations of red king crab around Kodiak Island, along the western Alaska Peninsula, and on the shallow shelf of the southeastern Bering Sea. Interspersed throughout this wide geographic range are areas where low concentrations of red king crab occur. One low density area occurs from Yakutat to the study area (Figure 1). The reasons for the geographic variations in abundance are not described but the previous studies of larvae suggested that the type of planktonic food web present in an area determines the feeding success of first zoeae (Paul et al. 1989, 1990). One common characteristic of the low-density king crab habitat like Prince William Sound and the Kenai Fjords (labeled study area on Figure 1) is that they are deepwater areas and thus not likely to have plankton communities similar to those of shallow shelf areas. The objective of this study was to examine the ability of the plankton community in one deep fjord, situated well within the geographic range of red king crab, but not containing noteworthy populations of the species, to support their zoeae.

The previous studies in which red king crab zoeae were reared in natural communities (Paul et al. 1989, 1990) were done in a shallow bay (50 m depth) in southeastern Alaska where growth rates of zoeae was 5 to 10% dry body weight per day (Paul et al. 1990). That plankton community had high phytoplankton counts (> 1,000 cells per ml) during the spring bloom (Paul et al. 1989) and *Thalassiosira* spp., a preferred food of the larvae (Paul et al. 1989, 1990) was a major member of the diatom assemblage. In that bay much of the spring bloom phytoplankton sank to the benthos ungrazed (Laws et al. 1988) because the copepod community consisted primary of small species that do not begin rapid reproduction until after the bloom (Coyle et al. 1990). In lower Cook Inlet and the mid-shelf region of the southeastern Bering Sea, both good king crab producing areas, much of the spring diatom bloom also sinks to the benthos ungrazed (Chester and Larrance 1981, Goering and Iverson 1981, Sambrotto and Goering 1983). These observations suggest that king crab larvae survive best in food webs where there are relatively high diatom concentrations, and little competition from other grazers, during the spring phytoplankton bloom.

The deepwater plankton communities of the Alaskan fjords are poorly described but the limited measurements (Horner et al. 1973) suggested a plankton community with relatively low cell counts during the spring phytoplankton bloom. Since king crab larvae require relatively high concentrations of specific types of phytoplankton to survive (Paul et al. 1989, 1990) they may be unsuited to compete in deepwater planktonic food webs. King crab larvae generally hatch in the spring, but they exhibit some interannual variation in the time that they hatch and a

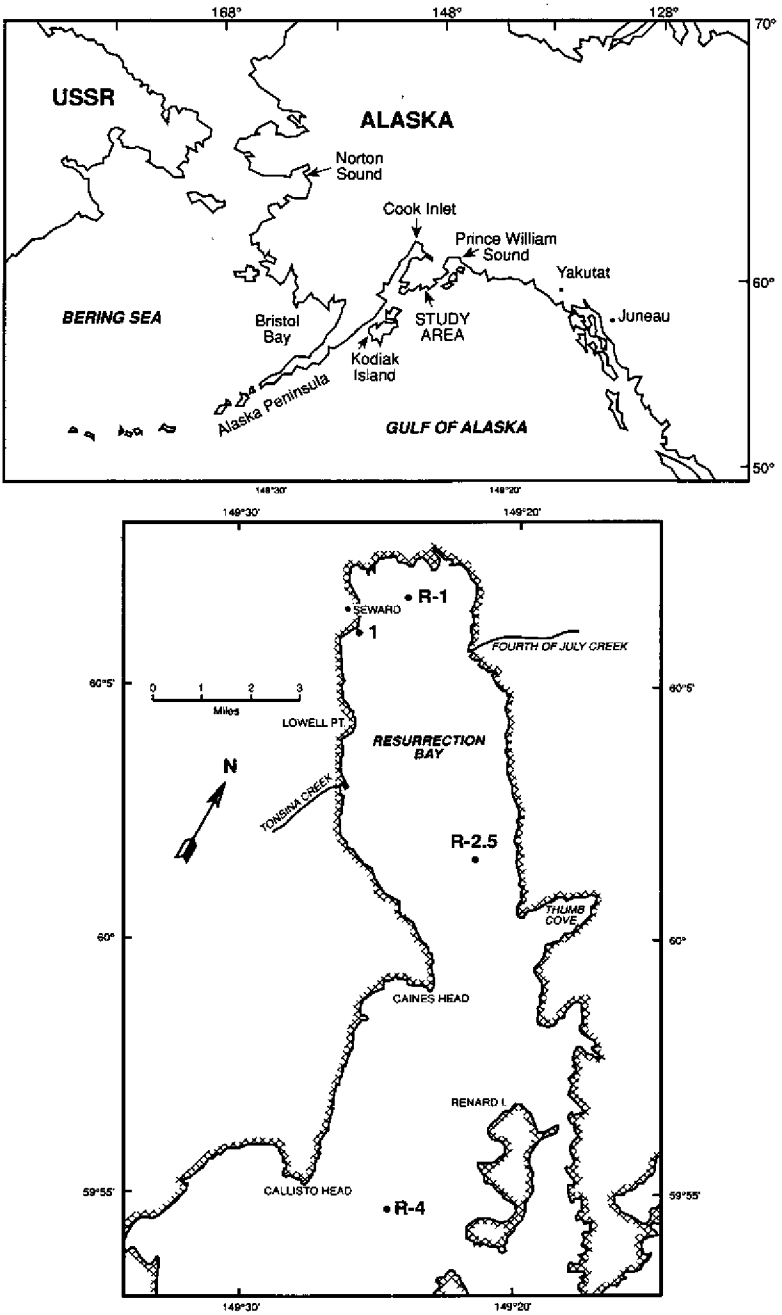

Figure 1. Map of Alaska (upper) and stations at the study site in Resurrection Bay (lower).

larval period that lasts 56 to 113 days in the Gulf of Alaska depending on temperature (Shirley and Shirley 1989a).

Methods

Study site

The work was done in Resurrection Bay in the northern Gulf of Alaska (Figure 1). There is no fishery for red king crab in the bay due to their absence or very low abundance. Thus the site was ideal to pose the question, "was the absence of the species related to the suitability of the planktonic food web?"

Resurrection Bay is a fjord estuary approximately 30 km long, 6 to 8 km wide, and oriented in a north-south direction. An inner basin, 290 m deep, is separated from the outer reaches of the fjord by a sill at approximately 250 m depth and the outer basin opens directly onto the Gulf of Alaska. Previous information on the physical oceanography of the study area is included in Heggie et al. (1977). Generally there is temperature and salinity stratification in the upper water column beginning in April resulting from summer warming, snow melt, and freshwater run-off. Much of the melt water comes from glaciers. By the end of May there is usually a strong pycnocline in the 20-25 m depth region (Heggie et al. 1977). The geology of the area protects the bay from east and west winds and the prevailing north and south winds are generally mild during May and June, so the mixed layer depth is probably shallower than the pycnocline. Thus by mid-May the water column is generally stable in the vertical plane.

General methods

The suitability of a plankton community to supply energy to first feeding king crab zoeae was tested with a short-term growth bioassay. Red king crab larvae are usually found in the upper 15 m of the water column during their daily feeding period (Shirley and Shirley 1988, 1989b). The weekly growth bioassay measured changes in dry body weight of first-feeding larvae reared in water pumped from the upper 15 m of the fjord. In 1991 zoeae first began to hatch on 29 March, and 22 April was the last date that enough larvae were available for a growth assay.

On the evening prior to a growth assay, five egg-carrying female king crabs were placed in a freshly filled seawater tank and the next day 24 hour old zoeae I were collected for the experiment. Twenty zoeae were placed individually on weighed pieces of aluminum foil and dried to a constant weight at 60°C, then reweighed on an electro balance to obtain their dry weights. This calculation provided the estimate for the cohorts' initial dry weight. Zoeae I from that cohort were placed in

125 liter tanks filled with 1,000 μm filtered seawater pumped from 5, 10, or 15 m depth at Station 1 (Figure 1). There were four zoeae per tank and they were reared for three days in this water. The predicted intermolt period for stage I at 5°C is approximately 8 to 12 days (Kurata 1960). In three days a weight gain around 30% dry body weight would be expected if the larvae are receiving adequate nutrition (Paul et al. 1990). Measurement of changes of weight of this magnitude are well within the capacity of an electrobalance. Air gently passed through an air stone at the bottom of each chamber kept prey from settling. In addition, gentle stirring every hour during the light cycle was done with a paddle. Grazing chambers were held in a controlled temperature room at 5.0°C (sd = 0.5). The room had a 12 h dark and light (5 lux) cycle. There was no zoeae mortality in growth assays.

Phytoplankton concentrations in the growth bioassays were determined from triplicate samples taken from each rearing tank on days one and three, then all six values were averaged to estimate cell concentration in the assay. Phytoplankton cells were counted with an inverted microscope (Lund et al. 1958). After three days in the growth chamber the larvae were dried and weighed and the difference in dry weight between 24 h and four day old zoeae was obtained and converted to the daily average change in body weight (BW per day).

A fourth group of larvae were set up at every assay to demonstrate that each cohort of larvae had the potential to grow if enough food was present. These were zoeae treated in the same manner as above but held in tanks in which the plankton, from a vertical tow from 20 m depth to the surface with a 200 μm 0.5 m ring net, served as the prey. After capture the wild plankton was passed through a 300 μm mesh screen to remove any predators and other zoeae. Copepod (all stages) concentrations in all well-fed groups greatly exceeded 200 per liter, a concentration that allows first-feeding king crab larvae to be carnivorous (Paul et al. 1979).

Results

In the 1991 growth assays unidentified pennate shaped diatoms were the most abundant type of cell and the genera *Chaetoceros*, *Cylindrotheca*, and *Melosira* were present in low numbers (Table 1). Cell concentrations, at all depths, and from the beginning to the end of hatching period were consistently low with total cell counts never exceeding 118 per ml (Table 1). With such low cell counts, all four cohorts of zoeae reared in 5, 10, and 15 m depth water either barely maintained their weight or lost weight (Figure 2). All weekly groups reared with > 200 copepods per liter grew at 5% dry BW per day, or more, indicating that the larvae had the capability to grow if enough food was present.

Table 1. **Average phytoplankton (cells per ml) and crustacean (no. per liter) abundance from natural plankton communities, taken from 5, 10, and 15 m depth, in Resurrection Bay, Alaska, and used as food in red king crab larvae growth assays.**

Assay date	Taxa	Food abundance at depth		
		5 m	10 m	15 m
1 April	*Chaetoceros* spp.	0.6	0.9	0.1
	Cylindrotheca closterium	0.5	1.1	0.7
	Melosira sp.	1.0	0.5	0.1
	Unidentified pennates	3.0	7.4	4.1
	Skeletonema costatum	2.0	0.0	0.0
	Thalassiosira spp.	0.3	2.2	0.3
	Total phytoplankton cells	8.2	13.5	7.3
	Crustaceans	2.5	2.0	1.0
8 April	*Chaetoceros* spp.	0.6	0.5	0.6
	Cylindrotheca closterium	1.1	1.7	0.6
	Melosira sp.	0.6	1.0	2.9
	Unidentfied pennates	4.1	9.7	7.0
	Skeletonema costatum	0.0	0.0	0.0
	Thalassiosira spp.	0.1	0.6	0.0
	Total phytoplankton cells	8.0	17.1	17.5
	Crustaceans	4.5	1.5	0.5
15 April	*Chaetoceros* spp.	1.1	0.9	1.0
	Cylindrotheca closterium	2.3	3.7	4.5
	Melosira sp.	0.5	2.8	5.1
	Unidentfied pennates	10.3	27.0	89.4
	Skeletonema costatum	0.0	0.0	0.0
	Thalassiosira spp.	0.8	0.9	1.1
	Total phytoplankton cells	17.9	39.6	118.2
	Crustaceans	2.0	2.5	3.5
22 April	*Chaetoceros* spp.	0.9	1.4	0.4
	Cylindrotheca closterium	1.7	3.1	2.8
	Melosira sp.	1.3	0.0	0.5
	Unidentfied pennates	3.5	2.5	10.9
	Skeletonema costatum	0.0	0.3	0.0
	Thalassiosira spp.	1.0	2.1	1.3
	Total phytoplankton cells	11.3	11.3	21.1
	Crustaceans	7.0	8.5	8.0

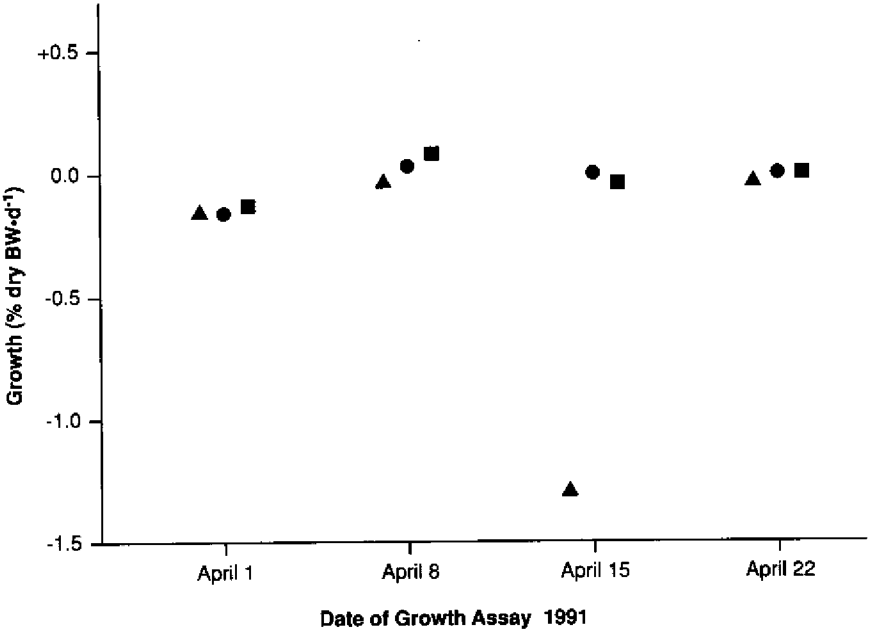

Figure 2. Growth (percentage of dry body weight per day) of stage I zoeae of Paralithodes camtschaticus reared on natural plankton collected at 5 (triangle), 10 (circle), and 15 m (box) depths in Resurrection Bay during 1 April to 22 April 1991.

Discussion

In known good king crab larval rearing areas large diatoms like *Thalassiosira* spp. are common and dominate the spring bloom (Chester and Larrance 1981; Goering and Iverson 1981; Paul et al. 1989, 1990; Sambrotto and Goering 1983). These type of diatoms are preferred food of king crab larvae (Paul et al. 1989, 1990). In natural communities king crab zoeae I need about 1,000 *Thalassiosira* spp. cells per ml for maximal growth (Paul et al. 1990). In shallow Auke Bay, *Thalassiosira* spp. often exceed 1,000 cells per ml (Paul et al. 1990) but in the deep fjord this level of abundance was never observed. In pure culture experiments (Paul et al. 1989) *Chaetoceros debilis* concentrations had be about 4,300 cells per ml for king crab zoeae to obtain a maintenance ration and only 10% of the zoeae would molt when held at that concentration. Cultured *Skeletonema costatum* concentrations had to be 13,240 cells per ml to provide a maintenance ration for zoeae (Paul et al. 1989). In the 1991 growth assays in Resurrection Bay concentrations of these genera of phytoplankton were far lower than the above stated values. Kurata

(1959) reported that pennate diatoms such as *Nitschia* sp. (genus spelling from original text) were not good foods on which to rear king crab larvae for aquacultural purposes. Pennate diatoms were common in Resurrection Bay. Thus in addition to low cell counts, the types of phytoplankton in Resurrection Bay during the 1991 spring bloom were not the most suitable taxa for king crab zoeae. The role of temporal variations in phytoplankton taxa on meroplankton survival is little studied but this report and another showing that phytoplankton species composition affects survival rates in barnacle larvae (Barnes 1956) suggest that it is a topic worthy of further study.

Chamber size can affect growth rates of grazers but the cell counts in the growth assay chambers at the start and end of the experiments generally showed no significant difference. This suggests that feeding activity by the zoeae was not a major factor in restricting them to prey. A growth assay done in phytoplankton-rich Auke Bay used 8 L chambers holding 5 zoeae for 5 days and growth rates of around 10% dry BW per day were common (Paul et al. 1990). To compensate for community differences the volume of the growth assay containers for this study was increased to 125 L for only 4 zoeae in this experiment and the rearing period reduced to three days. We do not think that further increasing chamber size would have greatly changed growth rates. Rather, the poor growth for all dates and depths assayed suggests that the plankton community of Resurrection Bay was not well suited for rearing king crab larvae, at least during this survey.

Obviously doing the growth assays during only one spring precludes a full understanding of how well king crab larvae can find food in deep fjords. However, given that in Auke Bay every growth assay produced positive growth rates, it seems that the growth failures observed in Resurrection Bay indicate the community structures must be quite different. Factors such as the formation of a strong pycnocline, diatom sinking phenomena, wind mixing, and nutrient fluxes have been previously shown to modify phytoplankton abundance and thus feeding success of king crab larvae. The results of this experiment suggest geographical variations in plankton community structure can be added to this list needing further study to understand king crab recruitment.

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High Latitude Crabs: Biology, Management, and Economics
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Modeling Advection of Dungeness Crab *(Cancer magister)* in Dixon Entrance and Northern Hecate Strait, British Columbia

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Abstract

Major Dungeness crab fisheries in British Columbia (BC) are relatively discrete and separated geographically. The most northerly fisheries are on Dogfish Banks in Hecate Strait, the Skeena River delta, and McIntyre Bay in Dixon Entrance. Earlier studies have shown that both current pattern and diel migratory behavior of megalopae predominantly influence Dungeness crab recruitment in southern BC areas. However, the dynamics of stock recruitment in northern BC is less certain. McIntyre Bay has supported a significant annual fishery (≈ 340 t y^{-1}) for decades, while Dogfish Banks has only recently become extremely productive (> 4,000 t y^{-1}) after 25 years of virtually no landings. The Skeena fishery has increased modestly over time, but remains relatively small at ≈ 250 t y^{-1}.

Extensive oceanographic studies and numerical simulations of currents have revealed the presence of a basin-wide recirculating current, called the Rose Spit Eddy, in Dixon Entrance. This eddy appears able to retain crab larvae until their settlement in Dixon Entrance, thereby allowing for possible movement of larvae by appropriate winds into northern Hecate Strait. Northward flowing, late winter currents may transport crab larvae to northern BC from the west coast of Vancouver

Island. However, these latter currents cease in April, prior to most larval settlement. Our study suggests why Dungeness crab settlement occurs consistently in Dixon Entrance, but with available oceanographic and meteorological data, we cannot explain why 1989 was an exceptional year of crab settlement in northern Hecate Strait. The source of that exceptional settlement in Hecate Strait remains uncertain, but possibilities are discussed.

Introduction

The Dungeness crab (*Cancer magister*) population of the Queen Charlotte Islands, British Columbia, is located predominantly in McIntyre Bay in Dixon Entrance and on Dogfish Banks in Hecate Strait (Figure 1). These stocks are geographically isolated from other populations along the west coast of North America, with the closest substantial Dungeness crab population being a much smaller one to the east in Chatham Sound on the delta of the Skeena River. Queen Charlotte Island Dungeness crab have shown a unique recruitment pattern over the past 30 years. While the McIntyre Bay population has been relatively consistent in production (≈ 340 t y^{-1}), the Dogfish Banks population was largely collapsed (Jamieson 1985) from the late 1960s to late 1992. Exceptionally large landings unique to Hecate Strait have occurred there since 1992, landings so disproportionately large (> 4,000 t y^{-1}) that they exceed the long-term average annual landing from all of British Columbia (1982-1991: 1,406 t) 3 to 4-fold (Figure 2).

The cause of the late-1960s collapse of the Dogfish Banks crab population is unknown, but is presumed to be environmental rather than fishery related. This is because the adjacent McIntyre Bay crab fishery has remained consistent over recent decades. With extensive pelagic larval dispersal characteristic of Dungeness crab, there has probably always been an adequate abundance of larvae for potential substantial larval movement and subsequent settlement in Hecate Strait. The larval period of Dungeness crab is 3-4 months and, since the megalopal stage, at least, is in near-surface waters (Jamieson et al. 1989) for much of the time, larval dispersal in outer coast areas at least is considered to be extensive. Given the relatively strong, wind-driven longitudinal currents that characterize northern Hecate Strait (Crawford et al. 1988) through the early larval crab period (January-March), it thus seems unlikely that the Dungeness crab population on Dogfish Banks is, or ever was, an isolated, self-sustained population. Locally hatched larvae would probably be rapidly transported away, although if larvae were retained in Dixon Entrance, some might drift back into Hecate Strait when average wind direction reverses after the spring transition.

With the ocean current structure (Figure 3) in McIntyre Bay and northern Hecate Strait, relatively stable recruitment of Dungeness crab populations in these areas would require either (1) larval crab emigra-

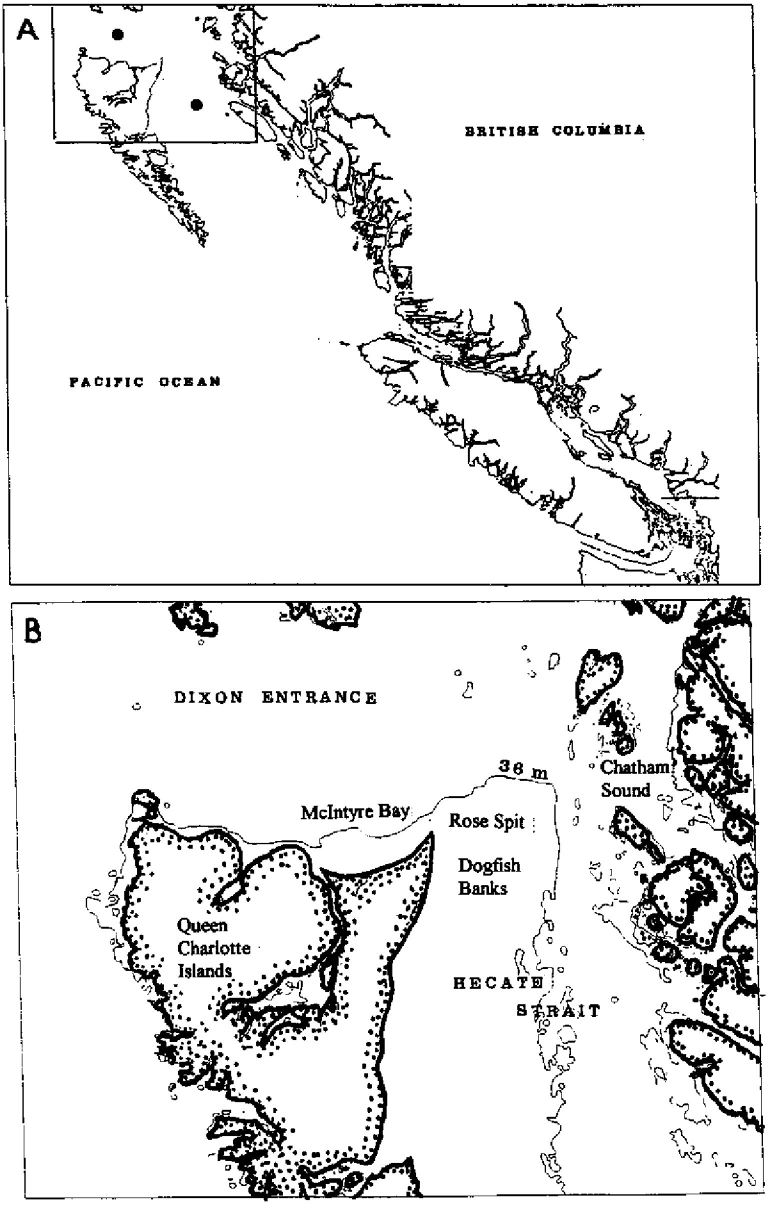


Figure 1. A. Location of Dixon Entrance and Hecate Strait in British Columbia, Canada. Box shows region shown in Figure 1B. The symbol ● denotes locations of weather buoys 46145 and 46183. B. Region of study, showing the 36 m contour that defines the outer boundary east of Rose Spit of Dogfish Banks.

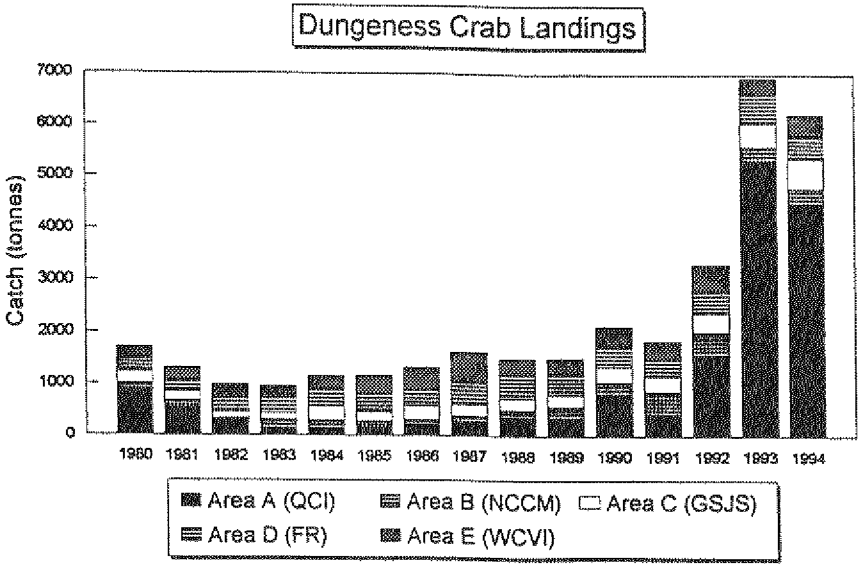


Figure 2. Annual Dungeness crab landings (t) by management area in British Columbia. Area A = Queen Charlotte Islands; Area B = northern and central mainland coast; Area C = Strait of Georgia (excluding the Fraser River delta) and Johnston Strait; Area D = Fraser River delta; and Area E = west coast of Vancouver Island.

tion from local populations during the early larval period, and subsequent crab immigration, which might include locally hatched larvae, from more distant sources during the late larval period, or (2) some indigenous larval crab retention mechanism, either solely oceanographic or an oceanographic event coupled with unique indigenous larval crab behavior. Currents would otherwise likely transport locally hatched larvae permanently away from these areas into the open Pacific Ocean.

Jamieson and Phillips (1993) documented an example of a larval crab retention process for Strait of Georgia Dungeness crab. Exit from this largely enclosed body of water is primarily through Juan de Fuca Strait, and it was shown that Strait of Georgia megalopae can maintain themselves in inside waters through vertical migration in the estuarine circulation of Juan de Fuca Strait. The vertical migratory depth range of megalopae produced outside the Strait of Georgia (≈ 25 m) keeps outer coast larvae entirely in the mostly outward-flowing surface waters of Juan de Fuca Strait, largely preventing their movement into the Strait of Georgia. In contrast, Strait of Georgia megalopae show a much larger vertical migratory depth range (≈ 160 m), largely keeping them in the inward flowing deeper waters of Juan de Fuca Strait. This adaptation to local oceanographic conditions appears to retain most Strait of Georgia crab larvae in inside waters and minimizes their mixing with outer coast crab larvae.

We have not investigated whether northern British Columbia Dungeness crab larvae have a comparable unique vertical depth range behavior, but such a behavior would seem less likely to exist in Dixon Entrance and Hecate Strait crab populations for a number of reasons. First, northern Hecate Strait waters are generally shallower than those in the Strait of Georgia and Juan de Fuca Strait, with no persistent differences in shallow and deepwater currents comparable to those found in Juan de Fuca Strait. Second, Dixon Entrance forms an oceanographically wide strait, within which the estuarine circulation differs from that of Juan de Fuca Strait. Rather than a surface outflow and deep inflow of oceanic replacement water, Dixon Entrance is so wide that the effect of the Coriolis force is to deflect the surface outflow of brackish water to the northern side of Dixon Entrance, and the inflow of oceanic water to the southern side, into McIntyre Bay. A key difference is that both outflow and inflow are surface currents, and so megalopae need not migrate vertically to remain in Dixon Entrance. They may be retained by surface currents if there is exchange of water between these two flows. Such a mechanism does exist, and we discuss it below.

In this paper, we explore the effects of currents on larval crab dispersal in northern British Columbia through a model incorporating current pattern over time and probable vertical distribution of megalopae. We investigate whether there are mechanisms that can retain crab megalopae within Dixon Entrance and northern Hecate Strait. Zoeae are not considered, as there are no adequate field data to indicate their diel vertical distribution in the water column.

Dungeness Crab Life History

Dungeness crab hatch their eggs in late winter. The larval stage consists of five zoeal stages and one megalopal stage. Duration of the zoeal period is unknown but is estimated to be 80-95 d (Reilly 1983). Hatfield (1983) indicated the duration of the megalopal stage to be 28 d at temperatures ranging from 13 to 17.5°C. It is assumed that northern British Columbia megalopae have a vertical distribution similar to that of outer coast megalopae off the west coast of Vancouver Island (Jamieson et al. 1989), i.e., in the top half meter of the water column at night and at a depth of about 25 m during daylight hours. The limited sampling of Dixon Entrance Dungeness crabs conducted to date (Booth et al. 1985) supports this assumption.

Although the seasonal occurrence of megalopae in the study area has not been specifically studied, megalopae appear to occur there throughout the summer. In McIntyre Bay, Booth et al. (1985) found megalopae during July 6-17, 1984. On Sept. 2, 1994, about 75 megalopae

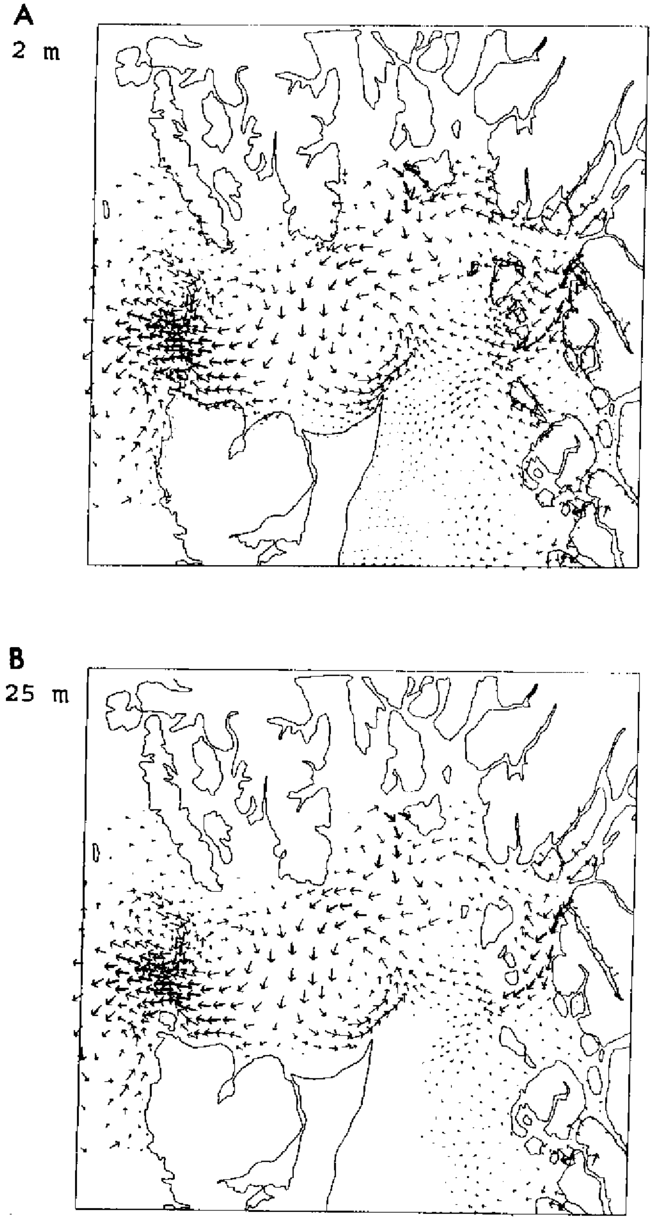
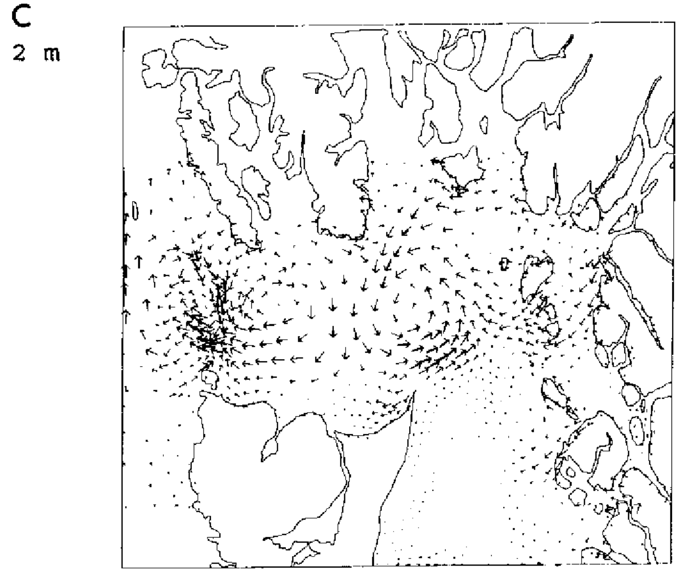


Figure 3. Simulated baroclinic currents in Dixon Entrance and northern Hecate Strait. Boldness of the current vectors represents general current strength; a thin, full length vector represents a 10 cm s^{-1} current and stronger currents are represented by thicker vectors. A. June-July 1991, 2 m depth. B. June-July 1991, 25 m depth. C. December 1991, 2 m depth. D. December 1991, 25 m depth.



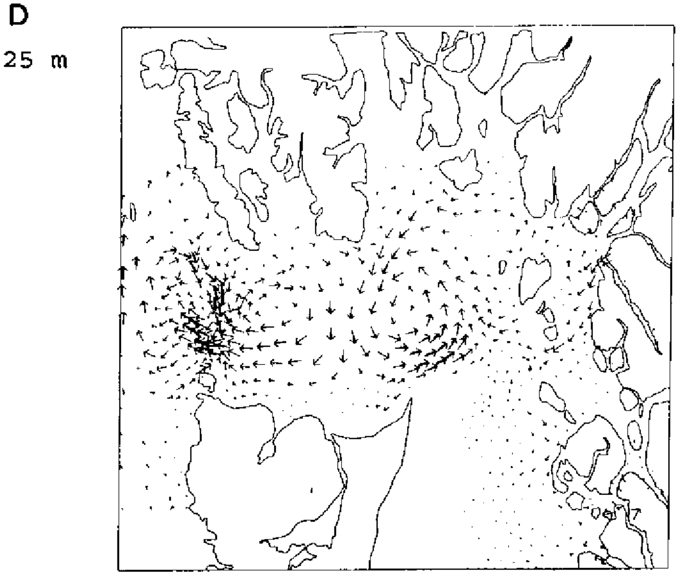


Figure 3. (Continued.)

were collected in 1.5 h of neuston towing between 2200 and 2330 h at night in McIntyre Bay near Rose Spit (A. Phillips, Pacific Biol. Sta., Nanaimo, BC, pers. comm.). However, none were collected by Phillips (pers. comm.) on Sept. 7, 1994, in 1 h of similar nighttime towing on Dogfish Banks in Hecate Strait. Jamieson and Phillips (1988) reported megalopae from April 16 to August 24 off the west coast of Vancouver Island, with the period of highest abundance being May and June. Whether this also applies to northern British Columbia waters is unclear. In this paper, megalopae are assumed to be present in Dixon Entrance in greatest abundance in June and July.

Northern Coastal British Columbia Oceanography

The oceanographic features of Dixon Entrance have been well studied over the past 30 years. Crean (1967) described an eddy which he labeled a "vortex" in the geostrophic surface current during September to October 1962. This eddy, located north of McIntyre Bay, has come to be called the Rose Spit Eddy, named after the point of land at the extreme northeast corner of the Queen Charlotte Islands, which separates Dogfish Banks from McIntyre Bay.

The next study of these waters, using current meters, drifters, and water property measurements from 1984 to 1985, revealed that this eddy penetrated to at least 50 meters depth and persisted through the summer (Crawford and Greisman 1987) and, although in a weaker state, even into the winter (Bowman et al. 1992).

The southern arc of the Rose Spit Eddy flows eastward through McIntyre Bay. Although Crawford and Greisman (1987) showed that a portion of the persistent eastward current in McIntyre Bay could be attributed to tidal forcing only, through a process termed "tidal rectification," they were unable to account for the origin of the Rose Spit Eddy itself. Their study of currents in Dixon Entrance and winds measured in McIntyre Bay revealed little correlation between fluctuations in the wind and basin-wide motions such as the eddy.

Bowman et al. (1992) investigated the origin of the Rose Spit Eddy using a barotropic simulation of tidal motion in an idealized basin. Although the eddy was present in the rectified tidal currents of their simulation, its speed was so slow that a complete circuit of the eddy by passive drifters such as crab larvae would take more than 100 days. They attributed quicker speeds observed in field studies of the eddy (Crawford 1996) to estuarine circulation.

During an extensive drifter study of Dixon Entrance, northern Hecate Strait and Chatham Sound in the summer of 1991 (Crawford 1996), several drifters were entrained in the eddy, with some completing one or more circuits of the Rose Spit Eddy with circuit times varying from 5 to 43 days (regression analysis of circuit diameter versus circuit travel time shows each increase of 1.5 km in circuit diameter requires an extra day of travel [$r = 0.88$]). In contrast to this persistent eddy in Dixon Entrance, drifters in northern Hecate Strait revealed almost no average motion, but instead drifted with the wind, flowing southward with winds from the north or northwest and reversing direction during winds from the south. Any exchange of water between Hecate Strait and Dixon Entrance during this drifter study was of short duration, and was set up by fluctuations in local winds. These findings agree with observations of northward transport through Hecate Strait by Crawford et al. (1988).

During the above drifter studies in northern Hecate Strait, we noticed that while drifters moved with the prevailing winds north-south, there was little movement east-west. Drifters in the central part of the strait did not appear to be readily transported onto Dogfish Banks.

Methods

Data and hydrodynamical models

Observations in the summer of 1991 form the most extensive set of water property, drifter, current meter and wind observations in these waters. Using water property data from 300 measured temperature and salinity profiles during June, July, and August 1991, Ballantyne et al. (1996) constructed a three-dimensional, diagnostic, finite element model of steady-state baroclinic currents, using methods similar to Foreman et al. (1992). The 300 profiles were used in two separate simulations for summer, one for June-July 1991 (denoted summer 1991a by Ballantyne et al. 1996) and another for July-August 1991 (summer 1991b), and for one winter simulation for December 1991. In Figure 3 we present currents simulated at 2 and 25 m depth by this model for June-July 1991 and December 1991. The Rose Spit Eddy clearly emerges in the field of vectors as an elongated gyre in the middle of Dixon Entrance, stretching across the complete north-south span of the strait. Surprisingly to us, all three data sets produced similar current fields in the simulations. Currents from the two simulations of the summer of 1991 agree well with drifter-observed velocities taken simultaneously (Ballantyne et al. 1996). We selected the 1991 June-July simulations to provide a set of current vectors for megalopae drift simulations.

In the model used for diagnostic baroclinic simulations noted above, and using the same grid, Ballantyne et al. (1996) also computed fields of tidal and rectified tidal currents for the barotropic case. This research is a continuation of the studies of Foreman et al. (1993). These latter model simulations also provide sets of tidal current and rectified tidal current vectors for megalopae drift simulations.

Megalopa drift simulations

We used velocity vectors produced by these hydrodynamical models in Crabview, a larval drift simulation model described below. It displays the tracks of up to 50 simulated larvae on a PC computer screen. Input variables (1) and (2) below are based on the Ballantyne et al. (1996) model. Input variables (3) and (4) below are unique to Crabview. The velocity vectors are added to each other to produce cumulative megalopae displacements at 10-min intervals. Positions are plotted at 24-h intervals.

Diagnostic currents

Crabview applies the baroclinic current field for June-July 1991, which is stored as an array of several thousand vectors, each representing the time-averaged baroclinic flow at a node of the computer simulation of the Ballantyne et al. (1996) model as described previously. This flow field represents a seasonal average response for 1991 to buoyancy input from the Skeena and Nass rivers, surface heating, evaporation and rainfall, and wind stress over the water surface.

Tidal currents

Amplitudes of time-varying current vectors for tidal constituents M_2, S_2, N_2, K_1, O_1, and P_1 are defined for the same grid and applied every 10 minutes by the model. Tidal fields are time varying, but this was found to contribute little to the long-term drift patterns of larvae. Nevertheless they are retained in the simulation to introduce dispersion, and to represent realistic currents near Rose Spit where tidal currents are strong (up to 1.5 m s^{-1}.). Crabview also applies steady, rectified tidal currents (denoted as the tidal constituent Z_0), defined at the same nodes as the diagnostic currents.

Vertical migration of megalopae

Crabview assumes that larvae drift at 2 m depth during an 8-h night and at 25 m depth during a 16-h daylight period. If water depth is 10 m or less, larvae drift with the current at 2 m depth and are influenced by wind day and night. If bottom depth is deeper than 10 m, it is assumed that during the day, larvae drift with the nearest 25 m current and are not influenced by wind at this time.

Wind-driven motion

We have chosen to represent daily fluctuations in wind influence by moving megalopae at a constant fraction of wind speed while they are near the surface at night. For Dixon Entrance in summer, we chose the fraction to be 2% of wind speed. During summer, the wind-mixed layer is typically in the order of 10 m deep, and it seems reasonable to assume currents at 25 m to be little influenced by daily fluctuations in wind stress. A drift rate of 2% is less than the nominal value of 3% used for oil spill simulations because we assume that even at night, megalopae are not always right at the surface.

Winds were determined from hourly observations at meteorological buoys 46145 at 54°22.998'N, 132°25.362'W in Dixon Entrance, and 46183 at 53°37.00'N, 131°6.18'W in northern Hecate Strait (Figure 1A) for the period April 1991 to December 1994, as described by Cherniawsky et al. (1995). A time series of daily average wind stresses was computed at each buoy, centered at Noon Universal Time (J.Y. Cherniawsky, Inst. Ocean Sci., Sidney, BC, pers. comm.) The stress at each node is statistically interpolated by Crabview from a weighted mean of these two time series, where the weighting is determined by the distance to each buoy using a Gaussian weighting system.

Wind stress was converted to wind speed at 10 m height using a drag coefficient of 1.2×10^{-3}. When computing wind drift, it is often assumed that surface currents move at some angle to the right of the wind, due to the Coriolis effect. Here, we kept this angle at zero due to the influence of the nearby shoreline. Winds blew more from the west at the Dixon Entrance buoy than they did at the northern Hecate Strait buoy.

Drift simulations

We focus on June and July for our simulations of larval drift, since this is the seasonal time period megalopae appear most likely to be present. We ran simulations for a period of 30 days, starting at 1 June, 15 June, 1 July, and 15 July, for the years 1991 to 1994, comprising 16 simulations. We used the wind fields from 1991-1994 and the baroclinic field from 1991.

Results

To evaluate how much dispersion might result from tidal action alone, individual megalopae were released at the same location at hourly intervals and subsequent simulated movements plotted (Figure 4). This movement can be extensive, even over time intervals as short as two days. However, the converse can also be true, as shown in the 10-d plot, where for 10 drifters released at one location, dispersal was extensive for the first 4 drifters but virtually nil for the last 6. In Figure 5, drift tracks are estimated where tidal movement has been smoothed out.

Sample simulation results from 1991 and 1994 are presented in Figures 6 and 7. Although Crabview permits up to 50 drifters, for clarity we display five or so at a time for each simulation. Generally, few drifters escaped Dixon Entrance to the west, but several hit the model's southern boundary across Hecate Strait, where they either stalled or drifted north once the winds reversed. Realistic tracks are thus not produced once this southern boundary is encountered. Any drifter launched in McIntyre Bay has a high probability of beaching along the shore of the

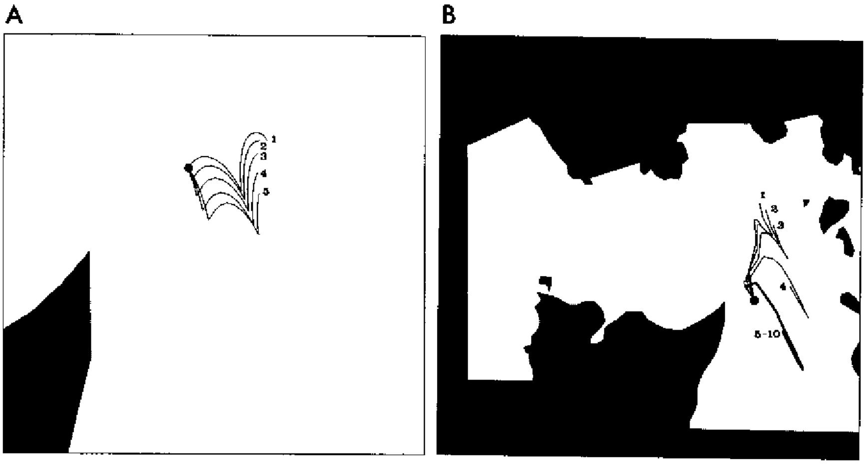


Figure 4. *Simulated drift tracks to demonstrate the amount of dispersion generated by tidal motion. An individual megalopa is released from each starting point at an hourly interval; megalopae are at the surface for 8-h nights and at 25 m depth for 16-h days. A. Two-day plots, plotting positions once an hour, starting at midnight, July 1, 1994. B. Ten-day plots, plotting positions once a day, starting at midnight, July 1, 1991. ● = start locations; numbers are consecutive drifter releases.*

bay. No drifter launched in Dixon Entrance found its way onto the beach of Dogfish Banks.

Discussion

On the basis of larval crab dispersal patterns presented here, the Rose Spit Eddy appears capable of retaining Dungeness crab larvae within Dixon Entrance, at least for a period of 30 d. In this sense, Dixon Entrance crab larvae may be benefiting from the horizontal estuarine circulation pattern in Dixon Entrance in a manner similar to how Strait of Georgia larvae benefit from the vertical estuarine circulation pattern in Juan de Fuca Strait. In both cases, larvae are able to maintain their relative geographic position in a complex current regime. Since the eddy appears to be a stable feature in winter, it may be able to retain all Dungeness crab larval stages during the four-month larval developmental period.

A contrasting situation appears to occur in Hecate Strait. Before the spring transition in flow direction (usually April), currents in northern Hecate Strait appear to offer little opportunity for larval retention. Drifting objects are relatively rapidly transported through the Strait into

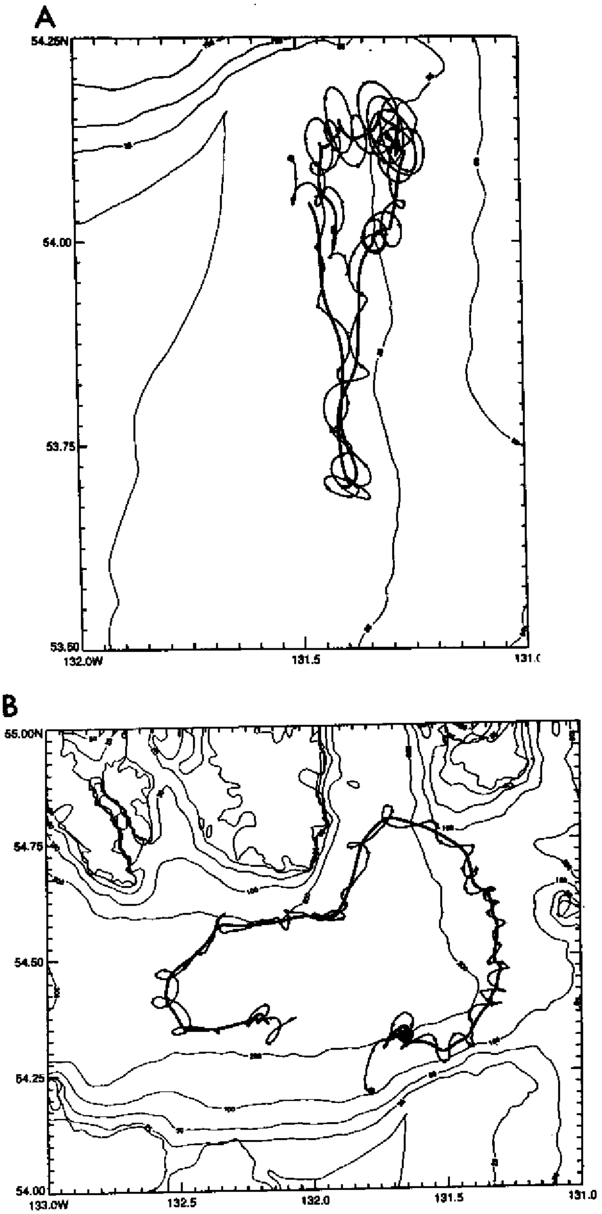


Figure 5. Sample drifter tracks (thin lines) from July 1991, and the estimated track where tidal motion has been smoothed out (thick line).
A. northern Hecate Strait near Rose Spit.
B. Dixon Entrance. Depth contours in meters.

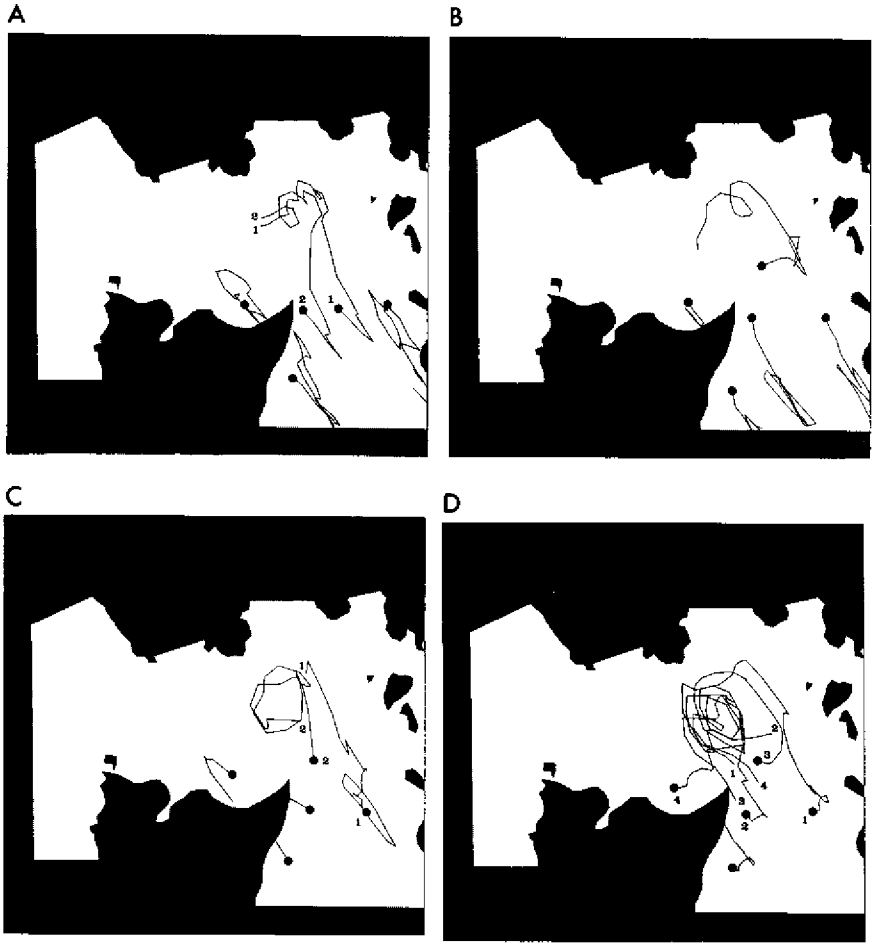


Figure 6. Simulated 30-day drift tracks, plotting positions once a day, for megalopae that are at the surface for 8-h nights and at 25 m depth for 16-h days in 1991. Drifting start dates: A. June 1. B. June 15. C. July 1. D. July 15. ● = start locations; numbers indicate start and end points of specific tracks for easier identification.

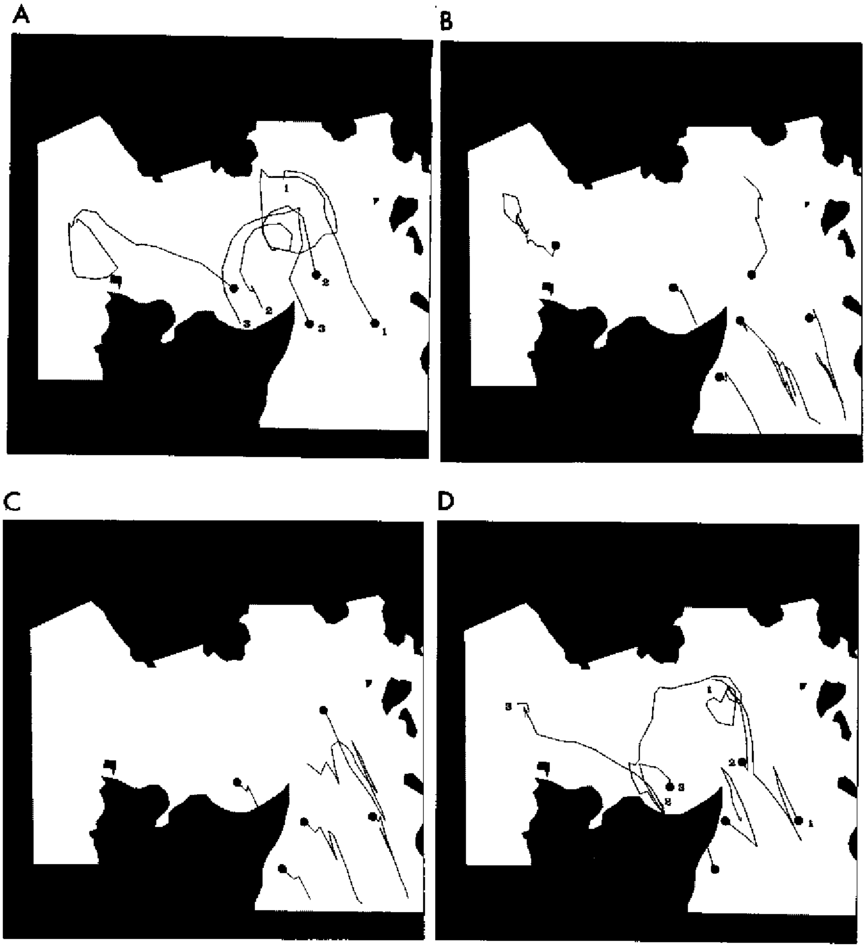


Figure 7. *Simulated 30-day drift tracks, plotting positions once a day, for megalopae that are at the surface for 8-h nights and at 25 m depth for 16-h days in 1994. Drifting start dates: A. June 1. B. June 15. C. July 1. D. July 15. ● = start locations; numbers indicate start and end points of specific tracks for easier identification.*

Dixon Entrance. Dungeness crabs off Washington and British Columbia start hatching their larvae in late winter, when it is possible for larvae to drift northward from off Vancouver Island into Hecate Strait and then into Dixon Entrance. Evidence for such movement is provided by a drift card study carried out in 1992 (C. Ebbesmeyer, Evans Hamilton Consultants, Seattle, WA, pers. comm.). Several thousand surface drift cards were released in several regions of Juan de Fuca Strait, more than 900 km to the south of Dixon Entrance. About 100 drifters were found a month later on the shores closest to Dogfish Banks, on Rose Spit and in McIntyre Bay. The currents that pushed these drifters north exist only in winter, though, and by about mid-April the general direction of coastal flow has changed (Crawford et al. 1988) and long northward drift tracks become unlikely.

The current pattern we report here for northern Hecate Strait also contrasts to that reported by Crawford et al. (1990) for southern Hecate Strait in winter. They described an eddy which they believed was capable of carrying ichthyoplankton across the strait.

During the June-July period considered in this study, simulated drift of larvae in Hecate Strait resulted in no clear pattern of overall movement. The best opportunity for large-scale larval retention in northern Hecate Strait would appear to result if most crab egg hatching occurred after the spring transition, either because of later-than-expected egg hatching or a particularly early spring transition. We have no data at this time to suggest either of these events occurred around 1989, thereby allowing the exceptionally large year class now being fished in Hecate Strait at this time to settle there. Unfortunately we are unable to model larval crab transport in the whole of Hecate Strait to evaluate how long larvae might be retained, as the detailed water property components required to run the model in the central and southern parts of Hecate Strait are unavailable. There is a suspicion that the modeled residual tidal currents on Dogfish Bank are somewhat larger than actual tidal currents (P. Cummins, Inst. of Ocean Sciences, Sidney, BC, pers. comm.), but we believe this discrepancy will not influence the conclusions outlined here.

The oceanographic data we use are from 1991, and we have at-sea wind data extending back only to 1991. There are wind data from land-based stations extending back further in time, but such data are difficult to extrapolate to wind conditions at sea, particularly given the size of the study area. Consequently, it is impossible for us to state what factors led to the 1989 large crab settlement in Hecate Strait. No comprehensive crab surveys have been conducted there, so we do not know if year classes subsequent to 1989 are also well above the recent long-term average settlement number (as indicated by fishery landings). Consequently, we do not know if the large crab settlement in 1989 was the result of an unusual oceanographic or meteorological event, or was the result of a sustained change in general oceanographic pattern in comparison to the average pattern present in the preceding decade. Although our oceanographic data were collected in 1991, our data base, as mentioned above, does not include all required Hecate Strait components, so we cannot simulate ultimate destinations of crab larvae located in Hecate Strait as a whole. Settlement of megalopae on Dogfish Banks may require winds toward the west at the appropriate time for larval settlement, much as substantial megalopal settlement in nearshore areas around Tofino appears to require southeasterly storm winds (Jamieson et al. 1989).

Acknowledgments

Crabview is our name for the Dixon Entrance version of Tideview/WIN Professional®, developed for this project by Adrian Dolling of Channel Consulting of Victoria, BC, Canada. Drifter and water property measurements were taken with the assistance of Axys Environmental Consulting and the Canadian Hydrographic Service. Current vectors in Figure 3 were provided by Anne Ballantyne. We thank Ian Perry and Patrick Cummins for their constructive reviews of this manuscript.

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High Latitude Crabs: Biology, Management, and Economics
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Does Intense Male Harvest Limit Egg Production of Protected Female Stocks of Dungeness Crabs?

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Extended Abstract

In many crab fisheries, commercial harvest of female crabs is prohibited, but harvest of male crabs above a minimum size limit is unrestricted. In Dungeness crab fisheries from California through British Columbia, resulting commercial fishery exploitation rates on male crabs have exceeded 90% of the preseason abundance of legal size males in some recent years (Gotshall 1978, Methot and Botsford 1982, Hankin 1985, Smith and Jamieson 1989). Although minimum size limits for male Dungeness crabs are in principle designed to allow male crabs to mate at least once prior to fishery vulnerability, Smith and Jamieson (1991) proposed that large female Dungeness crabs (those exceeding 140 mm carapace width) might have difficulty finding suitable large mates. If females did experience difficulty finding mates in intensely exploited populations, then a shortage of large males might lead to reduced egg production of females and consequent long-term reduction in recruitment.

Smith and Jamieson's (1991) proposition relied substantially on measurements of male and female crabs collected in premating embraces (Butler 1960). In this species, male crabs can apparently sense that female crabs are near molting and they clasp females in a premating embrace until the time that the female molts. Just after the female molts, mating takes place between the soft-shelled female and the hard-shelled male. Thus, the actual size of a female at time of mating is reflected by her postmolt carapace width, whereas typical premating embrace measurements are for the hard-shelled carapace width of females prior to molting.

In this paper, we critically examine the merits of Smith and Jamieson's (1991) proposition with respect to Dungeness crab populations and fisheries in northern California and in the Fraser River area, British Columbia. Evidence we consider in this examination consist of the following: (a) measurements of carapace widths (CW) of male and female Dungeness crabs collected in premating embraces in northern California in 1992, 1993, and 1995, and in British Columbia in the 1950s; (b) molt increment data for the same periods that allowed observation or prediction of the postmolt sizes of females collected in premating embraces; (c) size frequency data for adult female Dungeness crabs collected from nonselective experimental traps (see Diamond and Hankin 1985) fished in northern California in 1982, 1983, and 1992-1995, and in British Columbia during 1969-1970; (d) dissections of reproductive tracts of 587 adult female Dungeness crabs collected shortly following the molting/mating season in 1995; (e) fitted fecundity vs. carapace width regressions for northern California crabs collected in 1983, 1992, and 1993; and (f) hypothetical calculations of total egg production among a sample of female crabs believed to represent population size structure during 1992.

Our examination of the evidence listed above has led us to the following conclusions: (1) Based on premating embrace data, minimum carapace width of mating male Dungeness crabs generally exceeds the postmolt carapace width of female Dungeness crabs. Thus, intensive fisheries on males might limit mating opportunities among female crabs exceeding minimum legal size for males (154 mm CW in British Columbia and 159 mm CW in California, Oregon, and Washington), but are unlikely to restrict mating among smaller female crabs. (2) In northern California and in the Fraser River area, British Columbia, female crabs in excess of the minimum legal size for male crabs comprise a very small percentage (generally less than 2%) of the total population of female Dungeness crabs. (Also, Hankin et al. [1989] and Mohr and Hankin [1989] reported that annual molting probabilities are close to zero for female Dungeness crabs > 155 mm CW.) (3) Presence of sperm plugs in vaginas and presence of sperm in spermathecae of large (> 150 mm CW) freshly molted female Dungeness crabs was no less than presence in smaller female crabs; 39 out of 40 such large crabs had evidence of sperm plug presence, a definitive indicator of recent mating. (4) Hypothetical calculations of total egg production of female crabs showed that even in the most extreme scenario, if no adult females in excess of the minimum size limit (159 mm CW) for males were mated, impact on total egg production would be small (< 5%).

We conclude that there is no evidence in support of a proposition that intensive harvest of male Dungeness crabs limits mating success of females in the northern California and Fraser River area, British Columbia, fisheries. Because sizes of female crabs in Oregon and Washington appear similar to those in California (Hankin et al. 1989), we believe that this conclusion applies also to fisheries in Oregon and Washington. In Alaska, however, female Dungeness crabs appear to grow to larger sizes and the minimum size limit for male crabs is approximately 165 mm CW (T. Shirley, Univ. Alaska, Juneau, pers. comm.). We suspect that our conclusions apply also to Alaskan Dungeness crab fisheries and populations, but the larger size of females in that area warrants an independent examination of this important issue.

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Conceptual Modeling of Brood Strength of Red King Crabs in the Bristol Bay Region of the Bering Sea

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Abstract

Productivity of red king crab (*Paralithodes camtschaticus*) in terms of brood strength fell off following the mid-1970s, well before the heaviest catches of the late 1970s and 1980, and prior to the decrease in mature stock biomass. This indicates that the fishery was not responsible for the decline of productivity, though it contributed to the final decline in mature biomass. A statistically significant relationship was found between brood strength and intensity of the Aleutian Low atmospheric pressure system. From a regional workshop we developed a stage-by-stage table of life history events with ecological processes pertaining to productivity and survival rates. The information included the location and timing of eight life stages, along with the coincident physical oceanographic and biological factors that could influence the productivity and survival rates of the stages. Hypotheses emerged relating survival to physical factors: (1) a critical number of degree-days is necessary to bring on ovarian maturation; (2) after fertilization cool temperatures will delay hatching, and high temperatures will increase egg mortality; (3) a high percentage of successful hatch is linked to an optimum temperature; (4) timing of hatching depends on a chemical cue that is related to the abundance of a particular diatom; (5) for the larval stages, water-mass mixing due either to tide or Ekman transport increases nutrients used in primary production and consequent larval growth and survival; and (6) high-profile, rocky bottom with sessile fauna is critical for survival of the glaucothoe larval stage during settling, and consequently, an increase in the strength of currents moving larvae away from this bottom type would increase mortality. Other hypotheses were related to predation and biological factors. These ecological relationships were redesigned as graphical functions and set into the structure and logical flow of the conceptual aspects of a simulation model. The comprehensive conceptual model showed the simultaneous influence of particular factors on several life stage processes. Inferences were drawn for decadal period dynamics, implications for fishery management, and needs for at-sea research to clarify understanding.

Introduction

The objectives of this paper are (1) to develop the accumulated body of information on year-class strength formation and survival of the red king crab (*Paralithodes camtschaticus*) into the conceptual structure of a simulation model and (2) from the synthesis of the conceptual model, to form proposals for new process-oriented studies that could improve understanding of formation of year-classes, i.e., brood strength. The data and information on processes surrounding formation of brood strength have been well developed through many years of research by many people. We invited a number of specialists to a modeling workshop in 1994 (Tyler and Kruse 1995) to develop a unified information base and a set of hypotheses from existing knowledge. The workshop allowed an intensive review of knowledge on mortality, growth, productivity, and life history of king crabs.

After the workshop we expressed these hypotheses as graphical and mathematical functions of processes that apply to several stages of development from egg to adult, and then put these functions into a logical flow of a conceptual simulation model. Because we were able to fit parameters to very few of the functions, we operated on a graphical basis rather than a dynamics basis. As a consequence we chose to leave equations out of this paper and to explain the work in a graphical manner.

This exploratory model was used to examine the possible effects of physical and biotic factors on year-class strength formation in the Bristol Bay (i.e., Eastern Bering Sea) stock of red king crab. The model was developed by first specifying life history stages that seemingly have varying, stage-specific rates of survival associated with environmental changes from year to year. Processes were incorporated into the model in eight stages as follows: development of fecundity; mating success; fertilization rate; hatching success; survival of zoea larvae, glaucothoe larvae, juveniles, and adults. We will show that the model gives insight into the observations and experiments necessary for understanding the changes in year-class strength and age structure and also highlights processes that lead to change.

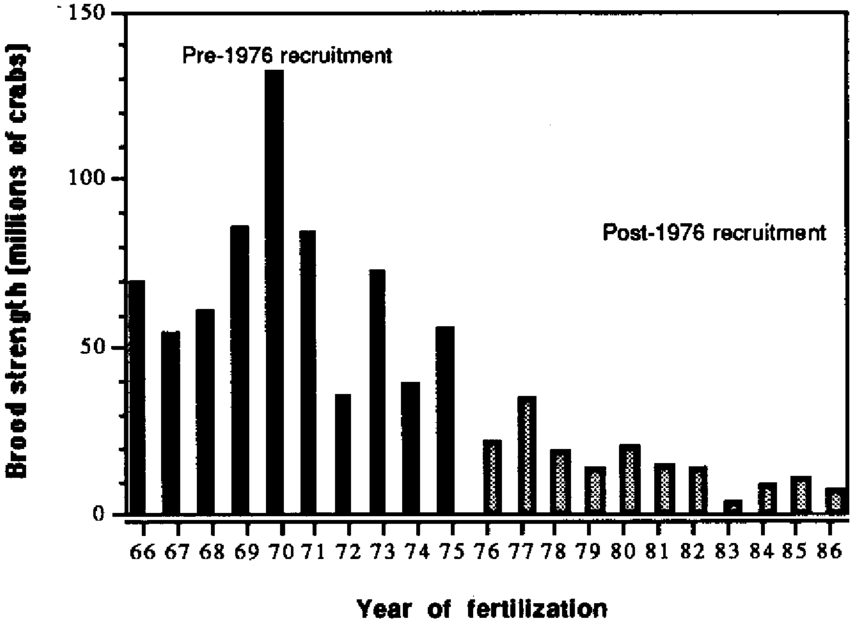


Figure 1. Brood strength of Bristol Bay red king crab determined at age-7 and plotted on the year of fertilization. The period of high brood strength, or recruitment, is given with dark columns, and the period of low brood strength is given with open columns for emphasis.

Statistics of Brood Strength and Catch

Brood strength for the period 1966 to 1986 has been previously estimated with a published length-based model (Zheng et al. 1995). The time series shows a decade of high brood strength followed by a decade of weak brood strength (Figure 1). The period of consistently low brood strength seems to have begun in 1976. Zheng et al. (1995) compared this recruitment series with the spawning biomasses that produced the year-classes in a plot of brood strength versus spawning biomass (Figure 2). They fitted a Ricker stock-recruitment function to the data, and concluded that the stock could be showing density dependence. It appeared that once the stock reached a low level due to very large catches in 1979 and 1980 (Figure 3), the stock lost its ability to recover in the face of continued low catches. The relationship between brood strength and spawning stock is not random (Figure 2), but that the large broods of the late 1960s and early 1970s brought about an increasing spawning biomass through 1978 despite the high catches of as much as 40,000

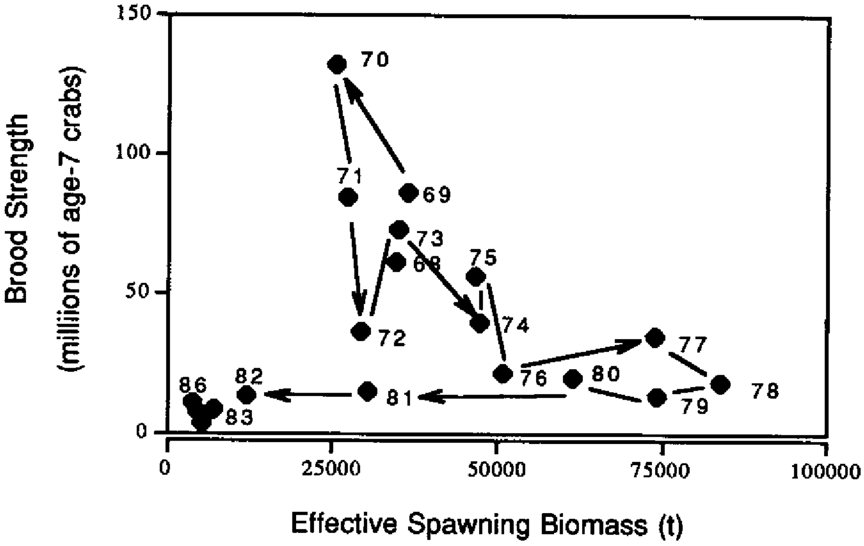


Figure 2. Relationship between brood strength and spawning biomass. Numbers beside points indicate year of fertilization, while arrows show the sequence of years.

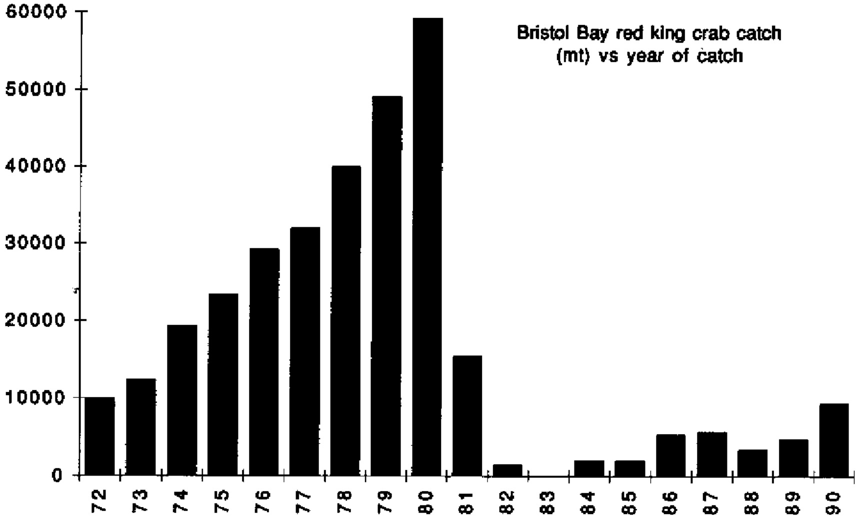


Figure 3. Bristol Bay catch of red king crab (metric tons) plotted on year of catch.

metric tons in this period. Productivity expressed as brood strength fell off after the mid-1970s, well before the heaviest catches of the late 1970s and 1980, and prior to the lowering of the biomass of the mature stock (Figures 2 and 3). The moderate stock size of 1981 and the lower stock sizes thereafter did not result in subsequent high brood strength. It is likely that the stock was so depressed that the small catches plus the bycatch mortality in some trawl fisheries served to prevent the rebuilding of the stock under the new, lower reproductive capacity.

It is possible, however, that other factors entered the picture in the mid-1970s to lower the productivity of the stock. From the plot of brood strength versus spawners (Figure 2) one might ask: why didn't the 1981 stock biomass produce the same size broods as did similar stock sizes in the late 1960s and early 1970s? Were the low brood strengths produced from 1976 through 1980 due just to density dependent interference, or was productivity lowered due to a coincident change in ocean factors? Either the hypothesis of density dependence or extrinsic environmental factors can be supported.

It is well known now that a shift in ocean climate occurred in the North Pacific Ocean in the mid-1970s. A change in the intensity and position of the Aleutian Low occurred that in turn brought about a number of other physical changes (Trenberth and Hurrell 1994). We plotted the January pressure anomalies for the North Pacific since 1966 for the area of the Pacific Ocean between 20° and 60°N latitude (Figure 4; Niebauer, University of Alaska Fairbanks, unpublished data). Except for three years the pressure was above average from 1966 though 1975 inclusive, and from 1976 to 1988 the pressure was lower than normal. It was during this intense low pressure that brood strength was progressively reduced. When we linearly regressed the king crab brood strength against the atmospheric pressure changes (Figure 5), we found a significant relationship ($r = 0.596$, $p < 0.01$, d.f. = 18). In making this calculation we removed the single 1970 brood strength outlier. Of course atmospheric pressure changes do not kill king crab, and so we have not found the specific cause of mortality. It is likely that a combination of events have acted simultaneously through the complex life history of the species to produce the lowered brood strength. Unfortunately many measures will correlate with this fairly simple decline in brood strength and barometric pressure. Therefore we suggest that further exploration of correlation statistics will only produce many significant coefficients but no new understanding.

Warmer winters were also a result of the low pressure. Several other species began a decline in biomass at this time in the eastern Bering Sea, including Greenland turbot (*Reinhardtius hippoglossoides*), fishes of the family Zoarcidae (Bakkala 1993), red-legged and black-legged kittiwakes (*Rissa brevirostris, R. tridactyla*) (Springer 1993), and Pribilof fur seals (*Callorhinus ursinus)* (Castellini 1993). Salmon showed increases in stock sizes (Beamish and Bouillion 1993), as did several species of groundfish

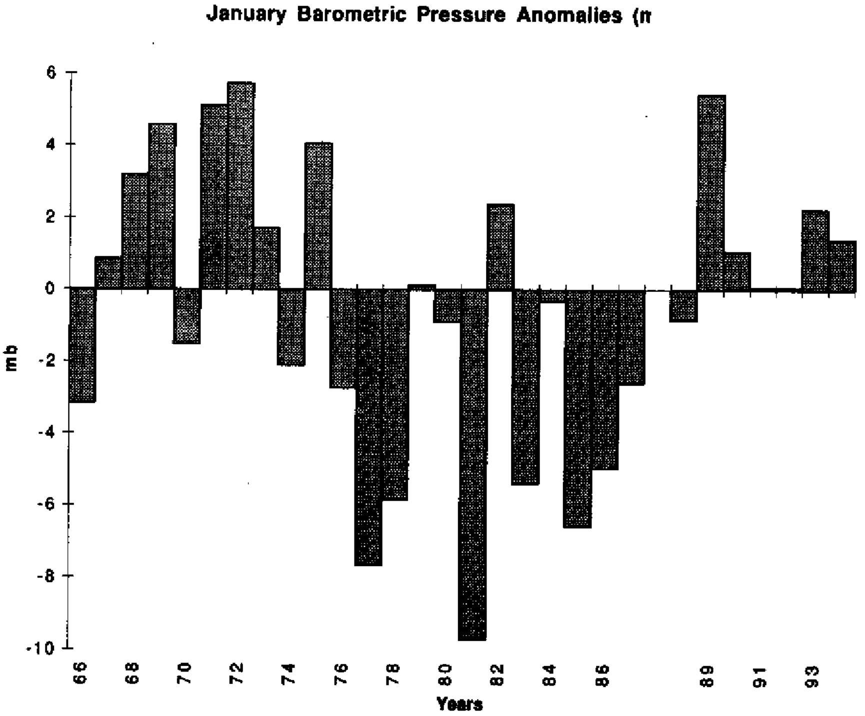


Figure 4. North Pacific barometric pressure anomalies for January 1966 to 1994. Each column is the value of the mean pressure in January over the area 20°N to 60°N over the Pacific Ocean. Data are from the Climate Research Group (D. Cayan) Scripps Institute of Oceanography, University of California, San Diego.

including rock sole (*Pleuronectes bilinearis*) and Pacific cod (*Gadus macrocephalus*), both known to be predators on young king crab (Bakkala 1993). The source of these broad changes is to be sought in wide ranging phenomena such as would accompany climate shifts.

Development of Hypotheses for the Model

To avoid a somewhat mechanical statistical procedure of correlating many data-series with brood strength, we re-examined accumulated biological information about red king crabs and developed a comprehensive conceptual model of processes. We identified the key phases of crab life history that have processes contributing to year-class strength, and wrote a stage-by-stage description of the life history events for the red king crab. The events included location and timing of the life stages,

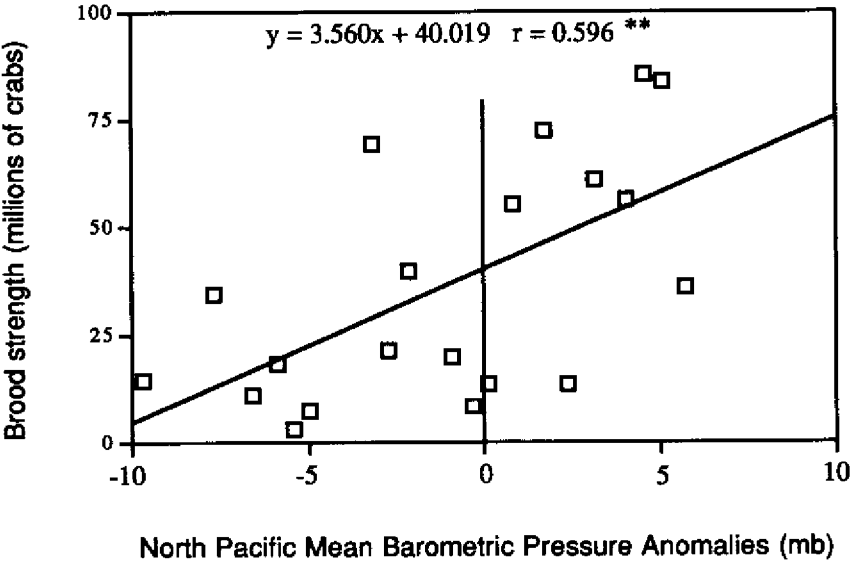


Figure 5. Brood strength versus mean barometric pressure anomalies in mb for the period 1966 to 1986 inclusive. The point for 1970 has been deleted from the fit because it was an outlier and out of the series. The correlation coefficient is significant at the 1% level.

plus the coincident physical oceanographic and biological events that could influence the productivity and survival rate of the stages. The result was a series of hypotheses related to year-class strength expressed in a table called an Events-Time Table (Table 1). We call this approach to model development the Events-Time Modeling Procedure (Tyler 1992). The statements and hypotheses about biological relationships are given in Table 1, and were all contributed by the workshop participants. These hypotheses will be discussed in the next section in the context of the functional relationships that result from them.

Development of Functional Relationships

A functional relationship is expressed as a mathematical equation describing the change of a dependent variable (y) with changes in the values of an independent variable (x). The form may be a difference equation or a differential equation showing a rectilinear or curvilinear response of y with change in x. These relationships can also be expressed graphically, the form that we have chosen for this paper.

The modeler turns the hypotheses of the biologists into functional relationships that can be used in a quantitative model. The functional

Table 1. Events-Time table of life history stages, their depths, the months of occurrance(Jan=1, Feb=2, etc.), and hypotheses.

STAGE / ACTIVITY	DEPTH	MONTHS	OCEANOGRAPHIC HYPOTHESES	BIOLOGICAL HYPOTHESES
1. Fecundity-development of egg clutch vs barrenness. Generally 0 to 350 K eggs / female.	30 -200 m	7 - 1	-warm water may give an increase in egg mortality due to development of parasites and disease. -there is a critical level of degree-day accumulation for full maturation - very cold temp may delay maturation of eggs to biennial spawning -maximum fecundity may depend on an optimum temp.	- fecundity is related to crab size - higher fecundity is linked to number of previous spawnings - senescence is possible in older animals - a molt may be skipped if egg development is delayed and eggs are resorbed - fecundity may depend on rations - parasites and pathogens may cause reduction of fecundity or sterility
2. Mating and egg fertilization	20 - 100 m	2 - 6	–	- fertilization rate is higher with larger males - the first female mated gets more sperm than does last female mated by one male. - female's aggregate, but males not always distributed in the same way as females. - Timing of mating depends on female's previous reproductive history as well as the water temperature.
3. Hatch timing	20 - 200 m	4 - 6	- For the temp range 2 - 5 C egg development time depends on accum. degree-days	- Primiparous spawners hatch eggs, then multiparous crabs - Need a water quality cue, perhaps from the diatom *Thalassiosira*
4. Percentage successful hatch	–	–	- at 28 C & higher larvae are not viable. There is a temperature level optimizing % viable hatch	- parasites (*Carcinonemertes*) may reduce fecundity

Table 1. continued

STAGE / ACTIVITY	DEPTH	MONTHS	OCEANOGRAPHIC HYPOTHESES	BIOLOGICAL HYPOTHESES
5. Larval survival (zoea)	<100 m	4-8	- Bristol Bay - Mixing due to high tidal currents of 40 - 50 cm/sec increases productivity; low non-tidal currents of only 3 - 5 cm/sec. - Wind from south can cause Ekman transport into Bristol Bay. - A lack of solar energy due to heavy cloud cover can delay the peak chlorophyll concentrations by 5 - 7 days.	- High concentrations of specific, concentric diatoms are needed, or starvation can result in 4 days. - Predation is by pollock, salmon, T. raschii - Diel vertical migration may be a retention mechanism
6. Settling larvae (glaucothoe)	0 - 50 m, on active bottom with sediments of rock, shell, boulder, often with a complex of high relief organisms like soft coral,	6-8	- Currents that move larvae away from the required habitat can increase larval mortality. Habitat seems obligatory.	- Cannibalistic nature of settled larvae leads to density dependent mortality. - Predation by sea stars, Pycnopodia
7. Juveniles. Age-1 to 6. Note, some age 5 crabs are likely mature.	age-1, 0-60 m age-6, 20-100 m	–	- Increased temperature gives increased molt frequency and size at age.	- Depth of habitat increases with age. - Food competition is likely with some flatfish species with major biomass increases in the 1980s. - Predation by Pacific cod, sole spp and sculpins include appendages of large molting crabs and whole crabs in smaller instars. - Sea otters are major predators
8. Mature stages. Ages 5 to 15 (possibly older)	–	–	- Molting frequency of males may drop as stock size decreases	- females grow more slowly than males. - Mature females are obligate spawners, molters subject to more predation if ratio of males to females is decreased

relationships of interest are expressions of the basic processes that in turn lead to temporal changes in a product of interest. In this case the product is brood strength. The basic processes are the physical or chemical events at a particular time, life history stage, or place that lead to changes in the survival or productivity of the animal. There may be biological factors such as predation that change survival rates. As an example of a functional relationship, the mortality rate of zoea larvae is postulated to be linked, among other things, to the concentration of diatoms of the genus *Thalassiosira* during May and June. Below a critical minimum concentration zoea survival is low (Figure 9, Fcn Q). Diatom concentration is positively related to survival rate, but with a progressively shallow slope so an asymptotic relationship is generated. That is, unit increments at low concentrations bring about greater survival change than do unit increments at high concentrations. More food brings about better health; however at higher diatom concentrations, unit increases would not be used as efficiently by the larva behaviorally or physiologically, and so would not have the same effect (the diminishing returns principle).

Thirty-five functional relationships have been identified that describe the hypothetical processes influencing brood strength (Figures 6 through 12). The relationships can be considered as two groups: those that are likely to bring about substantial interannual variation and those that are likely to cause little variation. The term "interannual variation" includes year-to-year and decadal-scale changes.

The following is the list of critical relationships. The letters refer to the functions given in figures 6-12. Some relationships are not included here but presented in a separate list of non-critical relationships.

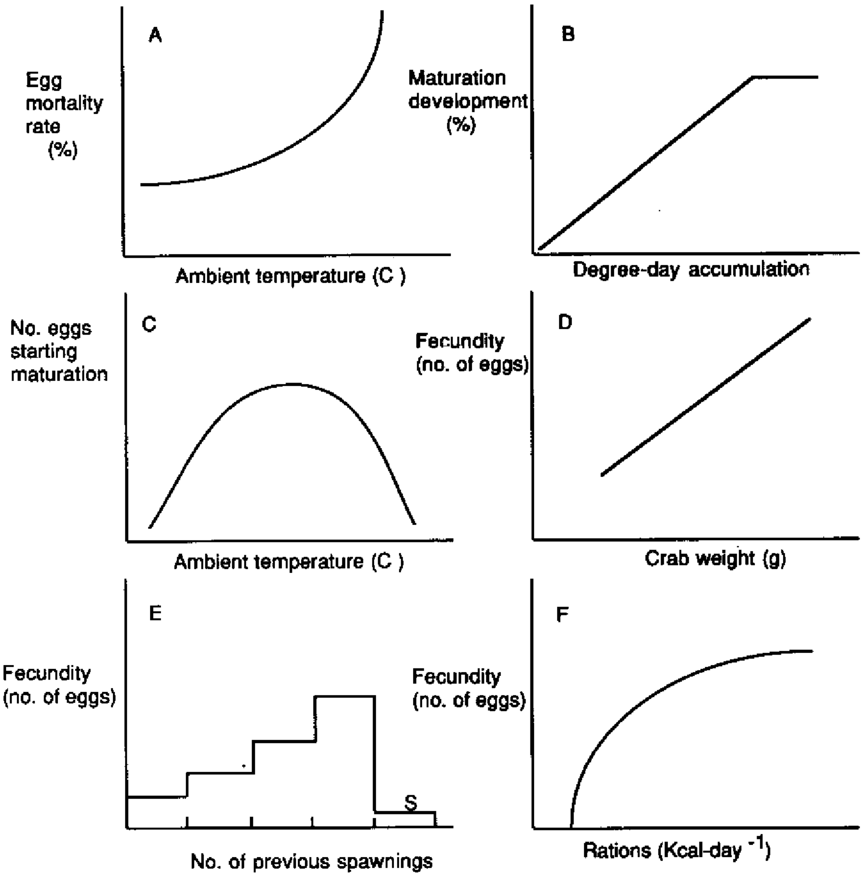
A. Egg mortality rate increases exponentially with ambient temperature. Climate change could cause high temperatures through several years and as a result effect increases in disease and parasitism to developing eggs, e.g., via the egg parasite, *Carcinomertes* sp.

B. Oocyte maturation is a function of degree-day accumulation. A reduction of accumulated degree-days is likely, at times, to cause some individuals to skip spawning, and in cold years, to interfere with reproduction potential of the stock.

C. Number of eggs starting the maturation process is a function of temperature.

D. Fecundity increases linearly with crab weight. Factors that cause decreased growth or decreased numbers of older, larger crabs, e.g., the fishery, will influence this relationship.

F. Fecundity increases asymptotically with rations (rate of food intake); the combined effects of ambient temperature and rations could cause changes stock fecundity.



Development of fecundity and the maturation process

Figure 6. Hypotheses expressed as functional relationships related to brood strength formation for Bristol Bay red king crab for the life history stages relating to fecundity and maturation processes.

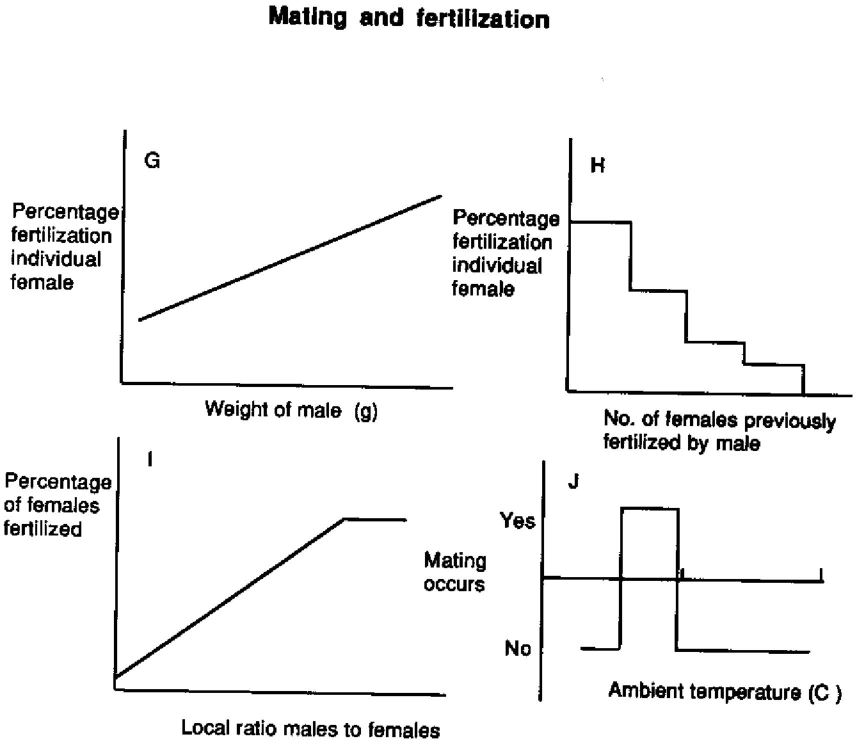


Figure 7. Hypotheses expressed as functional relationships related to brood strength formation for Bristol Bay red king crab for the life history stages relating to mating and fertilization processes.

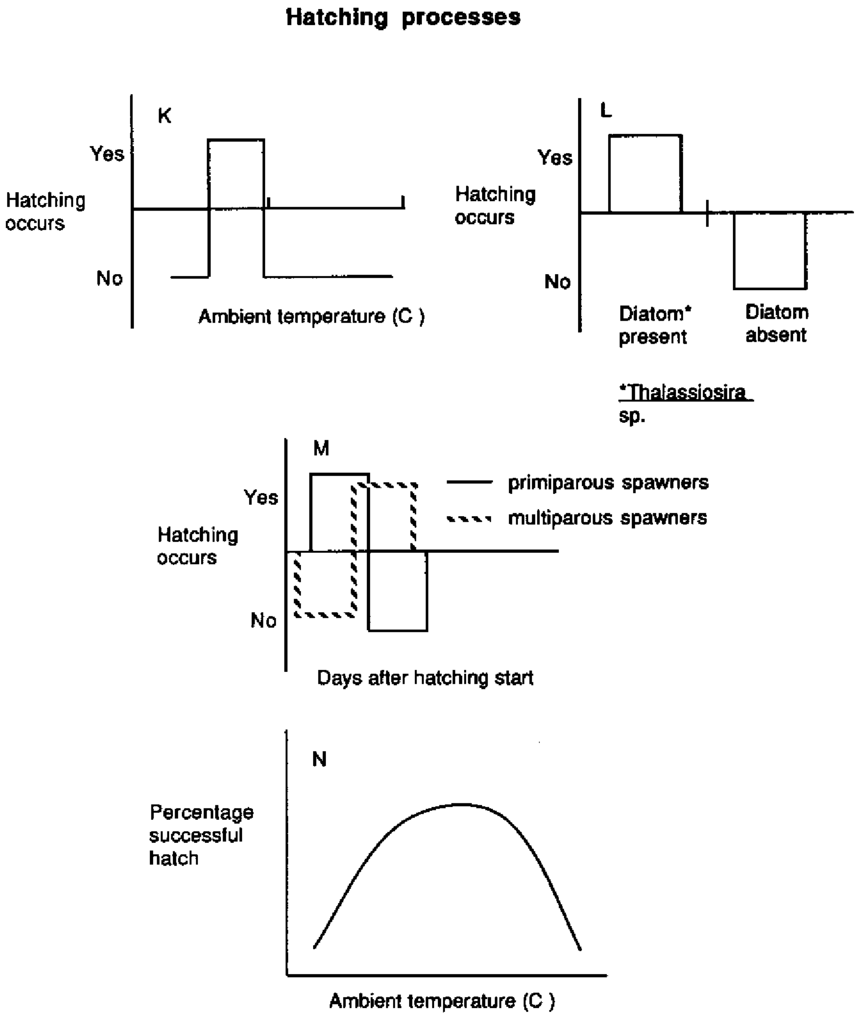


Figure 8. Hypotheses expressed as functional relationships related to brood strength formation for Bristol Bay red king crab for the life history stages relating to hatching processes.

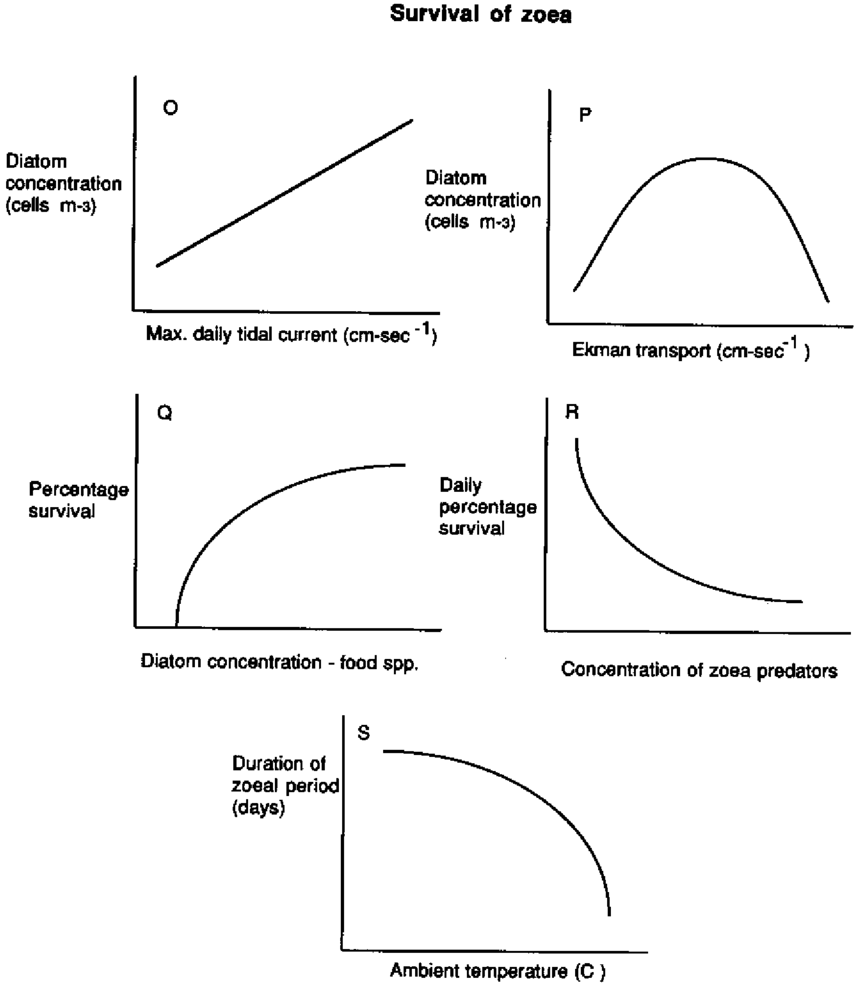


Figure 9. Hypotheses expressed as functional relationships related to brood strength formation for Bristol Bay red king crab for the life history stages relating to survival of zoea stage larvae.

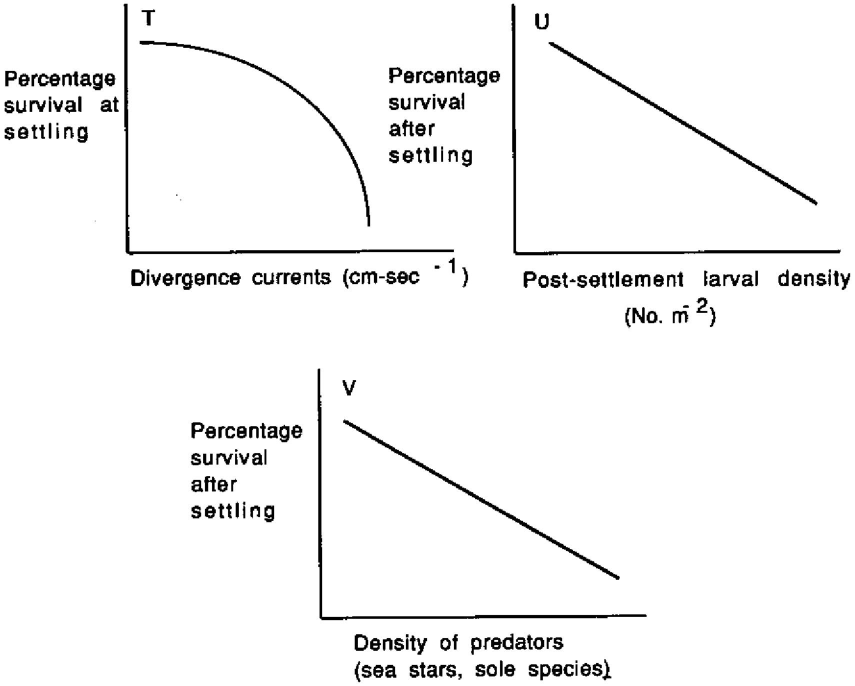


Figure 10. Hypotheses expressed as functional relationships related to brood strength formation for Bristol Bay red king crab for the life history stages relating to survival of glaucothoe larvae.

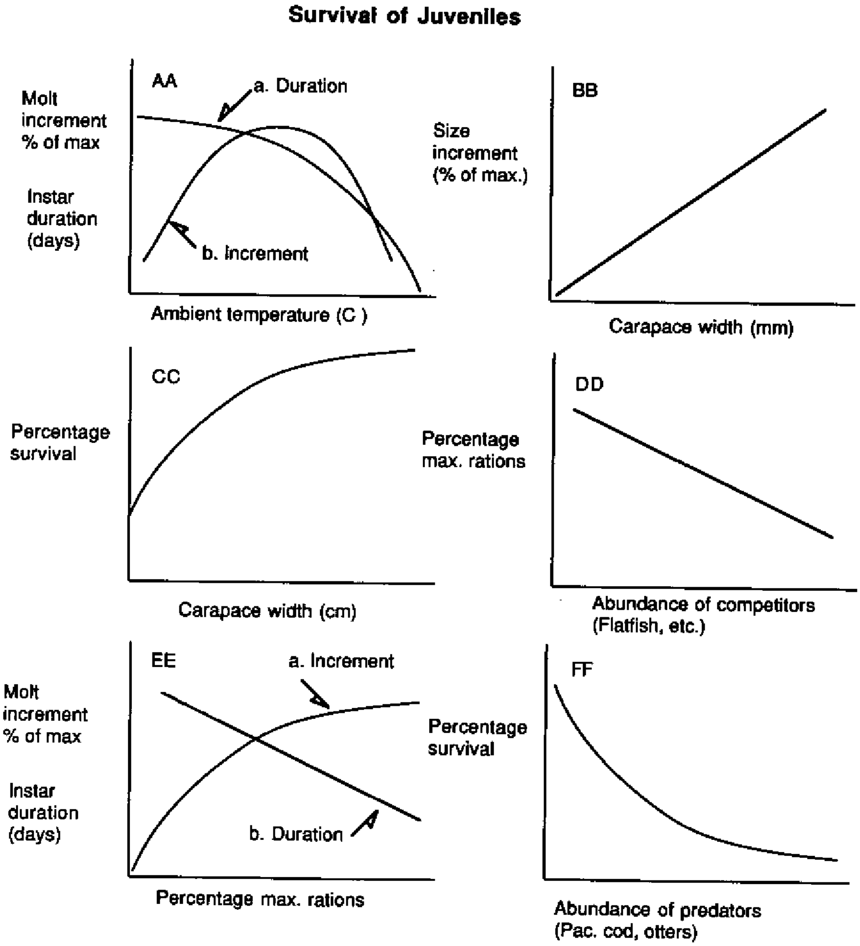


Figure 11. Hypotheses expressed as functional relationships related to brood strength formation for Bristol Bay red king crab for the life history stages relating to survival of juveniles.

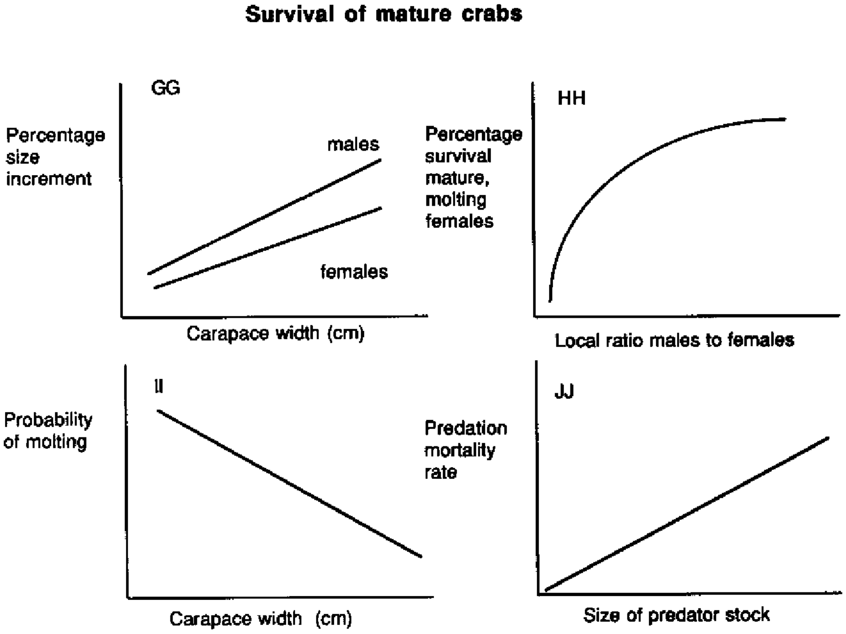


Figure 12. Hypotheses expressed as functional relationships related to brood strength formation for Bristol Bay red king crab for the life history stages relating to survival of mature crabs.

G. Percentage of eggs fertilized in a single female may depend on the weight of the male. Larger males have more sperm mass. The influence of the fishery will be felt through decreases in abundances of large males, effecting lowered fertilization rates.

H. Percentage of eggs fertilized in a single female depends on the number of females recently fertilized by the male. If he has fertilized two or three, the next female is likely to receive a smaller sperm mass. The number of copulations by a single male is less with a reduced male to female ratio as possibly influenced by the intensity of the male-only fishery.

I. The percentage of females mating and fertilized depends on the ratio of males to females in any small area, and is influenced by the abundance of males and the intensity of the fishery.

K. Hatching will not occur outside a specific temperature range. Because eggs require two years of nurturing, each egg represents a substantial bioenergetics investment. Fcn's K and L could determine the interannual variation in hatch timing, and therefore larval survival rate.

L. The presence of concentrations of diatoms of the genus *Thalassiosira* may be necessary for egg hatching.

N. Percentage of successful hatch depends on the ambient temperature.

P. Diatom concentration is a function of mixing generated by wind-driven Ekman upwelling. The survival of zoea depends on conditions for primary productivity.

Q. Percentage survival increases asymptotically as a function of primary productivity and diatom concentration.

R. The daily survival rate declines with the size of the predator stocks. Young walleye pollock and sockeye salmon are predators that occur in sufficient abundance to influence zoea numbers.

S. The duration of the zoeal period declines with increasing temperature. This relationship works in conjunction with Fcn R, a higher duration having increased predation mortality.

T. Glaucothoe survival depends on whether currents carry settling larvae to suitable habitat, specifically large rock substrate encrusted with a community of sessile invertebrates. The extent of this habitat is limited in Bristol Bay. If currents are strong in some years, the larvae could be swept beyond the nursery habitat and brood strength would be decreased.

U,V. The survival rate after settling, depends on post-larval density and the cannibalistic nature of the settled glaucothoe and also the density of predators. High densities would have greater percentage rates and could actually cause decreased brood size.

The juvenile and adult survival functions are all labeled with double letters.

AAa. The survival rate of juvenile stages due to predation decreases with increased instar duration, a function of temperature, and growth. Survival rate is dependent on crab size, larger sizes having higher survival.

AAb. The size of the molt increment is a function of the temperature.

BB. Size of molt increment also depends on starting size.

CC. Predator avoidance success increases with crab size.

DD. The potential rations for the crabs are dependent on the stock sizes of competitors.

EEa and EEb. Molt increment and instar duration also depend on ration size. Rations in turn are dependent on density of the competitors, DD.

FF. Survival rate is also dependent on the abundance of predators, particularly the abundance of fish and mammalian predators.

GG. The size increment at molting is dependent on the starting size of the crab.

HH. Survival rate is a function of the ratio of males to females because recently molted females are protected by males which grasp and defend molting females from predation by large fishes.

II. The probability of molting is dependent on the starting size of the crab.

JJ. The predation mortality rate is also dependent on the abundance of predators.

The less critical functional relationships are as follows:

E. Fecundity is dependent on the number of previous spawnings.

J. Although an acceptable range of temperature is required for mating, temperatures outside the range might be a rare event.

M. The graph gives the timing differences between primiparous and multiparous spawners, not likely to have interannual variation.

O. Tidal mixing would be about the same each year and so would not bring about interannual variation in biological response.

V. Survival of glaucothoe is related to benthic predators. It is not clear whether strong variability in population size occurs among benthic predators as a group. When some predators become scarce others may increase.

The Flow Logic of the Model

The model is represented with a flow chart of the Main Model and separate flow charts for each of the submodels. The Main Model flow chart (Figure 13) shows the sequence of the submodels as well as the physical oceanographic factors and predation rates that affect processes within each of the submodels. The Reproductive Submodel (Figure 14) is the first in the sequence and deals with the development of fecundity, the

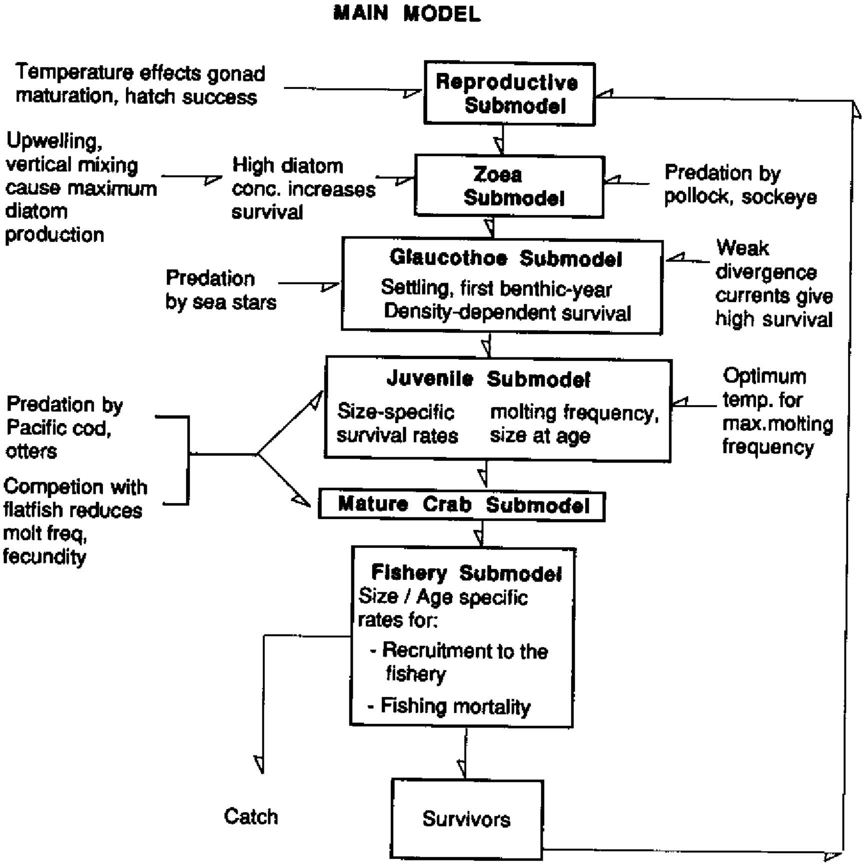


Figure 13. Flow chart of the cycle of modeled hypothetical relationships that lead to the formation of year-class strength of red king crabs. The model is iterated once per annum. The variables of the central boxes are influenced by relationships described to the sides of the chart. Only predation and the physical oceanographic factors are shown in this figure. More detail of all factors is given on individual model flow charts. The flow starts with the Reproduction Submodel and follows through to adult survivors.

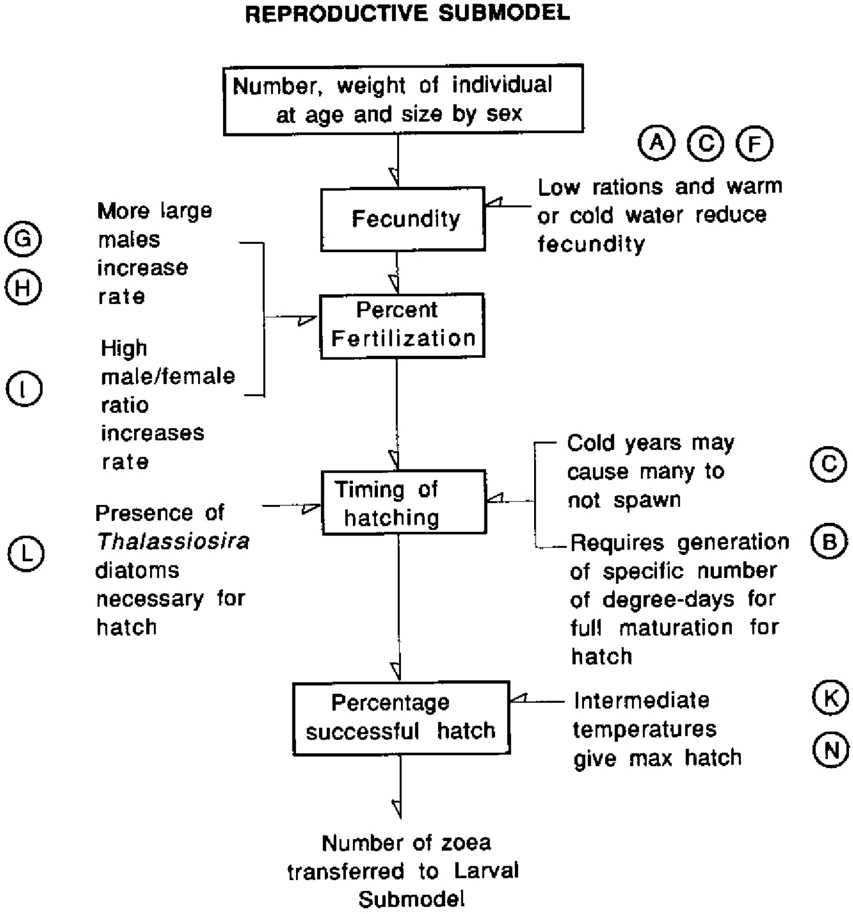


Figure 14. Flow chart for the annual Reproduction Submodel for year-class strength formation of red king crabs. The variables of the central boxes are influenced by relationships described to the sides of the chart. Letters refer to critical functional relationships. Key variables are likely to be temperature in Fcn's B and C as well as the presence of a diatom concentration, Fcn L. Both influence the timing of hatching and the linking of larvae with conditions for survival.

percentage of the eggs that are fertilized, the timing and percentage of the eggs that hatch successfully. The functional relationships are the processes of productivity and survival, and are represented by the letters described in the last section as depicted in Figures 6-12. Only the critical functional relationships are given on the model flow figures, and only these will be discussed in this section.

Fecundity is affected by the number of eggs that start maturation (Figure 14, Fcn C), the egg mortality rate of those eggs that start maturation (Figure 14, Fcn A), and the rations (Figure 14, Fcn F). The next step in the flow diagram is percentage fertilization. This is affected by size of the fertilizing male (Figure 14, Fcn G), the number of females recently fertilized by the male (Figure 14, Fcn H). The percentage of females fertilized depends on the availability of mature males (Figure 14, Fcn I). Once the eggs are fertilized and deposited on the female's abdomen, a specific number of heat units measured in degree-days is required for the development of the eggs to hatching (Figure 14, Fcn B). Because of this function, and also because of Function C, cold years may cause many crabs not to spawn. The presence of a concentration of the diatom, *Thalassiosira,* is necessary for hatching to commence (Figure 14, Fcn L). Optimum temperatures give maximum hatch (Figure 14, Fcn K and Fcn N).

The number of zoea hatched is entered into the zoea submodel (Figure 15). The daily zoea mortality rate is likely dependent on two factors: the availability of diatoms as food (Figure 15, Fcn Q), and the concentration of predators (Figure 15, Fcn R). The availability of diatoms is in turn dependent on the diatom concentration that varies with the intensity of Ekman transport (Figure 15, Fcn P). The duration of the zoea period decreases with increase in ambient temperature up to a point where further increase interferes with molting (Figure 15, Fcn S). The number of survivors is a function of the stage duration and the daily mortality rate.

The next life-history period is the benthic larva or glaucothoe stage, which is represented in the Glaucothoe Submodel (Figure 16). The zoea larvae at the end of the zoeal stage settle to the bottom to begin the glaucothoe stage. The success of settlement is influenced by the portion of the zoea that find critical hard-bottom habitat, influenced by the currents. If the currents are divergent from the needed habitat, higher mortality occurs (Figure 16, Fcn T). Glaucothoe undergo mortality from predation by other species (Figure 16, Fcn V) and from density-dependent cannibalism (Figure 16, Fcn U).

In the Juvenile Submodel (Figure 17), mortality is influenced by the length of time each brood spends at small instars because small sizes are vulnerable to predation. The smaller the size increment and the longer the duration of small instars, the higher the mortality. Effects of rations and temperature on growth rate and instar duration (Figure 17, Fcn EEa and Fcn EEb) are important processes in determining mortalities

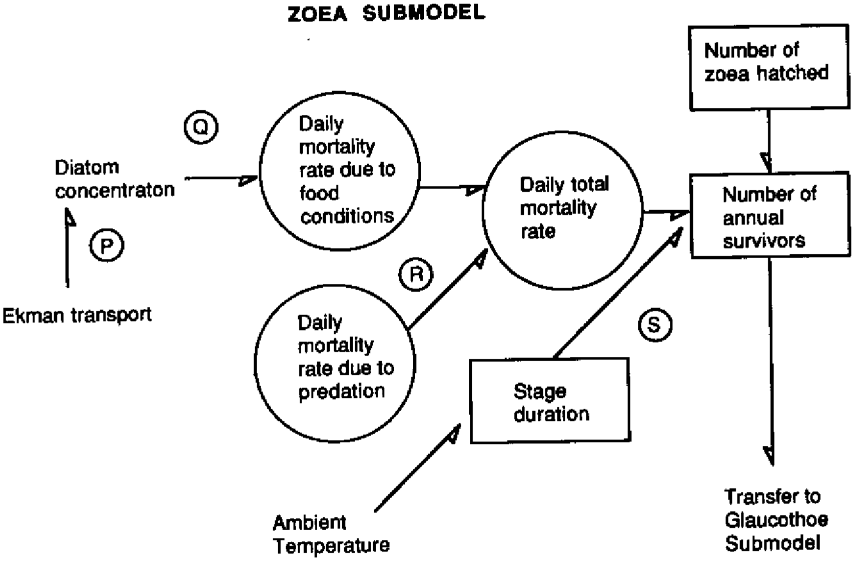


Figure 15. For the zoea stages the daily mortality rate is considered dependent on two main factors: the availability of diatoms as food (Fcn Q), and the concentration of predators (Fcn R). The availability of diatoms is in turn dependent on the diatom concentration that varies with the intensity of Ekman transport (Fcn P). The duration of the zoea period decreases with increase in ambient temperature up to a point where further increase interferes with molting (Fcn S). The number of survivors is finally a function of the stage duration and the daily mortality rate.

(Figure 17, Fcn AAa and Fcn AAb). The size of the competitor populations and the predator populations are, in turn, directly related to the number of survivors (Figure 17, Fcn FF).

The mature crab submodel (Figure 18) is the simplest of the system. The natural mortality depends on the portion of crabs in the softshell state at any time because of predation on these individuals. The portion of individuals molting is estimated depending on the initial size (Figure 18, Fcn II). The mortality rate also depends on the abundance of the predators (Figure 18, Fcn JJ), mainly Pacific cod and other large fishes. It also depends on the degree of protection provided to molting females given by the males. The ratio of males to females sets the portion of females protected (Figure 18, Fcn HH). A portion of the unpaired, molting females are eaten. Those having successful molts and surviving go on to a new size in the model (Figure 18, Fcn GG). A portion of the molting

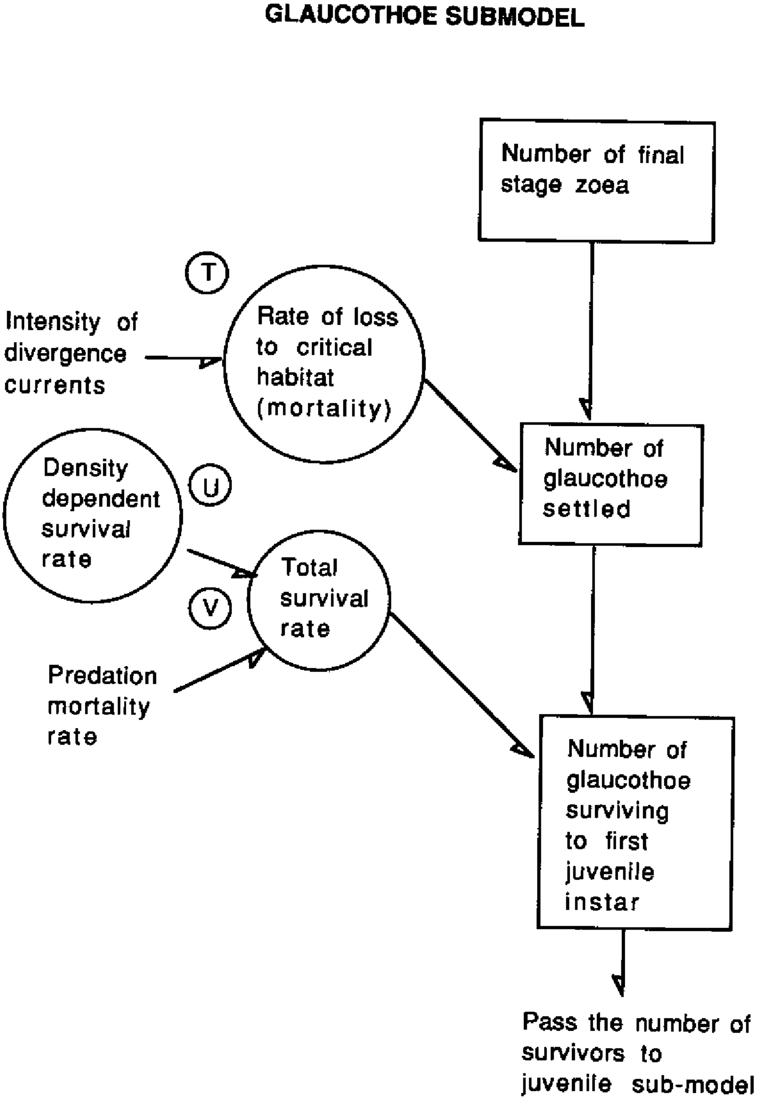


Figure 16. The life-history period of the benthic larva—the glaucothoe stage—is represented here. The final zoea stage molts and settles to the bottom in this new instar. The success of settlement is influenced by the portion of the zoea that find critical hard-bottom habitat, influenced by the currents. If the currents are divergent away from the needed habitat, higher mortality occurs (Fcn T). When the larvae are settled they undergo mortality due to predation by other species (Fcn V); they also experience density dependent cannibalism (Fcn U). Only critical functions are indicated by letters within circles.

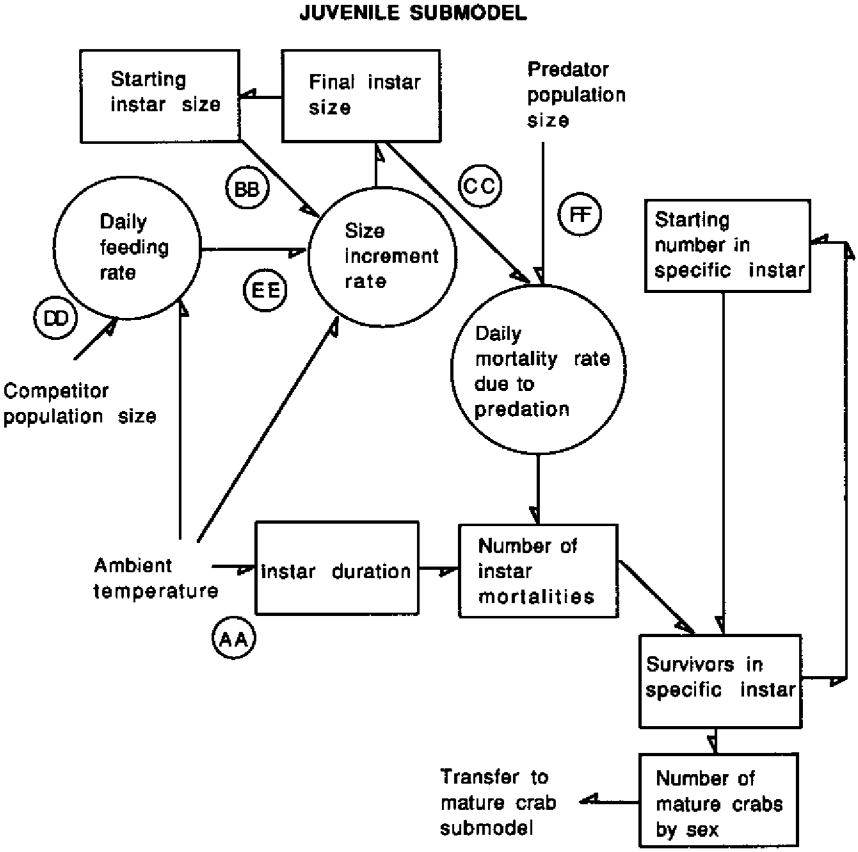


Figure 17. Mortality of juveniles is influenced by the length of time each brood spends at small-sized stages, because small sizes are vulnerable to predation. Growth rate and instar duration are important processes in determining the mortalities, in particular the relation between rations and molt increment and instar duration (Fcn EEa and EEb); and the relation between temperature and molt increment and instar duration (Fcn AAa and AAb). In turn the sizes of the competitor populations and the predator populations are directly related to the number of mortalities (Fcn FF). Only critical functions are indicated by letters within circles.

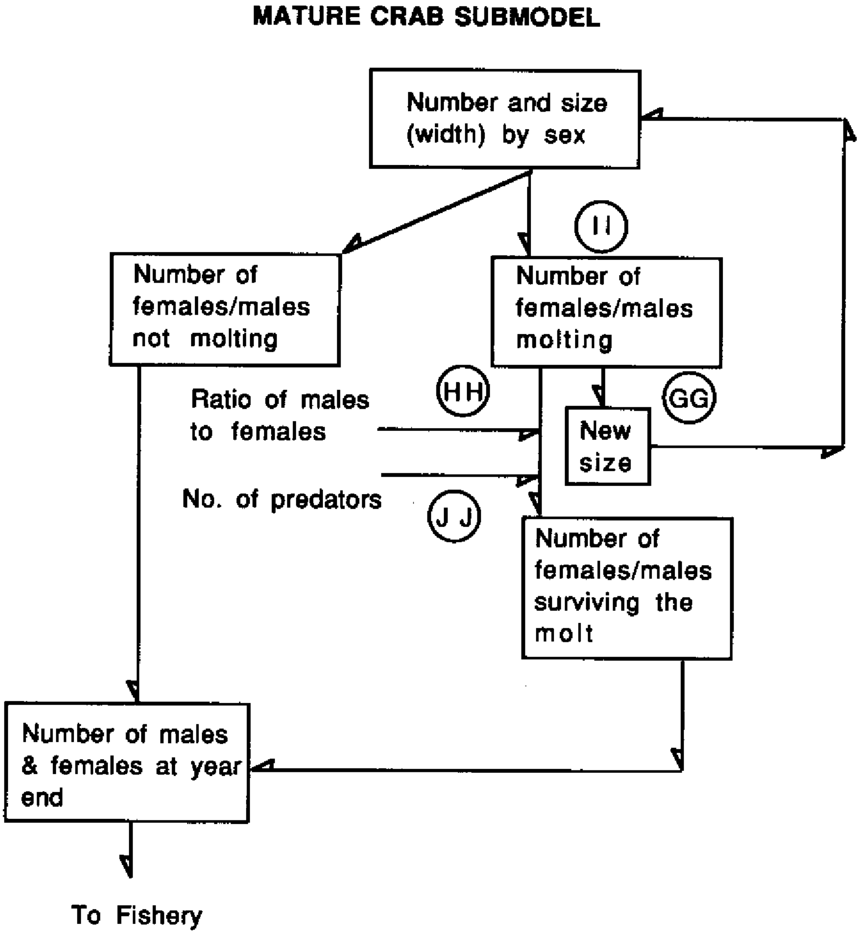


Figure 18. This Adult Submodel is the simplest of the system. The natural mortality depends on the portion of crabs in the softshell state. Mortality is due to predation on these individuals. The portion of individuals molting depends on the size (Fcn II). The mortality rate also depends on the size of the predator stock (Fcn JJ), mainly Pacific cod. It also depends on the degree of protection of molted females provided by the males. The ratio of males to females sets the portion of females protected (Fcn HH). Those having successful molts, and that survive, go on to a new size in the model (Fcn GG). A portion of the molting males also succumbs to predation, and as well a portion are taken as bycatch in the fishery. The catch is calculated with the standard Baranov catch equation. Only critical functions are indicated by letters within circles.

males also succumbs to predation, and as well a portion are taken as bycatch in the fishery. The catch is calculated with the standard Baranov catch equation.

Discussion

Red king crabs have a far more complex life history than the abundant groundfish that surround them and have been more common subjects of fishery oceanography studies. These extra complexities need to be included among the processes which model the natural history of the crabs and lead to brood strength variability. The females develop their unfertilized eggs for a year or more, then carry developing embryos for a year, a reproductive energy output not shared by most ocean fishes. Unlike most crabs that have a maturity molt and mate once at that time, mature red king crabs have the complexity of molting and mating each year. Mating and carrying embryos is more similar to the reproductive biology of the rockfishes (genus *Sebastes*). However they are far more complex than the rockfishes in that they have two types of larvae, the zoea instars and the glaucothoe instars.

Several predation hypotheses emerged from our synthesis. Indeed, predation, starvation, and advection are the three most commonly cited hypotheses to explain year-to-year variations in recruitment of marine species (e.g., Wooster and Bailey 1989). With regard to the egg stage, it was suggested that optimal temperatures might promote outbreaks of the egg predator, *Carcinomertes*. Kuris et al. (1991) found high rates of prevalence of *C. regicides* and three other undescribed nemertean egg predators in the mid-1980s in some areas of Alaska, such as Southeast Alaska and Kachemak Bay. A significant correlation between egg mortality and intensity of infestations led the authors to speculate that nemertean egg predators could impact recruitment in some local areas.

It was postulated that zoea mortality increased with predator density, such species as pollock and salmon. In a recent study, Wespestad et al. (1994) proposed that outmigrating juvenile sockeye salmon (*Oncorhynchus nerka*) may adversely impact red king crab brood strength by predation of larvae. This premise is based on a negative correlation between sockeye salmon abundance (lagged 4 years earlier) and king crab recruits (lagged 8 years earlier). Although the potential for salmon-crab interactions is intriguing, these lags are questionable. Stevens (1990) showed that king crab recruits enter the Bristol Bay fishery over ages 7-12 depending on temperature. Further, depending on the stock and brood year, sockeye salmon from Bristol Bay lake systems smoltify as 1- or 2-year-olds, or in their second or third year if measured from time of egg deposition, and return to spawn after spending 2-3 years at sea (Burgner 1991). Because peak cycle runs are dominated by fish that spent two years at sea (Eggers and Rogers 1987), the appropriate lag from adult salmon to juvenile outmigrants is 2 years not 4 years prior.

This 2-year lag causes the abundance of outmigrants from strong salmon runs prior to 1970 to coincide with years of high crab recruitment, contrary to the recruitment hypothesis.

Unfortunately, few field studies on feeding habits of outmigrating sockeye salmon have been conducted. In Bristol Bay, total prey consumption and growth rates of juvenile sockeye salmon are very low until they pass through the inner bay to offshore waters (Straty 1974). In Bristol Bay (Straty 1974) and the Strait of Georgia (Healy 1980) larval decapods (i.e., crabs and shrimps) generally constitute small percentages of food of juvenile sockeye salmon, but these studies reported stomach contents by volume rather than number of prey.

Other predation hypotheses involved glaucothoe, juvenile, and adult king crabs. As with salmon, hypotheses about effects of groundfish predation on red king crab year-class strength emerged from observations of recent increases in the abundance of some groundfish species (Bakkala 1993). Frequently invoked groundfish predation hypotheses regarding red king crabs involve Pacific cod, yellowfin sole (*Limanda aspera*), sculpins, and Pacific halibut (*Hippoglossus stenolepis*).

Livingston (1991) and Livingston et al. (1993) reported on king crab predation from samples of fish stomachs collected primarily during May through September 1984-1989 by trawl gear on research and commercial vessels. Among nine groundfish predators investigated, these studies found that Pacific cod are the primary predator of red king crabs; many of the red king crabs consumed were softshell females. Walleye pollock (*Theragra chalcogramma*) and yellowfin sole are minor predators of king crabs and consume mostly glaucothoe and small juveniles. Livingston (1989) estimated that 3.8%, 2.8%, and 1.4% of the female red king crab stock were consumed by Pacific cod in 1981, 1984, and 1985, respectively. These predation rates led her to conclude that cod were not the major factor behind the crash of the red king crab population in Bristol Bay during the early 1980s. More recently, Livingston et al. (1993) estimated that cod consumed 3.8%, 4.8%, and 14.3% of female red king crabs in 1987, 1988, and 1989, respectively. In the Gulf of Alaska, red king crabs occur infrequently in stomachs of Pacific cod sampled off Kodiak Island (Jewett 1978) and Southeast Alaska (Clausen 1981) during summer.

Jewett and Powell (1979) examined the stomachs of sculpins, *Myoxocephalus* spp. and *Hemilepidotus jordani*, during summer 1973-1975. Red king crabs were never found in stomachs of *Myoxocephalus* spp. and they were found infrequently in stomachs of *Hemilepidotus jordani*.

Gray (1964) found an individual halibut with a distended stomach caught during a trawl survey in April 1962. This fish had eaten three mature female red king crabs all of which had recently molted. Despite occasional impressive reports, published studies of stomach contents of Pacific halibut reveal low incidences of predation on red king crabs (Simenstad et al. 1977, IPHC 1985, Best and St-Pierre 1986).

Our attempts to reconcile predation hypotheses with available data helped us to identify gaps in understanding. Most of the shortcomings result from limited field studies designed to identify the prey of fishes rather than the predators of red king crabs. We recommend predation studies to focus on several life history stages of red king crabs: pelagic larvae, glaucothoe in shallow water habitats, and molting juvenile and adult males and females. Studies of predation on larvae should include abundant pelagic fish species and be conducted in April through August. Although incidences of predation by walleye pollock and yellowfin sole on blue and red king crab glaucothoe have been documented (Livingston 1991, Livingston et al. 1993), it is likely that predation on glaucothoe is grossly underestimated because fisheries tend not to occur in shallow water habitats occupied by young-of-the-year red king crab. We recommended shallow water sampling of fishes and sea stars in June through August. Most incidences of adult red king crabs in fish stomachs are newly molted females. This finding may reflect the fact that king crab morphology prevents consumption of hardshell animals by most predators, plus the fact that fish stomachs are almost always sampled in summer by which time males (and some females) have hard exoskeletons and so would not be consumed by predators. Therefore, we recommend sampling of potential fish predators in February through June in habitats occupied by molting crabs of both sexes.

The change in weather pattern that occurred in the mid-1970s (Trenberth and Hurrell 1994) effected a decreased barometric pressure and intensification of the Aleutian Low (Figure 4). This coincided with a decrease in brood strength of red king crabs (Figure 5). An accompanying increase in water temperature was correlated to decrease in the red king crab stocks of Kodiak and Bristol Bay (Müter et al. 1995), though the relationship appears more related to availability of crabs to the fishery and changes in fishing effort. There are several hypotheses presented here that relate temperature change to change in productivity of red king crabs. Drawing on inferences from northern ocean fishes (e.g., for Pacific cod see Tyler 1995), increase in temperature is sometimes associated with decrease in fish fecundity (Figure 6, Fcn C). An increase in temperature could cause an increase in egg mortality (Figure 6, Fcn A). The optimum temperature for embryo development of red king crabs is 3-8°C (Nakanishi 1985). For ocean fishes, hatch success (Figure 8, Fcn N) is often highest at an intermediate temperature, with decreases at higher temperatures (Alderdice and Forrester 1971). Cumulative exposure to optimal temperature is sometimes necessary for both egg and embryonic development (Figure 6, Fcn B) of some fish (for English sole, Kruse and Tyler 1983). In unusually warm years spawning may be skipped because a temperature cue is needed (for English sole, Kruse and Tyler 1983) or degree of maturation is insufficient (Figure 6, Fcn B) (e.g., for Pacific cod, see Tyler 1995). An optimum temperature might also maximize molting frequency and body growth (McMurray et al. 1984). Thus warming beyond optimum could actually bring about increased duration of larval and juvenile stages and subsequent increase in exposure to predation mortality. The mechanisms of response to warming that might bring about a decrease in brood strength are manifold. Specifics for the red king crab are wanting, and so it is not possible to rule out hypotheses presented here. We suggest that temperature effects on processes at the more advanced stages of reproductive productivity, and larval survival, should be investigated. For example, embryo clutch size just before hatching could be measured in relation to ambient temperatures; this would have to be carried out in the laboratory and also at sea over several years. Duration of zoea instars in relation to rations and temperature could be investigated in at-sea and laboratory situations. Diatom concentration would have to be determined in the at-sea sampling along with ambient temperature. These measures might produce the functional relationships proposed here, and could be used to validate statistically parts of our model.

Other physical factors that could be of major influence are advection and mixing. Advection is critical to the development of brood strength in processes related to hatching, to survival of zoea, and to the settling of the glaucothoe stage. The prevailing currents flow to the northeast along the Alaskan Peninsula toward Bristol Bay then turn northward and flow along the Alaskan coast of the Bering Sea (Stabeno and Reed 1994). Concentrations of diatoms are generated by the mixing of nutrients and diatoms in the euphotic zone. The mixing could be tidal or possibly be from Ekman upwelling along the north coast of the Alaskan Peninsula caused by winds from the northeast, though this is not documented. The fertilized embryos of red king crab will hatch only if there are concentrations of diatoms present, as though a chemical cue were necessary (T. Shirley, University of Alaska Fairbanks, Juneau Center, unpublished). Investigations of advection along the north coast of the Alaska Peninsula, and of conditions that effect phytoplankton blooms, would be valuable. High concentrations of diatoms would provide the rations for copepods. Zoea consume both diatoms and copepods, depending on instar (Paul and Paul 1980, Paul et al. 1979). With high rations zoea would grow faster and molt more frequently, achieving the settled glaucothoe stage sooner. A reduced duration in the vulnerable zoeal stage would lead to reduced mortality and higher brood strength. The bottom type along the north shore of the Alaska Peninsula is favorable for the settlement as glaucothoe, because it is rocky and encrusted with organisms favored by that stage (Powell and Nickerson 1965). Our hypothesis is that if currents through this area are strong in some years, last stage zoea would be carried past these bottom types and out over muddy areas with resultant reduction in favorable settlement and increased mortality. It would be useful to look at the settlement rates of glaucothoe in this area in much the same way it has been done recently in the Kodiak area by the Alaska Department of Fish and Game (Blau 1992).

Acknowledgments

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Postlarval Red King Crab Density Dependence in Artificial Collectors, Kodiak, Alaska

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Extended Abstract

Red king crabs *(Paralithodes camtschaticus)* supported one of the most lucrative commercial fisheries in the world until a dramatic decline in the early 1980s. Regardless of cause, a rebound in stock abundance will be realized only through successful recruitment coupled to a sound management strategy. Ability to forecast an influx or decline in recruitment to a stock would improve management and benefit harvesters and processors. Changes in recruitment to lobster (*Panulirus cygnus*) and blue crab (*Callinectes sapidus*) stocks have been predicted through use of artificial collectors. In Alaska, sausage-shaped artificial collectors (SACs) have been deployed in Chiniak Bay, Kodiak Island, since 1990 to monitor settlement, index abundance, and estimate growth of age-0 red king crabs. The goal of this long-term research study was to determine if a correlation exists between age-0 red king crab abundance in a given year and the abundance of mature crab captured four or more years later in the annual Alaska Department of Fish and Game trawl survey of Chiniak Bay. The project assumed that density on SACs was the same as on the natural substrate after settling and initial density dependence. However, habitat limitations could affect interpretation of abundance indices because the majority of larval red king crab settle to a benthic ex-

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istence during late June and early July in Chiniak Bay, but age-0 crab abundance was not measured until late September to mid-October. During the elapsed time, interactions between crabs, hydrographic conditions, and the SAC habitat may yield a measure of the carrying capacity of the SAC rather than an index of abundance. If one of these factor's effects varies with population density so that the proportion of crabs influenced changes with density, then the factor is said to be density dependent. The purpose of this study was to experimentally test for density dependent effects on the number of age-0 red king crabs in the SACs.

To test for density dependence, 15 replicate SACs were seeded with 5, 10, or 30 crabs in the fall of 1992. SACs were set on the ocean bottom in 14 to 18 m of water and retrieved after 15 to 16 days. We hypothesized that, if density dependence was occurring, then subsequent densities following initial seeding would converge. The experiment was repeated in the summer of 1993 to test for density dependence immediately following peak settlement of glaucothoe red king crabs to the SACs. To identify timing of peak settlement additional SACs were set in May 1993 at two sites in Chiniak Bay: (1) Trident Basin, where age-0 red king crab abundance per SAC had been moderately low, and (2) Gibson Cove, which consistently had the highest annual abundance of any index site. The Gibson Cove site was in the immediate proximity of a fish reduction plant effluent pipe known to introduce significant quantities of pulverized fish waste. To assess settlement, multiple SACs were retrieved weekly through June, then every 2-4 days through August. When peak settlement had been identified in late July, replicate SACs were seeded with 15 or 30 crabs, set at depths of 12 to 14 m, and retrieved 8 ($n = 9$) or 23 ($n = 13$) days later. Carapace lengths (CL) of crabs were measured before seeding and after retrieval of SACs to assess growth.

Complete convergence of the three-treatment densities was not observed in fall of 1992. A one-way analysis of variance of the mean density retrieved was significant ($P = 0.0001$). SACs seeded with 10 and 30 crabs had both experienced significant reductions in crab densities when retrieved ($P < 0.0001$ in paired comparison t-tests) accompanied by a significant increase in the mean size of crabs from 5.1 mm to 5.9 mm carapace length ($P < 0.001$). Peak settlement during the summer of 1993 was difficult to establish in Trident Basin because of low and variable numbers of crabs caught per SAC. On sampling dates coincident to both areas, crabs per SAC in Gibson cove were up to 79% higher than in Trident Basin. Peak settlement was identified as having occurred when crabs per SAC had peaked in Trident Basin and begun to decline in Gibson Cove. Treatment densities did not converge in the summer of 1993. Two sample t-tests between mean retrieval densities were significant for both intervals at $P = 0.0001$. However, paired comparison t-tests of the treatment densities indicated set and retrieval densities of crabs for both intervals declined significantly ($0.0001 < P < 0.0064$). The percent reduction was variable between treatments within and between intervals. These disparities could be attributed to the proximity of SAC retrieval to the molting event and the proportion of crabs that molted. Two modes in carapace length of crabs seeded in SACs were identified, one at 2.7 mm CL and another at 3.6 mm CL, indicating a molt event was in progress. After the 8-day period 73% of the crabs had molted to a mean size of 3.5 mm CL. Sixteen days later after a 23-day period, 54% of the crabs had molted resulting in two modes: 3.3 mm CL and 4.1 mm CL.

Density dependence was observed on SACs used to index abundance of age-0 crabs in Chiniak Bay, Alaska. Of the SACs sampled in the fall of 1991 to index abundance of age-0 crabs, 63%, had less than 2 crabs per SAC, 62% in 1992, and 61% in 1993. In comparison, only 5% of the SACs sampled in the summer of 1993 had less than 2 crabs per SAC. Average density of crabs in the three fall samples was 2.4 crabs per SAC, whereas average density in summer of 1993 was 7.6 crabs per SAC. The decreasing density of crabs between peak settlement and the fall sampling period indicates SACs should not be used to estimate an abundance index over a protracted period. The significant decreases in crabs per SAC and the significant increases in mean size of crabs between set and retrieval of treated SACs could be caused by any one or combination of three possible factors. (1) Space demands could increase as crabs molt and grow, reflecting density dependent regulation of crab numbers per SAC; however, the significantly greater density of crabs on collectors in Gibson Cove adjacent to the fish reduction plant compared to Trident Basin suggests food availability could modify density dependence. (2) Decreased densities may be a direct consequence of cannibalism, which is known to occur in young-of-year red king crabs, predation, or other factors reducing population abundance. (3) Emigration and dispersion of crabs into other habitats could have lowered densities on SACs.

Effects of density dependent regulators on using SACs to index age-0 red king crabs could be reduced by retrieving SACs as close to peak settlement time as possible and timely retrieval of SACs. This practice should enable these collectors to be used to identify changes in recruitment and location of crab nursery areas.

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Bitter Crab Hemolymph Studies: Indications of Host Physiological Condition

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Abstract

Motile dinospore stages of the parasitic dinoflagellates (*Hematodinium* spp.) which cause bitter crab disease (BCD) in southeastern Alaska Tanner crab, *Chionoecetes bairdi*, were observed exiting heavily infected hosts via the gill lamellae. Loss of the integrity of the gill in heavily infected and sporulating crabs appears to be the reason for the observed changes in the hemolymph physiological parameters studied. Heavily infected and moribund Tanner crabs which had sporulated had tissue osmolalities similar to seawater, elevated Na^+ ion concentrations, reduced hemocyanin levels, and lower glycogen concentrations. Light to moderately infected and uninfected Tanner crab hosts appeared to retain their locomotory abilities, had similar hemolymph osmolality, Na^+ and K^+ ion, hemocyanin, mean protein, ninhydrin positive substances, and glycogen concentrations. Light to moderately infected crabs may be equally as marketable as uninfected.

Introduction

Bitter crab disease (BCD), a blood-borne dinoflagellate infection of southeastern Alaskan Tanner crabs *(Chionoecetes bairdi)* causes off-flavor and mortality that results in a significant annual loss to the commercial fishery. An average of 4% of the commercial Tanner crab harvested from southeastern Alaska during the last six seasons has been unmarketable due to BCD, representing losses of about $150,000 annually (Cathy Bothello, ADF&G, Juneau, AK, Jan. 1995, pers. comm.). Upper Lynn Canal near Skagway, Alaska, and the Auke Bay, Alaska, area have reported disease prevalence of greater than 90% during certain years (Meyers et al. 1987, Love et al. 1993). In certain areas of the Bering Sea as much as 60% of the total animals sampled were found to be infected with dinoflagellate parasites (Frank Morado, NMFS-NWFSC, Seattle, WA, Oct. 1995, pers. comm.). This fishery is the most highly valued invertebrate fishery in Alaska, averaging 218 million pounds annually between 1991 and 1995 (Hermann Savikko, ADF&G, Juneau, AK, Sept. 1995, pers. comm.). Although an active culling and disposal program during the Tanner crab fishery in southeastern Alaska appears to be reducing the prevalence of disease, BCD has not been eradicated. Loss of marketable product and disease-related mortality still threaten commercially important southeastern Alaska and Bering Sea crab fisheries.

Dinoflagellate parasites similar to *Hematodinium perezi* have been described from a wide range of decapod hosts and many geographically distinct areas. *Hematodinium perezi* was first described parasitizing the portunid crabs *Carcinus maenus* and *Portunus (Liocarcinus) depurator* from the Atlantic coast of France (Chatton and Poisson 1931). In northern France, dinoflagellate parasitism has been reported from *Cancer pagurus* and *Liocarcinus puber* (Latruite et al. 1988, Wilhelm and Buolo 1988). Norway lobster (*Nephrops norvegicus*) from the west coast of Scotland were recently found to be infected with *H. perezi* and infections have been reported in the Australian portunid crabs *Portunis pelagicus* and *Scylla serrata* as well as two species of xanthid crabs (Field et al. 1992, Shields 1992, Hudson et al. 1993). In North America, *H. perezi* infects *Callinectes sapidus* along the eastern coast of the United States (Newman and Johnson 1975, Couch and Martin 1979) as well as the lady crab (*Ovalipes ocellatus*) and the rock crab (*Cancer irroratus*) (MacLean and Ruddell 1978). Infections of spot prawns (*Pandalus platyceros*) and pink shrimp (*Pandalus borealis*) from British Columbia and Alaska have also been reported (Bower et al. 1993, Meyers et al. 1994). In Alaska, *H. perezi* infects snow crab (*Chionoecetes opilio)* and Tanner crabs (*C. bairdi),* causing off-flavor and economic losses to commercial fisheries (Meyers et al. 1987, Meyers et al. 1990).

External clinical signs in heavily infected Tanner crabs include a pink abdomen and carapace, white lines along the underside of each merus, and milky hemolymph filled with the amoeboid *Hematodinium* sp. parasites. Lightly infected crabs hosted uninucleate cells with a dinokaryon-type nuclear morphology (Chatton and Poisson 1931). The amoeboid stages of these parasites resided in the hemolymph for 6 to

18 months, causing considerable damage to the vascularized connective tissues of antennal glands, hepatopancreas, cardiac muscle, endocuticle, gill epithelia, and to circulating hemocytes (Meyers et al. 1987, Love 1992). As the disease progressed, hemocytes decreased in number and multinucleate cells having prominent chromatin and no apparent nuclear membranes were observed (Eaton et al. 1991). Prevalence and intensity of infection increased from January through September, at which time the multinucleate cells metamorphosed into either or both of the micro- or macrospore stages which exited the crab via the gills through the exhalent openings of the branchial chamber (Love et al. 1993, Love 1992). Hosts did not survive sporulation. Both the micro- and macrospores survived 2 to 3 months and vegetative stages survived about 5 days following injection into sterile seawater (Meyers et al. 1987). These micro- and macrospores were not produced meiotically from the amoeboid stages (Eaton et al. 1991), and did not appear to fuse thus forming planozygotes as do other free-living dinoflagellates, but instead may represent genetically discrete non-recombining syngens (Pfiester 1984). The parasite appears to spread to uninfected hosts via the motile dinospores through the water column and also via the ingestion of recently dead, infected crabs. However, disease expression in control animals 6 months into the yearlong epidemiological experiments has clouded a clear description of the life cycle of this parasite (Love, unpublished). Beyond this, little else is known about *Hematodinium* spp. life cycles or specific impacts on Tanner crab physiology by amoeboid cells while resident in the hemocoel or immediately following dinospore release.

Decapod hemolymph is a complex liquid "tissue" essential for ion regulation, for maintaining a proper internal pH balance, for the transport of oxygen and metabolic wastes, and in the recognition of "nonself" followed by an appropriate immune response (Mantel and Farmer 1983). Components of decapod hemolymph include several types of hemocytes, ions such as Na^+ and K^+, serum proteins and hemocyanin, free amino acids and by-products of protein metabolism, phospholipids and neutral lipids all suspended in a liquid matrix (Johnson 1980). As such, hemolymph represents chemically the tissues it supports within the hemocoel. Previous taste test experimentation at Auke Bay Laboratory indicated that consumers could not distinguish between uninfected and lightly infected Tanner crab (Moles, Thomas, and Love, unpublished). This means that a portion of the Tanner crab harvest currently discarded due to off-flavor may be marketable in some form, or the fishery could be undertaken during seasons when the intensity of epizootics are lower. It is not known whether BCD parasites deplete hemolymph proteins, utilize crab glycogen, or in what manner cause changes in hemolymph composition and physiological condition prior to killing the host. This study investigated the effects of parasitism by BCD dinoflagellates on the composition of hemolymph and physiological condition of Tanner crabs to determine the extent to which uninfected crabs differed chemically from infected.

Methods

Female Tanner crabs were captured by submerging 2 m × 2 m conical commercial Tanner crab pots for 12 to 36 h in waters 90 m in depth from the Auke Bay area, southeastern Alaska. Captured animals were held at Auke Bay Biological Laboratory in flow-through seawater aquaria (6-10°C). Hemolymph was drawn from each captured crab at the intersegmental membranes at the base of the right coxa using a disposable 1 cc syringe. A drop of hemolymph was used immediately upon collection to make smears on numbered glass slides, which were dried and stained using a Wright-Giemsa (Diff-Quik™) histological stain. Intensity of *Hematodinium* sp. infection was determined for each sampled crab per Meyers et al. (1987) using a numerical code from 0 to 4. A value of 0 meant that no parasites were found in sampled hemolymph, 1 denoted that 1 to 10% of all cells present in an average of 10 fields of view (400×) were parasites, 2 denoted 11 to 40%, 3 meant 41 to 70%, and 4 meant that more than 70% of all cells were *Hematodinium* sp. parasites. To facilitate analysis, crabs having infection intensities of 1 through 3 were then categorized as lightly to moderately infected while level 4 crabs were designated heavily infected. These criteria were also used during previous taste test experiments at Auke Bay Laboratory (Thomas, Moles, and Love, unpublished)

Physiological measures included: righting response (10 uninfected and 10 infected animals) wet weight, dry weight, shell weight, wet and dry tissue weights, ovary weight, osmolality (mmol), Na^+ and K^+ concentration (mmol/L), hemocyanin (gm%), ninhydrin positive substances (nm/ml), and glycogen concentration (mmol/L). Measures were taken from newly molted as well as terminal molt animals. Newly molted animals had clean, iridescent pink exoskeletons lacking epifauna. Terminal molt crabs often had worn, darkened exoskeletons and ectocommensals such as barnacles, *Notostomobdella* leeches, and leech egg cases.

Anatomical and gross physiological measures

Triplicate measures were taken of the time required for each of 10 infected and 10 uninfected Tanner crabs to right themselves once placed dorsal side down in a large volume tank. Wet weights of individual crabs to the nearest milligram were obtained using a Mettler digital scale. Hemolymph used for physiological measures was drained from each infected and uninfected crab by severing and immobilizing the first merus of the third or fourth walking legs, allowing the hemolymph to drain into a sterile beaker chilled in crushed ice. The resulting hemolymph samples were centrifuged at 6,000 rpm for 2 minutes and the serum supernatant frozen at –29°C. Crabs were then killed by separating the carapace from the legs and abdomen. Ovaries were removed and weighed. All portions of the crab were placed in an oven for 2 days at 60°C to obtain dry weight. Shell weight was determined via KOH digest and tissue weight (wet and dry) calculated by subtracting shell from total weight.

Hemolymph physiological measures

Plasma osmolality was determined using a Wescor 5100 series vapor pressure osmometer. Sodium and potassium levels of hemolymph sera were determined using an Orion 1020 Na^+/K^+ analyzer. Analyzer values were converted to equivalent values of a flame photometer with a conversion coefficient of 0.941. This conversion coefficient was based on previously reported plasma protein and lipid values determined for blue crab (Jack Martinez, Aquatic Consultants, Seattle, WA, 1988, pers. comm.). Ninhydrin positive substances were determined using the method of Moore and Stein (1954) as modified by Rosen (1957). Hemolymph hemocyanin concentrations were measured spectrophotometrically using methods reported by Shirley et al. (1986). Protein concentrations were determined with a colorimetric protein assay kit (Sigma 690-A) using bovine albumin standards. Total protein used Ohnishi and Barr (1978) modification of the Lowry method (Lowry et al. 1951) wherein a dilute biuret reagent reacts with peptide bonds and is read colorimetrically at 550-770 nm (Sigma No. 690-A). Glycogen contents were analyzed following the method published by Wedemeyere and Yasutake (1977) with some modification. Anthrone and KOH were prepared as described. Ethanol was saturated with KCL. Glycogen powder (Sigma No. 115-A) was used to prepare standard curves. Glycogen concentrations in the standard curves ranged from 0 to 102 µg/ml.

To test whether physiological parameters differed by level of infection, we compared mean blood parameter values using one-way analysis of variance. If the effect of infection was significant, different levels were compared using Scheffe's test. All data are presented as mean ± standard error.

Results

Dinoflagellate parasitism did not affect general fitness of host crabs until BCD dinospores were released from the gills. Triplicate trials of the time required for 10 uninfected (11.3 ± 1.6 min.) and 10 heavily infected (10.1 ± 1.9 min.) Tanner crab to right themselves when placed upside down were not significantly different based on two-way analysis of variance ($F = 3.07$, $P < 0.05$). No additional measures of fitness were taken, although feeding and ambulatory behavior of infected crabs did not

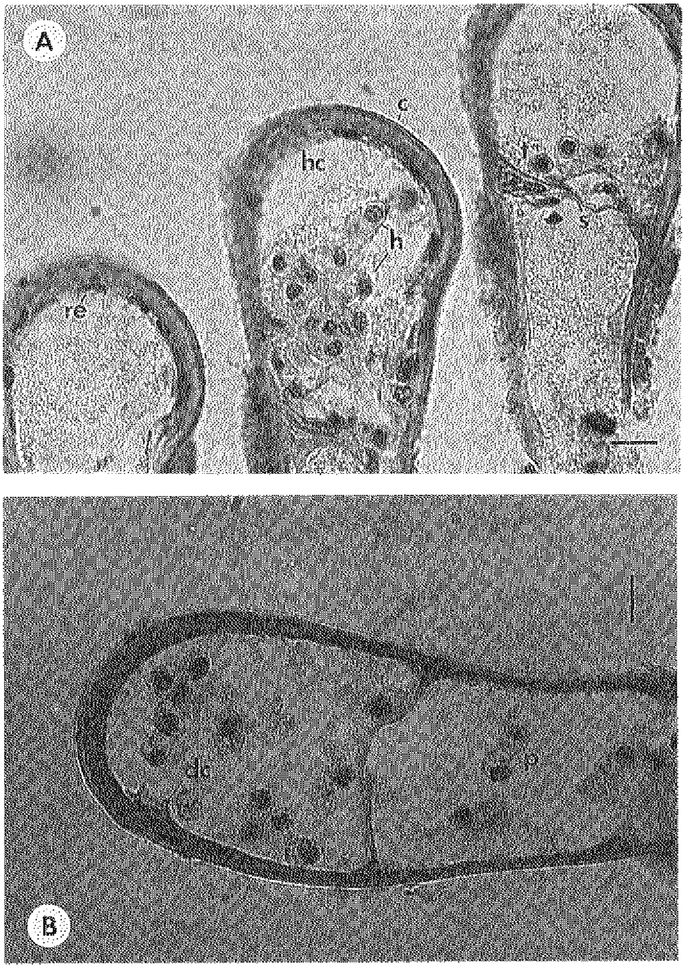

Figure 1. Histological sections of crab gills taken from uninfected crabs and crabs infected with the dinoflagellate parasite responsible for bitter crab disease (BCD) in southeastern Alaskan Tanner crabs (Chionoecetes bairdi). (A) Uninfected gills had hemal channels (hc) containing numerous hemocytes (h), intact cuticle (c) and respiratory epithelium (re) and granular-looking hemolymph. Septae (s) and associated trabecular cell (t) are evident within the lamellae. (B) Gills from heavily infected crabs contained less hemolymph, had degenerate respiratory epithelium (dc) and numerous vegetative stages of the BCD parasite (p). Epicuticle is still evident. Hematoxylin-Eosin stain. Bar = 25 μm. (Modified from Love 1992.)

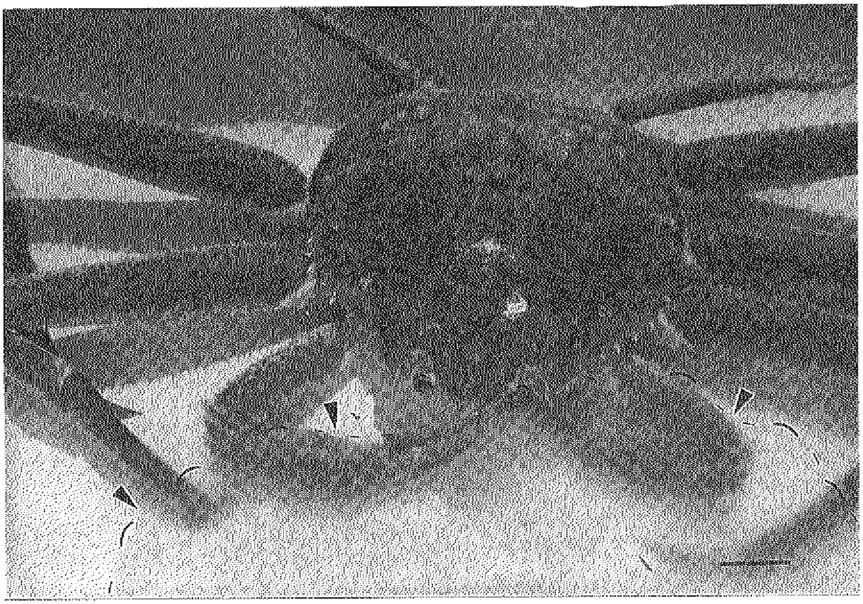

Figure 2. Tanner crab (*Chionoecetes bairdi*) infected with *Hematodinium* sp. dinoflagellate parasites which cause bitter crab disease (BCD) in southeastern Alaska, releasing BCD dinospores into the water column via the gill lamellae and branchial chamber. Bar = 20 mm. (Modified from Love 1992.)

seem different from uninfected until immediately prior to BCD sporulation when crabs became lethargic and inappetent, and died.

Prior to BCD sporulation, hemolymph from heavily infected crabs contained noticeably fewer hemocytes than uninfected when observed under the light microscope and eventually turned opaque and milky as the number of parasites increased in abundance. Heavily infected gill tissue had degenerate respiratory epithelia, hemal channels filled with numerous parasites, and a lamellar cuticle which seemed more fragile than uninfected gill to section for histological examination (Figure 1). Heavily infected crabs were observed in seawater aquaria releasing milky hemolymph containing the dinospore stage of the BCD parasite from the gill prior to death of the host (Figure 2). Released hemolymph was opaque, appeared milky, and contained 1.5×10^5 motile parasites ml^{-1} based on hemocytometer counts. Many crabs appeared to have lost hemocoel hydrostatic pressure as hemolymph was lost at the gill, evidenced by sunken intersegmental membranes. Within the hemocoel, milky hemolymph was replaced by a clear, acellular fluid, presumably seawater.

Table 1. Means and standard errors of the mean for hemolymph physiological measures of uninfected Tanner crab (*Chionoecetes bairdi*) and Tanner crab infected with *Hematodinium* sp. parasites.

	Osmolality (mosmol)	Na^+ (mmol/L)	K^+ (mmol/L)	Mean protein (mg/dL)	Hemo-cyanin (gm %)	NPS (nM/ml)	Glycogen (μ/mg)
Uninfected							
n = 61							
mean	843.64	381.48	9.63	30.94	13.81	2.39	109.75
SE	12.86	5.24	0.15	2.08	0.75	0.13	6.50
Light/med							
n = 135							
mean	834.49	380.07	9.75	33.94	15.39	2.71	109.88
SE	12.17	4.64	0.13	1.19	0.42	0.12	3.85
Heavy							
n = 22							
mean	893.29*	404.23	9.95		8.62***	2.76	74.75***
SE	43.30	16.70	0.46		1.13	0.21	5.39
Sporulating							
n = 25							
mean	902.80**	432.48***	9.76				
SE	6.96	3.84	0.14				

Measures from newly molted and terminal molt crabs are combined. Seawater osmolality during week-long period when crabs were sacrificed ranged from 896 to 898 mosmoles/L. NPS denotes ninhydrin positive substances. Very highly significant (P = 0.001) denoted by ***, highly significant (P = 0.01) denoted by **, and significant (P = 0.05) differences denoted by *.

Reflecting the sporulation event, some hemolymph physiological measures of ion regulation from heavily infected and sporulating Tanner crabs differed from uninfected and crabs with light-moderate infections (Table 1). Osmolality was significantly higher (893.29 ± 43.3 mosmols) in heavily infected than in uninfected crabs (843.64 ± 12.86 mosmols) while Na^+ ion concentrations were not significantly different. Although not significantly different than in uninfected and light to moderately infected, Na^+ ions in heavily infected crabs were intermediate in concentration to sporulating crabs. Differences in osmolality (902.8 ± 6.96 mosmols) and Na^+ concentration (432.48 ± 3.84 mosmols) in sporulating crabs were highly and very highly significant as compared to uninfected crabs. The osmolality of the seawater in the holding tanks ranged from 896 to 898 mosmol/L during the week in which the crabs were sacrificed. K^+ ion concentrations were not significantly different for any of the infection levels compared. Concentrations of hemocyanin and glycogen, which may also exert some osmotic pressure, were also

Table 2. Means and standard errors of the mean for wet weights (g) and percent measures of uninfected Tanner crab (*Chionoecetes bairdi*) and Tanner crab infected with *Hematodinium* sp. parasites.

	Wet weight (g)	% Ovary weight	% Dry weight	% Shell weight	% Wet tissue	% Dry tissue
Uninfected						
n = 61						
mean	282.09	8.79	24.28	12.05	87.40	12.63
SE	7.16	0.45	0.30	0.18	1.27	0.46
Light/Med						
n = 135						
mean	292.52	8.77	25.07	12.65	87.51	13.16
SE	4.57	0.29	0.20	0.12	0.33	0.61
Heavy						
n = 22						
mean	198.27***	12.35**	21.90***	8.63***	91.39*	20.30***
SE	7.18	2.25	0.82	0.33	0.33	0.95

Measures from newly molted and terminal molt crabs are combined. Very highly significant (P = 0.001) denoted by ***, highly significant (P = 0.01) denoted by **, and significant (P = 0.05) differences denoted by *.

significantly lower in heavily infected crabs. All of these physiological measures remained significantly different regardless of molt stage, indicating that physiological effects occurred regardless of molt cycle.

Light to moderately infected crabs as well as uninfected crabs did not differ significantly from one another in any of the anatomical and physiological measures taken based on one-way analysis of variance (Tables 1 and 2). In addition, Na^+ ion concentration, K^+ ion concentration, and ninhydrin positive substances also were not significantly different between heavily infected and uninfected crabs (Table 2). Mean protein measures were not taken for heavily infected crabs and were not significantly different between uninfected (33.4 ± 2.1 mmol/L) and lightly to moderately infected (33.9 ± 2.4 mmol/L).

Heavily infected crabs (198.3 ± 7.2 g) were significantly smaller than uninfected and light to moderately infected crabs (285.7 ± 6.7 g), thus impacting any other comparative measurements based on percentage of wet weight. Sporulating crabs were similar in size to uninfected and light to moderately infected. Anatomical measures included wet weight, percent dry weight, percent dry and wet tissue weight, percent shell, and percent ovary. Percent shell and percent ovary by weight were significantly higher in the heavily infected animals (8.6 ± 0.3 and 12.4 ±

2.3 % by weight, respectively) sampled than in uninfected (12.2 ± 0.2 and 8.9 ± 0.4 % by weight). Infected crabs (198.3 ± 7.2 g) were significantly smaller than uninfected crabs (285.7 ± 6.7 g).

Discussion

Currently, processors and fishermen may inadvertently be harvesting and selling lightly infected crab, as quality of the meats may not be impacted and exterior clinical signs used to sort crab at the dock are not evident in low level infections. This may not be bad news for industry as taste tests indicate that consumers could not tell the difference between uninfected and lightly infected crab. However, transport of infected crab in flow-through holding tanks and processing of lightly infected animals may aid in dissemination of the parasite to new areas and certainly impacts physiological condition of the host.

Loss of the integrity of the gill in heavily infected and sporulating crabs appears to be the reason for the observed changes in the hemolymph physiological parameters studied. Osmolality concentrations similar to seawater and higher Na^+ ion values in sporulating and heavily infected crabs are probably the result of seawater flooding of the gill hemal sinuses and hemocoel. Although not as striking as in sporulating crabs, heavily infected crabs often had numerous amoeboid cells and BCD plasmodia within the hemocoel, histological damage to gill and other internal organs and reduced osmotic ability. Nonetheless, host crabs seemed quite resilient physiologically. Despite reported extensive histopathological damage (Meyers et al. 1987), cardiac function did not appear to be compromised as infected, dinospore-laden hemolymph was pumped out of the gill during sporulation until little remained in the hemocoel. Efferent valves of the gills which regulate lamellar hemolymph flow are present in other brachyuran crabs, including *Carcinus maenus* and *Ovalipes catharus* (Taylor 1990). Destruction of valves such as these in sporulating Tanner crabs would result in an inability to prevent most of the hemolymph from being expressed following rupture of the gill epithelia and epicuticle.

Hemolymph Na^+ ion, hemocyanin, and glycogen concentrations in heavily infected crabs were significantly different from uninfected and light to moderately infected crabs. Assuming physiological differences between new molt and terminal molt animals, comparisons of the smaller-sized heavily infected crabs to the terminal molt uninfected and light to moderately infected crabs cannot be considered valid. Samples from terminal molt, heavily infected animals are needed to clarify disease impacts on hemolymph composition. Assuming new molt, heavily infected animals to be representative, significant losses of hemolymph translates into concurrent losses of hemal proteins such as hemocyanin which may indirectly be important for maintaining an osmotic gradient across the gill membrane. Assuming similar hemal protein ratios for *C. bairdi* hemolymph as are reported for the blue crab, *Callinectes sapidus*, hemocyanin represents 85-90% of the volume of hemolymph proteins (Johnson 1980). Osmolality concentrations similar to seawater and higher Na^+ ion values in sporulating and heavily infected crabs are probably the result of seawater flooding of the gill hemal sinuses and hemocoel. It is also possible that BCD parasites are feeding on or destroying hemocyanin and glycogen directly, although this is not yet known. The vegetative stages of this parasite have been successfully cultured in vitro using sterilized Tanner crab hemolymph (Meyers et al. 1987).

Hemocytes of *Carcinus maenus* appear to be major sites of glycogen storage and carbohydrate metabolism (Johnston et al. 1973). Spongy connective tissues of *Callinectes sapidus* may be equally as important for glycogen storage as the hemocytes, based on histological evidence (Johnson 1980). Both spongy connective tissue and hemocytes in *C. bairdi* are destroyed or damaged by BCD parasites over the several-month course of infection, regardless of which tissue is actually involved in glycogen storage and metabolism in this species (Love 1992).

Heavily infected crabs were all smaller, newly molted animals unlike the uninfected and light to moderately infected crabs which were terminal molt animals; size differences preclude a meaningful comparison of anatomical measures which are based on percent by weight. The long-term effect on tissue growth (dry weight) and reproduction (ovary dry weight) would require measurements on the same size females; unfortunately, we could not get enough crabs of the right size categories for comparisons. Different levels of infection in different size females suggest that parasite infection levels cycle in the population. Prevalence of disease in newly molted crab appears to be higher in samples taken from Kodiak, Alaska, since 1990, which would appear as a cyclic occurrence in random samples (Dan Urban, ADF&G, Kodiak, AK, Oct. 1995, pers. comm.).

Tanner crab hosts appeared to retain their locomotory abilities, continue to ion-regulate, and have normal hemolymph chemical makeup throughout the time during which BCD vegetative stages reside within the hemocoel. Gross measures such as righting response may not be precise enough and appear to be of limited value in assessing host-parasite physiological interaction throughout all but the final moments of infection just prior to BCD sporulation. Heavily infected crabs were able to right themselves as quickly as uninfected. Hemolymph osmolality, Na^+ and K^+ ion, hemocyanin, mean protein, ninhydrin positive substances, and glycogen concentrations were quite similar between uninfected and light to moderately infected crabs, which had hemolymph that was slightly hypoosmotic as compared to seawater and heavily infected or sporulating crabs. Light to moderately infected crabs as well as uninfected crabs did not differ significantly from one another in size or in any of the anatomical and physiological measures taken based on one-way analysis of variance.

Tanner crab condition does not seem to be compromised until the final stages of disease during late summer and fall when dinospores are released, thus allowing host crabs to release currently held clutches of eggs prior to dying. This indicates the host-parasite relationship is highly evolved. *Hematodinium* sp. parasites may elicit no humoral or cellular disease response, or the tough dinoflagellate pellicle, exterior to the cell membrane, may prevent hemocyte destruction. The physiological components of hemolymph were practically identical, with small relative standard errors of the mean, between uninfected and light to moderately infected Tanner crabs. Although chronic parasitism appears to be relatively widespread in Tanner crab from southeastern Alaska, the physiological consequences of disease may be minimal for much of the time that the parasite resides within the hemocoel prior to sporulation. Research on the long-term impacts of parasitism on host growth and recruitment to reproductive and harvestable sizes has not been done. If management is to make conservative decisions regarding sustainable harvest of these crab populations, continued physiological, epizootiological, and parasite life cycle related research is needed.

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Sea Otter Predation on Dungeness Crabs in Glacier Bay, Alaska

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Abstract

Sea otter (*Enhydra lutris*) populations are increasing and expanding into areas of Southeast Alaska where Dungeness crabs (*Cancer magister*) are commercially harvested. Although sea otters are known to feed on Dungeness crabs, their effects upon crab demography have not been quantified. We censused Dungeness crabs in adjacent areas within Glacier Bay National Park and Preserve with and without sea otters in April 1993, 1994, and 1995 to investigate the effects of sea otter predation. Two different crab survey techniques were used. Commercial crab pots with sealed escape rings and baited similarly were soaked for 24 hours to measure CPUE in 0-25 m depths. A minimum of 50 pots was used for each site; 25 additional pots were used in 1994 and 1995 to sample crabs to 95 m depths. Divers censused crabs along belt transects (2 m × 100 m) laid perpendicular to shore from 0 m depth to 18 m; 15 transects were surveyed at each site on each date. Sea otter numbers were estimated from aerial surveys and boat observers. Prey types and feeding rates of sea otters were made from telescopic observations. In Outer Dundas Bay, where 46, 39, and 40 sea otters were present in 1993, 1994, and 1995 respectively, CPUE of Dungeness crabs in pots was 0.04, 0.04, and 0.2 crabs per day, respectively, at depths to 25 m, but was higher (4.0 crabs per day) at deeper depths (95 m). Only two Dungeness crabs were observed in 45 diver transects surveyed during three years in Outer Dundas Bay, however Dungeness crabs were a common prey item (15%) of sea otters. Approximately 16 km N in Inner Dundas Bay, where no sea otters were observed any year, CPUE of Dungeness in pots was 2.7, 1.8, and 2.5 crabs per day for 1993, 1994, and 1995, respectively. Adult crab density estimated from diver transects was 236, 78, and 50 crabs/ha in 1993, 1994, and 1995, respectively. Significantly lower crab densities and CPUE occurred in the site occupied by sea otters. Our data imply that sea otter predation decreases Dungeness crab abundance and may induce movement of crabs to greater depths. A depth refuge for crabs from sea otter predation may vary with local bathymetry.

Introduction

Since their reintroduction to southeast Alaska beginning in 1965 (Burris and McKnight 1973), the population of sea otters (*Enhydra lutris*) has been increasing and their range expanding into inside waters, where a majority of the southeastern Alaska commercial Dungeness crab (*Cancer magister*) harvest occurs. Sea otters were eliminated from southeast Alaska by the fur trade before 1900. Between 1965 and 1968, 402 animals were translocated to six sites on the outer Alaskan coast (Burris and McKnight 1973, Jameson et al. 1982). The population remained low until 1987 when it began a period of rapid growth (Pitcher and Imamura 1990).

Sea otters are known to have a diverse diet (Doroff and DeGange 1994, Ebert 1968), but in most parts of their Alaskan range sea otters have been documented as feeding primarily on sea urchins (Estes and Duggins 1995) and bivalves (Kvitek and Oliver 1992, Kvitek et al. 1992). Although sea otters have been reported to prey heavily on Dungeness crabs in Prince William Sound, Alaska (Garshelis 1983, Garshelis et al. 1986), the effects of their predation upon crab demography have not been quantified.

The Dungeness crab supports a substantial commercial and sport fishery in southeastern Alaska. In 1992, 243 commercial crabbers held permits to fish in Southeast Alaska, harvesting over 3 million pounds of crab. With the limited-entry program for the Dungeness fishery in 1997, 308 crabbers will be eligible for permits (S. Shirley, Commercial Fisheries Entry Commission, pers. comm.). If sea otter predation on Dungeness crabs in southeastern Alaska is of the same magnitude as it was in Prince William Sound, an average of 14 crabs per adult sea otter per day (Garshelis et al. 1986), the effects upon the commercial fishery could be devastating. If the estimated population of 10,000 sea otters consumed only Dungeness crabs, the 1995 commercial harvest of Dungeness crabs could be consumed in less than two weeks. We expect that such calculations are absurd, but they do serve to emphasize the magnitude of the potential problem.

Beginning in April 1992 we conducted surveys of Dungeness crab populations twice annually at locations in or adjacent to Glacier Bay National Park and Preserve as part of a long-term study (MADS, Multi-Agency Dungeness Study) implemented to study the effects of commercial crabbing upon several attributes of Dungeness crab biology (Leder 1994, Leder and Shirley 1995, O'Clair et al. 1995, O'Clair et al. 1996, Schultz 1996, Schultz and Shirley 1996, Schultz and Shirley in press). The five study sites, Gustavus Flats, North Beardslee Islands, South Beardslee Islands, Berg Bay, and Bartlett Cove (Figure 1), at the time had no or a low historical incidence of sea otters. With the advent of sea otter sightings and the concern of additional sea otters moving into our study areas, two additional sites, Outer and Inner Dundas Bay, were added in April 1993 (Figure 1). Outer Dundas Bay has been populated by sea otters since at least 1989 (Pitcher and Imamura 1989) while sea otters have not been observed in the upper reaches of Dundas Bay, approximately 16 km NW, hereafter referred to as Inner Dundas Bay.

The objectives of this study were to: (1) compare CPUE and abundance of Dungeness crabs in adjacent areas with and without sea otters and to compare to values collected with similar methodology in 1989 by the Alaska Department of Fish and Game (Pitcher and Imamura, 1990); (2) compare depth distribution of Dungeness crabs in areas with and without sea otters; and (3) examine the diet of sea otters in southeastern Alaska.

Methods

Dungeness crab abundance was assessed by two methods, commercial crab pots and scuba diver transects. At each site 50 commercial Dungeness crab pots were soaked for 24 hours: 25 pots were set in depths of 0-9 m and 25 pots were set in 10-25 m. At Outer Dundas Bay, which has greater depths available, an additional 25 pots were set at depths of 64-95 m in 1994 and 1995. The pots were baited similarly with a mixture of herring and squid and hanging bait of salmon and cod. The escape rings of all pots were sealed in order to retain small crabs. All pots were numbered and the depth and location of each pot was recorded. Catch per unit effort (CPUE) was determined per pot standardized to a 24 h soak period.

Crabs were identified by sex and females were classified as ovigerous (with an egg clutch under the abdominal flat) or nonovigerous. Carapace width was measured with vernier calipers to the nearest millimeter immediately anterior to the tenth anterolateral spines. Carapace condition was categorized as soft (recently molted), new (sharp spines and

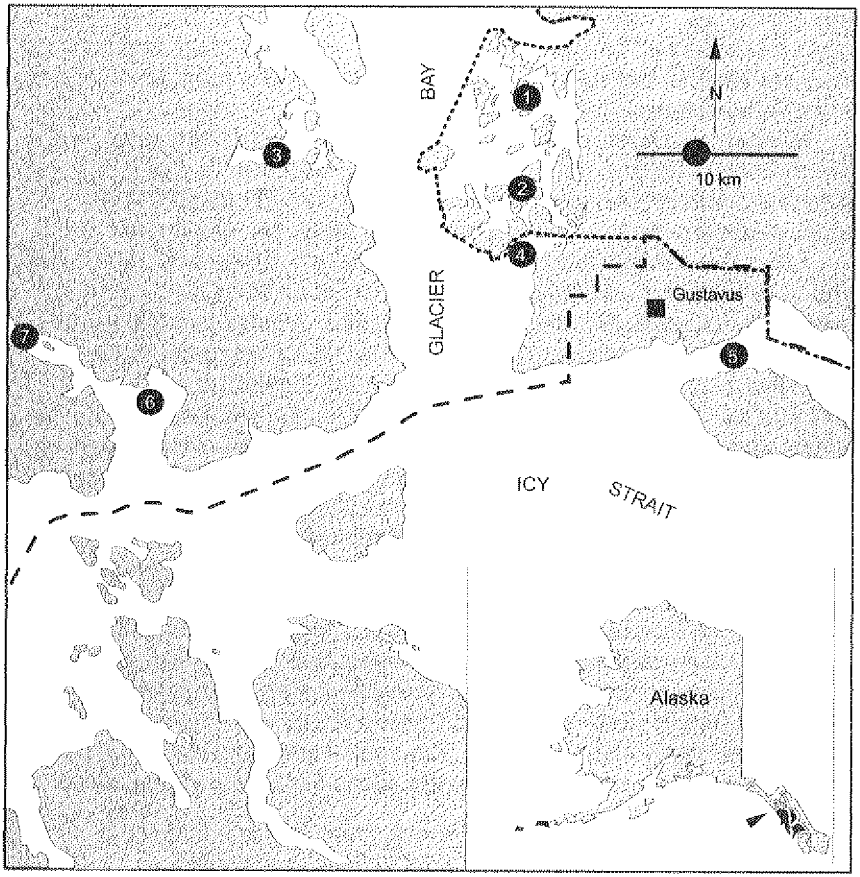

Figure 1. Study locations in and adjacent to Glacier Bay National Park and Preserve. Numbered locations are: (1) North Beardslee Islands, (2) South Beardslee Islands, (3) Berg Bay, (4) Bartlett Cove, (5) Gustavus Flats, (6) Outer Dundas Bay, (7) Inner Dundas Bay.

bright colors), old (dull spines and colors, with some fouling organisms) and very old (dull spines, heavy fouling, larger barnacles and often with macroalgae) (Shirley and Shirley 1989). Carapace and appendage damage and evidence of regeneration of appendages was also recorded. More detail of the variables measured and techniques are provided by Leder (1994) and Schultz (1996).

Divers using scuba gear censused crabs along belt transects (2 × 100 m) perpendicular to shore from the shallow subtidal (0 m, MLLW) to 18 m depth or until the end of the 100 m transect, whichever came first (O'Clair et al. 1995, O'Clair et al. 1996). Fifteen randomly placed transects located within the area where pots had been located were conducted at each study site. Crab number, sex, reproductive condition, and number of legal-sized males were counted by 10 m quadrats along each transect.

Sea otter abundance was determined by aerial and small boat surveys. Sea otter diet was assessed by telescopic observation by trained observers.

Crab and sea otter surveys were conducted at approximately the same time in the third week of April in 1993-1995. Diver transects were conducted concurrently with the pot survey in 1993, but followed by 1-5 days in 1994 and 1995. All values are reported as mean ± standard error.

Results

In Outer Dundas Bay, CPUE was uniformly low in pots at 0-25 m depth, being 0.04 ± 0.03 crabs per pot per day in both 1993 and 1994 and 0.2 ± 0.1 in 1995 (Figure 2). At the deeper depths, CPUE increased, from 0.4 ± 0.2 crabs per pot per day for pots in 20-60 m depth in both 1994 and 1995, and to 3.9 ± 0.8 and 4.0 ± 1.0 crabs per pot per day for pots from 60-90 m depth in 1994 and 1995, respectively (Figure 3). In sharp contrast, Inner Dundas Bay had CPUEs of 2.7 ± 0.4, 1.8 ± 0.3, and 2.5 ± 0.5 crabs in 1993, 1994, and 1995, respectively. The bathymetry of Inner Dundas Bay is shallow, so that no pots can be set at deeper depths for comparison; however, the CPUE of crabs in pots from 0-10 m was twice that of pots from 10-20 m depth.

The low CPUE of crabs in pots from Outer Dundas renders consideration of sex ratio of questionable value. Two males were caught in pots at 0-25 m depth in Outer Dundas in both 1993 and 1994, while 8 males were collected in 1995 from the same depths. In the 25 pots set deeper (25-95 m), 40 males and 1 female were collected in 1994, but 42 males, 1 nonovigerous and 3 ovigerous females were collected in 1995. In Inner Dundas Bay, 104 males and 30 nonovigerous females were collected in 1993; 59 males and 24 nonovigerous females were collected in 1994; and 113 males, 8 nonovigerous, and 5 ovigerous females were collected in 1995.

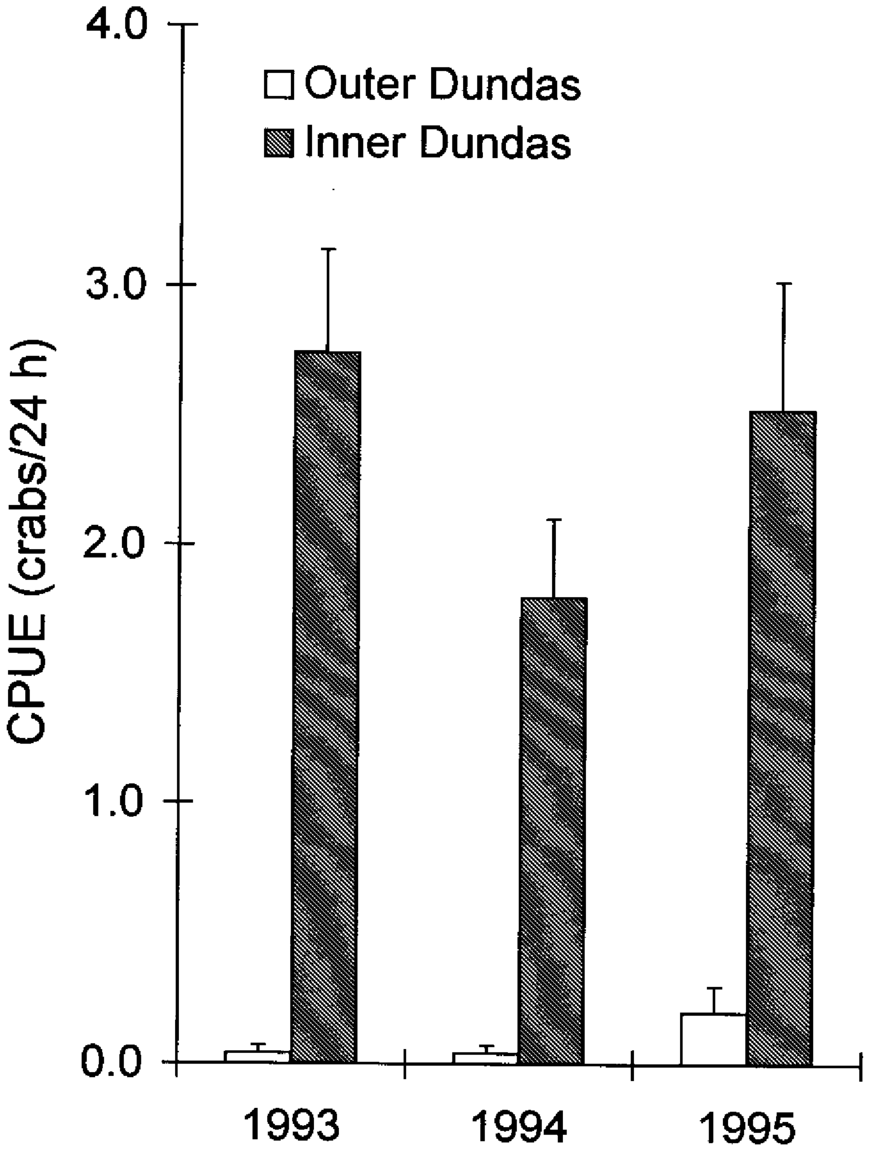

Figure 2. Mean catch per unit effort (CPUE) of crabs/24 h in commercial crab pots (n = 50 pots) in Outer and Inner Dundas Bay from 1993 to 1995. Vertical bars represent one standard error.

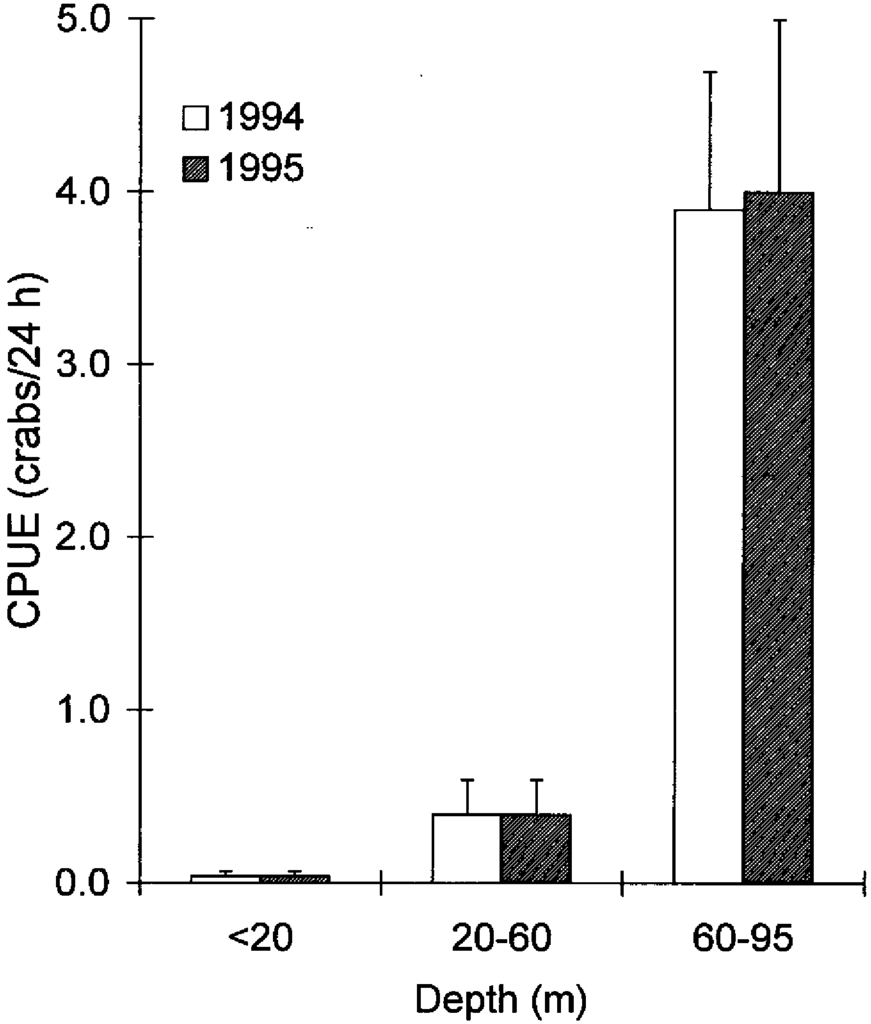

Figure 3. Mean CPUE of crabs/24 h in commercial crab pots by depth in Outer Dundas Bay in 1994 and 1995. Means are for 50 pots at depths < 20 m, 15 pots for 20-60 m depth, and 10 pots for 60-95 m depth.

Crab abundance in diver transects followed similar trends as the CPUE reported for pots. No crabs were found in a total of 30 transects conducted in 1993 and 1994 and only 2 in 15 transects in 1995 in Outer Dundas Bay, in contrast to an abundance 236 ± 88.7, 78.1 ± 30.4 and 50 ± 22.9 crabs per hectare in 1993, 1994, and 1995, respectively, in Inner Dundas Bay (Figure 4).

Numbers of sea otters in Outer Dundas Bay remained relatively constant, with minimum counts during aerial surveys being 46 in 1993, 39 in 1994, and 40 in 1995.

Prey composition of sea otters in Outer Dundas Bay was 65% bivalves (*Saxidomus* sp., *Macoma* sp. and *Prototheca* sp.), 15% crustaceans (*Cancer magister* and *Chionoecetes bairdi*) and 20% other (green sea urchins, sponge, sea cucumbers, octopus, sea stars, and snails). Of the crustaceans consumed, 95% were Dungeness crabs (Figure 5). The above values represent an overall average of prey composition. Three sites were sampled within Outer Dundas Bay for prey composition of sea otter diets and the proportions varied among the sites as follows: (1) 26% bivalves, 46% crustacean, 28% other; (2) 96% bivalves, 1% crustacean, 3% other; and (3) 58% bivalves, 7% crustacean, 35% other.

Discussion

Dungeness crabs have large spatial and temporal variations in abundance (Botsford 1986, Johnson et al. 1986) that complicate interpretations of the impact of sea otter predation on crab abundance. Also, different spatial scales of dispersion (i.e., degree of aggregation) for different sex and life history stages of Dungeness crabs have been reported to vary with location within Glacier Bay (O'Clair et al. 1996). Interannual variations in the CPUE of different sex and life history stages of Dungeness crabs in five different bays within and adjacent to Glacier Bay were documented by Leder (1994) and Schultz (1996). In addition, the harvest of the commercial crab fishery should be expected to affect the abundance of crabs. The total harvest varies not only in response to interannual variations in abundance of crabs, but also in response to market demand.

The results of our survey suggest that sea otter predation affects the abundance and bathymetric distribution of Dungeness crab. The lack of multiple, paired sites and circumstantial nature of our data limit the inferences which can be derived; however, strong patterns are evident. In the presence of sea otter predation in Outer Dundas Bay, the CPUE of crabs was not significantly different from zero. Similarly, scuba divers found only 2 crabs in 45 scuba diver transects during 1993-1995 in the area where sea otters were present. In the upper reaches of the same bay (Inner Dundas) where otters are not observed or rarely present, CPUE varied from 1.8 to 2.7 crabs per pot during 1993-1995. The abundance of crabs in scuba diver transects declined steadily from

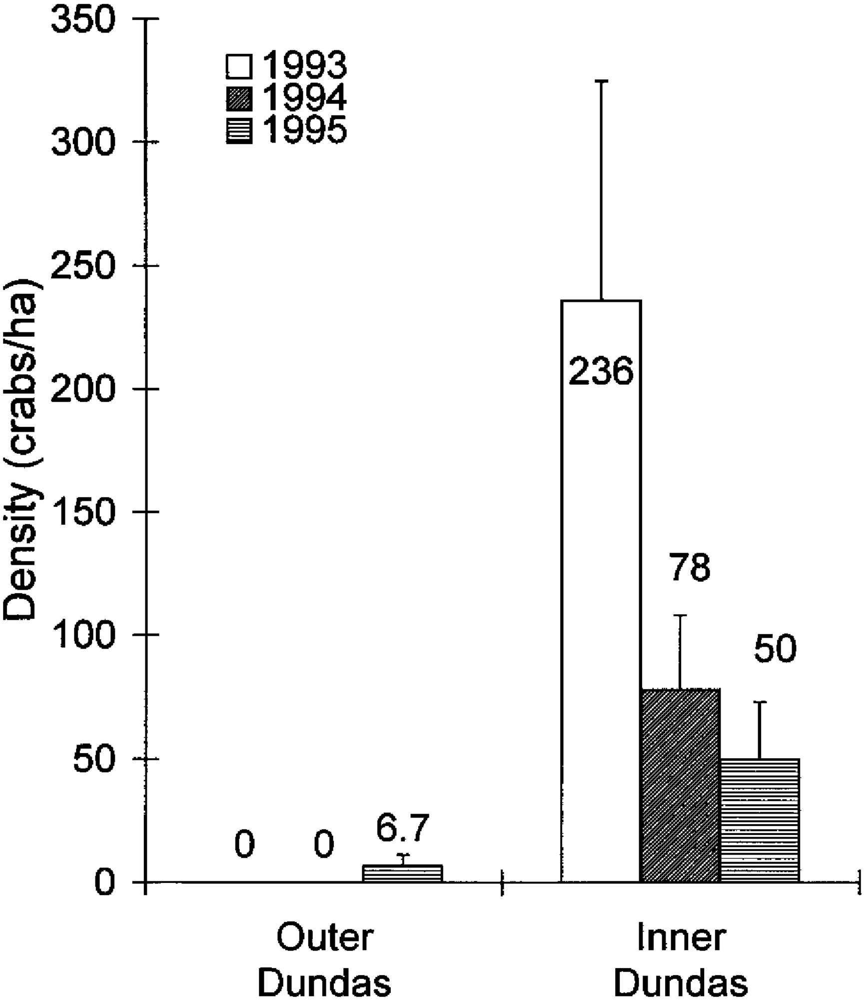

Figure 4. *Mean Dungeness density in diver transects (n = 15 diver transects per value) in Inner and Outer Dundas Bay in 1993-1995. Transects terminate at 18 m depth or shallower.*

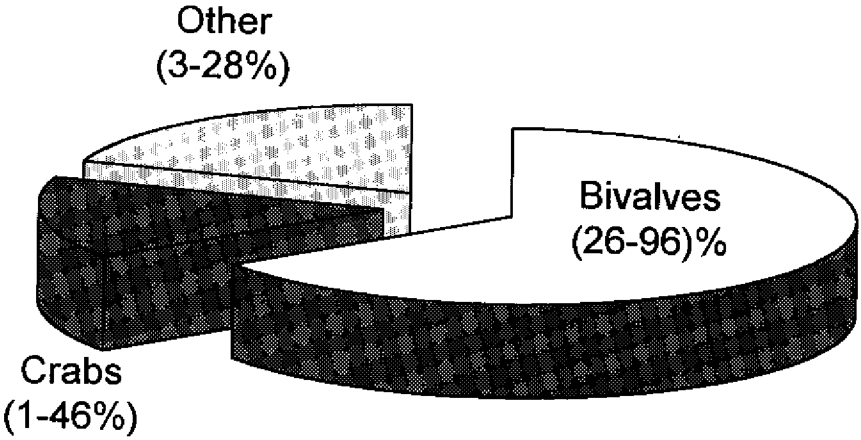

Figure 5. Mean composition of sea otter diet in Outer Dundas Bay in 1993. Values are averaged from telescopic observations at three locations. Other includes sea urchins, sea cucumbers, sea stars, snails, sponge, octopus.

236, to 78, then to 50 crabs per hectare in 1993, 1994, and 1995, respectively, in Inner Dundas Bay. We do not know if the decline is related to predation or resulting from long-term trends in population abundance.

The CPUEs that we report for both Outer and Inner Dundas Bay are sharp declines from the 1989 CPUE in Dundas Bay reported by Pitcher and Imamura (1990) of 10.49 ± 11.75 (mean ± standard deviation) crabs per pot per day. Although our crab pots were baited and set for 24 h in an identical manner as those of Pitcher and Imamura (1990), the values are not strictly comparable because crab pot locations and depths were not the same.

Sea otters were first reported in Dundas Bay by Pitcher and Imamura (1990). The CPUE they reported for Dundas Bay (10.49 crabs per pot per day) was one of the higher values they reported for areas along Icy Strait that did not have sea otters. It is likely that sea otters had not yet significantly decreased the numbers of Dungeness crabs in Dundas Bay at the time of their sampling, as the CPUE they reported for Dundas Bay in 1989 differs little from our overall CPUE from 5 bays within Glacier Bay during 1992-1995 of 9.4 crabs per pot per day (unpublished data). Pitcher and Imamura (1990) hypothesized that the low CPUE of Dungeness crabs in two other bays along Icy Strait, Idaho Inlet and Mud Bay, were likely the result of sea otter predation and predicted that substantial numbers of sea otters would populate Dundas Bay within three years and have a negative effect on Dungeness crab abundance. Our data corroborate their hypotheses and prediction.

A strong aspect of our study is our observations of sea otter diet in our crab study area. Sea otters were actively feeding on Dungeness crabs even though our divers could not find them in transects and few were collected in our crab pots. On average, 15% of the sea otter diet in Dundas Bay was crabs, of which 95% was Dungeness crabs. If crabs had been more abundant within Outer Dundas Bay, predation rates might have been considerably higher. Our sea otter feeding rates on crabs should be considered conservative, as some sea otters have been reported to feed nocturnally when Dungeness crabs are more active (Ralls et al. 1995), when telescopic observation of diet is not possible.

The increase in CPUE of Dungeness crabs with depth in Outer Dundas Bay has several implications. One inference is that depth may be a refuge from predation for the crabs. Although Dungeness crabs have been reported to 179 m depth (Hart 1982), they are generally found in nearshore areas and most of the commercial fishery in Alaskan waters occurs in less than 25 m depth (unpublished observations). In most of our other study locations in or near Glacier Bay, bathymetry prevented us from setting crab pots in deeper depths; however, in the South Beardslee Islands, CPUE of Dungeness crabs decreased with increasing depth to 60 m in 1995 and 1996 (unpublished observations). The diving depth of sea otters can exceed 100 m (Newby 1975) but most dives are in shallow water (VanBlaircom and Estes 1988, Kvitek et al. 1992, Ralls et al. 1995). As an interesting aside, we found Dungeness crabs in commercial Tanner crab pots at 183 m depth in Outer Dundas Bay (unpublished observations). In our April 1996 sampling in Outer Dundas Bay, the largest number of Dungeness crabs collected were in our deepest pot at 123 m. Another consideration of a possible depth refuge is that predation by sea otters may be biased towards certain sex and life history stages of Dungeness crabs. Ovigerous females tend to bury in dense aggregations, often in shallow water (O'Clair et al. 1996, Schultz 1996), perhaps rendering them more susceptible to sea otter predation. O'Clair et al. (1995) did find seasonal differences in sex distribution of Dungeness, but not significant differences in depth distribution between ovigerous and nonovigerous Dungeness crabs. However, the depth range studied was restricted to < 18 m. At our deep set of pots in Outer Dundas in 1995, 3 of 4 females collected were ovigerous.

Whether Dungeness crabs move to deeper depths in response to sea otter predation, or have substantial abundance at depth are questions that would have significant implications to the commercial fishery and to management agencies. The impact of sea otter predation may manifest itself only in movements of the crab populations, or conversely, a deep-dwelling population of Dungeness crabs may serve as a buffer against overexploitation.

The colonization of the inside waters of southeastern Alaska by sea otters has been relatively slow in comparison to their expansion along the oceanic coast. Similarly, sea otters do not seem to frequent some embayments such as Inner Dundas, even though sea otters are common in adjacent waters. Kvitek and Oliver (1992) suggested that high levels of paralytic shellfish toxins may protect some clam populations and limit the distribution of sea otters in some areas.

Most of the considerations of the effects of sea otter predation has been that of direct effects upon a commercially harvested species, Dungeness crab. More profound community level effects have been proposed (Kvitek et al. 1992). Sea otters reduce the size and abundance of their prey, and foraging-related disturbance and facilitation may enhance the abundance of other species. Removal of a large generalist predator such as the Dungeness crab may greatly affect the densities of its prey and competitors. Foraging pits created by the sea otters may facilitate predation by sea stars such *Pycnopodia helianthoides* which appear attracted to sites of sea otter activity (Kvitek et al. 1992). We have observed unusually high densities of *Pycnopodia helianthoides* in Outer Dundas Bay. High numbers of bivalve shells discarded by foraging sea otters increases the hard substratum available to benthic sessile species (Kvitek et al. 1992). Many of these community level changes could have impacts on possible later recolonization by Dungeness crabs. Additional community level studies of the impact of sea otter predation are needed.

We suggest that the long-term impact of sea otters on Dungeness populations may depend upon local bathymetry and recruitment source. In areas where crab recruitment is exogenous or where the bathymetry offers a refuge from predation, sea otter predation may not be as deleterious. Clearly additional study of this difficult but important topic is warranted. Long-term surveys of locations where sex and life history dispersion patterns of Dungeness crabs are known before, during, and after sea otter invasion may be one method of addressing the challenge.

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Effects of Handling and Discarding on Mortality of Tanner Crabs *(Chionoecetes bairdi)*

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Abstract

The substantial bycatch of female and sublegal male Tanner crab (*Chionoecetes bairdi*) in Alaskan commercial pot fisheries has been a subject of some concern. The process of crab capture, deck handling, and discard can result in damage that causes mortality. This study evaluated the separate effects of dropping crabs into water, inducing leg or carapace injuries, and repeatedly capturing crabs on the mortality of sublegal and legal size male Tanner crabs. After a 60-day holding period there was no significant difference in the percent of Tanner crabs dying in treatment groups (0-6%) and control groups (1-12%). Tanner crabs readily autotomize limbs that have been injured. Eighty-five percent of crabs with a merus/carpus joint injured had autotomized that leg within 24 hours, and 94% had done so by the 14th day.

Introduction

The Tanner crab (*Chionoecetes bairdi*) is one of the most important commercial crab species in Alaska. Over the 10-year period 1984-1993, the eastern Bering Sea alone accounted for 66,000 mt with an ex-vessel value of $228 million (ADF&G 1994). The Tanner crab fisheries use pots to target mature males greater than or equal to 140 mm (5.5 inches) carapace width (minimum legal size statewide except Prince William Sound, where the size limit is 5.3 inches) (ADF&G 1993). There is no minimum pot mesh size restriction, although in some areas two escape rings 121 mm in minimum inside diameter must be sewn into the mesh. In both Tanner and king crab fisheries, large numbers of sublegal-size male and female Tanner crabs are caught and must be returned to the sea. In the 1994 eastern Bering Sea Tanner crab fishery which captured

3.8 million legal males, an estimated 5.9 million sublegal male and 3.6 million female Tanner crabs were caught and released (Tracy 1995a). In 1993, the red king crab (*Paralithodes camtschaticus*) fishery on the same fishing grounds caught almost as many sublegal male and female Tanner crab (1.8 million) as it did legal king crab (2.0 million) (Tracy 1995b). If many of these incidentally caught crabs die, this could be a substantial source of population mortality.

There are many individual components of the capture, handling, and discard process that can injure crabs or cause them to be less fit. These forms of damage, individually or in combination, can cause immediate (occurring right after handling) or delayed (occurring after the crab has been returned to the sea) crab mortality. Some damage is grossly observable: broken spines, cracked, crushed, or punctured shell, or autotomized limbs. Other types of damage are less visible, and would include those caused by desiccation or temperature changes. Numerous studies have addressed mortality and injury to decapod crustaceans captured in fishing gear. Trawl gear has been shown to cause injury and mortality in Tanner crab (Stevens 1990) and Dungeness crab (*Cancer magister*) (Reilly 1983). Capture in pot fisheries has been shown to injure snow crab (*Chionoecetes opilio*) (Miller and Watson 1976) and western rock lobster (*Panulirus cygnus*) (Brown and Caputi 1983). For Tanner crab, Byersdorfer and Watson (1992) reported an injury (torn limb segment or broken carapace) rate of 3.0% and an immediate mortality rate of 0.5% in a 1991 research pot survey in the eastern Bering Sea. Of 834 Tanner crabs carefully examined from a similar pot survey in 1992, 16% had newly punctured, crushed, or cracked carapaces or legs (NMFS unpublished data). Potential mortality from repeated pot capture and discard of non-target crabs within a single season has also been cause for concern (Kruse 1993, Zhou and Shirley 1995).

Autotomy and regeneration, the severance of an appendage at a preformed breakage plane and its regrowth over several molts, are common among brachyuran crabs and in many species are the normal response to limb injury distal to the autotomy plane (Bliss 1960, McVean and Findlay 1979). Tanner crabs commonly autotomize chelate and walking limbs in response to a variety of stimuli including injury, external tension applied to limbs, and cold air exposure (Pers. obs., Carls and O'Clair 1990). Edwards (1972) found that 39% of Tanner crabs examined in the eastern Bering Sea had at least one autotomized limb. The conditions under which Tanner crabs autotomize and regenerate limbs have not been adequately studied.

The most common pot used in Alaskan Tanner crab fisheries is a large (0.9 m × 2.1 m × 2.1 m) steel frame cage weighing about 300 kg (Otto 1981). While the handling procedures for pots on deck vary considerably among vessels, a generalized scenario is as follows. When a pot is retrieved over the side of a vessel, it is lowered onto a hydraulically operated, articulated pot launcher at the rail. A hinged side door on the pot is opened and the crabs fall and are pulled out either into containers on deck or onto a raised table. The articulated launcher can be used to shake the crabs out of the pot. Crabs that are "stuck" in the pot are often removed by hand. At this point, the male crabs are sorted by size, with legal males being dropped or slid by chute into live-tank openings in the deck. Sublegal males and females are shunted overboard either by being carried to the rail and dropped overboard, placed in the stream of live-tank overflow water that washes overboard at deck level, or by being slid down a discard chute that ends just above water level. Crabs that are dropped over a vessel's rail can fall 2 m or more before hitting the water. In addition to a wide variety of physical deck arrangements for handling crabs, there is variation in handling that results from differences in the quantity of crabs caught per pot, the number of pots fished per unit time, weather conditions (including freezing temperatures), and the overall level of care with which crabs are handled by the crew.

Little is known about the mortality rates of Tanner crabs caught and discarded in pot fisheries. This paper examines male Tanner crab mortality that occurred within 59-60 days of specific handling processes or types of injury that are known to occur in Tanner crab pot fisheries. In three experiments, we examined mortality rates of crabs (1) dropped once or four times from a height of 2.5 m into seawater, (2) physically injured by tearing tissue at the merus/carpus joint of one leg ("bent" group), severing tissue of one coxa ("pinched" group), or cracking the lateral margin of the carapace ("cracked" group), (3) placed in a crab pot and lowered to, then raised from the ocean floor four times over a period of 3 days to simulate repeated capture and release in a fishery.

Methods

The three experiments, ordered 1, 2, and 3, are hereafter referred to as the Drop, Injury, and Elevator experiments. For all experiments, Tanner crabs were collected with commercial crab pots from depths of 70 to 150 m in Chiniak Bay (latitude 57°43′N, longitude 152°15′W), near the town of Kodiak, Alaska. Because few female crabs were caught, only males were used in our experiments. Several selection criteria determined which males were used. No softshell crabs or very oldshell crabs (crabs judged not to have molted within the previous 48 months) were used (except in the Elevator experiment, where 17 vigorous but very oldshell crabs were used because sufficient newer shelled crabs were not available). Also rejected were crabs with both chelipeds missing (autotomized), any number of very recent autotomies (autotomy plane membrane soft and white), more than two autotomies of any age, or crushed, cracked, or punctured shell. Experimental crabs were measured for carapace width (excluding lateral spines) and right chela height, coded for shell age, and the number and location of autotomized limbs was noted. A numbered Peterson disc tag was attached with a plastic tie to the distal end of a walking leg merus on each crab.

In all experiments, post-treatment crabs were held for 59-60 days in a covered outdoor live-tank system. This system consists of four circulating seawater tanks, each containing six plastic mesh baskets in which crabs were placed. Raw seawater circulated through each tank at a rate of 19 gpm. Water temperature, salinity, and dissolved oxygen level were monitored at least every 5 days. Tank water temperatures varied between 1.8 and 6.0°C during the three experiments. The number and duration of aerial exposures varied from experiment to experiment. The longest exposures were generally at the time of treatment, ranging from a mean of 19 seconds in the Injury experiment to 8 minutes in the Elevator experiment. Mean exposure times at tagging and measuring were 30 seconds and 106 seconds for the Drop and Elevator experiments, respectively. Air temperatures at exposure ranged from −3.0 to 3.9°C but almost all temperatures were above freezing. Crab were fed herring ad libitum every third day. Baskets were examined every day for mortalities.

There were enough dissimilarities in the handling of crabs in the three experiments that the methodology of each will be discussed separately at this point.

Drop experiment

Eighty crabs were used in two treatment and one control group for a total of 240 crabs (Table 1). Crabs caught on 8 December 1993 were carefully removed from the capture pots, placed in containers supplied with circulating seawater, and transported ashore to the live-tanks. The crabs were allowed to acclimate in the tanks for 5 days, at which time they were measured, autotomies were assessed, and they were tagged. On the following day, crabs were allocated to the baskets by size, with the three smallest crabs being split among the two treatment groups and the control group, and so on, until all of the crabs were allocated. In each group, 80 crabs were equally divided among eight baskets. The baskets were distributed among the 24 basket positions by randomized block design. In the two drop treatments, crabs were removed from the baskets and dropped from 2.5 m above a tote filled with seawater. All crabs were released from a horizontal position, and almost all impacted the water on their ventral surface. After all 10 crabs in a basket were dropped, they were removed from the tote and immediately returned to the tanks. Crabs in the 4-drop group were first dropped on 15 December, then every 48 h through the fourth drop on 21 December. Also on 21 December, the 1-drop group crabs were dropped and the control crabs were "sham-dropped." The sham-drop consisted of removing a control basket from a tank, gently placing each crab in the seawater-filled tote, then returning the crabs to the basket and tank. This process

Table 1. Characteristics of Tanner crabs used in three handling mortality experiments and experiment dates.

A. Sample size, crab size, and holding period.

Experiment	Group	Sample size	Number legal[a]	Size range mm	Mean size mm	Days held
Drop	Control	80	40	109-177	140	59
	1-Drop	79[b]	42	109-173	139	59
	4-Drop	80	44	109-182	141	59
Injury	Control	71[c]	15	107-164	131	59
	Bent	72	12	108-164	130	59
	Pinched	72	13	99-162	130	59
	Cracked	72	13	107-167	130	59
Elevator	Control	75	48	99-167	139	60
	4 lifts	69[d]	53	104-164	138	60

[a] Legal crabs are ≥ 140 mm carapace width.

[b] One crab died from injuries sustained during holding.

[c] One crab died from injuries sustained while molting in tank.

[d] Five crabs escaped and one was killed when a board covering a pot tunnel entrance broke free during treatment.

B. Treatment and holding dates.

Experiment	Treatment date(s)	Holding tank dates
Drop	15-21 Dec 1993	21 Dec 1993-18 Feb 1994
Injury	16 Mar 1994	16 Mar-14 May 1993
Elevator	5-7 Jan 1995	7 Jan-8 Mar 1995

simulated the drop treatment except that each crab was placed gently in, rather than dropped in, the tote.

Injury experiment

In the Injury experiment, 72 crabs were used in three treatment and one control groups for a total of 288 crabs (Table 1). Crabs were captured on 9 March 1994 and transported to the live-tanks as in the Drop experiment. On 14 March, they were measured, and their autotomies were assessed, tagged, and allocated as in the Drop experiment to individual baskets. Each group contained 12 crabs in each of six baskets. On 16 March the injuries in the three treatment groups were induced. In the bent group, the carpus of a middle walking leg was rotated on the end of the merus to a position 90 degrees beyond its normal, fully extended position. This tore the arthrodial membrane and underlying tissues and caused considerable loss of hemolymph. In the pinched group, the coxa of a middle walking leg was cut with a pair of wire cutters. This cut was made perpendicular to the axis of the coxa and severed the ventral half of the shell and muscle mass. In the cracked group, each crab was placed on a hard surface and hit with a metal rod on the lateral margin of the carapace directly above the posterior gill filament. The force was sufficient in all cases to crack the carapace and tear the underlying epidermis. Most cracks were straight, and began at the outside margin of the carapace and extended towards its center. Crack measurements on 63 crabs ranged in length from 21 to 47 mm (mean 33 mm). In approximately 73% of these crabs, the cracks forked or the impact created a small hole in the carapace. The fourth group was a control in which crab remained in the tanks for the duration of the experiment. In order to determine whether injuries would induce autotomy, all crabs in this experiment were examined 24 hours, and again 14 days after the treatment day.

Elevator experiment

Seventy-five crabs were used in single treatment and control groups for a total of 150 crab (Table 1). Crabs captured on 5 January 1995 were gently removed from the pots and pairs of approximately equal size were divided between two containers of seawater on deck. The treatment crabs were removed from one of the containers, measured, and autotomy assessed. Then they were placed in a modified crab pot covered with 77 mm stretch mesh webbing and with covers over the tunnel entrances to keep crabs from escaping. This pot was then lowered to the bottom of the bay. It was allowed to free-fall for the first 45 m, then was lowered slowly to the bottom on its buoy line. The control group crab were transported ashore to the live-tanks where they were measured, injury assessed, tagged, and placed 10 crabs to a basket in the tanks. The next day, 24 hours after the treatment pot was lowered to the bottom of the bay, it was pulled to the surface and brought on deck three more times with 1 hour intervals of bottom time. When the pot reached the surface on the second lift, one of the wood covers to the tunnel entrances was found to have come loose, killing one crab and allowing 5 crabs to escape, leaving 69 crabs in the treatment group. Each time the pot was brought on deck, it was placed on the pot launching rack which was raised just enough that the pot door could be opened above two totes laid end to end below it. The crab fell or were pulled out of the pot and allowed to drop the 0.6 m into the totes. Any crabs that were hung up in the pot web were carefully extracted by the crew and dropped in the tote. Immediately after removing the last crab from the pot, the crew lifted the crabs out of the totes, placed them back in the pot, and closed the pot door. The pot was then launched overboard. The fourth and final pot lift was made the next day, 7 January. The treatment group crab were then transported ashore to the live-tanks where they were measured and injury assessed again, tagged, and placed 10 crabs to a basket in the tanks. This was day 0 of the holding period.

Data analysis

Results of survival tests were analyzed using the log-likelihood ratio statistic, or G^2, which is approximately χ^2 distributed (Bishop et al. 1975, Agresti 1990). Initial analysis was conducted as a 2 × n contingency table, using outcome (survived, died) vs. group (including control). Secondary analyses were conducted as 2 × 2 tables by comparing each treatment vs. control separately, and by combining all treated crabs vs. controls. Analysis of autotomies was conducted similarly, except that data used were numbers of crabs that did or did not autotomize a leg. Results of the G^2 tests were considered to be significant if they had an alpha level = 0.05.

Results

Mortality

Drop experiment

Percent mortality and number of mortalities in the control, 1-drop, and 4-drop groups was 6.3% (5), 5.1% (4), and 2.5% (2), respectively (Figure 1). The G^2 statistic for all groups was not significant (Table 2), indicating no relationship between treatment type and the proportion of deaths in each group. Comparisons between controls and each treatment were also not significant, as was the comparison between controls and all treated crabs. Therefore, we conclude that dropping of crabs from a height of 2.5 m did not cause any significant mortality.

Injury experiment

Percent mortality and number of mortalities in each group was: control, 4.2% (3); bent, 1.4% (1); pinched, 1.4% (1); and cracked, 12.5% (9) (Figure 1). The G^2 statistic for all groups was significant (Table 2), indicating that the proportion of crabs dying was not independent of treatment. This significance is due to the difference between cracked crabs (mortality rate higher than that of control) and bent and pinched crabs (mortality rate lower than that of control). However, the relevant comparison is whether any treatment group exhibited mortality different from the control group. Comparisons between the control and each treatment group were not significant, nor was the comparison between the control and all treated crabs combined. Therefore, we conclude that injured crabs did not exhibit significantly greater mortality than uninjured crabs.

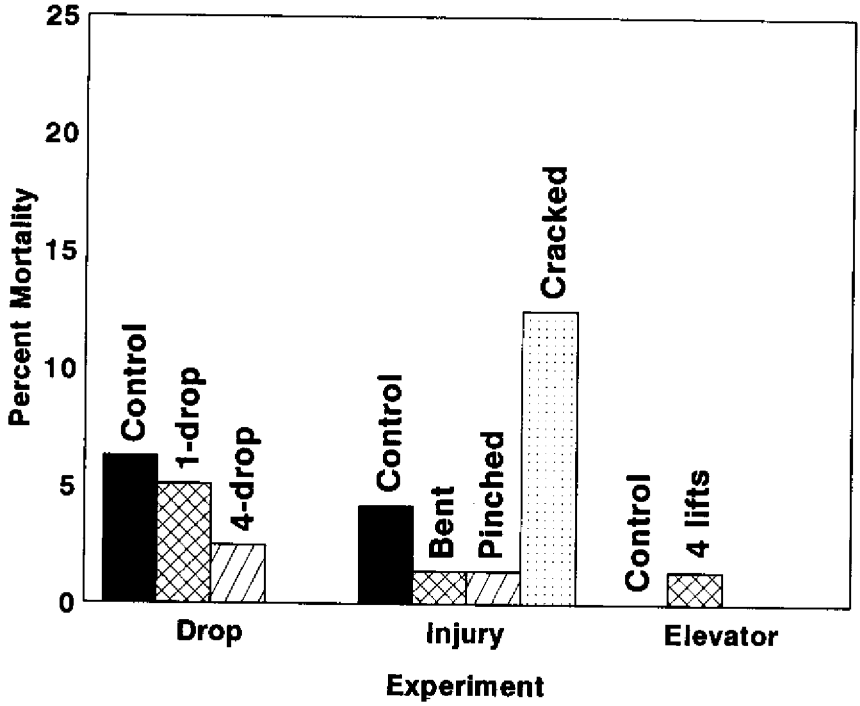

Figure 1. Percent mortality in control and treatment groups in three Tanner crab handling mortality experiments.

Elevator experiment

Only 1 of the treated crabs died, while none of the controls died. These numbers are too small to conduct a G^2 test, and the difference in mortality is considered not significant.

Autotomy

In the Drop experiment, the number of crabs with new autotomies (by day 59) was 23 in the control group, and 18 in both treatment groups. The incidence of autotomies was not significantly different among experimental groups ($G^2 = 1.05$, P-value = 0.59; Table 3).

In the Injury experiment, autotomies numbered 7, 70, 7, and 10 in the control, bent, pinched, and cracked groups, respectively. Bent crabs had a significantly higher rate of autotomy than crabs in the other two treatment groups and the control (Table 3; $G^2 = 195.1$, P-value < 0.001). Sixty-nine of the 70 bent crabs that had new autotomies had autotomized the injured leg. Of these 69 crab, 61 (88%) had done so within 24 hours of treatment and by the 14th day, 68 (99%) had done so.

Table 2. Results of G^2 tests for mortality in each of three Tanner crab handling mortality experiments.

Experiment	Comparison	G^2	P-value
Drop	All groups	1.443	0.486
	Control vs. 1-drop	0.105	0.746
	Control vs. 4-drop	1.387	0.239
	Control vs. all dropped	0.711	0.399
Injury	All groups	11.688	*0.008
	Control vs. bent	1.104	0.293
	Control vs. pinched	1.104	0.293
	Control vs. cracked	3.323	0.068
	Control vs. all treatments	0.089	0.765
Elevator	Too few deaths to compare	–	–

* indicates result is significant at $P < 0.05$.

Table 3. Numbers of crab with autotomies, sample size, and G^2 test results for autotomy in each of three Tanner crab handling mortality experiments.

			With autotomies	
Experiment	Group	N	Number	Percent
Drop	Control	80	23	29
$G^2 = 1.05$, $P = 0.59$	1-Drop	79	18	23
	4-Drop	80	18	22
Injury	Control	71	7	10
$G^2 = 195.1$, $P < 0.001$*	Bent	72	70	97
	Pinched	72	7	10
	Cracked	72	10	14
Elevator	Control	75	7	9
$G^2 = 2.74$, $P = 0.10$	Elevated	69	13	19

* indicates $P < 0.05$.

In the Elevator experiment, there was no significant difference ($G^2 = 2.74$, P-value = 0.10) in autotomy rates between controls (7 of 75) and elevated crabs (13 of 69; Table 3).

Discussion

There are many factors that by themselves, or in some combination, could potentially affect the survival of Tanner crab discarded from commercial pot fisheries. In our crab Drop and Injury experiments, we chose to narrow the focus of the treatment so that any observed mortality could be better linked to one treatment factor. The Elevator experiment linked a number of handling factors together and more closely resembled a commercial handling regimen.

Dropping crabs either one or four times into still water on their ventral surface did not increase mortality in our experiment. While we didn't simulate the drop from a moving vessel (crabs are usually discarded overboard from a vessel as it travels between pots), the height that we dropped from (2.5 m) was somewhat higher than the 1.7 m average rail height in a sample of twelve eastern Bering Sea crab vessels (Leslie Watson, Alaska Dept. Fish. and Game, Kodiak, Alaska, Dec. 1993, pers. comm.). Two recent experiments with red king crab also found no mortality associated with water impacts. Zhou and Shirley (1995) simulated deck handling and discard with a process that included an aerial drop into water and found no increase in mortality with up to three handlings. When Watson and Pengilly (1994) dropped tagged legal size red king crab from a height of 1.7 m from a vessel moving through the water at 7.5 knots, the rate of tag return from the commercial fishery was the same as for crabs that they dropped only 37 cm into still water. These experiments taken together would suggest that hard-shelled crabs are not damaged by water impacts alone.

Our Injury experiment was designed to isolate three common injury types from other handling factors. While no treatment group suffered significantly higher mortality than control crabs, it is possible that injured crabs or even uninjured crabs released into the natural environment would not have fared as well as tank-held crab. Gooding (1985) observed a high rate of fish predation on uninjured spiny lobsters (*Panulirus marginatus*) released from pots that resulted primarily from their vulnerability while falling through the water column and disorientation upon landing on the bottom. Fish predation in the eastern Bering Sea, however, may not be a problem. Food habits studies of Pacific cod (*Gadus macrocephalus*) (Livingston 1989) and of nine common groundfish predators (Livingston et al. 1993) have shown that while small Tanner crab are common fish prey, almost no crab over 60 mm carapace width are taken. In the Gulf of Alaska, Jewett (1978) found that while Tanner crab was the most frequently occurring species in Pacific cod stomachs, the largest crab taken was 70 mm, and 78% of crabs were between 7 and

28 mm. Since almost all male Tanner crab discarded from the eastern Bering Sea pot fisheries are larger than 70 mm (Tracy 1995a, 1995b), there is no evidence that, injured or uninjured, Tanner crab would be highly vulnerable to Pacific cod predation.

Autotomy is a common response to limb injury in Tanner crabs, and this was certainly the case with the bent group in the Injury experiment. Ninety-six percent of the crab in this group autotomized the injured leg. The 85% autotomy rate within 24 hours of treatment and the extremely low (1.4%) experimental mortality rate of these crabs suggests that leg injuries that lead to autotomies will seldom result in mortality.

The Elevator experiment was designed to simulate repeated capture of crabs in a pot as closely as possible. One substantial deviation, of course, was that the crabs rode the pot both up and down through the water column. By avoiding rough handling each time the pot was brought on deck, emptied, and refilled, we avoided some physical damage that might itself have caused mortality. No crab sustained body damage as a result of the elevator treatment and most leg damage was remedied by autotomy, as only three crabs had minor leg damage. Repeated retrieval of crabs through the water column followed by air exposure on deck as a significant source of mortality is not supported by this study.

There are several additional issues that need to be considered when evaluating these experiments and their relevance to actual fishery conditions. Only males were used in the experiments although females made up 38% of the 9.6 million Tanner crab discarded in the 1994 eastern Bering Sea Tanner crab fishery (Tracy 1995a). When Hayes and Reid (1974) held trawl-caught Tanner crabs on deck in air or buried in bins of fish, they found that, overall, egg-bearing females had a lower mortality rate than males. Because of their more compact shape, pot-caught females might also be less subject to limb injury and autotomy than males. Among trawl-caught "adult" Tanner crabs, Edwards (1972) found that 43% of males and 23% of females had autotomies. The discard mortality rate of large females is probably no greater than for large males.

The size of males that we used was dictated largely by what we could catch. The percentage of legal size males used in the Drop, Injury, and Elevator experiments was 52, 18, and 60%, respectively. Both sublegal and legal-size males are discarded in Alaskan commercial crab fisheries. The State of Alaska has, however, attempted to minimize crab bycatch by allowing the take of legal size Tanner crab during the most recent (1993) Bristol Bay red king crab fishery (Tracy 1995a).

No softshell and very few very oldshell crab were used in these experiments. Do commercial pots catch substantial numbers of these crabs, and if they do, might their mortality rates be higher? Observer data from the eastern Bering Sea Tanner crab fishery from 1991 through 1994 show that no softshell crabs of either sex are caught (Tracy 1995a). This is probably because few crabs are soft-shelled when the late fall fishery occurs, but softshell crab might also be less likely to enter pots to begin with. It is unclear whether very oldshell crabs, which made up about 1% of all crabs caught in the fishery (Tracy 1995a), would sustain higher mortality rates than newer shelled crabs.

The effect of cold air exposure on Tanner crab mortality was not addressed by this study. Most of our aerial exposures were to temperatures between 0.0 and 4.0°C, with the most extreme single exposure in the Drop experiment, where all crab were exposed to –3.0°C for less than a minute. This time-temperature combination was well below the mortality threshold demonstrated for Tanner crab by Carls and O'Clair (1990).

The assessment of crab fishery discard mortality of Tanner crabs is made difficult by the wide variety of conditions that exist during commercial harvests and by the difficulty researchers have in trying to simulate fishery conditions in their experiments. Our experiments suggest that some handling factors that were potential agents of mortality appear, in fact, to be fairly benign. Whether or not these factors, when included in complete handling regimens, would have resulted in mortalities different from those we observed remains unknown. Another question that remains unanswered is whether return of our treated crabs to the marine environment would have resulted in different mortality rates. There is a clear need for additional studies. To more closely simulate release into the natural environment, some future studies should hold treated crabs in underwater enclosures or tag and release them for subsequent recovery in commercial fisheries.

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Is Handling Responsible for the Decline of the Red King Crab Fishery?

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Abstract

A large number of female and sublegal-size male crabs are caught in the red king crab fishery and must be discarded to comply with the state's regulations on sex and size limitation. Before being returned to the sea, these crabs suffer aerial exposure, crushing, and deck and water impacts. In this study we examined the potentially deleterious handling effects of commercial fishing procedures on female and sublegal male red king crabs. We estimated that on average 64.6% king crab in the catch are females and sublegal males. The deck impact distance is approximately 60 cm, and the water impact distance is approximately 2 m if crabs are returned from the rail of vessels, or averages 71 cm if returned from the chute. Maximum aerial exposure duration averages 2.33 min. We simulated handling procedure in the laboratory to test the effects on discarded crabs. There were 5 treatments: handled once, handled twice, handled three times, modified handling (no deck impact and return to the seawater via a ramp), and controls. Crabs were categorized in 3 groups: ovigerous females, juvenile females, and sublegal males. After receiving handling treatments, crabs were maintained for 4 months while damage, righting response, feeding rates, weight change, carapace length increment, and mortality were monitored. Body damage increased significantly with increased handling. One crab died within 24 hr of the first handling treatment. However, there were no significant differences in righting responses, feeding rates, weight gain, carapace length increment, or long-term mortality among the five treatments. Normal handling of red king crabs during commercial crabbing activities may not have detrimental effects on the stock.

Introduction

The Alaska red king crab (*Paralithodes camtschaticus* Tilesius, 1815) fishery collapsed in the early 1980s. Since then the stock has remained at low abundance and shows no definite sign of recovery (Otto 1990). Several hypotheses have been proposed to explain this decline. Of these hypotheses, lethal and sublethal effects of handling during commercial crabbing have been suggested, and handling is suspected of continuously depleting the resource (Thomson 1990, Kruse 1992).

Red king crabs are commercially harvested by crab pots in Alaska. Only male king crab of legal size (≥ 121 to 178 mm CW, depending on the statistical area) can be taken or possessed (Alaska Department of Fish and Game, 1994-1995). In comparison to other fishing gear (e.g., trawl), pots have many advantages. However, a large number of females and sublegal-size males are incidentally caught in this male-only fishery. A field survey using king crab pots in Kodiak, Alaska, reported that 75% of king crabs caught were female, and, of the males captured, 26% were sublegal size (Blau 1988). This means that 81.5% of the king crab captured had to be returned to the sea. The sex ratio in the catch in Bristol Bay varied from year to year. The male:female ratio in a 1991 survey was 47:53. In the 1992 survey, although the male:female ratio was high (70:30), and 62% of males caught were legal-size (> 165 mm CW) (Byersdorfer and Watson 1992), as high as 57% of the red king crabs caught had to be returned to the sea.

Before they are released, these female and sublegal-size male red king crabs are exposed to aerial desiccation and temperature differences between the air and seawater. They may also crush each other, and sustain damage when dropped on the deck and into the sea during sorting and release operations. The amount of physical trauma received from impact with the vessel deck, and that crabs later endure when dropped from commercial vessels above the water surface, is unknown. Handling impact may have delayed sublethal effects on activity, feeding rate, growth rate, and long-term survival.

Red king crabs are vulnerable to autotomy (Edwards 1972, Kurata 1963, Niwa and Kurata 1964). The Alaska Department of Fish and Game conducted experimental fishing with pots in 1991 and reported that 2% of crabs were injured and 0.1% died immediately after handling (Byersdorfer and Watson 1992). There was no report on the incidence of handling-induced injury or mortality during commercial fishing with pots. The immediate mortality (47.3%) of king crabs captured by commercial sole trawls was high (Stevens 1990).

Prior investigation of handling effects on Dungeness crabs in southeastern Alaska demonstrated that increased handling resulted in higher mortality, culminating in 100% mortality after crabs were handled four times with techniques simulating those used in the commercial fishery (unpublished data, T. Shirley). The mortalities were not due to acute injuries, but rather occurred over a 4-month period following the handling. The average number of missing limbs and percentage of the population with missing limbs increased as the Dungeness crab season progressed (Shirley and Shirley 1988). Because red king crabs are larger and heavier than Dungeness crabs, and would be expected to have fewer adaptations to aerial exposure and impacts because of their subtidal lifestyle, the effects of handling may be more deleterious.

Our research hypothesis is that handling has lethal and sublethal effects on discarded female and sublegal-size male red king crabs. First we measured the crab vessels' dimensions related to potential impacts that discarded crabs would suffer. We estimated the aerial exposure duration from field observations, and we estimated the number of crab discarded and the immediate injury and death rate by analyzing data from the king crab observer program. Second, we simulated handling in the laboratory and examined the effects of handling on: (1) body damage which includes limb damage and autotomy; (2) vigor and activity; (3) feeding rate; (4) growth rate; (5) carapace increment after molt; (6) long-term survival; (7) the effects of repeated handling on these indices; (8) whether handling impacts can be ameliorated by alteration of handling techniques.

Methods

Field data collection

Crab vessels were measured prior to the opening of crab season when vessels were in the harbor. Rail-deck height (the distance from the rail to the deck), and rail-water height (the distance from rail to the water surface), chute-water height, sorting table dimensions, and tote dimensions were measured.

A minimum and a maximum aerial exposure time were measured for each pot with a stop watch. The minimum aerial exposure time was from the time the pot was lifted from the water to when the first crab was returned to the sea; the maximum aerial exposure time was from when the pot was lifted from the water to when the last crab in the pot was returned to the sea. Also the total number of crabs and number of legal crabs were counted for each pot. Water temperature and air temperature were recorded sporadically at different times of the day. Occasionally some crabs fell from the pot onto the deck; this impact should have a more detrimental effect. The number of crabs falling to the deck was recorded for each pot as an index of abnormal handling.

The Mandatory Shellfish Observer Program of Alaska Department of Fish and Game provided the data collected during the commercial red king crab fishery. Four years' data from 1990 to 1993 were used to estimate the impact of commercial crabbing on discarded crabs. The observer deployed on the catcher/processor vessel randomly selected approximately 5 pots per one hundred pulled, counted all of the crab according to the pertinent categories, species, and sex. If less than 100 crabs in any category were in the pot, all were measured for biological length. All crabs were examined for damage and death.

Laboratory experiments

Sublegal male and female red king crabs were collected near the laboratory in Auke Bay and Barlow Cove, Alaska, with commercial and sport pots, handled gently, and maintained in seawater during transport to the laboratory. Within the laboratory, crabs were kept in tanks with flowing seawater from a –30 m intake and fed a mixed diet of fish, squid, and mussels ad libitum. All crabs were acclimated to laboratory conditions for at least two weeks prior to experimentation.

Each crab was individually numbered with a numbered cinch tag attached to the basis of the right third walking leg. Sex, wet weight, and carapace length were recorded for each crab. No new autotomy resulted from initial capture and during maintenance in the laboratory. Crabs with missing leg(s) were not used for the experiment. The experiment consisted of 5 treatments, and 27 crabs were used in each treatment: 9 ovigerous females, 9 juvenile females, and 9 sublegal males. Crab sizes were selected so as to have similar-size crabs within each treatment, and the placement of crabs into each treatment was determined by randomized block design. The carapace length of these crab ranged from 70.3 to 125.0 mm with a mean size of 99.8 mm (± 14.1 SD), and the wet weight ranged from 258 to 1481 gram with a mean weight of 804.9 g (± 312.5 SD). Deck impacts and water impacts were studied by treating crabs in a manner similar to that experienced onboard commercial vessels. The handling procedures for the 5 treatments were as follows.

Treatment 1: handled once. Twenty-seven crabs were placed in a simulated commercial pot (approximately ½ size, 92 × 92 × 45 cm, but of similar box shape). The pot was stood on a height of 60 cm and subsequently tilted at a 45° angle. The door of the pot was opened and crabs fell (were dumped) into an empty tank. Crabs tangled on the pot-mesh were shaken to cause them to fall and none was pulled out by hand. Crabs were then dropped from 3 m height into seawater onto their dorsal surface.

Treatment 2: handled twice. All crabs in this treatment received the same handling as Treatment 1. Three days after the first handling, crabs were handled in the same way as the first handling, except that they were dropped onto their ventral surface. This permitted crabs in this group to experience one dorsal water impact and one ventral water impact.

Treatment 3: handled three times. All crabs in this treatment received the same handling as Treatment 2. Three days after the second handling, crabs were repeatedly handled in the same way as during the first handling.

Treatment 4: modified handling. Crabs were placed in a pot and dumped from 60 cm height into a tank filled with seawater of 40 cm depth (the distance between the pot and water surface was 20 cm). Then crabs slid on their ventral surface into seawater from a 45° tilted ramp of 3 m height rather than being dropped.

Treatment 5: control. This group received no handling or aerial exposure after the initiation of experiments, other than that used for determining weights and measurements.

During these four treatments, water temperature varied between 7.8° and 8.6°C and air temperatures varied between 7.6° and 15.3°C. Aerial exposure time for the last crab returned to the water varied from 10-14 min. in Treatment 1 and Treatment 3.

Crabs from all treatments were returned to laboratory holding tanks for examination. Crabs used for feeding measurements and crabs undergoing molting were kept in individual compartments.

Body injury and limb autotomy, if any, were recorded for each crab immediately after each experimental treatment. Mortality was recorded daily.

One day after treatment, the righting time that each crab required to turn over when placed on its back underwater on the bottom of the tank was recorded. We considered the righting time to be an indicator of general well-being of the crab as an integrated coordination of muscles and sensory perception is required for rapid righting. Righting time was measured weekly until week 12. Feeding rates were measured by placing known weights of cut squid into each crab container and weighing the remainder 24 hr later. Before it was weighed, the food was blotted dry with paper towels. Measurements were made of control food soaked for 24 hr in a tank without crabs to determine weight changes due to immersion, and consumption was corrected accordingly. Feeding rates were measured twice a week for a subset of 9 crabs in each treatment until week 13. At the termination of the experiments (4 months after experimental treatments), wet weights and carapace lengths were recorded for all crabs.

Several statistical methods were used to analyze different experiment indexes according to the data characteristics. All data were diagnosed by graphic methods before and after statistical tests. Data transformation was applied if statistical assumptions were violated. Statistical power was calculated for some experimental indexes.

Results

Impact of commercial fishery

During commercial crabbing, pots are pulled to the deck and the contents dumped onto a sorting table or into a tote. After sorting the legal-size male are kept while females and sublegal males are slid down from the sorting table to a chute below the deck surface with overflow water

Table 1. Measurements (cm) of deck and water impact distances.

	Rail-deck (N = 63)	Table-chute (N = 10)	Chute-water (N = 60)	Rail-water (N = 61)
Minimum	76	73	18	130
Maximum	147	96	153	282
Mean	104	86	71	198
SD	14.50	7.42	31.4	37.37

from the tank, and then dropped from the chute to the sea or thrown out from the rail to the sea.

The major impacts include the dumping of crabs onto a sorting table or into a tote, and sliding from the sorting table to the chute. The distance from lower edge of the pot door to the table is less than 30 cm. A typical tote has dimensions of 81 (wide) × 142 (long) × 53 (high) cm. The distance from the lower edge of the pot door to the bottom of the tote is about 60 cm. The mean height of a sorting table is 61 cm and the chute is approximately 25 cm lower than the deck surface (Table 1). Crabs usually slide down to the chute through a ramp at approximately 45°.

Water impact distances were measured when boats were fully or partially loaded with pots and their holding tanks were partially filled with water. Two vessels with a rail-water height of 3.05 m were treated as outliers because they were unloaded and had no water in tanks. The water impact distance varied with the size of vessels (Figure 1). The larger vessels generally had a greater water impact height. If crabs are returned to the sea from the chute, the mean water impact distance was < 1 m, but if crabs were thrown back from the rail, the mean water impact distance might exceed 2 m (Table 1).

Crabs are exposed to air from when pots are lifted from the water until the crabs are returned to the sea. The number of crabs in the pot affects the aerial exposure duration (Figure 2). The first crab can be returned to the sea within 2 min. (mean 1.3 ± 0.23 SD, N = 97) , and the last one within 4 min. (mean 2.3 ± 0.47 SD, N = 134). During the 1994 fishing season, the air temperature in Bristol Bay varied from 0.5°C to 6.6°C with a mean of 3.0°C (± 2.13 SD, N = 20), while the water temperature was more stable, from 3.5 to 4.4°C with a mean of 4.0°C (± 0.30 SD, N = 6).

Some crabs suffered abnormal handling during crabbing. When the pot door was opened quickly, crabs hanging on the door might be tossed high into the air. An average of 1.41 ± 1.32 SD (N = 108) crabs dropped to the deck rather than into the sorting table. These crabs suf-

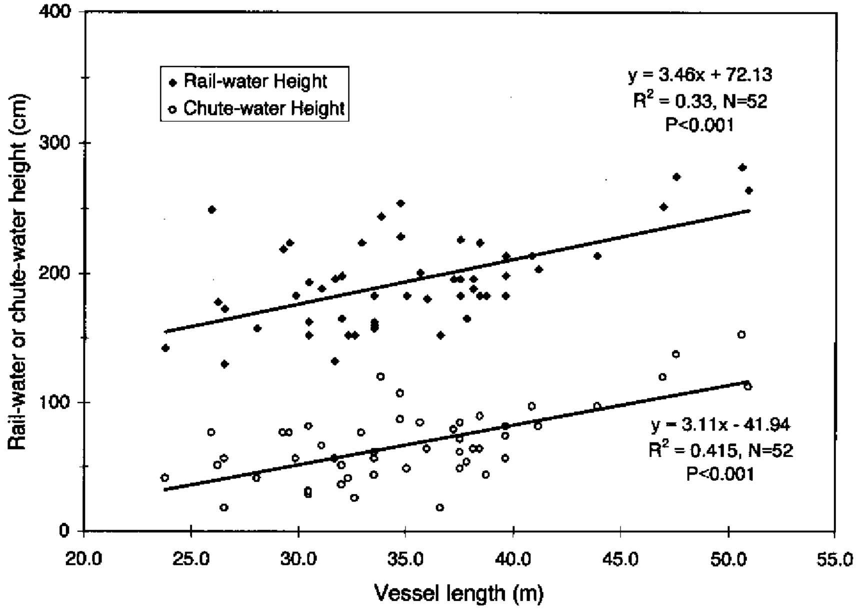

Figure 1. Water-rail height and water-trough height of commercial crab vessels.

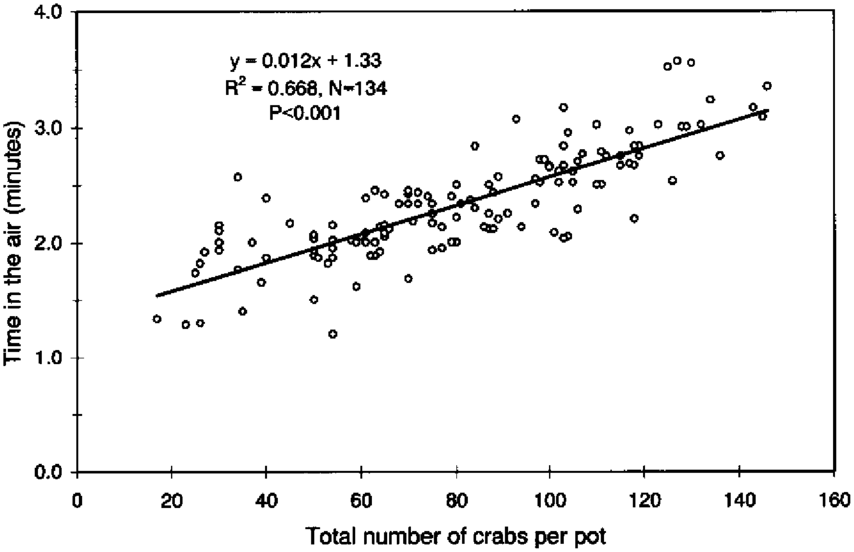

Figure 2. Maximum aerial exposure duration in commercial fishery.

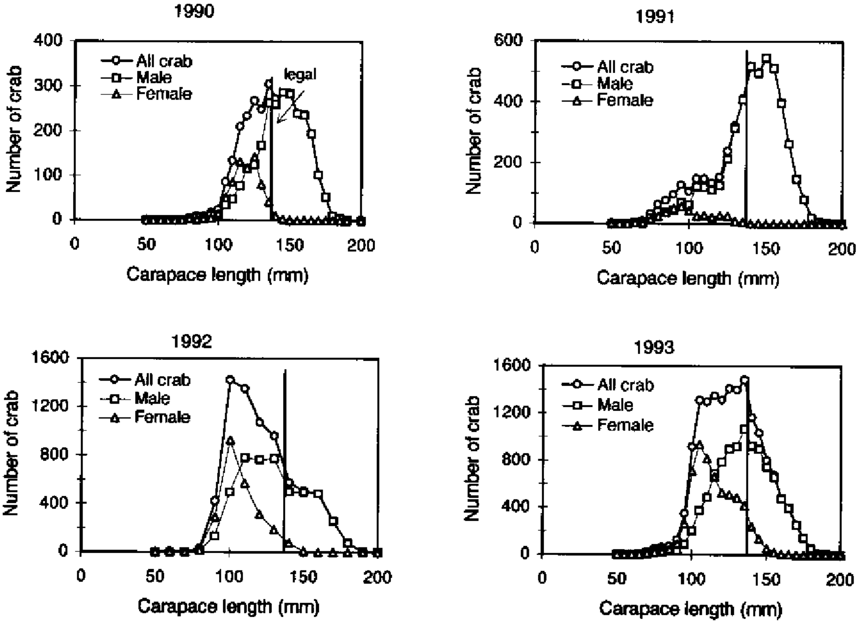

Figure 3. Carapace length distribution of red king crab in Bristol Bay fishery with regard to the legal size.

fered longer aerial exposure, and might be kicked, smashed, or thrown back to the water from the rail.

Red king crabs as small as 65 mm in carapace length can be retained in crab pots, but few crabs less than 85 mm CL are caught (Figure 3). Although the size distribution of the catch varied from year to year, a significant number of female and sublegal male king crab were caught in red king crab fishery. The minimum legal size was 6.5 inch or 165 mm carapace width including spines in the Bristol Bay district (Alaska Department of Fish and Game 1994-1995). If the relationship of $CL = 0.81 \times CW + 3.57$ was applied (S. Zhou, unpublished data), the legal size was 137 mm in carapace length. Crabs smaller than this size must be released (Figure 3).

From the average number of crab caught in each pot (Figure 4), we calculated that an average of 64.6% (± 18.60 SD for 4 yr) of the catch would be discarded, if only the red king crab is considered. As an example, in 1990, 3,120,326 legal males were landed in Bristol Bay red king crab fishery, and in 1991, 2,630,446 legal males were landed (Westward Region Shellfish Staff 1992). By applying the average discard rate, we estimated that in Bristol Bay 6.6 million crabs in 1990 and 4.8 million

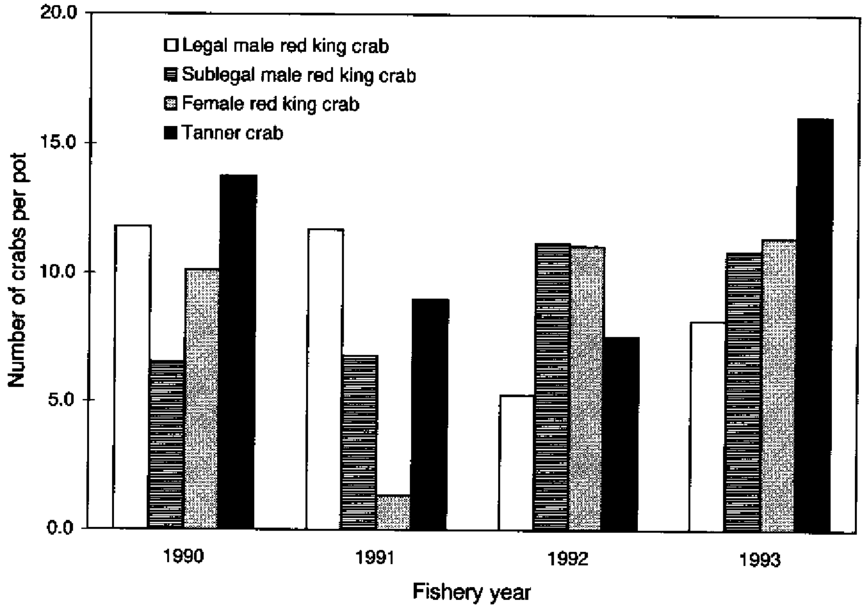

Figure 4. Average number per pot of legal male, sublegal male, female, and Tanner crab in Bristol Bay red king crab fishery.

crabs in 1991 were discarded. If the Tanner crab, *Chionoecetes bairdi* (another commercially important species), is also considered, an average of 75.3% (± 12.2 SD for 4 yr) of the catch had to be returned to the sea. Besides these discards, the fishery caught a small amount of other economically important crab species such as snow crab (*Chionoecetes opilio*), Korea hair crab (*Erimacrus isenbeckii*), blue king crab (*Paralithodes platypus*), and golden king crab (*Lithodes aequispinus*). These crabs also would have been discarded.

The injury rate and death rate were low in the red king crab fishery. We calculated that only 0.2% ± 0.002 (mean ± SD) crab sampled were freshly injured, and only 0.02% ± 0.0002 (mean ± SD) crab were dead during 1991, 1992, and 1993.

Laboratory experiments

Handling caused damage, and damage increased with repeated handling (Figure 5). Spines were most vulnerable to the damage. A significant difference in damage among the Treatments 1-4 occurred for all damage types combined ($\chi^2 = 50.6$, df = 3, $p < 0.001$) and for the spines damage alone ($\chi^2 = 37.84$, df = 3, $p < 0.001$). Due to low damage rates in the rostrum, leg, and carapace, one-tailed Fisher's exact test was conducted to

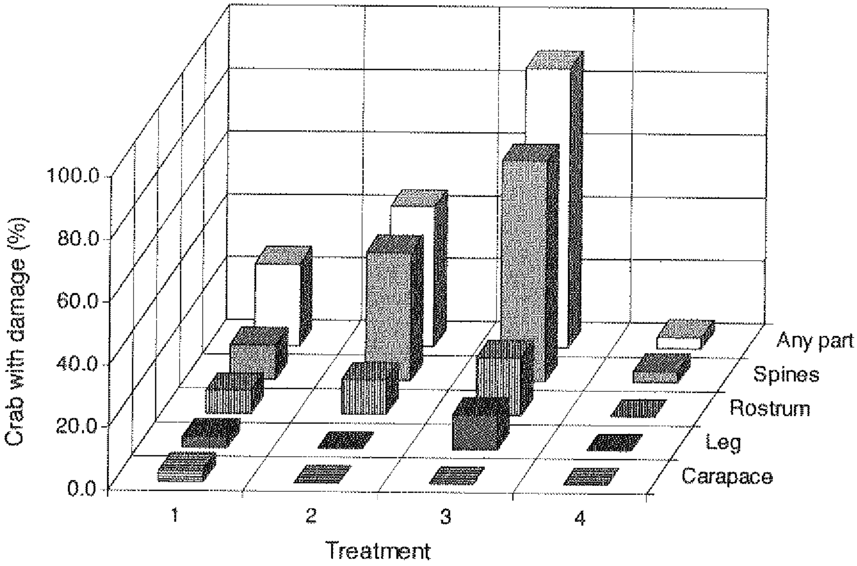

Figure 5. Percent crabs with damage after handling in the laboratory. Treatment code: 1 = handled once, 2 = handled twice, 3 = handled three times, 4 = modified handling.

test the damage in Treatment 1-3 as comparing to either Treatment 4 or Treatment 5. For rostrum damage, Treatment 1 and 2 were not significantly different from the control (1-tailed Fisher's exact test, $p = 0.246$ and $p = 0.118$ respectively), while Treatment 3 was ($p = 0.026$). There were no significant difference for leg ($p > 0.10$) or carapace damage ($p = 0.50$). Eighty-nine percent of the crabs handled three times had damaged body parts, either spines, legs, rostrum, or carapace; while only 26% of the crabs handled once had damage to body parts. Crabs in the modified handling treatment (without deck impact and returned to water by means of a slide) had the least damage, approximately 4%.

Red king crab can promptly right themselves after being placed on their back. During the experiment, 67% of crabs righted themselves within 2 seconds, and 89% within 3 seconds. Some individuals required a longer time to turn over, but the maximum righting time was 7.8 seconds. Data transformation was performed to improve normality. Righting time did not differ significantly among the treatments (regression analysis, df = 515, $p > 0.10$). However, the righting time was affected by both days after handling and sex (N = 518, $p < 0.001$). Further tests with Scheffe's methods indicated that only the males' righting time differed from both ovigerous females and juvenile females (df = 515, $p = 0.020$ for male vs. ovigerous female, and $p < 0.001$ for male vs. juvenile fe-

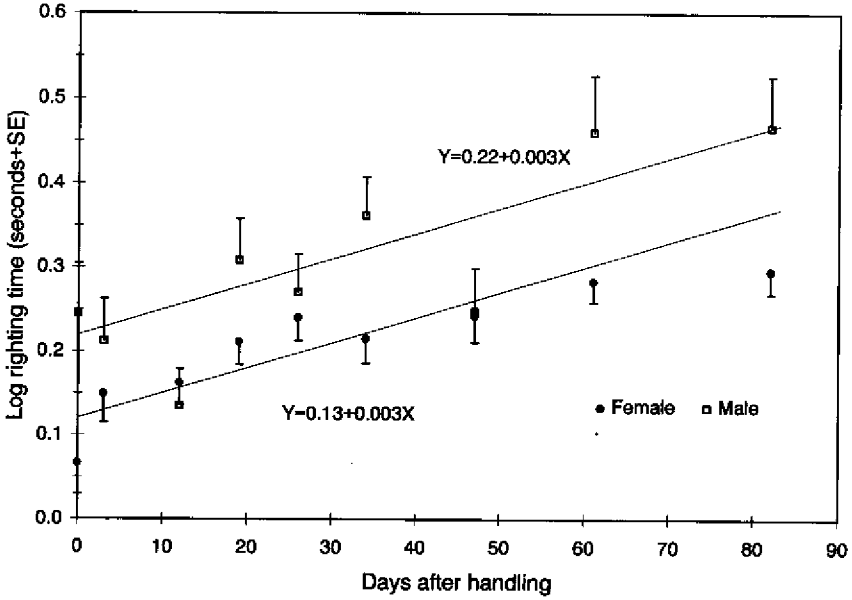

Figure 6. Log righting time of male and female king crabs over time after handling.

male), while the righting time between ovigerous females and juvenile females was not ($p = 0.056$). A linear regression with a dummy variable Z was fitted to the data:

$$\text{Log(Righting time)} = 0.224 + 0.003 \times \text{Day} - 0.093 \times Z$$

where $Z = 1$ when females, and $Z = 0$ when male (N = 518, $r = 0.364$, $p < 0.001$, Figure 6). During the three months after handling, males took 0.3 to 0.6 seconds longer to turn over than females, and the average righting time increased from 1.7 to 3.0 seconds for males and from 1.4 to 2.4 seconds for females.

Feeding rates did not differ significantly among the treatments, after feeding rates were standardized to grams of food consumed per kilograms of crab wet weight per 24 hours (Stepwise regression or ANOVA, N =751, df = 4, $p > 0.10$, Figure 7). No significant differences in average feeding rates occurred among the treatments over time (Regression analysis, N = 751, $p = 0.494$, Figure 8). There was also no significant difference between the sexes when feeding rates of each single day were analyzed by two-way ANOVA ($p > 0.05$). However, a significant difference existed between sex categories with a regression method (N = 751, df = 4, $p = 0.001$), and males had significantly lower feeding rate than females (Scheffe's test, df = 743, $p = 0.002$ between males and ovigerous

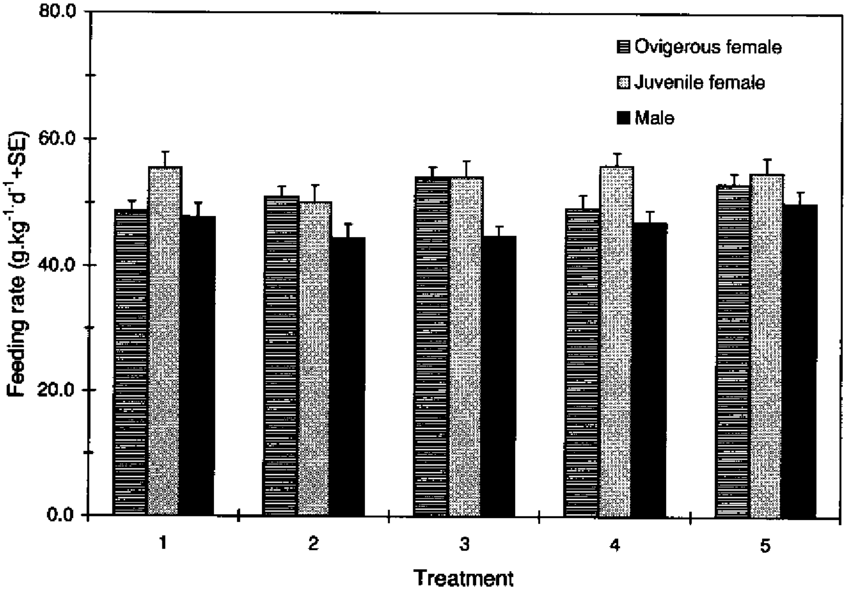

Figure 7. Average feeding rate (g × kg^{-1} × d^{-1}) of red king crabs. Treatment codes are the same as in Figure 5, and code 5 = control. No significant difference existed between treatments.

females, and $p < 0.001$ between males and juvenile females), but no difference existed between ovigerous females and juvenile females. Average feeding rates were 51.3 g × kg crab^{-1} × d^{-1} (± 12.9 SD) for ovigerous females, 54.4 g × kg crab^{-1} × d^{-1} (± 17.4 SD) for juvenile females, and 46.4 g × kg crab^{-1} × d^{-1} (± 13.5 SD) for sublegal males.

All crabs were weighed at the beginning and at the end of the experiment. Stepwise regression was performed to analyze the effects of treatment, sex, and original weight on final weight for the following model:

$$W_2 = \text{Constant} + \text{Treatment} + \text{Sex} + W_1 + \text{Treatment} \times \text{Sex} + \text{Treatment} \times W_1 + \text{Sex} \times W_1 + \text{Treatment} \times \text{Sex} \times W_1,$$

where W_1 = weight at the beginning, W_2 = weight at the end of the experiment. Only sex and W_1 were significant factors (N = 101, $p < 0.001$ for both sex and W_1). Neither significant difference between treatments, nor interaction between any factors was found in the model (N = 101, $p > 0.10$). Since more than 50% of the male king crabs molted during the 4-month experiment, the growth data were further analyzed separately by sex.

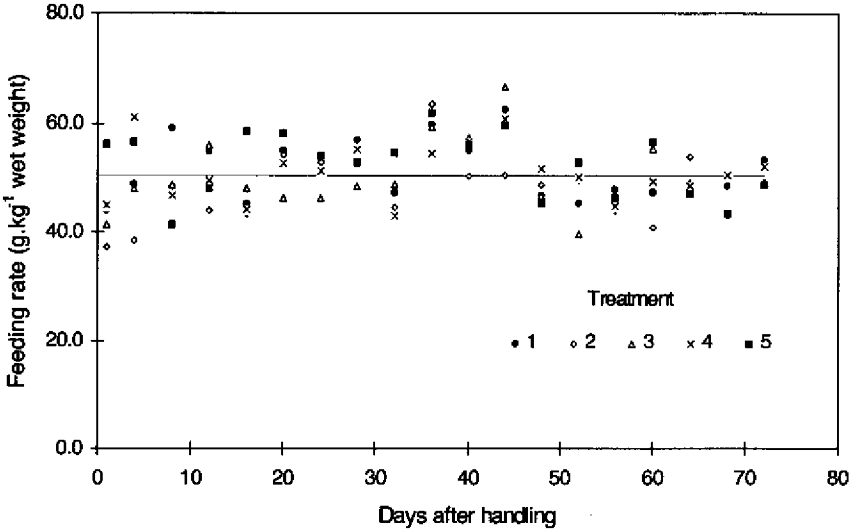

Figure 8. Feeding rate (g × kg^{-1} × d^{-1}) of red king crabs over time. The treatment codes are the same as in Figure 7. No significant difference existed between treatments and over time.

The relationship between W_2 and W_1 was significantly different between ovigerous female and juvenile female (ANCOVA, N = 74, $p = 0.005$, Figure 9). Two linear regression equations were fitted, ovigerous females: $W_2 = 1.05W_1 + 26.8$ (N = 34, $R^2 = 0.9889$, $p < 0.001$); and, juvenile females: $W_2 = 1.05W_1 - 6.2$ (N = 39, $R^2 = 0.9965$, $p < 0.001$). Ovigerous female king crabs gained more weight than juvenile females did in the 4-month period, and larger crabs gained more weight than smaller ones in the same category.

During 4 months and after one molt, the wet weight of males increased from an average of 785.6 g (± 284.5 SD, N = 20) to a mean wet weight of 1093.4 g (± 347.7 SD, N = 20) in the manner of $W_2 = 1.21W_1 + 141.4$ (N = 20, $R^2 = 0.9833$, $p < 0.001$, Figure 9).

For female king crabs, the growth rate, expressed by $(W_2 - W_1)/W_1$ in g × kg^{-1}, did not differ among treatments (ANOVA, N = 72, df = 4, $p > 0.10$), but differed significantly between ovigerous and juvenile (ANOVA, N = 72, df = 1, $p = 0.004$), and W_1 had interaction with these two categories of females (ANOVA, N = 72, df = 1, $p = 0.036$). Ovigerous females had a higher growth rate but it slightly decreased with an increase in crab size; juvenile females had a lower growth rate but it slightly increased with crab size (Figure 10).

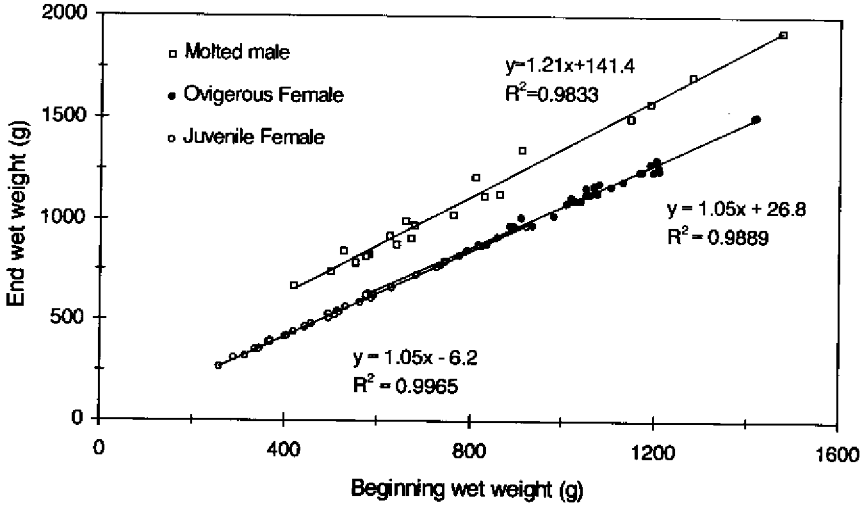

Figure 9. Relationship between wet weight at the beginning and at the end of four-month experiment. No significant difference existed between treatments.

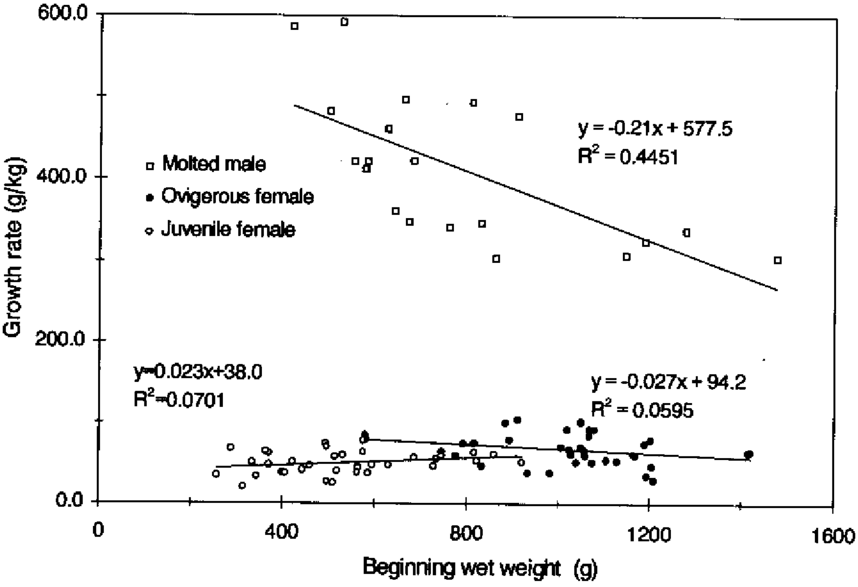

Figure 10. Growth rates (wet weight gain/wet weight at the beginning of the experiment) during the 4-month experiment. No significant difference existed between treatments.

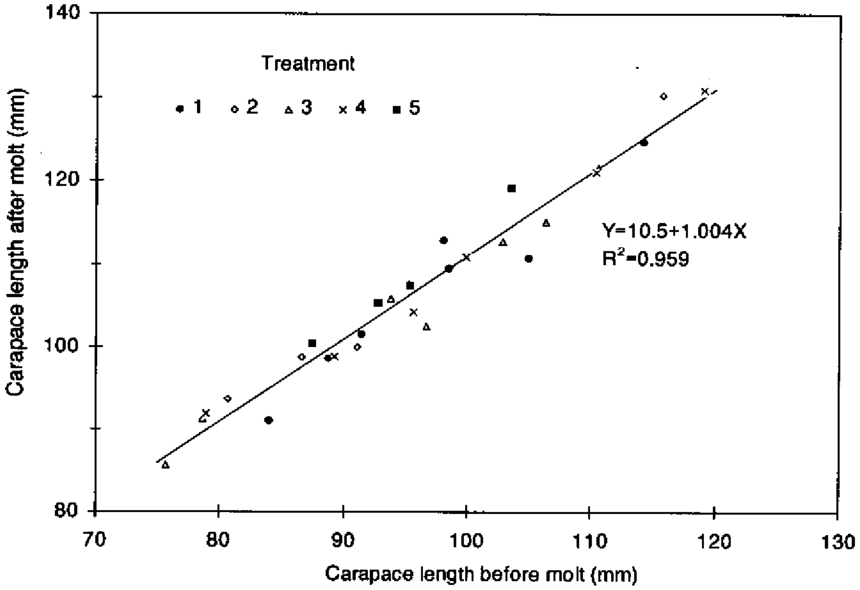

Figure 11. Carapace length increment of molted male crabs. The treatment codes are the same as in Figure 7. No significant difference existed between treatments.

Molted male king crabs did not have different growth rates among treatments (ANOVA, N = 20, df = 4, $p = 0.051$). The largest difference in growth rates occurred between Treatment 4 (Modified handling) and Treatment 5 (Control) where crabs in Treatment 5 had a mean growth rate 111.6 g × kg^{-1} greater than crabs in Treatment 4, but the difference was not significant (Scheffe's test, df = 14, $p = 0.115$). Growth rate decreased with crab weight in the manner of Growth rate = 577.5 − 0.21 × W_1 (N = 20, $R^2 = 0.445$, $p = 0.001$, Figure 10).

Carapace length after molt (CL_2) was only related to carapace length before molt (CL_1) (ANCOVA, N = 28, df = 1, $p < 0.001$) and was not affected by treatments (ANCOVA, N = 28, df = 4, $p = 0.122$). The relationship was: $CL_2 = 10.5 + 1.004 \times CL_1$ (N = 28, $R^2 = 0.959$, $p < 0.001$, Figure 11). The mean growth data were summarized by sex categories (Table 2).

Mortality was relatively low in all treatments. A total of 18 crabs of the 135 crabs used in the experiment died over the 4-month study; 6 of the mortalities were due to experimental error. There were 2 mortalities (7.4%) of unknown causes in each treatment, except in Treatment 2 which had 4 mortalities (14.8%). In the treatment handled once, one crab died within 24 hr of the handling treatment and was considered to be acute mortality. All other unknown mortalities were considered delayed

Table 2. Summaries of growth during the four months experiment.

	Growth rate (g × kg^{-1} wet weight)			CL increase (mm)
	Ovigerous female (N = 35)	Juvenile female (N = 37)	Molted male (N = 20)	Molted male (N = 28)
Mean	66.6	50.4	412.3	10.9
SD	19.4	14.5	89.6	2.4

mortalities. There were no significant differences in mortality among the five treatments (G-test, df = 4, $p = 0.695$), even when the mortality in Treatment 2 (14.8%) was compared to mortalities in other treatments (one-tail Fisher's exact test, $p = 0.335$).

Statistical power (1–β) was calculated for experimental indexes (Cohen 1988, Search-Bernal 1994). When α was set at 0.05, and the two-tailed power test was adopted, the (1–β) value was between 0.6 and 0.8 for most of the indexes; for example, 0.72 for feeding rate, 0.75 for male growth rate. When we examined all of the indexes by sex categories for each treatment, we did not see any index (the response was expressed in mean value) had an increasing or decreasing trend in the order of control-modified handling-handled once-handling twice-handled three times, after other factors were considered.

Discussion

More than 60% of the catch in the red king crab fishery are female and sublegal-size male crabs, and they must be returned to the sea. These crabs experience a fall from nearly 30 cm height from the pot to a sorting table, sliding from about 90 cm height to the chute, and dropping to the water surface from approximately 1 m height if from a chute or 2 m height if dropped from the rail. Also they will be exposed to air for 1-4 min. Although the injury rate and immediate mortality, 0.2% and 0.02%, respectively in the fishery, are very low, the numbers of discards are tremendous. Is there any lethal and sublethal effect to these discards over the long term? Our laboratory study suggested that there were no significant differences in activity (measured in righting time), feeding rate, weight gain, carapace increase, and mortality among the five treatments. Although body damages significantly increased with handling, the damages were limited to spines and rostrum, and did not affect crab's survival. Male king crab had longer righting time and lower feeding rate than females. We explained this difference as a result of the males' molting activity, even though we excluded the data measured ten days before and after when a crab molted. Between September 15 and

January 15, 29 males molted, while only 3 juvenile females molted and no ovigerous female molted. The slight differences, although statistically significant, may have little biological significance.

Our results of no significant effects of handling contrast with many other studies in crustacean fisheries. In these mimic experiments, after handling and aerial exposure, crabs and lobsters had increased injury, reduced vigor, decreased growth, and increased mortality (Brown and Caputi 1983, 1985; Davis et al. 1978; Kennelly et al. 1990; Simonson and Hochberg 1986).

Besides the probable difference in tolerance of stress between red king crab and the other species studied, the conservative handling techniques in our laboratory experiment might contribute to this contrast. In other mimic experiments, the animals were treated detrimentally or lethally. For example, in a mortality study of declawed stone crab (*Menippe mercenaria*), 47% of the declawed crabs died from the trauma of double amputation and 28% from single amputation (Davis 1978). Declawing caused high mortality; however, it should be noted that the stone crab has large chelae that constitute 51% of the total weight of an intact crab. Amputating two chelae left a crab less than half its original weight. Also a significant amount of body fluid was lost due to declawing. In another declawing study of stone crabs (Simonson and Hochberg 1986), the animals were exposed to the air for 2-6 hr and then the chelae were amputated. Mortality increased to 100% for crabs suffered aerial exposure for 6 hr and finally being declawed. However, if these crabs were wetted with seawater once every hour during the exposure before being declawed, the mortality decreased to 23%. The long aerial exposure plus declawing (which was more than 25% body weight for one claw) was fatal to crabs.

Removing one cheliped of blue crab (*Callinectes sapidus*) did not alter the molt increment, percent wet weight increase, or molting frequency. Multiple limb loss significantly reduced the molt increment and percentage weight increase in the first molt after amputation, but did not affect the duration of the intermolt. By the second molt following amputation, molt increments for crabs missing four limbs did not differ significantly from those of intact animals (Smith 1990).

Kennelly et al. (1990) found that 60-70% of spanner crab (*Ranina ranina*) with one or more dactyls removed died within 50 days, while 100% of crabs with whole limbs removed died after 8 days. This crab's high vulnerability to death is probably related to its reluctance to autotomize limbs.

In a laboratory experiment of effects of aerial exposure on rock lobster (*Panulirus cygnus)*, an expected time for 50% mortality within two weeks was 233 to 99 min. with increased temperature, and a time of 387 min. for lobsters exposed to air under shade (Brown and Caputi 1983). However, no mortality was evident when exposure time was less than 40 min. even under direct sunlight at the highest temperature regime of the experiment (31-35°C). In another study of rock lobster exposed to air, all 8 crabs exposed for 60 min. at high temperature (34-35°C) died before their second molt after the exposure; however, no difference in mortality was observed for crabs in 0, 15, and 30-min. exposure at 34-35°C. There was also no difference in mortality for the rock lobster exposed to air for 0, 15, 30, 60, and 120 min. when the air temperature was mild (20-21°C). The observed effect was that increasing aerial exposure duration decreased growth increment (Brown and Caputi 1985).

Aerial exposure experiments on red king crab and Tanner crab demonstrated that exposure to cold air reduced vigor, feeding rates (Tanner crab), and growth (king crab) (Carls and O'Clair 1990). Exposure also caused limb autotomy in Tanner crabs, and mortality in both species in severe situations. However, the exposures were severe, and in contrast, mortality measured 128 days after exposure for king crab did not increase significantly unless temperatures were below −4.6°h (the unit means the product of temperature and duration of exposure) exposure, and for Tanner crab until −3°h. Vigor did not significantly decrease until −4.6°h for king crab and −2.2°h for Tanner crab. Tanner crab did not feed significantly less until −2.7°h. King crab emersed at temperatures greater than freezing showed no trend in growth with exposure. Tanner crab weights did not correlate with exposure. Exposure of ovigerous crabs generally did not affect eggs or mortality of subsequently released zoeae unless the female died.

In an aerial exposure study of Dungeness crab (*Cancer magister*), after exposure for 5, 15, 30, and 60 minutes, hardshell crabs did not have significant differences in recovery rate among exposure periods. Although softshell crabs had a significantly lower recover rate, tests for differences among exposure periods for softshell crabs could not be made due to small sample size (Kruse et al. 1994).

More direct support for our results came from two recent studies of the effects of handling and discarding on mortality of Tanner crabs (MacIntosh et al. 1996). In the first study with three treatments, one group of crabs was dropped once into seawater from a height of 2.5 m, one group was dropped four times at two-day intervals, and one group was not handled. In the second study with four treatments, three groups received physical injury to the merus/carpus joint, coxa, or carapace, respectively, while the fourth was an unhandled control. There was no significant differences in mortality between the control and any treatment group in either experiment after 60 days.

These results suggest that commercial crustacean species have the capacity to endure stresses within certain magnitudes without detrimental effect. Our laboratory simulation was comparable to typical handling procedures in the commercial fishery. Deck impacts, aerial exposure, and water impact should have minimal effects on discarded female and sublegal red king crabs, *if* these crabs are handled in the normal manner which we have described.

In contrast to the normally handled crabs, some crabs experience abnormal handling. A few crabs will fall to the deck from the pot or sorting table, and some may be tossed high into the air when the pot door is quickly opened. The crabs dropping on the deck may be kicked, smashed, or thrown back to the water from the rail. In most commercial crabbing situations, these crabs will remain aerially exposed for a long time before being returned to the sea. The size of the sorting table comparing to the width of the pot door will affect the number of crabs receiving abnormal handling. Also, the fishermen's skill and concern are important factors. It is assumed that these crabs receiving abnormal handling will suffer much more, and the impact will be more severe. Further study should estimate this subpopulation and quantify the impact to these crabs. It is also essential to educate fishermen to take greater care of female and sublegal male crabs.

Our results do not implicate handling in the decline of red king crabs. But, can we blame discarding for the decline of the red king crab? Before this question can be answered, additional information on what happens to the returned crabs is required. During pot retrieval, hundreds of seabirds are waiting for the discarded bycatch and old bait; whether birds cause damage to the crabs is unknown. More important, are there any predators that feed on these returned crabs when they descend from the water surface to the benthos? Predators have been reported to be particularly voracious on crab (Kennelly et al. 1990) and lobster (Brown and Caputi 1983) while these benthic species were sinking in the water column. Also, what effect does disorientation have on feeding and responses to benthic predators once the crabs have reached the bottom? Many of these potential indirect effects on crab survival warrant investigation.

Acknowledgments

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Development of Artificial Reefs for the Horsehair Crab

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Abstract

This study surveyed the history of crab fisheries in Hokkaido, which has the most crab fishery grounds in Japan, and introduced preliminary work on artificial reefs to preserve the horsehair crab *(Erimacrus isenbeckii)* resources.

Fisheries started in the late nineteenth century for the red king crab (*Paralithodes camtschaticus)*, and *E. isenbeckii* also has been harvested for more than 60 years. These crabs were canned for an important export item. The crab fishermen were compelled to reduce catches due to overharvest and because of international agreements. Recently the crab catch has decreased so much that the fishery cannot supply domestic demand, and some crab species are imported from foreign countries. In 1991 the Japanese consumed about 16% of the crabs captured from all parts of the world.

Artificial reefs are expected to give two advantages for the preservation of the *E. isenbeckii* resource: the prevention of illegal fishing and providing the crabs shelter. We tested the attractant effects of reefs for *E. isenbeckii* using an artificial reef, which we designed. The reef was made of fiber-reinforced plastics and had 12 shelters of the 2 different interior structures. Seven *E. isenbeckii* were released into the tank in which the reef was settled, and the crab behavior observed with a video camera. Although the native crab habitats are sandy and muddy bottom, some crabs stayed in the shelter for long periods, suggesting that the establishment of artificial crab reefs may be beneficial. However, the reef design must be improved before use to increase the number of crab

homes, because the crabs usually used the shelters only on the lowest floor.

Introduction

Many commercial crabs such as the red king crab (*Paralithodes camtschaticus*), the spiny king crab *(P. brevipes)*, the snow crab (*Chionoecetes opilio*), and the horsehair crab (*Erimacrus isenbeckii)* are distributed in the waters of northern Japan, and the crabs are an important seafood for Japanese historically. In the 1930s Japan produced a large volume of canned crab (Hokkaido Government Fisheries Department 1957). Only a small part was consumed by domestic residents, and most was exported to various countries (chiefly the United States) to get foreign money. After the crab canning industry declined in the 1970s, the price of boiled crabs abruptly increased in the domestic fishery markets. Then Japan began to import fresh or boiled crabs from foreign countries. In 1991 the Japanese consumed about 16% of the world crab products (1,140,000 metric tons) (FAO 1992). Thus, Japan is an important market for the world crab fisheries. In the present paper, we survey the history of crab fisheries in Hokkaido, which has the largest crab fishery ground in Japan, and report the preliminary study on artificial reefs for *E. isenbeckii.*

History of crab fisheries in Hokkaido

The crab fishery in Hokkaido began in the late nineteenth century (Hokkaido Government Fisheries Department 1957). The crabs were caught nearshore by boats without an engine and consumed by the local people. At that time the catch of crab was small. Since the technique for canning crabs was developed in the 1900s, the demand of canned crab increased as stored food. By that time motorized boats were common, and the supply of crabs increased with demand. The boats captured the red king crab and the spiny king crab from the coastal regions of Hokkaido, Sakhalin, and southern Kuril Islands.

As early as 1910 the king crab resources around Hokkaido began to decrease from overharvest, and Hokkaido prefecture began to regulate the number of crab fishing boats. Unfortunately for the crabs, the United States, which was the most important export country for canned crabs, needed more canned crab than ever because its crab fisheries were limited then. The chief crab canning companies in Japan advanced a program to get greater profits by canning crabs captured offshore from a ship. A fishing group consisted of a mothership equipped with a canning factory and some crab catcher boats. This fishery program overharvested the king crabs inhabiting the Okhotsk Sea. The total length of gillnets a catch boat used reached more than several hundred

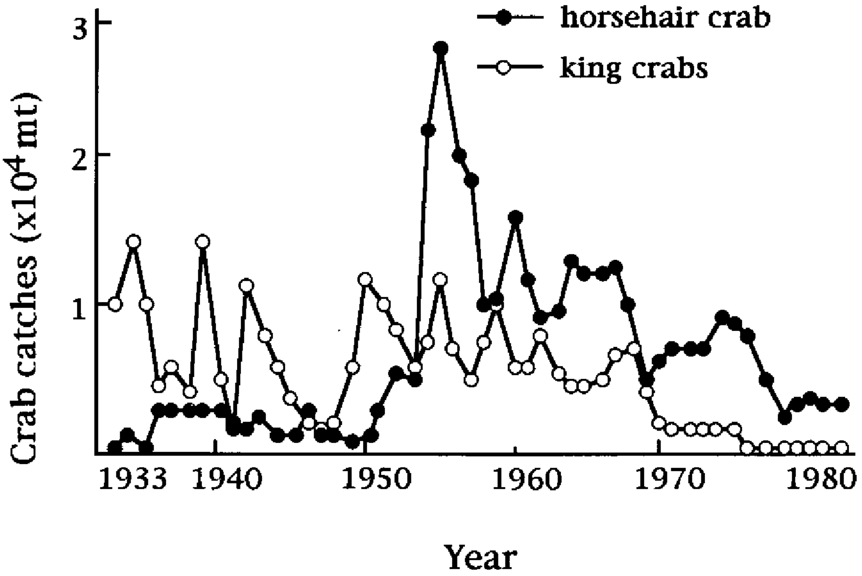

Figure 1. Yearly changes in catches of king crabs and horsehair crabs. Spiny king crabs were included with king crabs prior to 1952 (from Abe 1992).

kilometers. By the end of World War II nearly 10,000 mt of red king crab and spiny king crab were captured per year, with some fluctuation (Figure 1).

Horsehair crab canning had not been done industrially until the test products from crabs in Funka Bay succeeded in 1933 (Matsuya 1969). Possibly the canning process for the horsehair crab required more time and expenditure than for the king crab, because of the small body size. Then, the horsehair crab fishery gradually expanded to other regions of Hokkaido, and the Okhotsk Sea supplied the majority of the crab catches from Hokkaido (Domon et al. 1956). Horsehair crab and king crab were important canned exports after World War II (Figure 1). The catch of horsehair crab abruptly increased to 3,000 mt in 1951 when the horsehair crab fishery was fully operational. The peak of harvest was recorded at 29,500 mt in 1955, and then the catch slowly decreased with small fluctuations until 1977 (Abe 1992).

The crab fisheries in Japan underwent some international negotiations since the Russo-Japanese war. Japan got the fishing rights to the Japan Sea and the Okhotsk Sea around the Russian provinces, when Japan concluded the Japan-Russia Fishery Treaty in 1907. Many fishing boats competed to catch crabs from these regions by the beginning of World War II. Japan lost the fishing ground around Sakhalin and South Kuril Islands in 1945, and then Japanese fishing companies exploited some crab fishing grounds around the Aleutian archipelago and the Alaska peninsula. However, the crab fishery was compelled to accept new regulations under the Continental Treaty in 1964. The catch of crab in these regions was controlled by the international negotiation between Japan and America every year. The fishery for red king crab was also prohibited by the Soviet Union that same year. Crab canning industries depended on resources within the provincial waters of Japan, and tried to utilize the other crabs around Hokkaido, but the populations of these crabs were not large enough to support canning factories. Finally, Japanese crab fishing boats were excluded from the fishing grounds within the economic zones of foreign countries in 1977 when the 200 Mile Economic Zone Treaty was established internationally.

Japan had exported 1,000-7,000 mt of canned crabs by 1972, corresponding to 80% of the total catches. In recent years the catch of crabs was small due to the above reasons, with the result that crab canning is no longer an important industry. However, the decline of exportation of canned crabs was due not only to the decrease in catch, but also because of increasing domestic demand. This trend caused a sudden rise of the domestic market price, and unfortunately the crab resources around Hokkaido became abruptly reduced because of overharvest and secret fishing. Most caught crabs are boiled and sold in the markets of big cities, but the demand is never satisfied. Therefore, the importing of live, boiled, and frozen crabs, especially the red king crab from the United States and Russia, has increased every year (Figure 2). Nowadays Japan has the biggest crab market and imports a large volume of crabs.

Preliminary experiments on artificial crab reefs

Background

E. isenbeckii has been the most harvested crab species in Hokkaido since 1977 (Figure 1). In order to preserve and enhance this precious resource, some kinds of fishery regulation, rearing and release of artificial seeds, and ecological study for estimating resource abundance have been applied (Nishiuchi 1991). In spite of these efforts, the official catch of the crab hardly increased at all. The effects of the recovery program for the crab resource may be canceled by illegal secret fishing and unintended catch by gillnets or trawl.

E. isenbeckii lives on or in the sandy and muddy bottom above 150 m depth (Nishiuchi 1991), and many more crab were found nearer reefs (Ueda et al. unpublished data). This research was started on the

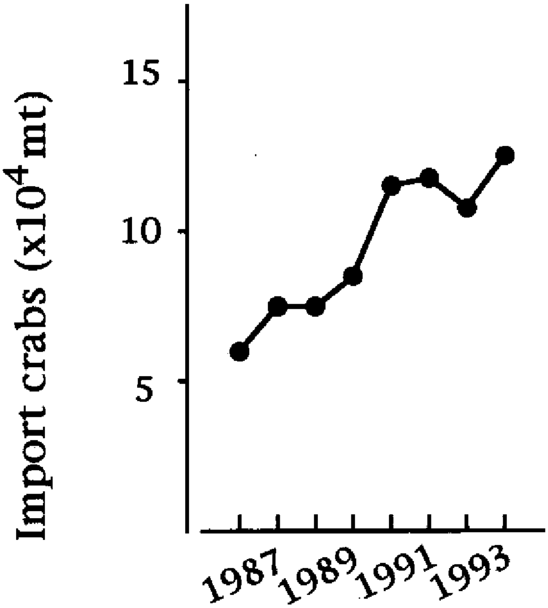

Figure 2. Yearly changes of import of crabs (from Fishery Agency 1989, 1991, 1993, 1994).

basis of the hypothesis that establishment of artificial reefs may enhance settlement for *E. isenbeckii.*

The projects on artificial fish reefs began in 1955, with much hope for increasing the fishery (Kakimoto 1984). Because Hokkaido has many large fishing grounds, as much as 140 billion yen was invested into Hokkaido fishery enhancement during 1988 to 1993 (Hokkaido Government Fisheries Department 1992). When artificial reefs are established on the bottom, not only does the reef produce new habitat for benthic animals, it also attracts pelagic animals by generating upwelling currents (Kato 1984, Ogawa 1984). If the surface area of the reef increases the possibility of settlement for benthic animals, the number of homes will increase several times. This is the first advantage of artificial reefs for the crab. Second the crab resources may be protected from secret fishery and trawl or gillnet catch, because reefs damage nets. Such predictions encourage us to promote the establishment of artificial crab reefs.

Following is a report on a preliminary experiment for design of artificial crab reefs carried out in an aquarium tank.

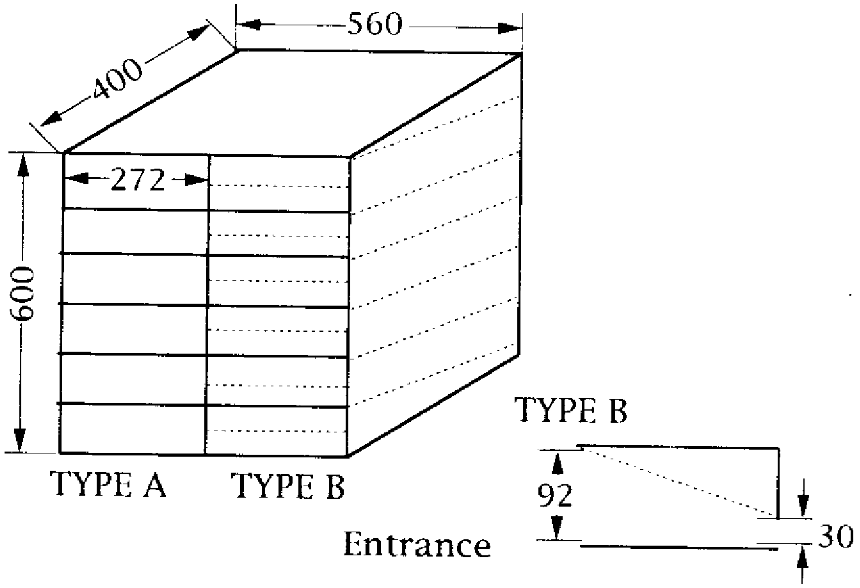

Figure 3. Measurement (mm) of the artificial reef tested in this study.

Materials and Methods

The 7 crabs of *E. isenbeckii* used in this study were obtained in November 1993 by trapping from the Funka Bay, southern Hokkaido, Japan. All the crabs were male, and their carapace lengths were within the range of 62.0 to 95.4 mm. Colored ribbon tags were coiled at one or both claws of all crabs for individual discrimination and detection of crab buried in the sand. All experiments were carried out in Usujiri Fisheries Laboratory, Hokkaido University.

The artificial reef was made of fiber-reinforced plastics, and sand was glued on its interior surface so that the crabs did not slip. The reef has 6 floors containing 2 different shelters in the interior structure, and a total of 12 shelters were prepared (Figure 3). One type (Type A) shelter was formed so that the ceiling paralleled the floor, and the ceiling of the other type (Type B) lowered toward the inside. The lowering ceiling was designed so a small crab would have contact with his carapace. The width and height of both shelters was large enough so the biggest crab could enter.

The artificial reef was placed in a tank (180 cm w × 60 cm h × 90 cm d), in which the water temperature was kept at about 5°C. Two experiments were carried out (Figure 4). Experiment I was intended to assess the attractiveness for the crab of the reef in an open area. In experiment

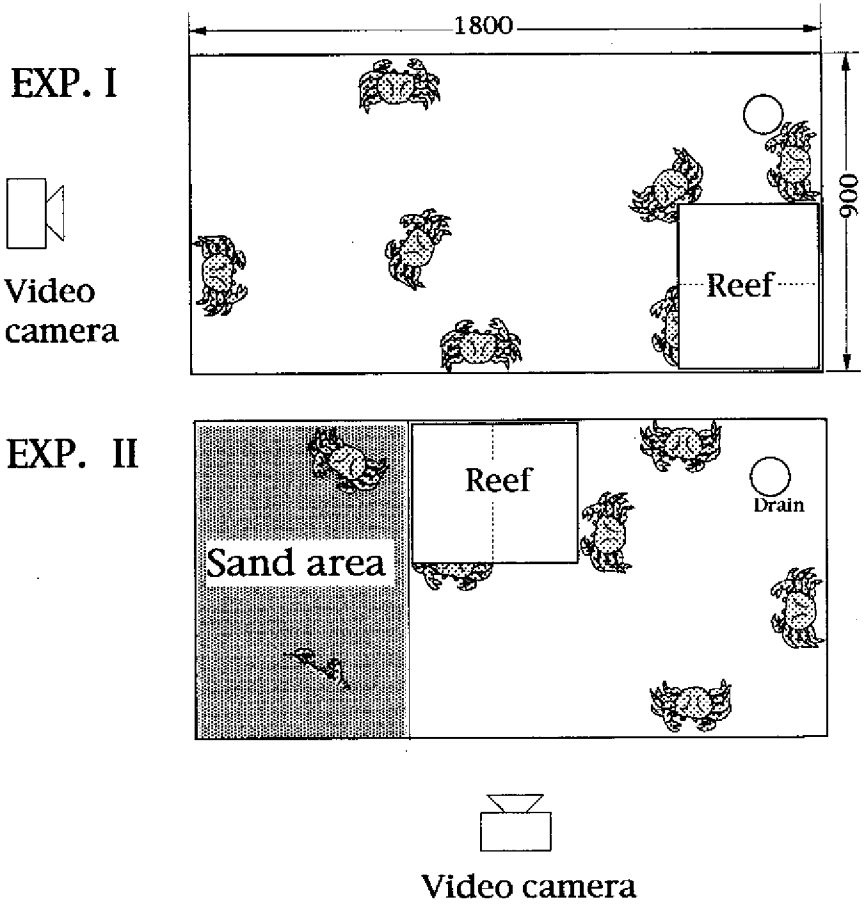

Figure 4. Arrangement of the reef and the sand area in the experiment tank (units are mm).

II one-third of the bottom of the tank was covered with sand to a depth of about 10 cm, and it was ascertained whether the reef could attract the crab even with a sandy bottom. The crab was released into the tank after adding the reef and sand, and observations were started the next day. Experiment I lasted for 6 days, and experiment II for 9 days. Experiment II was started 2 days after the finish of experiment I. The actions of each crab were recorded by a video recorder during the lighted hours (the totals of 72 hrs and 108 hrs in experiment I and experiment II, respectively), and the positions and the movements were individually analyzed. The light was applied from the ceiling of the tank, and its

Table 1. Frequency of movements along walls and across open area of the horsehair crab in the experiment tank.

Day	Along walls	Across open area	Total
Exp I			
1	31	16	47
2	39	24	63
3	26	16	42
4	16	8	24
5	16	9	25
6	25	10	35
Exp II			
1	2	26	29
2	3	12	15
3	2	14	16
4	3	11	14
5	7	13	20
6	7	14	21
7	4	11	15
8	2	7	9
9	3	8	11

intensity was about 1,000 lux on the surface of the water during lighted time (7:00-19:00), and about 1 lux during dark time.

Results

Experiment I

All crabs spent much of their time with their back or face contacting the wall of the tank or the artificial reef, and they stayed in the open only 1.0% of the time with the range of 0.3 ± 2.1% (n = 7). The crabs seldom changed their position, and they usually went along the walls while moving (Table 1). The movements were in a low frequency of 0.51 times/hr per individual, and 153 (67.6%) and 83 (32.4%) out of the 236 times during 72 hrs were along the walls and across the open area, respectively. The movement was frequently observed just after the light came on, caused perhaps by the disturbance of abruptly turning on the light. No diurnal change of movement was observed.

The 7 crabs stayed in shelter for the total time of 95 hrs 5 min, which was 19% of the total observation time (6 days × 12 hrs × 7 crabs)

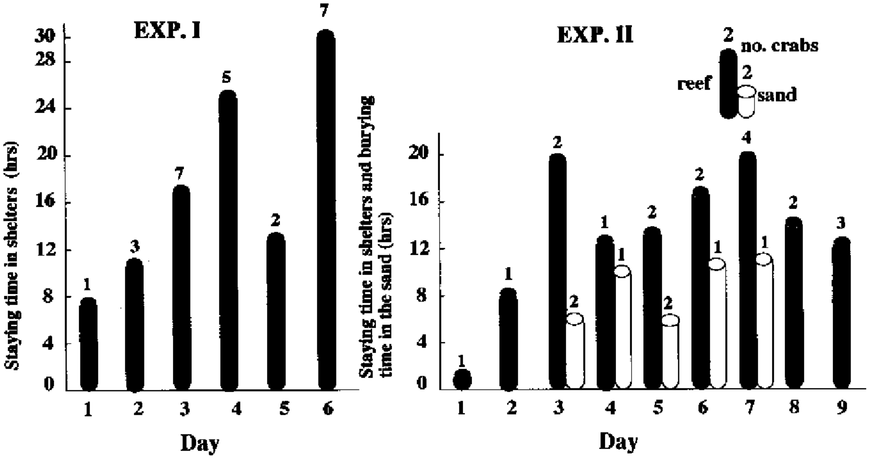

Figure 5. Total time of crabs staying in the shelters and crabs burying in the sand.

on all crabs (Table 2). Of 95 hrs 5 min, 65 hrs 42 min (69%) were recorded in the latter 3 days (Figure 5). Five crabs stayed in shelter throughout the lighted time. A crab was observed to stay in the same shelter during the 3rd, 5th, and 6th days, and the other 2 crabs occupied shelters during the 4th day and the 6th day. Thus, the reef provided the crabs with a comfortable home (Figure 6). Two shelters at the lowest level were most favored by the crabs, especially in the type A shelter which was occupied for 64 hrs 14 min by any crab, 89.2% of the total observation time (Figure 7). On the other hand, the type B shelter at the 3rd floor and the type A at the 6th floor were used for only 5 min and 12 hrs, respectively, and no crabs entered into the other shelters.

Experiment II

In experiment II the crabs spent a little more time in the open area. The movement frequency of the crabs was 0.20 times/hr per individual, and its value was only 40% of that in experiment I (Table 1). The total times of crabs sitting in any shelters and burying into sandy bottom was 128 hrs 6 min (17% of the total observation time [9 days × 12 hours × 7 crabs]) and 56 hrs 18 min (7% of the total observation time), respectively. Both habitats were used more frequently on latter days than on the first day (Figure 5).

Only 4 of the 12 shelters were used (Figure 7). In the type A shelter the lowest level was most favored like in experiment I (104 hrs 24 min). This shelter was concurrently utilized by 2 crabs for 8 hrs 16 min. The 2nd most favored shelter was the type B shelter lowest floor, which was

Table 2. Staying time of individual crabs in shelters and into sand.

		Exp I		Exp II			
		Shelters		Shelters		Sand area	
Crab no.	Carapace length (mm)	hrs	min	hrs	min	hrs	min
1	95.4		5	4	23	13	8
2	94.8	1	52		8	14	3
3	88.4	49	40	20	27	19	34
4	87.2	4	55	49	51		0
5	85.3	11	2	26	54		0
6	78.9	13	1	15	55		0
7	62.0	14	30	10	28	9	33
Total		95	5	128	6	56	18

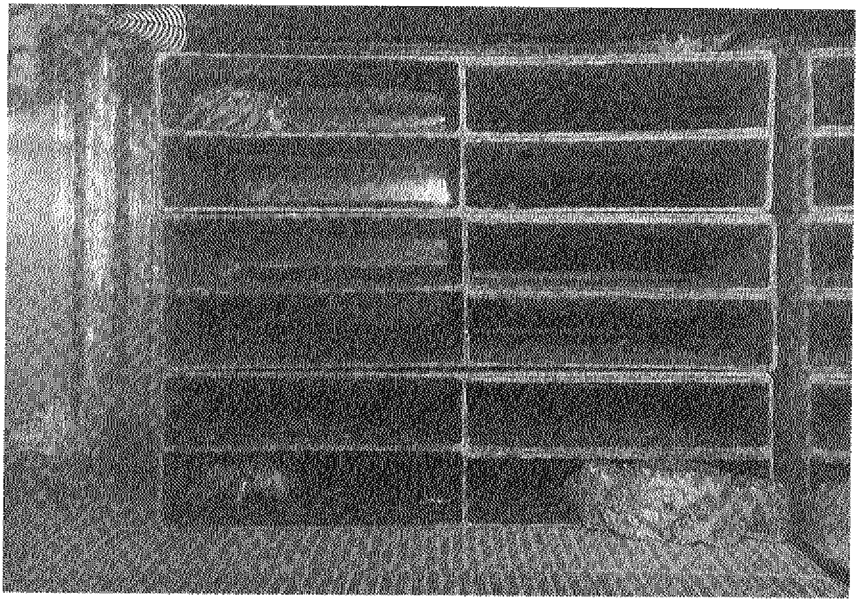

Figure 6. Three crabs staying in shelters.

EXP I			EXP II	
TYPE A	**TYPE B**	**FLOOR**	**TYPE A**	**TYPE B**
12 hrs 0 min **(16.7 %)**		6	**2 hrs 57 min** **(2.7 %)**	
		5		
		4	**2 min** **(0.0 %)**	
	5 min **(0.1 %)**	3		
		2		
64 hrs 14 min **(89.2 %)**	**18 hrs 46 min** **(26.1 %)**	1	*** 104 hrs 24 min** **(89.0 %)**	**20hrs 43min** **(19.2 %)**

*Figure 7. Staying time of individual crabs in shelters and buried in the sand. * The total time includes a duration (8 hrs 16 min) for which the shelter was concurrently used by 2 crabs, but the percent is calculated without it.*

used for 20 hrs 43 min. The 6th and 3rd floor of type A shelter were used for only 2 hrs 57 min (2.3%) and 2 min (0.1% below), respectively (Figure 7).

In both the reef and the sand area the results varied for individual crabs (Table 2), and the crabs that stayed in shelters for long periods also differed between experiments I and II. The length of stay was not related to carapace size of the crab. Fights were sometimes observed, but the identity of the fighters changed often and so did the winner. The crabs that stayed in shelters for long periods did not always indicate dominance.

Discussion

E. isenbeckii has a habit of burrowing into the sandy and muddy bottom (Nishiuchi 1991), but this study suggested that the crab keeps stability when its posterior body contacts any substrate, and that the reef attracted many more crabs than the sandy area. The attractant effect of the reef was less during the first day than for the latter days in both experiments, and the time of sitting in the reef differed with individuals. The crabs may utilize the reef more often after a couple of days of acclimation.

The reef did not multiply the crab habitats by several times. This may be partly caused by the crab's nature. The utilization rate of upper shelters probably depends on shelter form, because there was a difference in the attractiveness of type A and type B.

The establishment of artificial crab reefs may help preserve *E. isenbeckii* resources, although some more improvements of reef design must be made especially to encourage increased use of the higher shelters by individual crabs to develop useful artificial reefs.

Summary

More than 100 years have passed since the beginning of the crab fishery in Hokkaido. During this period fishing boats sought crabs from the coastal waters to the farther regions of Japan, and the coastal regions of foreign countries. Exploitation and overharvest were part of the history. Their cause may be attributed to the lack of efforts for the preservation of the crab resources and the lack of biological information on crab preservation. Not only fishing boats but researchers, therefore, are blamed for the current deterioration of the crab resources. All economically valuable crabs from high latitude habitats—the king crab, the horsehair crab, and the snow crab—take several years to grow to adults, and they need a couple of years to fulfill one reproductive cycle. To my knowledge, except for some mammals, few marine animals have such a low reproductive rate. The recovery of the crab resources must necessarily require a long period of research. Some projects promoted to preserve and replace the crab resources are release of seeds, development of a selective trap fishery for adult male crab using female pheromone, and so on. These projects never produce immediate visible effects, but these efforts ought not to be given up, because we have the responsibility to save crabs for the next generation.

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High Latitude Crabs: Biology, Management, and Economics
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Observations on the Biology of the Lithodid Crab *Paralomis spinosissima* from the Southern Ocean near South Georgia

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Abstract

The F/V *Pro Surveyor* conducted the first exploratory crab fishing in the South Georgia area of the Southern Ocean during the Antarctic winter and spring of 1992. The authors were aboard the vessel during the first month of the July to November fishing period. The pot fishery targeted *Paralomis spinosissima* although a smaller species, *Paralomis formosa*, was also taken in abundance. A total of 5,901 specimens of *P. spinosissima* were examined. Most were caught on the South Georgia grounds (n = 4,970) but a smaller sample was obtained near Shag Rocks (n = 931), 240 km to the west. Morphometric measurements, reproductive characteristics, prevalence of rhizocephalan parasites, and microsporidian infections were recorded for each specimen. Gross examination showed that a rhizocephalan, probably *Briarosaccus callosus*, infected 15% of the specimens examined while microsporidians infected 0.5%. Rhizocephalan parasites were hyper-parasitized by an undescribed species of isopod. Morphometrically, males infected with the rhizocephalan resembled females, while parasitized and unparasitized females were similar.

Examination of females showed that 50% were ovigerous at 62 mm carapace length. Ovigerous females at South Georgia tended to be larger than those at Shag Rocks. In both areas, ovigerous females carried embryos in a wide variety of developmental stages, suggesting that spawning occurs over a protracted period and perhaps occurs throughout the year. Based on chela allometry, size at maturity for males was 75 mm carapace length at South Georgia and 66 mm at Shag Rocks. Fishery management measures are examined relative to various biological parameters and in comparison to those implemented for other stocks of lithodid crabs.

Introduction

Fishing operations for Antarctic crab began in July 1992 with an initial trip by the F/V *Pro Surveyor* to South Georgia. All fishing was done with pots (traps) and both *Paralomis spinosissima* (Birshteyn & Vinogradov 1972), and *Paralomis formosa* (Henderson 1888) were captured during the initial trip. *P. spinosissima*, the larger of the two species, was targeted by exploratory fishing efforts and hence emphasized in biological collections. In subsequent trips, a few specimens of *Neolithodes diomedeae* (Benedict 1895) were also taken. All three species were previously known from the South Georgia area (MacPherson 1988, Dawson 1989). All fishing was conducted in accordance with a plan submitted to the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) (Delegation of USA 1991), and a permit issued by the United States under the terms of the CCAMLR Convention.

South Georgia is in the Southern Ocean on the Scotia Ridge northwest of the South Sandwich Islands. South Georgia shelf areas (including Shag Rocks) are relatively shallow by Antarctic standards and lie south of the Antarctic Polar Front which places them in the Antarctic Zoogeographic Region (Eastman 1993). Eastman (1993) also notes that the area around South Georgia is frequently referenced as a separate geographic province and is characterized by 30 to 40% endemic species in its fauna. Under CCAMLR, these waters are designated as Area 48.3.

The plan submitted by the U.S. delegation was intended to ensure orderly development of U.S. fisheries in accordance with the CCAMLR Convention. This was the first crab fishery conducted in the Convention Area, so there was no information on abundance and little biological data on crabs from the region (MacPherson 1988). The plan required logbooks and two National Marine Fisheries Service (NMFS) observers (the authors) to set size limits during fishing operations. Crab size limits were to be at least 10% larger than the size at maturity. Other provisions of the plan restricted the types of bait to be used, retention of non-target species, and limited crab landings to 400 t round weight. Under the CCAMLR Convention, fisheries must be conducted in a manner which strictly limits the potential for reducing populations to levels below those which ensure their stable recruitment, disrupting ecological relationships, or causing changes in the marine ecosystem. While the possibility of these things occurring during exploratory fishing was slight, strict permit provisions satisfied members of the Commission that they would not occur.

This report summarizes some of the results that were presented to CCAMLR after our examination of *P. spinosissima* during the first of three trips made by the F/V *Pro Surveyor* in 1992 (Otto and MacIntosh 1992, Anon. 1993).

Methods

The logbook system developed by the NMFS Antarctic Ecosystem Research Group was used to maintain a record of fishing operations. Fishing effort, commercial catch, position, depth, bait, and gear type were recorded for all strings of gear. These logbooks provided the basic data to which all biological observations were keyed.

Fishing took place near South Georgia between 53°30′S and 54°00′S latitude and between 36°20′W and 38°20′W longitude. While returning from the South Georgia area, 2 days were also spent exploring the area near Shag Rocks (53°10′S to 53°30′S and 41°50′W to 42°40′W). Fishing depths ranged from 118 to 551 m, but about 60% of the effort occurred between 300 and 400 m.

The F/V *Pro Surveyor* is a 53 m, steel-hulled fishing vessel that is used to catch, process, and freeze crabs. The steel-framed pots used were shaped like truncated cones and were covered by 10 cm nylon mesh. Approximate pot dimensions were 1.5 m base diameter, 0.9 m top diameter and a height of 0.8 m. Pots were fished by attaching them at intervals to a ground line. Each "string" of gear was buoyed and anchored at each end. Fishing gear was marked with radio buoys, as required under U.S./CCAMLR regulations. No pots were lost during the trip and gear loss was limited to a single buoy and one anchor. Pots were baited with frozen herring (*Clupea harengus* or *C. pallasi*) and usually fished for 18 to 24 hours.

During normal fishing operations, strings of gear are usually set about 926 m (0.5 nautical miles) apart. During exploratory fishing this interval was normally exceeded. Only large males or "commercial crabs" (greater than 102 mm carapace width, CW) of *P. spinosissima* were retained for processing. If sufficient concentrations of commercial crabs were located, at least some sustained fishing was attempted in order to determine the potential for commercial fishing in the area.

Estimates of total catch involve extrapolation from sampled strings to the total number of strings fished. We sampled 46 of 138 strings fished near South Georgia (33%) and 7 of 13 strings at Shag Rocks (54%). For each pot, the crew counted the number of commercial crabs that were retained and reported the counts to the bridge for recording. For each sampled string, observers tabulated the number of small male and female (non-commercial) *P. spinosissima* (and *P. formosa*) that were captured and either taken for biological sampling or returned to the sea. The ratio of non-commercial to commercial crabs in sampled strings was used to estimate the number of discards in unsampled strings. At times when catches were large the observer could not actually count the number of discards so a visual estimate of discards from each pot was made. This was necessary because pots frequently came aboard at 40 to

60 second intervals. Extrapolated totals for discards are less reliable than the totals for commercial males which should be accurate, apart from minor errors in counting or tabulation. Fish and cephalopod catches were extrapolated in the same manner as discarded crabs but all fish were counted in sampled strings and estimates are not subject to as much error.

Biological catch sampling consisted of removing up to five crabs from each pot in a sampled string. Since catch rates were varied, variable portions of the catch were sampled from each string. Sampling was representative of the size and sex of crabs caught except that we deliberately sampled as many very small crabs as possible. Very small crabs were uncommon in the catch but important for estimating size at maturity. Consequently, size-frequency data are biased in favor of smaller crabs, but we believe that bias is small relative to the general shape of the size-frequency distributions.

All sampled *P. spinosissima* were measured to the nearest millimeter for carapace length (CL; rear of right eye orbit to median posterior of carapace; see Wallace et al. 1949) and coded for shell condition using the following categories: (0) molting—portions of the old shell easily loosened from a well-developed new shell layer; (1) softshell—exoskeleton soft and pliable from recent molt; (2) newshell—exoskeleton firm, unscratched, little or no epifauna; (3) oldshell—exoskeleton firm, dactyls and spines worn, undersides of legs scratched and discolored, epifauna often present; (4) very oldshell—as in oldshell but more advanced, dactyls and spines very worn and rounded, more epifauna.

Females were classified into one of five categories of reproductive condition: (1) non-ovigerous—no embryos or their remnants on pleopod setae, the vast majority of these are immature; (2) uneyed embryos—embryos with no visible eyespot development; (3) eyed embryos—embryos with some visible eyespot development, includes hatching embryos; (4) empty embryo cases—no external embryos but remnants of embryo cases attached to pleopod setae, may include small numbers of dead embryos; (5) dead embryos—large numbers of dead embryos, not residual from a successful hatching. Crabs with dead embryos were rare; only 5 were found among all sampled crabs. In this paper, mature females are defined as those in categories 2-5 above. Embryo color was noted and the relative size of a clutch was determined on a five-point scale as follows: (1) trace to ⅛ full; (2) ¼ full; (3) ½ full; (4) ¾ full; (5) full.

All sampled crabs were examined for the presence of rhizocephalan externas and externa scars. The terms "parasitized" or "infected" refer to crabs with either rhizocephalan externa or externa scars. Crabs were also scored for the presence of a microsporidian disease, heavy infections of which were recognized as a white mass showing through the cuticle of the underside of the abdomen.

Additional measurements taken on some crab were carapace width (CW; maximum width of carapace including spines), right chela height (CH; see Wallace et al. 1949), and ovarian oocyte diameter (to 0.1 mm with ocular micrometer). Crab weights were taken to the nearest gram from newshell and oldshell crabs without missing or regenerating limbs.

Priority was given to determining size at maturity so that appropriate size limits could be set. Only unparasitized crabs were used in the determination of size at maturity. Female size at maturity was determined by plotting the proportion of mature females against size and determining the point of 50% maturity (SM50). Logistic curves were fitted using weighted, iterative regression (Somerton 1980).

For males, size at maturity was determined by examining the allometric relationship between carapace length and chela height, since mature male crab have relatively larger chela than immature crab. Size at maturity was quantified by fitting two regression lines to natural logarithmic plots of CH against CL and searching for the intersection point that minimized the combined residual mean square error (Somerton 1980). Standard deviations were determined using bootstrap techniques (Somerton and Otto 1986). Similar analyses for North Pacific lithodids include Somerton and MacIntosh (1983), Somerton and Otto (1986), and Otto and Cummiskey (1985).

Results and Discussion

Although catch rates varied considerably, *P. spinosissima* were caught in all strings of pot gear. The estimated total catch of crabs and fish taken during the first trip is shown in Table 1. The Patagonian toothfish (*Dissostichus eliginoides)* was the only species of nototheniid that we identified to species and was the most frequent incidental species of fish in the catch. Toothfish are known predators on crabs (Konforkin and Kozlov 1992), and conversations with scientists at the CCAMLR meetings indicated that toothfish are the only fish species in the area known to prey on juvenile and adult crabs. The largest toothfish that we saw weighed 27.5 kg and was 137 cm in fork length. The stomach of this fish contained two small octopuses while the stomachs of two others were empty. Based on a commercial crab catch of approximately 59.5 t, the extrapolated total incidental catch of *D. eliginoides* was 73 individuals or approximately 1.23 fish per ton of crab while that of all fish was 136 individuals or 2.26 fish per ton. In general, incidental catch of finfish was negligible and had no apparent influence on catch rates of crabs.

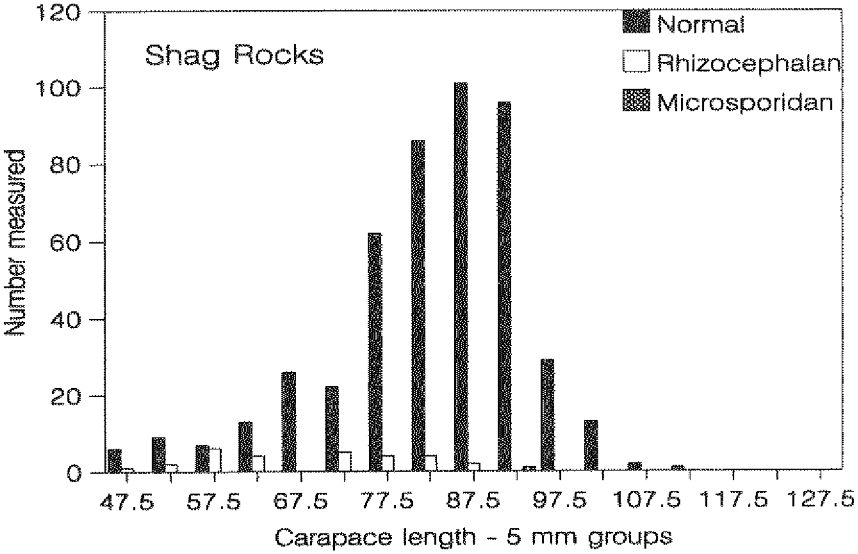
The high overall prevalence (15%) of rhizocephalan parasites on *P. spinosissima* was immediately and extremely striking. We assume that the rhizocephalan is *Briarosaccus callosus,* which has been described from near South Georgia on the host *Lithodes santolla* (Molina 1782) (as

Table 1. Number sampled and estimated total number of crabs, fish, and cephalopods caught by the F/V *Pro Surveyor* at South Georgia and Shag Rocks during July 1992.

	South Georgia		Shag Rocks		Grand total	
Item	Sampled	Total	Sampled	Total	Sampled	Total
Strings	46	138	7	13	53	151
Paralomis spinosissima						
Commercial	451	51,728	8	758	459	52,486
Discarded	4,519	83,239	905	8,203	5,427	96,390
P. formosa	668	34,768	0	2,152	668	38,084
Total crabs	5,638	169,735	913	11,113	6,554	186,960
Dissostichus eliginoides	22	65	4	8	26	73
Other toothfish	18	46	0	0	18	46
Rays	1	3	0	0	1	3
Flounders	1	3	0	0	1	3
Moray cod	1	3	0	0	1	3
Octopus	1	3	0	0	1	3

L. antarcticus) by Boschma (1962). We suspect, however, that because other investigators have not found *L. santolla* south of the Antarctic Polar Front (MacPherson 1988), and because we commonly found *P. spinosissima* but no *Lithodes* crabs in the area from which Boschma's samples were taken, that the host in his samples was probably *P. spinosissima.* Rhizocephalan infections were most prevalent in smaller individuals of both sexes and were more prevalent at South Georgia (18.7%) than at Shag Rocks (6.2%). These prevalences are among the highest reported for open-ocean populations of lithodids (see data in Hoggarth 1990). A species of isopod occurred as a hyperparasite on 26% of the rhizocephalan externa in our samples. Boschma (1962) previously observed the occurrence of an isopod hyperparasite on *B. callosus* from the South Georgia area. The isopod is an undescribed species but is perhaps similar to that noted by Pohle (1992) from externa attached to *Neolithodes grimaldi.*

The high prevalence of rhizocephalans complicated our attempts to determine size at maturity due to the rarity of small, normal (unparasitized) crabs in the catch (Figures 1, 2 and 3). *P. spinosissima* at South Georgia were larger than those at Shag Rocks, and within each area,



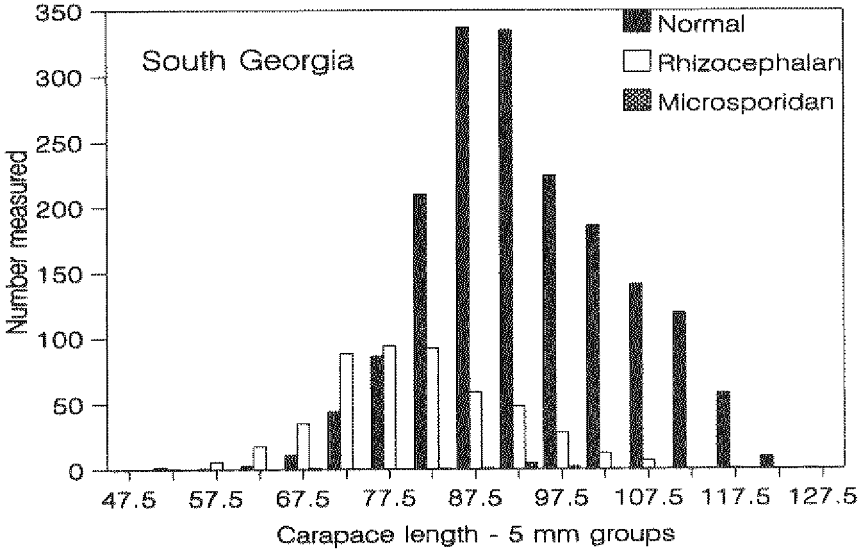


Figure 1. Size-frequency distributions for male Paralomis spinosissima sampled at South Georgia and Shag Rocks during July 1992.

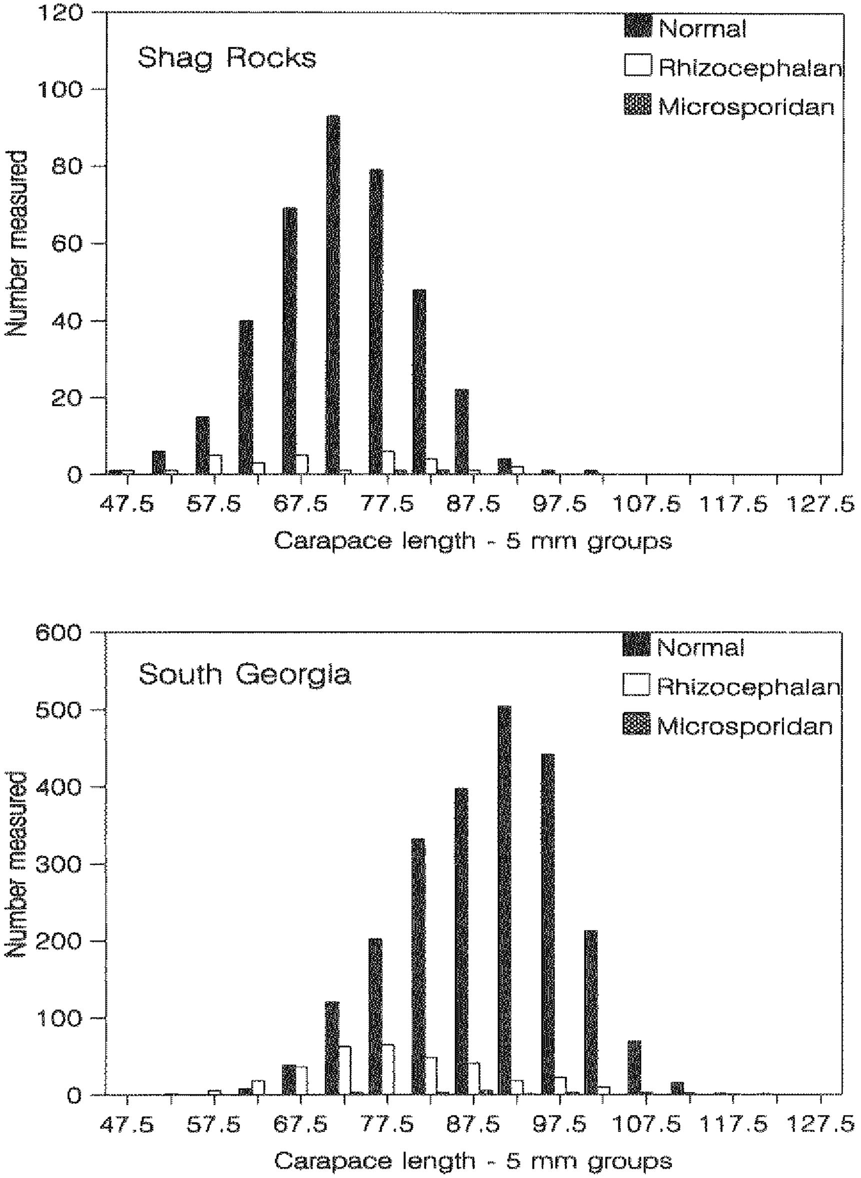


Figure 2. Size-frequency distributions for female Paralomis spinosissima sampled at South Georgia and Shag Rocks during July 1992.

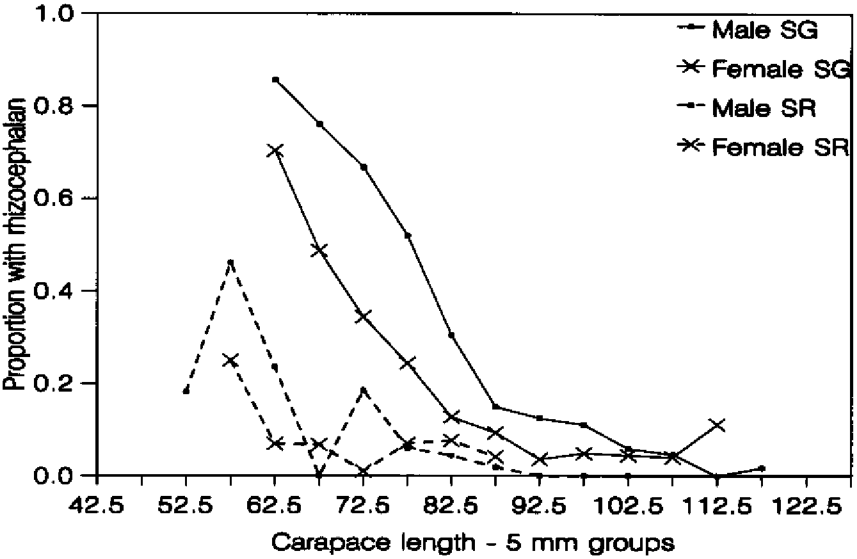


Figure 3. Prevalence of rhizocephalans on Paralomis spinosissima sampled at South Georgia (SG) and Shag Rocks (SR) during July 1992. Sample sizes ≤ 10 excluded from analysis.

those with rhizocephalans tended to be smaller than their unparasitized counterparts (Table 2). The diminished size of parasitized crabs almost certainly involves a reduced growth rate and may reflect increased mortality.

Small numbers of *P. spinosissima* were infected by a microsporidian that was grossly similar to a member of the family Nosematidae which infects *Lithodes aequispinus* in North Pacific waters (Sparks and Morado 1985). Crabs parasitized with microsporidians did not differ in size from their normal counterparts, although our sample size was small (Table 2).

Linear regression parameters for CW to CL and the natural logarithms of weight to CL are presented in Table 3. Regressions of CW on CL are nearly identical for all categories of *P. spinosissima*. Biologists studying lithodids frequently use CL to represent size because it is less subject to measurement error than CW. Commercial size limits, however, are usually expressed in terms of CW because it is the quickest measurement to gauge under fishery conditions. The regression of weight on CL is important relative to the size of crabs in the fishery, but is also of interest because it indicates changes in morphometry that accompany a rhizocephalan infection.

Table 2. Mean, standard error, and number of carapace lengths (mm) recorded for *Paralomis spinosissima* from South Georgia and Shag Rocks during July 1992.

		South Georgia	Shag Rocks	Mean difference	*t*	*p*
Normal males	Mean	93.5	82.9	10.6	18.3	< 0.001
	S.E.	0.3	0.5	0.6		
	N	1,768	473			
Males with rhizocephalans	Mean	80.4	67.2	13.2	13.2	< 0.001
	S.E.	0.5	2.3	2.4		
	N	489	29			
Difference relative to normal	Mean	13.1	15.7			
	S.E.	0.5	2.4			
	t	24.4	6.5			
	p	< 0.001	< 0.001			
Males with microsporidians	Mean	88.8	90.0	–1.2	–	NS
	S.E.	2.5	–	–		
	N	10	1			
Difference relative to normal	Mean	4.7	–			
	S.E.	2.5	–			
	t	1.9	–			
	p	NS	NS			
Normal females	Mean	89.3	72.5	16.8	36.5	< 0.001
	S.E.	0.2	0.4	0.5		
	N	2,347	379			
Females with rhizocephalans	Mean	78.9	70.4	8.5	3.7	< 0.001
	S.E.	0.6	2.4	2.3		
	N	340	29			
Difference relative to normal	Mean	10.4	2.0			
	S.E.	0.7	2.3			
	t	16.1	0.9			
	p	< 0.001	NS			
Females with microsporidians	Mean	85.3	79.0	6.3	2.7	NS
	S.E.	2.1	2.0	–		
	N	16	2			
Difference relative to normal	Mean	4.1	–			
	S.E.	2.1	–			
	t	1.9	–			
	p	NS	NS			

Table 3. Linear regression parameters for *Paralomis spinosissima* with and without a rhizocephalan parasite from South Georgia and Shag Rocks.

	Length to width				Log weight to log length			
	n	a	b	R-sq	n	a	b	R-sq
S. Georgia:								
Normal male	509	10.86	0.96	94.3	435	–8.66	3.36	97.9
Parasitized	189	4.96	1.04	93.6	159	–7.14	2.97	97.0
Normal female	337	6.18	1.00	93.5	255	–5.98	2.71	96.7
Parasitized	118	5.50	1.03	95.0	105	–6.84	2.90	98.2
Shag Rocks:								
Normal male	211	8.26	0.99	95.7	187	–8.54	3.32	98.6
Parasitized	19	2.54	1.07	96.5	20	–6.45	2.80	93.8
Normal female	145	5.13	1.02	94.3	134	–6.62	2.85	97.2
Parasitized	21	0.63	1.10	96.9	20	–7.43	3.02	98.2

Rhizocephalans cause feminization of parasitically castrated males and alter growth patterns (O'Brien and van Wyk 1985). We observed that parasitized males had broadened, apron-like abdomens that were much like those of females. Parasitized male abdomens also tended to be twisted to the right relative to the sagittal plane as was typical of females. Retransformed weight to CL relationships in Figure 4 show that parasitized males resemble females more closely than they do normal males and that parasitized and unparasitized females are similar. Male crabs with morphology intermediate between infected and normal individuals were not observed, suggesting that the parasite's effects on morphology occur at a single molt.

No parasitized females carried embryos or empty embryo cases. Observations on the condition of embryos suggest the mating season in *P. spinosissima* is protracted. In part, this is indicated by the diversity of embryo types observed for all sizes of females (Figure 5). Field observations showed that eyed embryos ranged from those with barely discernible eye spots to fully formed zoea, hence suggesting considerable variation in times of extrusion. Shell condition data from females also showed that some were in immediate pre-molt condition and some were softshell, newly molted crab. These two categories, however, made up less than 20% of the females observed. The vast majority of females were newshell crabs with uneyed embryos. Considerable numbers of females with empty embryo cases attached to their pleopods were also encountered and 35 of these were being grasped by males in a pre-mating embrace. Grasped females were all in pre-molt condition as deter-

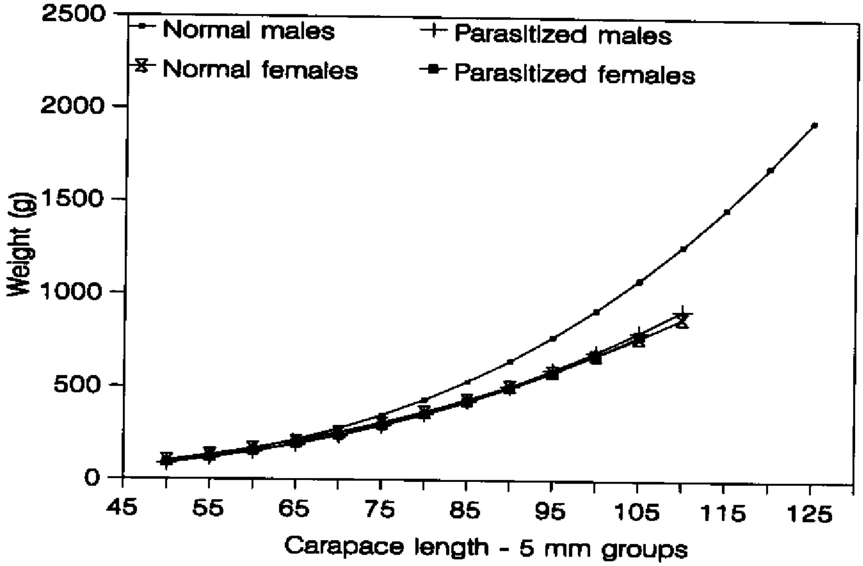


Figure 4. The relationship of weight to carapace length for normal and rhizocephalan parasitized Paralomis spinosissima sampled at South Georgia during July 1992.

mined by their well-formed second shells. Dissection of females from grasping pairs showed that they had large ovaries with oocytes that were grossly similar in size to embryos attached to pleopods.

Dissection of females with hatching zoea showed that their ovaries were large but that the mean oocyte diameter was about 85% that of oocytes in females from grasping pairs. This indicates that molting and mating occur considerably later than hatching of zoea. In two lithodids that spawn biennially, *Paralithodes platypus* and *L. aequispinus*, oocytes are roughly 75% of their maximum diameter in females with hatching zoea (Somerton and MacIntosh 1983, Otto and Cummiskey 1985). Assuming that the duration of embryo development is about 1 year, our observations also suggest that spawning does not occur annually in a given individual. Perhaps a longer than 1 year period of oogenesis contributes to a protracted or even year-round spawning period. Further observations will be necessary to determine how protracted the molting-mating period is and whether there is any seasonal component to it.

Size at sexual maturity was previously undescribed in *P. spinosissima* and its determination was an important part of our work. Unfortunately, insufficient numbers of small females were available at South Georgia and the fitted logistic curve failed to describe the data (Figure 6). For this reason the Shag Rocks and South Georgia data were com-

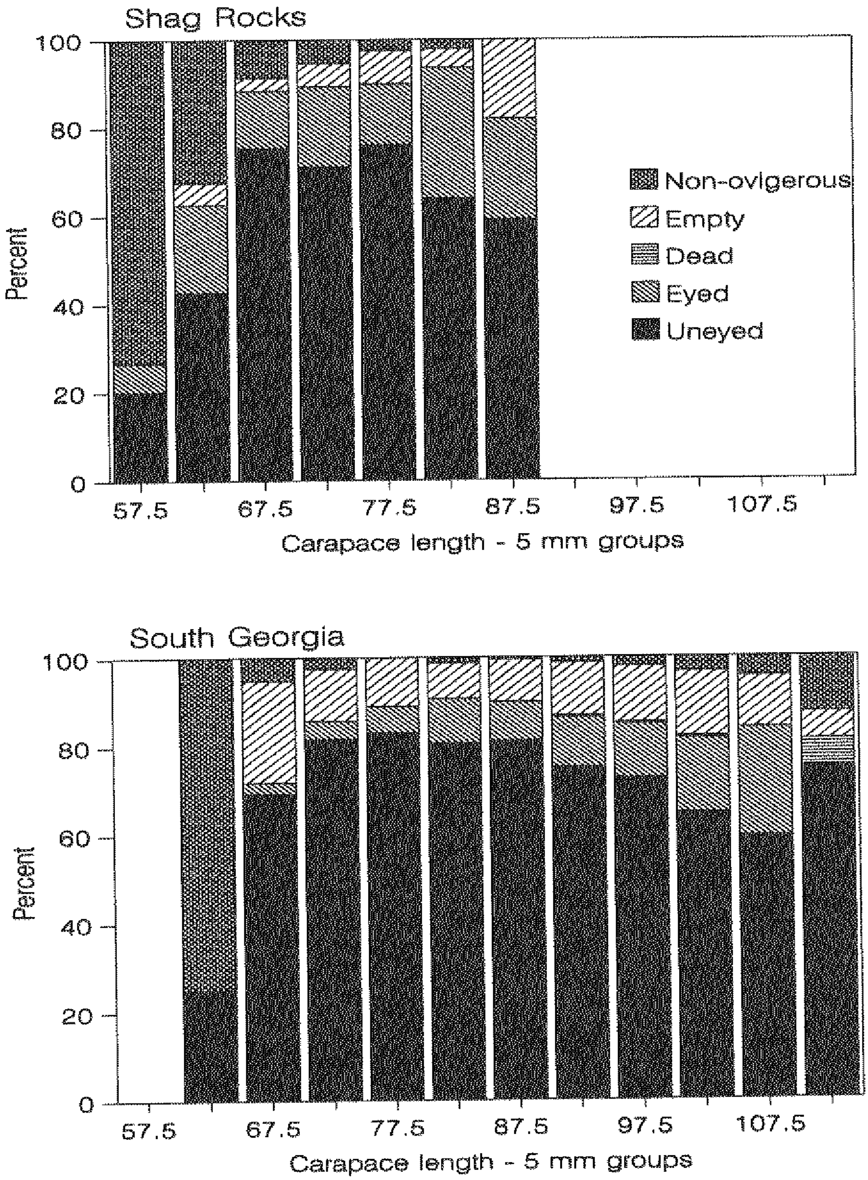


Figure 5. Reproductive condition of normal (no rhizocephalan) female Paralomis spinosissima sampled at South Georgia and Shag Rocks during July 1992. Sample sizes ≤ 9 excluded from analysis.

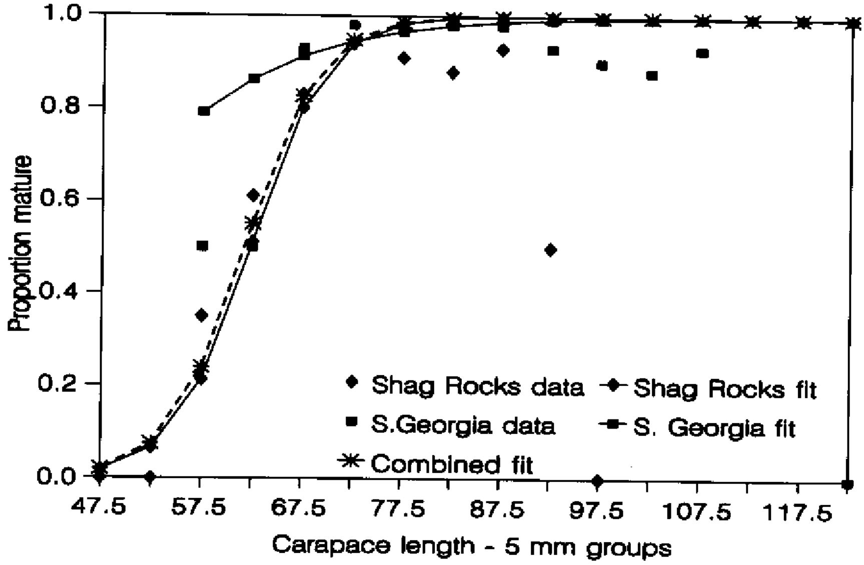


Figure 6. Proportion of mature Paralomis spinosissima sampled at South Georgia and Shag Rocks during July 1992. Fitted logistic curves were used to determine size at maturity (SM50).

bined to determine SM50 (Figure 6). The latter analysis yielded SM50 = 61.7 mm CL (*s* = 4.3 mm) but appears to be more reflective of conditions at Shag Rocks than at South Georgia. Females at Shag Rocks were significantly smaller than those at South Georgia (Table 2) and this is true of ovigerous females as well (Figure 7). The size frequency of normal South Georgia ovigerous females is noticeably skewed, however, probably reflecting the prevalence of rhizocephalans (Figure 7). While we believe that SM50 at South Georgia is greater than that at Shag Rocks, further research will be necessary to quantify this difference.

Size at maturity for males was quantified by fitting two regression lines to natural logarithmic plots of CH against CL. Fitted lines on retransformed axes (Figure 8) show intersections at 74.8 mm CL (*s* = 2.6 mm) for South Georgia and at 66.4 mm CL (*s* = 2.1) for Shag Rocks. Males apparently mature at slightly larger sizes than females. Both males and females apparently mature at smaller sizes at Shag Rocks

Under terms of the F/V *Pro Surveyor's* permit the minimum size limit had to be 10% greater than the size at maturity; that is, 82 mm CL or 90 mm CW at South Georgia and 73 mm CL or 81 mm CW at Shag Rocks. In North Pacific king crabs, growth per molt at maturity is about 15% in CL, which would lead to size limits of 94 mm CW at South Georgia and 84 mm CW at Shag Rocks. Assuming similar growth patterns, such limits

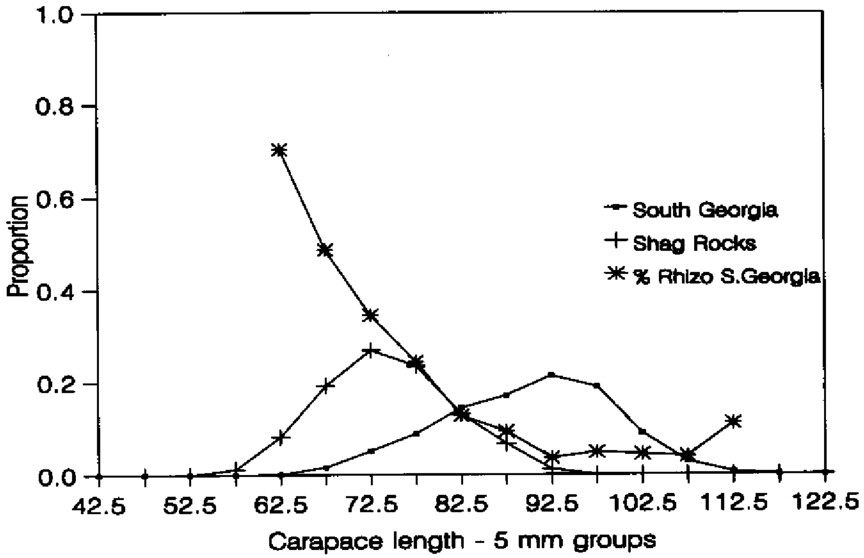
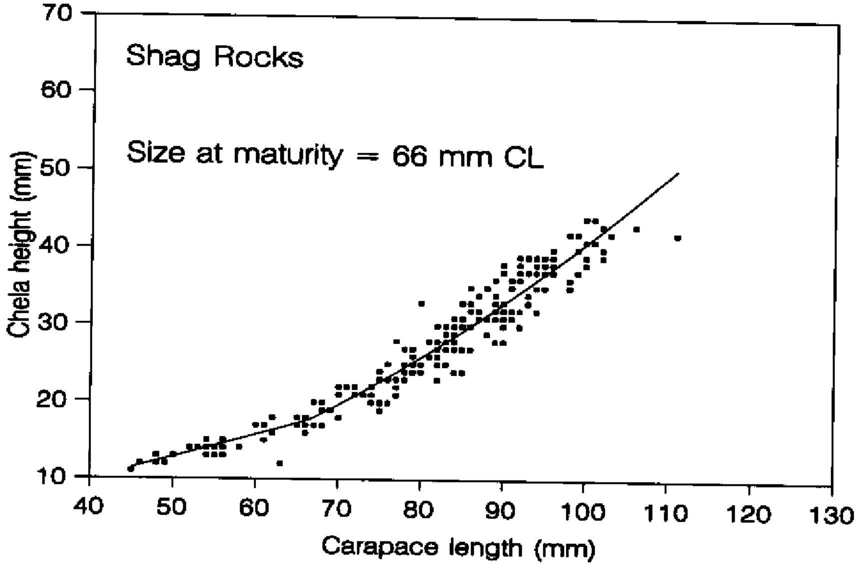


Figure 7. Size-frequency distributions for mature female Paralomis spinosissima sampled at South Georgia and Shag Rocks during July 1992. Superimposed prevalence of rhizocephalans indicates the cause of the skewed distribution at South Georgia.

would allow males to have, on average, at least one breeding opportunity before they become vulnerable to the fishery. Crabs retained by the F/V *Pro Surveyor* were greater than 101.6 mm (4.0 in) CW, which probably provides further breeding opportunities and hence protects reproductive potential. It may be necessary to refine size limits as more fishing grounds are explored.

Shell condition data provide information on relative growth rates because the intermolt period of mature male lithodids frequently exceeds 1 year. Such "skip-molt" crabs accumulate fouling organisms on their shells and can usually be detected by the degree of fouling, staining, shell hardening, or wear on various portions of the exoskeleton. Scoring shell condition is a subjective process, but experience in the North Pacific indicates that an oldshell crab has not molted for at least one year and very oldshell crab have not molted for two or more years. The pattern may differ for *P. spinosissima*, but an increased frequency of oldshell crab in our samples still indicates diminished growth rate (molting frequency) with increasing size (Figure 9). The prevalence of oldshell crab becomes appreciable soon after maturity and then tends to increase with size. Skip-molting also appears to begin at smaller sizes at Shag Rocks than at South Georgia.



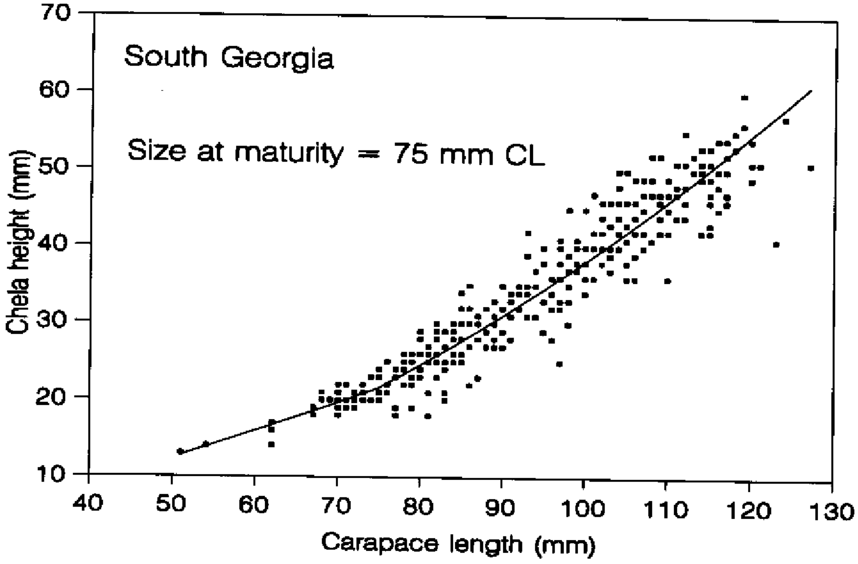


Figure 8. Chela allometry in male Paralomis spinosissima sampled at South Georgia and Shag Rocks during July 1992. The intersections of fitted curves were used to determine size at maturity.

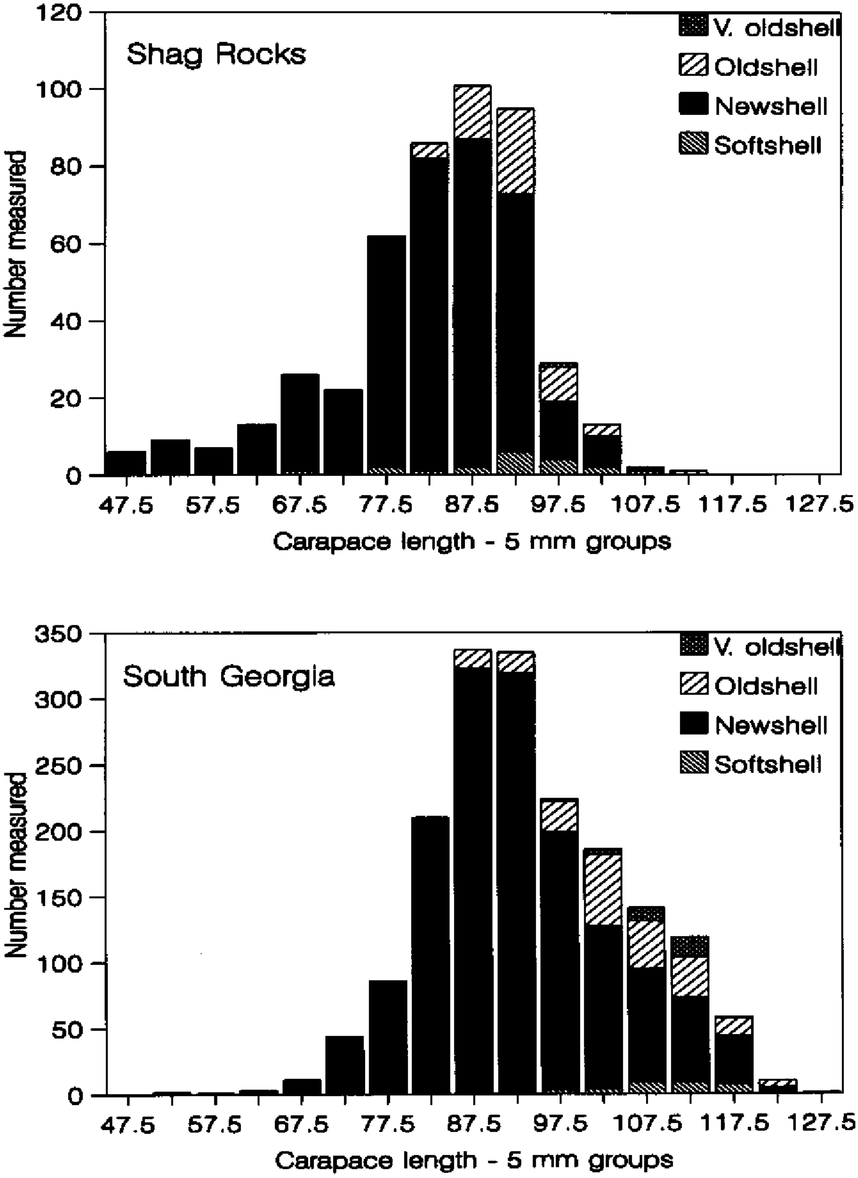


Figure 9. Shell conditions observed in male Paralomis spinosissima sampled at South Georgia and Shag Rocks during July 1992.

We have no information on mortality rates but suspect that the size at entry into the fishery that would maximize yield per recruit lies in the range where molting frequency is declining. Candidate size limits 15% greater than SM50 fall in this range while those 10% greater are slightly short of it. It is also worth noting that skip-molt crabs usually contain more meat than newshell crabs and hence provide a higher quality product. We recommended that size limits for *P. spinosissima*, in Area 48.3 be set at at least 115% of male SM50.

Minimizing the Risks to Antarctic Resources

Catches during the first trip of the F/V *Pro Surveyor* suggest that crab resources in Area 48.3 are large enough to provide a viable fishery. Catch rates were sustainable in the localized areas where trials were made, but the limited survey time precludes an understanding of how long they might be sustained. Crab per pot-lift rates encountered were typical of those in the Aleutian Islands fishery for golden king crab (*L. aequispinus*) over the past 10 years (Morrison and Gish 1994a, 1994b).

Management measures adopted by CCAMLR in the fall of 1992 included a catch quota, restrictions on size and sex of captured crabs, and a limitation on fishing gear to pots. The problem of an appropriate quota for crab stocks in Area 48.3 was not resolvable with the 1992 data at hand so a preemptive quota of 1,000 t was instituted. A minimum size limit of 102 mm CW for males allows them one or more breeding opportunities before harvest. While there is no strict biological reason to prohibit taking female crabs, mature females are smaller than mature males and processing mature females is not as economically feasible. A prohibition on taking females in concert with a minimum size limit on males will tend to preserve the natural characteristics of the stocks since only a small portion of a population can be removed. Crab pots allow nontarget females and small males to be returned quickly to the sea with a minimum of damage.

In some lithodids, especially *Paralithodes camtschaticus* (Powell and Nickerson 1965, Powell et al. 1974, Paul and Paul 1990), males are thought to be polygynous and it is not considered necessary to maintain a 1:1 sex ratio in the spawning stock. This may well be the case with *P. spinosissima*. Also, it appears that spawning is protracted which would make the sex ratio less important than it may be in a species where spawning occurs in a narrow time span.

Many crab and lobster pot fisheries have been conducted for decades, or even a century, with only a size limit or some combination of size, sex, and season restrictions. Populations of king crabs (*P. camtschaticus, P. platypus, L. aequispinus*) and fisheries for them in the North Pacific have frequently been unstable and many populations have declined and remained low for periods of more than a decade. North Pacific king crabs are managed with the size, sex, season, gear, and quota restrictions that are very similar to those implemented by CCAMLR for *P. spinosissima*. There is hence no real assurance that imposition of such restrictions will lead to stability in Antarctic crab populations or in their ecological relationships as is mandated by CCAMLR.

While the set of regulations adopted by CCAMLR is designed to minimize the effects of fishing, ecological conditions may already be destabilized or may affect the stability of crab stocks regardless of the effects of crab fishing. For example, there has been an inverse relationship between lithodid crab and many groundfish abundances in the northeastern Pacific during the past 25 years. CCAMLR annual reports show that most groundfish stocks near South Georgia (Subarea 48.3) have been heavily fished in the past and are considered depleted. Hypothetically, current abundance of crabs may not be sustainable if and when fish stocks recover.

Acknowledgments

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High Latitude Crabs: Biology, Management, and Economics
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Barents Sea King Crab (*Paralithodes camtschaticus*): Transplantation Experiments Were Successful

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Abstract

From 1961 to 1969 adults, juveniles, and larvae of king crab (*Paralithodes camtschaticus*), mainly from Peter the Great Bay near Vladivostok, were transplanted to the Kolsky Bay region off Murmansk. During the period 1974-1991 scattered incidental bycatches of king crab were made from about 40°E on the Kola coast to North Cape in Norway. Since 1992 king crab bycatches have become very numerous, especially in the gillnet fisheries. Coordinated Russian and Norwegian investigations have confirmed that a viable, growing stock of king crab is now well established in the southern Barents Sea. The main area of distribution has been inshore waters between 29°30′ and 35°E. In the most recent years the area of king crab distribution has gradually extended toward west and offshore, and since 1994 offshore trawl bycatches have become more common. At the Kola coast mainly juveniles are taken, the frequency of mature crabs increasing toward the west. Accordingly, large, mature crabs are most numerous in the Varangerfjord area, in both Russian and Norwegian waters, where exploratory trap and trawl fishing has yielded good commercial catch rates of large males. Successful reproduction is documented in both Russian and Norwegian coastal waters,

and young, immature crabs are abundant. Seasonal catch data suggest a similar annual vertical distribution as in the native North Pacific area, with migrations to shallow waters for molting and mating in winter and spring. Tentative stock assessments suggest a marked increase in abundance during the period 1993-1995. Female king crabs in the Barents Sea mature at a larger size than those in its native area of habitation. The main food items seem to be echinoderms, polychaetes, and small bivalves. Therefore, the Barents Sea king crab may be competing for food with the only other similar crab in the region, the stone crab, *Lithodes maja*, and possibly also with flatfish and catfish.

Background

No commercially exploited crab is native to the Barents Sea. In the 1930s the USSR, therefore, attempted to transplant the valuable king crab (*Paralithodes camtschaticus)* from the Far East to the Barents Sea. These attempts, however, all failed because of the inadequate long distance transportation facilities for live crabs of that time (Orlov and Karpevich 1965).

In 1961 a new transplantation experiment was started and during the period 1961-1969 about 2,600 adult specimens of king crab and 10,000 juveniles were transferred. In addition king crab eggs were incubated, and after hatching 1.5 million larvae were released. Most of the crabs used in this large experiment were caught in Peter the Great Bay near Vladivostok. They were transported in containers by air and/or rail and released, mainly in the Kolsky Bay region off Murmansk (Figure 1) (Orlov and Ivanov 1978). Again, in 1977-1978, 1,200 adult king crabs were transferred from the Far East to Kolsky Bay (Sennikov 1989).

On August 3, 1974, a large female king crab was caught in Kolsky Bay. Subsequently king crab bycatches in Russian coastal waters have been reported almost annually, and since early 1990 reports of one or more specimens have become more frequent. The crabs were mainly caught in the trawl fisheries for cod and in offshore scallop dredging. King crab observations were also made by sport divers and amateur fishermen.

The first king crab reported from Norwegian waters was a big male caught in 1976 with a halibut gillnet in the inner part of Varangerfjord. In the 1980s, Norwegian bycatches gradually became more frequent, especially in the coastal gillnet fisheries for cod in depths over 70 m during winter, and during spring for lumpfish in shallow waters less than 30 m. Sport divers have also frequently observed king crabs in the South Varanger fjords.

Until 1992 only single or very small numbers of king crab were taken. Then, in April-May 1992, gillnet fishermen started to get them by the hundreds in the South Varanger fjords. Since landings and sale of king crab are presently prohibited by law, this sudden bounty was just a menace to the fishermen, destroying their nets and, in the worst cases, effectively stopping gillnet fishing on traditional fishing grounds. Accordingly, the matter was brought to the attention of the Mixed Russian-Norwegian Fisheries Commission, which at its meeting in November 1992 requested both countries to intensify and coordinate their research efforts on king crab with the aim of providing advice to the Fisheries Commission on the state and harvest potentials of the Barents Sea king crab stock, and on the possible ecological impact of this new element in the marine fauna.

Russian and Norwegian Investigations 1992 to 1995

In August-September 1992 PINRO carried out a three-week coastal king crab survey. During the last three months of 1992, IMR collected data on incidental bycatches in the commercial fisheries and of king crab observations by sport divers.

From February to June, and again from August to December 1993, IMR organized monthly sample fishing with traps in Bugoyfjord, South Varanger (29°30′E), and in July carried out a three-week research vessel trap survey in the southern and western parts of the Varangerfjord. PINRO in August-September completed a six-week crab survey with traps, covering the inshore area from the Russian-Norwegian border at 30°48′E to 40°E on the Kola coast.

A scaled-down Alaska type king crab trap, 150 × 150 × 75 cm, was the sampling gear used till July 1993 by IMR, but thereafter also conical traps with a base diameter of 120 cm were operated. PINRO used similar conical traps throughout 1993.

The monthly sample fishing by IMR was continued from January to June in 1994. In July a four-week research vessel survey was conducted. This covered both sides of the Varangerfjord and a few localities east and north of the Varanger Peninsula. For 1994 the Fisheries Commission authorized a research quota of 22,000 male king crabs larger than 13 cm carapace width (CW) for a trial fishery to provide more extensive data on crab distribution and catch rates. The quota was divided evenly between the two countries. In Norway four small coastal vessels fished from August to end of December with conical traps of 140 cm base diameter. This trap was also the main gear used in the Norwegian research vessel survey. In the Russian trial fishing, conducted from August to October with two small trawlers, the same large conical trap was used in addition to bottom trawl. In August and November PINRO attempted to determine the fishing power of the king crab trap from underwater TV observations combined with parallel trawl and trap fishing experiments.

In 1995, the IMR sample fishing with traps in Bugoyfjord was continued once a month from January to June. PINRO in May carried out a stock assessment trawl survey covering the crab distribution area in Russian waters, and from mid-July to mid-August IMR repeated its annual research vessel survey in the South Varanger area.

The Mixed Russian-Norwegian Fisheries Commission for 1995 authorized the same trial fishing quota as in 1994, and in Norwegian waters trial fishing with four small coastal vessels started in mid-September.

The crabs caught in the Norwegian sample and trial fishing were sexed and samples of landed males (less than 13 cm CW) were measured and weighed. Females and undersized males were measured or, for large catches, the size range was recorded. Research vessel catches were sexed, measured (and weighed if landed) and some samples were examined with regard to stage of egg development and, from 1994, also condition (hardness) of exoskeleton. Similar measurements and observations were made during the Russian research vessel surveys. In addition, egg samples for fecundity studies were collected, and in 1993 and 1995 also stomach samples. In Russian coastal waters 172 crabs were tagged and released in 1993, and during the Norwegian research vessel survey in July-August 1995, 508 large male crabs were tagged and released in the South Varanger area.

Results and Discussions

In both countries king crab research efforts have until now been modest. The data material is limited and to some extent fragmentary with regard to area and time coverage, and detailed analysis is not yet completed. The findings presented here are therefore tentative.

Distribution

The coordinated PINRO and IMR investigations have established that the core area of king crab distribution includes the southern side of the Varangerfjord with tributaries, both in the Russian and in the Norwegian Extended Economic Zone (REZ and NEZ), Motovsky Bay (32-33°E) and the Murman coast from Kolsky Bay to Cape Teriberski (35°E) (Figure 1). The frequency of mature crabs is increasing toward the west. In the easternmost distribution area on the Kola coast, along the northern side of Varangerfjord and Varanger Peninsula, king crabs are present, but at low densities. Since 1994 offshore king crab bycatches have become more frequent than before in NEZ as well as in REZ, and a few king crabs have been taken as far west as in Kvaenangen (21°E) and in Porsangerfjord (26°E). Recently numerous gillnet bycatches of king crab have been taken in shallow waters in Tanafjord (28°E).

The 1995 PINRO trawl survey revealed that in the middle and end of May king crabs were present in locations with bottom temperature higher than 2°C and crab density increased in the offshore-inshore direction

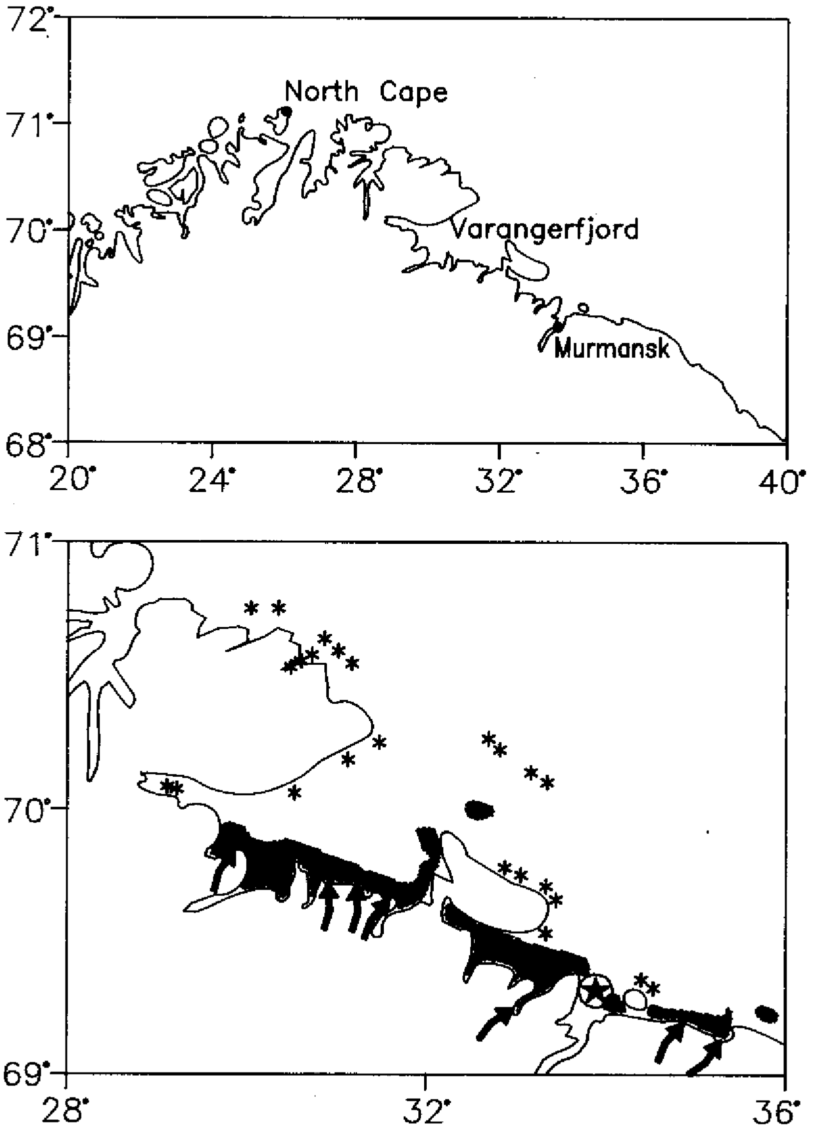

Figure 1. Top: area of king crab distribution in the Barents Sea. Bottom: 1994 distribution in core area. Large star within circle—main transplantation location; Dark shading—dense concentrations; Small stars—incidental bycatches; Arrows—locations of abundant small juveniles.

and from east to west. While a considerable part of the population seemed to be distributed in depths less than 40 m, shallow bays were beyond the reach of the trawl because of rough bottom. The Norwegian research vessel survey in July-August 1995 did not show any significant change in crab distribution from the two previous years. In conclusion, it would thus seem that while the main distribution area has remained practically unchanged from 1993 to 1995, the Barents Sea king crab is expanding both toward west and offshore.

Seasonal variations in depth distribution are evident. During spring, and again in September-October, gillnet bycatches of king crab, especially of berried females, are frequently made in shallow waters less than 30 m. From July to December both sexes are caught in depths beyond 90 m. Females are relatively rare in catches taken deeper than 200 m while large males have been caught in fair numbers down to 330 m. By the end of December females disappear from the trap catches and males become more scarce from February-March to June-July.

Small immature crabs below 10 cm CW have mainly been caught in depths less than 150 m in the many bays and fjords of both countries. Their distribution seems to be very patchy, and catches of 1,000 small crabs have sometimes been taken in one trap while no small crabs were caught in neighboring traps on the same line.

Accordingly, the Barents Sea king crab shows many traits of seasonal and vertical distribution which are very similar to those of king crab in its native North Pacific area. The Barents Sea population, however, is still in a transitional state of expansion toward west and offshore. By this expansion the king crab will gradually inhabit greatly increased areas suitable for feeding and reproduction and thereby enhance further population growth.

Abundance

Since no commercial fishery for Barents Sea king crab has yet started, only catch and effort data from the research vessel surveys and the exploratory (trial) fishing experiments are available. These were used for tentative stock assessments in 1993 and 1994.

The core area of crab distribution was divided into six sub-areas, for which average trap catch rates were estimated. While the data confirm that catch rates are clearly affected by soak time duration, the catch and effort records available do not suffice to make adjustments for variations in soak time in all sub-areas. Unadjusted mean catch rates have therefore been the basis for the assessments in both years. To convert crab mean catch rates into absolute crab densities, results of Russian trap/trawl comparisons in the Far East were applied (Nizyaev 1991). From these the nominal effective fishing area of a similar conical trap as used in the Barents Sea was estimated at 0.0023 sq. nautical mile. The total number of crabs is given by:

$$N = \sum_{x=1}^{n} Sa / q$$

where
S = size of sub-area,
a = mean catch per trap in sub-area,
q = nominal effective fishing area of trap used,
n = number of sub-areas.

In 1993 the total stock of crabs of the sizes encountered during the surveys and sample fishing was estimated at about 210,000, of which 75,000 were males above 13 cm CW. The corresponding figures for 1994 were close to 400,00 and 150,000 respectively, i.e., a doubling of the stock estimate from 1993 to 1994.

In these assessments only areas of "dense" concentrations (Figure 1) were included and their extensions were defined as the area between the 100 and 200 m isobaths. In 1995 crabs have been taken in fair numbers down to 330 m, and at all times of the year many crabs are present in shallower depth than 100 m. The size of the core area of distribution, therefore, was most likely underestimated in 1993 and 1994.

The trap fishing in 1994 was more extensive than in 1993, but in other respects the estimates of average catch rate for each sub-area are comparable between the two years. Accordingly, the conclusion of a substantial population growth from 1993 to 1994 is probably valid while the estimated magnitude of this increase is less reliable. Thus, the nominal trap fishing area of 0.0023 sq. nautical mile was derived from trap/trawl comparisons in a quite different area, probably with bottom topography much unlike that of the coastal fjords and bays in northern Russia and Norway. Furthermore, the general assumption of a constant catchability coefficient (usually set at 1.0 in trawls) regardless of size, sex, or kind of target species is not substantiated by fishing technology research. It is likely that the application of a fixed nominal trap catching area for all types of habitats and for all sizes of crabs results in an underestimated stock strength of unknown, but conceivably significant magnitude. Thus, in one of the Norwegian sub-areas, a fjord with a threshold preventing rapid crab migrations in and out of the fjord, the total number of male crabs over 13 cm CW was in 1994 estimated at 94 specimens while the total catch in three weeks fishing was 359.

The Russian trawl survey in May 1995 provided data for a new stock assessment in Russian waters. This was based on 104 stratified random sample tows of 30 minutes duration in depths from 35 to 300 m, assuming also here the trawl catchability coefficient to be 1.0. The result was a stock estimate of about 500,000 crabs or a biomass of 1,260 metric tons in REZ. It is noted that the area coverage was not complete with regard to inshore non-trawlable locations which are known to be inhabited by king crab.

A complementary estimate for NEZ has not yet been made since the exploratory fishing trials were just started in the middle of September. However, the catch rates obtained during the Norwegian July-August research vessel survey were 3 to 14 times higher than those for the same sub-areas and times in 1994. In particular the relative catches of large males was much greater in all localities. The catch rates obtained demonstrate high densities of crabs in the present core area of distribution which might sustain a profitable commercial fishery, but only for a very limited number of vessels. It is conceivable that the crab stock in the present core area may be approaching an upper limit in abundance, and that the Barents Sea king crab is to inhabit a much larger feeding and reproduction area to become a significant commercial resource.

Recruitment

Berried females are abundant in most of the tributary bays and fjords along the coast from Varanger to Cape Teriberski. The main reproduction potential appears to be in the Varangerfjord area (within both REZ and NEZ) and in the Motovsky Bay. Accordingly, the PINRO survey in August-September 1993 identified four locations with dense concentrations of young, immature king crabs of 6 to 9 cm CW. Similarly, from end of August to early December incidental high catches of juvenile crabs, up to 430 in one trap, were made in Bugoyfjord. Again in 1994, from June to December, small, immature crabs were common in Norwegian trap catches and were sometimes taken in very large numbers. Also in Russian waters good catches of small crabs were made, confirming that in 1994 they were plentiful and present in most bays and fjords of the core area of distribution in both countries (Figure 1). In 1995 small crabs were present from April onward in the Norwegian trap catches in most of the South Varanger tributary fjords, sometimes in very large numbers.

While during each of the last three years small crabs appeared to be abundant, the year by year progressions of distinct modal CW peaks in both males and females (Figure 2) indicate earlier large variations in annual recruitment to the Barents Sea king crab stock.

The predominant current system along the relevant Norwegian and Russian coastline is likely to transport the pelagic king crab larvae far out to sea and toward the eastern cold waters of the Barents Sea. It is proposed that the successful reproduction, evident by the abundance of small crabs in Norwegian and Russian fjords, might be facilitated by tidal eddies in the long and irregular fjords, the vertical tide difference in the region being about 4.5 m. Some of the king crab larvae hatched there may be trapped in the eddies and remain in the fjords where they find suitable depths and living conditions as glaucothoe larvae. Consequently, in this foreign environment the establishment of viable king crab subpopulations is enhanced in areas with complex fjord systems.

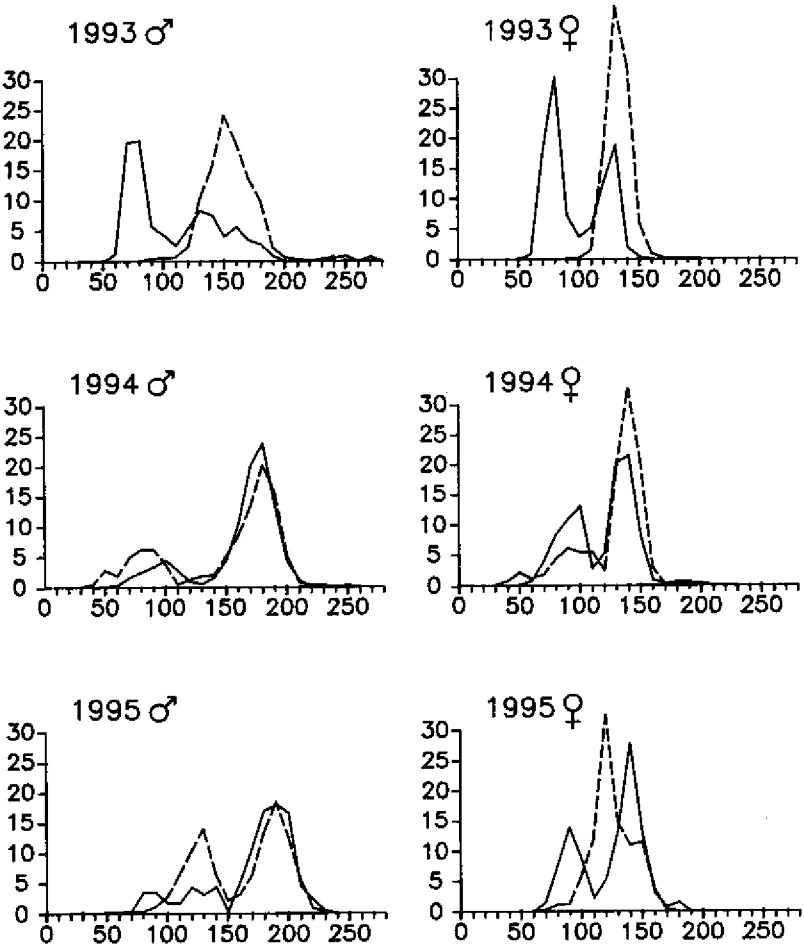

Figure 2. Percentage carapace width (in mm) distributions of Russian (solid line) and Norwegian (broken line) research vessel catches of king crab in 1993, 1994, and 1995.

Population structure

Figure 2 shows the overall frequency distributions of the carapace width measurements made in 1993, 1994, and 1995 of the crabs caught during the Russian and Norwegian research vessel surveys. The Russian distributions each year show a bimodal pattern including significant numbers of small crabs. In contrast, the Norwegian samples were practically without crabs of less than 10 cm CW, of both sexes in 1993 and of females in 1995. This may partly be due to the relatively large mesh size of the traps used by the Norwegian research vessel. The sample fishing in the last quarter of each year, however, has confirmed that small crabs were also abundant in NEZ throughout the three years.

The modal peaks in the distributions are progressing year by year toward higher CW values. In males this is most pronounced in the Norwegian data, where crabs of 14 to 16 cm CW were the most abundant ones in 1993, while they were almost lacking in 1995.

The Russian samples from different sub-areas demonstrate an increase in crab size from east toward west with mostly small immature crabs east of Cape Teriberski. No such trend has been detected in Norwegian waters and neither is there any distinct difference in size distribution between Russian and Norwegian catches in the Varangerfjord region.

Sex proportions may vary greatly between localities and even between neighboring traps on the same line. During the months July-November, males and females are on an average caught by traps in more or less equal numbers in most sub-areas, but one of the sexes may during short periods be taken in much larger numbers than the other. In the very large catches of small crabs which are sometimes made, the sex ratio is always close to 1:1.

Reproduction

In late January, and again in early April 1995, sport divers observed grasping pairs of king crab in depths of 15 to 40 m in a South Varanger fjord. In April numerous empty exoskeletons were also seen on the seabed. During the same period, extending into May, bycatches of females are frequently made in shallow waters. Nearly all of these have new soft shells, as have the crabs caught at that time of the year in the monthly Norwegian sample fishing. These observations suggest a molting and mating season for the Barents Sea king crab which is fairly similar to that of its native North Pacific waters. (e.g., Powell and Nickerson 1965).

The minimum carapace length for berried females was found to be 93 mm, and the size at which 50 percent of the females have become sexually mature (SM50) was estimated at a carapace length of 108 mm (about 118 mm CW). All females above 145 mm CW were mature (Figure 3). The estimated SM50 for Barents Sea king crab therefore exceeds those reported for different populations in its native areas of habitation (e.g., Blau 1990, Otto et al. 1990).

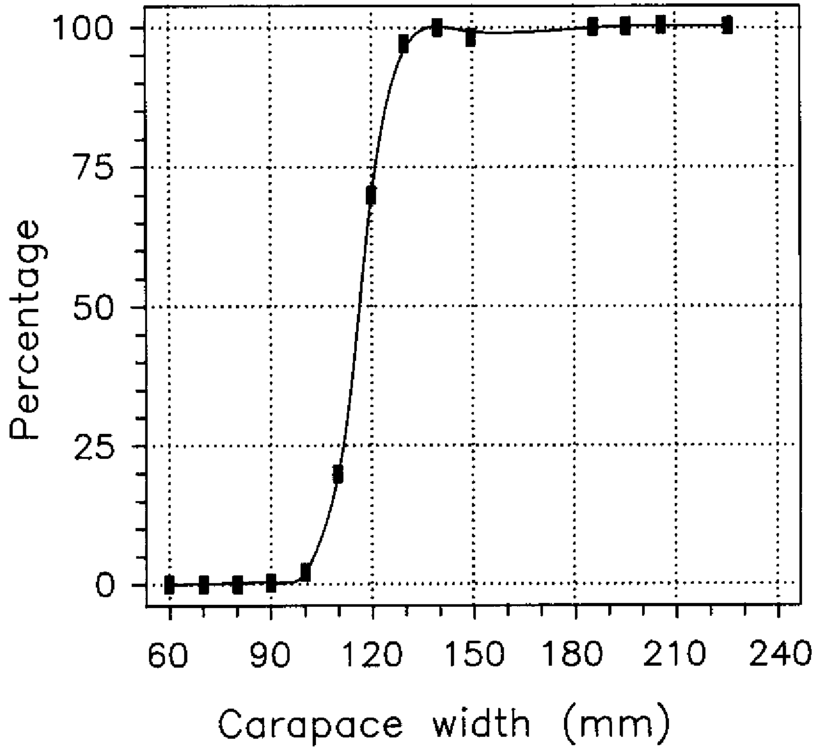

Figure 3. Frequency distribution of females carrying eggs as a function of crab size.

Measurements of chela height in small, immature male crabs are too few for determining the size at which relative male chela height starts to increase. The more extensive data for crabs above 7-8 cm CW of both sexes show that relative chela height differs between males and females in crabs above 10-11 cm CW. Assuming that the sex-determined difference in chela growth starts at the size of male maturity (e.g., Somerton 1980) the data therefore suggest that male Barents Sea king crab on average reach sexual maturity at 10-11 cm CW, which is similar to maturation sizes established by the same method for male king crabs in the Bering Sea.

Absolute individual fecundity in females of 112 to 220 CW ranged from 76,000 to 704,000 eggs. In other king crab stocks the fecundity is reported to vary within 25,000-500,000 (Kruse 1992, Haynes 1968).

The total number of eggs *(F)* can be expressed as an exponential function of carapace width: $F = a(CW)^b$. The estimated coefficients of this

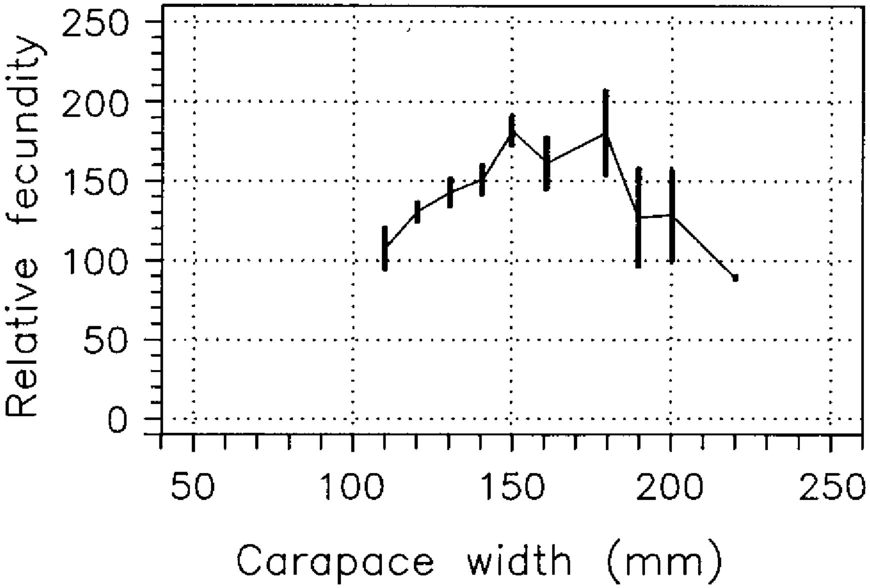

Figure 4. Comparison of relative fecundity with crab size.

equation were within the limits of variation reported for king crab in its native area (Takeuchi 1967, Haynes 1968, Rodin 1985, Klitin 1992), but while in 1993 and 1994 they were quite similar, they differed markedly in 1995. This may be related to the difference in sampling time, August-September in 1993-1994 and May in 1995.

Relative fecundity, determined as the ratio between absolute fecundity and female weight, was found to reach its maximum in females of 150 to 180 mm CW (Figure 4). This is consistent with observations made during the trial fishing in late 1995 of very large females (over 22 cm CW) carrying only a few eggs.

Food and feeding

The available data on stomach contents of the Barents Sea crab differs both with regard to time, areas, and methods of sampling. In August-September 1993, stomach samples were collected from crabs caught with traps, mainly in bays and fjords. The samples from May 1995 were all derived from trawl catches in the large bays (Motovsky Bay, Varanger-fjord) and in the open sea. The species composition of the food objects and their weights were determined. Feeding intensity was estimated by indices of stomach fullness and by the ratio of food weight to crab weight, expressed in perdecimille.

Table 1. Stomach contents of king crab in the Barents Sea.

Sampling dates	19 Aug-28 Sep 1993	18 May-26 May 1995
Sampling depth, m	25-128	47-270
Sampling method	trap	trawl
Average CW ± 1 SD	132.3 ± 43.3	150.8 ± 29.1
Number of stomachs examined	73	70
Empty stomachs	16	3
Dominant prey:	Frequency of occurrence from all crab examined (%)	
Bivalvia	49.4	39.4
Gastropoda	21.2	35.2
Scaphopoda	–	5.6
Crustacea	2.4	12.7
Paguridae	–	4.2
Amphipoda	1.2	2.8
Echinodermata	24.2	66.2
Echinoidea	22.4	15.5
Asteroidea	–	19.6
Ophiuroidea	1.2	26.8
Polychaeta	16.5	52.1
Sipunculoidea	–	28.2
Hydroidea	3.5	14.1
Bryozoa	–	5.6
Foraminifera	7.1	4.2
Fish	4.7	9.9
Fish eggs	–	5.6
Algae	36.5	28.2

It appears from Table 1 that echinoderms as well as molluscs are important food items for the Barents Sea king crab, both in spring and in autumn. In the samples from the spring trawl catches, polychaetes were also of great importance.

Males were found to feed more actively than females, their mean index of stomach fullness being about twice that of the females, 11.30/000 and 5.90/000, respectively. In May 1995 the index of stomach fullness in some cases exceeded 500/000. This shows a high intensity of crab feeding compared for example with the maximum stomach fullness of 190/000 reported for king crab off western Kamchatka (Kulichkova 1955).

A full evaluation of the ecological impact this new element in the Barents Sea marine fauna has had, or might have in the future, is premature at this stage of knowledge, before the king crab has become established in its total potential area of distribution. The present stomach analysis suggests that it is a potential competitor for food with the stone crab (*Lithodes maja*), the only other similar crab in the region, with catfish *(Anarrhichas* sp.), and with some of the flounders in the area, but not with any of the important commercial fish species.

Conclusions

In the Barents Sea, a viable population of king crab *(Paralithodes camtschaticus)*, is established, which is continuing to grow in abundance and area of distribution. Good recruitment of juvenile crabs is evident, and the overall size distribution and size at sexual maturity demonstrate favorable living conditions in the Barents Sea. Accordingly, further king crab population growth and extension of geographical distribution are to be expected.

In the present core area, the crab density is quite sufficient for catch rates required in commercial fishing. However, the stock strength today may only support an economically viable fishery for a very small number of vessels in each country. Russia and Norway have, therefore, mutually agreed to prolong the prohibition of king crab landings, and presently only catches required for research and stock assessments are authorized.

The crab density in the present core area may be approaching a limit, and further increase in stock strength might therefore be contingent on expanded crab distribution. Recent observations suggest that the Barents Sea king crab is indeed pushing both toward the heavily indented coastal regions west of the Varanger Peninsula as well as toward large new feeding areas offshore. Both are likely to enhance further population growth and the potential for subsequent commercial exploitation.

A reliable evaluation of the king crab's ecological impact is premature, but so far no observations have been forthcoming giving cause for alarm.

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Growth, Mortality, and Food Preference in Laboratory-reared Juvenile King Crab *(Paralithodes camtschaticus)*

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Abstract

The king crab (*Paralithodes camtschaticus*) is a new species in the Barents Sea. The crabs were caught in Norway for the first time in 1977. To evaluate the king crab as a new species for aquaculture in Norway we have conducted a study on growth, mortality, and food preference in juvenile crabs hatched and reared under laboratory conditions. Growth, measured as increase in carapace length, was lower than observed in wild juvenile king crabs, probably due to a nutritionally sub-optimal diet. High rate of cannibalism may also be related to low food quality and high cohort density. The juvenile king crabs displayed a significant food preference.

The present results are not sufficient to evaluate the potential of king crab in aquaculture in Norway. However, the results are promising and do not disqualify the king crab as a culture organism.

Introduction

In recent years the Norwegian fish farming industry has achieved great success with the production of Atlantic salmon (*Salmo salar*). In 1995 the production of this species alone will exceed 250,000 tons. It has, however, proved much more difficult to introduce marine species such as halibut (*Hippoglossus hippoglossus*), cod (*Gadus morhua*), and wolffish (*Ararhichas lupus*) into aquaculture, and although some progress has been made the development has been very slow. The attempts so far to commercialize aquaculture of two crustaceans, noble crawfish (*Astacus astacus*) and lobster (*Homarus vulgaris*), have failed, mainly because of cannibalism in these species.

Between 1961 and 1969 Russian scientists transferred king crab (*Paralithodes camtschaticus*) from the Sea of Okhotsk to the coast of the Kola Peninsula in the Barents Sea, about 150 km from the Norwegian border. The first occurrence of king crab in Norway was reported in 1977 (Orlov and Ivanov 1978). The king crab has now established a significant population in the northeastern fjords of Norway and is penetrating constantly southward along the coast.

The king crab shows a combination of properties which makes it very interesting as a new candidate for aquaculture in Norway:

- The king crab is able to grow at low temperatures. The wild populations of king crab are found in regions with water temperatures below 10°C, and at the larval stages the optimum temperature seems to be approximately 8°C (Nakanishi 1987). It should therefore be possible to rear king crab in Norway without heating water.
- The king crab has a high fecundity. Females normally carry between 150,000 and 400,000 eggs (Wallace et al. 1949). This is far more than the other crustaceans previously attempted in Norway. The high fecundity makes it easy to gain a sufficient number of larvae for rearing, and also makes mortality at the early stages less decisive for the success.
- The podding behavior of the king crab, and the observations that king crabs may even molt while podding without eating each other (Dew 1990) indicate that king crab may be less cannibalistic than other crustaceans. Cannibalism may still prove to be the most crucial factor for the possibility to bring the king crab into aquaculture.
- The king crab is a well-known delicacy throughout the world, and there is already a large market for the king crab. The problems of introducing a new product to the market should therefore not apply to the king crab.

Our main objective in this study has been to provide fundamental biological knowledge needed to evaluate the king crab as a possible candidate for aquaculture in Norway. Three different concepts for crab culture could be implemented: (1) Rearing post-larvae for release. (2) Rearing crabs from eggs to market size. (3) Fattening of wild-caught crabs. Alternative (1) is not possible until the ecological impact of the immigration of king crab in Norwegian waters is evaluated, and an enhancement program of the wild population is wanted. Our choice has been to study the rearing from hatching to market size. We are well aware that the Japanese have obtained good results in rearing of post-larvae for their enhancement programs (Nakanishi 1987). We have therefore concentrated on the grow-out phase from settling to market size. In the first year of our study we have focused on growth, mortality, and food preference.

Materials and methods

Ten ovigerous female king crabs were caught by pots in the Varanger Fjord, Northern Norway, in November 1994 and brought to the Aquaculture Research Station in Tromsø. At this station water temperature and salinity as well as light conditions can be fully controlled. The females were kept in a fiberglass tank (2 by 2 m) supplied with unheated sea water and fed a diet of fish meat and sea urchins. Hatching took place in February and March 1995. Three fractions of the hatched larvae were collected by taking advantage of their positive phototaxis and placed in conical tanks of about 30 L. The larvae were fed with decapsulated *Artemia salina* nauplii. We changed the water of the tanks every second day and kept the water temperature at 5-7°C.

After reaching the megalope stage the larvae were transferred to trays (40 by 40 cm) made for hatching of salmonid eggs. The trays have perforated bottoms with an upwelling water current. The water temperature in the trays was kept at 8-10°C, and the salinity between 32 and 35 ppt. There was no substrate or any other form of cover in the trays. After settling the crabs were fed a mixed diet consisting of fish meat, *Calanus finmarchicus,* and dry salmon feed.

Three groups, hatched 20 January, 8 and 13 February, were transferred to the trays, at 6 and 20 March and 3 April, respectively. At two to three weeks intervals we measured the carapace length and wet weight of random crabs ($n = 10$) from each of the three groups. At the same occasions the number of remaining crabs in the trays were estimated. Molting was assessed by visual observation and the first appearance of new stages registered. In order to compare these groups, time was expressed as days after megalope stage. The experimental period started 45 days after megalope stage and lasted to 175 days after megalope stage. In addition, each measure of carapace length and developmental stage was related to cumulative degree-days (dC) from hatching. Our growth data were compared with a growth model proposed by Stevens and Munk (1989): $\ln(CL) = -10.787 + \ln(dC)$, where CL is carapace length in mm and dC is cumulative degree-days after hatching.

Food preference was tested by placing individual crabs in small chambers (10 by 7 cm) and offering them a choice of five different food items. We used four replicates of two size groups (mean carapace length of 5.1 and 7.9 mm), with 6 crabs in each group. The food items were dry salmon pellets, moist pellets made from a mixture of salmon and *Calanus* meat, raw shrimp meat, shrimp waste (shell from the posterior end of the shrimp tail) and dry cod pellet (less fat than the salmon pellet). After offering this diet for one week we recorded what the crabs were eating four times a day. Food preferences were expressed as mean percent of eaten food items in each group.

The results of our study are expressed as mean ± standard deviation (SD).

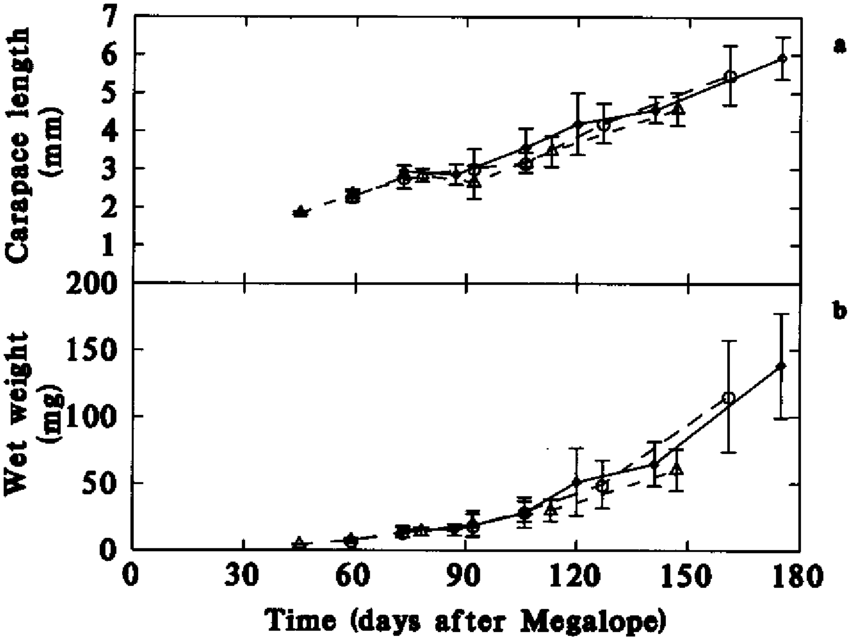

Figure 1. Growth in three groups of king crab (Paralithodes camtschaticus) after megalope stage. (a) Carapace length and (b) wet weight. The points and bars represent mean and SD (n = 10).

Results

The length and weight increase was very similar in all three groups during the experimental period, and there were no significant differences between the groups at any time (Figure 1). At the beginning of the experimental period (45 days after megalope) the crabs entered their second crab stage (C II) (Figure 2). At this point the mean carapace length was 1.8 ± 0.1 mm, increasing to 5.9 ± 0.6 mm 175 days after the megalope stage when the crabs entered the sixth crab stage (C VI). The corresponding wet weight increased from 4.3 ± 0.2 mg to 138.5 ± 39.4 mg.

There was high mortality in all three groups during the registration period (Figure 2). After 150-180 days the number of remaining crabs in the groups was reduced to 5, 9, and 14%, respectively. More than 50% of the crabs disappeared during the first 45 days of registration; thereafter the decline in number occurred at a slower rate. Visual observations revealed that cannibalism was the major cause of the mortality in the last part of the experiment.

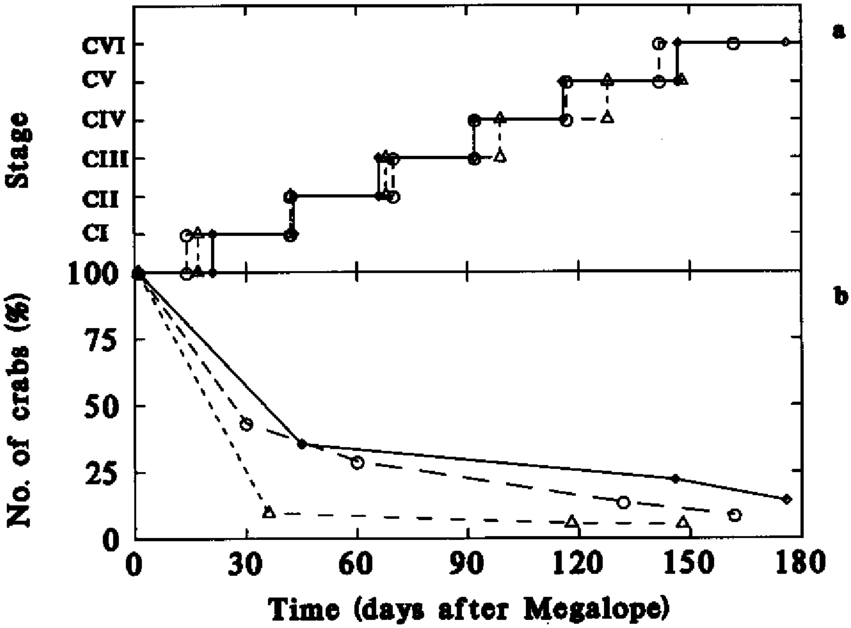

Figure 2. Development and survival of king crab (Paralithodes camtschaticus) after megalope stage. (a) Developmental stages and (b) no. of crab in percent of total numbers of crabs. The symbols correspond with the three groups in Figure 1.

The growth registrations of the present study cover a span from about 700 to 1,900 degree-days (dC) from hatching (Figure 3). Our first registrations fitted well with the growth model proposed by Stevens and Munk (1989), while our latest registrations fell somewhat below the predicted line. A straight regression line, fitted by the least square method, demonstrated a very good correlation between the carapace length increment and the cumulative degree-days ($r^2 = 0.94$, $p < 0.001$, $n = 18$), although we expect that a prolonged registration period will reveal that the relationship is best described by an exponential curve. The carapace length measured at 460 dC by Kurata (1960) seemed to fit well with our registrations. The molting was quite synchronous during the first crab stages, but became more asynchronous as the molting proceeded. The first crab stage (C I) appeared at 420 dC after hatching.

Both size classes of crabs displayed an obvious food preference, with shrimp meat as the most preferred food item (Figure 4). For the smallest crabs (mean carapace length of 5.1 mm) shrimp meat was eaten

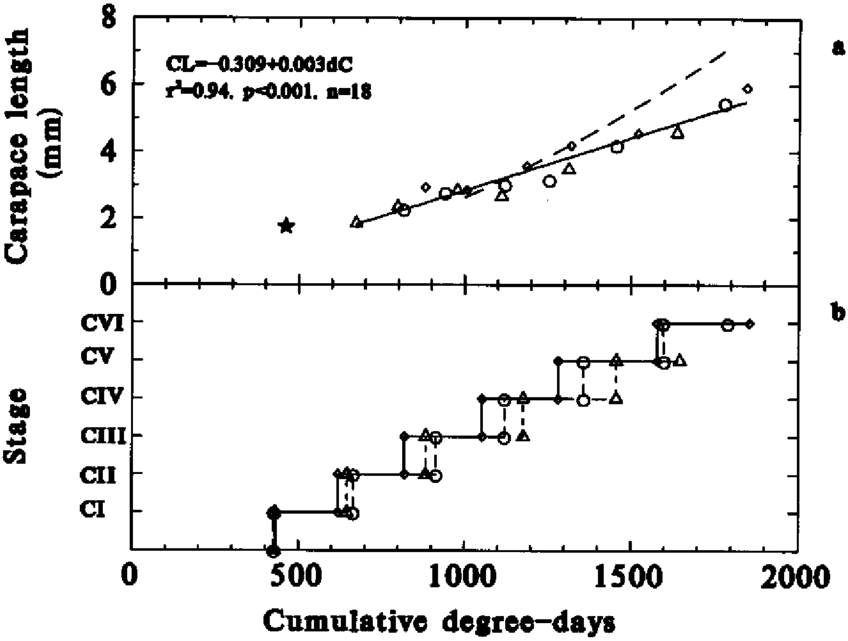

Figure 3. Growth and developmental stages in king crab (Paralithodes camtschaticus) related to cumulative degree-days after hatching. (a) Carapace length and (b) developmental stages. The solid line in Figure 3a represents the linear regression for the current results, the star represents the result from Kurate (1960), and the broken line represents the growth model proposed by Stevens and Munk (1990). The symbols correspond with the three groups in Figure 1.

in 30% of the observations, while the corresponding result for the largest crabs (mean carapace length of 7.9 mm) was 42%. Shrimp waste obtained the second highest score in both size classes with 12 and 8%, respectively. The other food items were chosen in less than 4% of the cases.

Discussion

Our first attempt to rear juvenile king crabs has brought promising results with regard to growth and development. With the exception of Kurata's (1960) registration of carapace lengths of stage C I reared king crabs we are not aware of similar growth data from cultured crabs covering the same development stages. Since the growth of juvenile king crabs is very temperature dependent (Kurata 1960), comparisons with

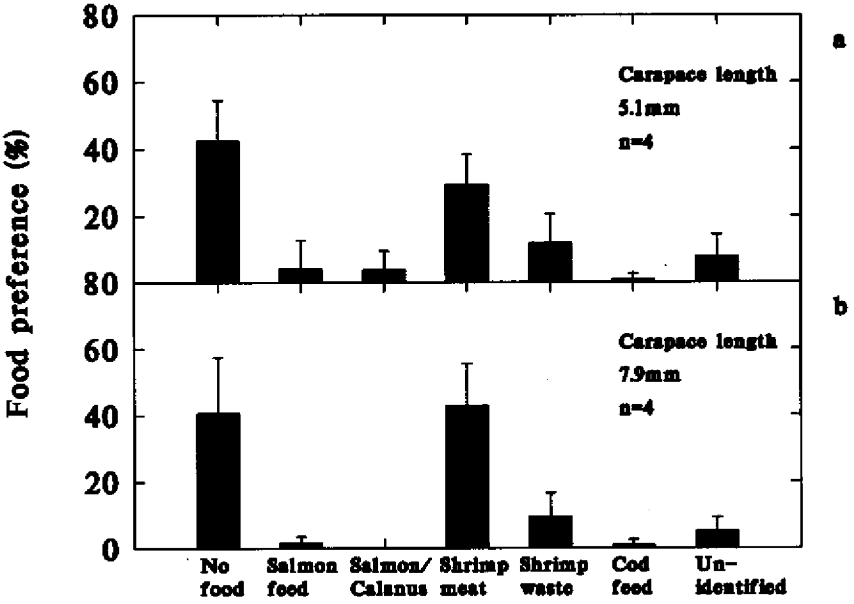

Figure 4. Food preference in king crab (Paralithodes camtschaticus). (a) Crabs with carapace length 5.1 mm and (b) crabs with carapace length 7.9 mm. The results represent mean ± SD of four replicate groups of crabs, observed at four different times.

plain growth registrations from wild crabs may be of minor value. Most of the growth registrations on king crabs are also made from larger crabs.

A more meaningful way to compare growth data is obtained if the growth parameters are related to cumulative degree-days (dC). By doing this the problems of differences in water temperatures are to a large extent avoided. When our data are subjected to this kind of comparison we find that the growth in carapace length in our experiment is somewhat lower than expected from literature values based on wild king crabs. Our results give a carapace length of 5.4 mm at 1,900 dC, while the growth models of Stevens and Munk (1989) and Stevens (1990) predict corresponding values of 7.9 and 9.9 mm, respectively. The values of these two studies are thus 46 and 83% above our value. From our data it is also possible to estimate the carapace lengths at different crab stages with a certain degree of confidence. It should, for instance, be fair to assume that the carapace lengths at 1,500 dC (4.2 mm) represent stage C V. In the study of Donaldson et al. (1992) carapace lengths of wild king crabs at stage C V was found to be 5.6 ± 0.4, which is 33% higher than our value. This result, together with the comparisons to the growth in the works of Stevens and Munk (1990) and Stevens (1990) indicate that our crabs suffered a lower growth rate than predicted both with respect to molting frequency and intermolt increments. The differences in growth rates may be explained in terms of food quality. Brodersen et al. (1990) found significant differences in growth rates between groups of juvenile king crabs given food of different quality. Crabs given nutritionally deficient food showed a significant longer intermolt time than crabs given a well balanced diet. It may well be that the quality of diet offered to our crabs was inferior compared to the diets of the wild crabs in the studies of Stevens and Munk (1989), Stevens (1990) and Donaldson et al. (1992).

In our study the first crabs reached stage C I at 420 dC. This is in good accordance with values obtained by Kurata (1960) from wild crabs (440 dC). This should indicate that the diet of decapsulated *Artemia* has not impaired the larval development.

The crabs in our experiment suffered from high mortality due to cannibalism. Several factors are known to affect the degree of cannibalism. These include cohort density, cover, food quality, and age. In our study the crabs were initially placed in trays at a density of approximately 3,000 animals/m^2. This is far above the density used by Rounds et al. (1990) where the highest density was 29 animals/m^2 and the lowest density 8 animals/m^2, and there the density was shown to affect the cannibalism. In the same study cover was shown to affect the cannibalism in 1-year-old crabs, but not in 2-year-old crabs, and the rate of cannibalism in the 2-year-old crabs was only half of that of the 1-year-old crabs. The older crabs often grouped in pods, while the younger crabs were seen to aggregate only at the end of the study when they were assumed to approach podding age. Our trays were not equipped with anything which provided cover for the crabs, and the crabs were probably too young to display podding behavior.

Brodersen et al. (1990) demonstrated that cannibalism in juvenile king crabs was strongly influenced by food quality. From the results of the growth registrations it is reason to believe that the diet eaten by our crabs was not optimal for growth, and hence may have been a reason for the high rate of cannibalism. In general, the rearing conditions in our study were not organized in order to keep the rate of cannibalism at a low level. This gives much room for improvements, and presents challenging tasks for future experiments.

The king crab is known to be an opportunistic omnivore. In nature food is not considered a limiting factor, while in laboratory-held crabs growth rate is shown to depend on the quality of the diet (Brodersen et al. 1989). We believe that if the king crab is food selective, preference studies may offer an easy way to find suitable food for the crabs. From the randomly chosen food items given to the crabs, shrimp meat and shrimp waste were selected in approximately 90% of the cases observed.

Shrimp meat or shrimp waste was not included in the diet given in the growth experiment, while the not-preferred fish food was. We take this to support the suggestion made above that we have fed the juvenile crabs with a nutritionally sub-optimal diet.

The results of the present study are in support of the following main conclusions:

- Juvenile king crabs are food selective.
- It is possible to obtain acceptable growth rates for king crabs in culture. Food quality is important to realize the growth potential.
- Cannibalism is a major problem in rearing juvenile king crabs, and further research is needed to reduce the problem.

The results so far do not disqualify king crab as a new candidate for aquaculture in Norway, but the current results are not sufficient to evaluate the potential of king crab as a culture organism.

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Summary Report of the International Workshop on Research Needs

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Two workshops associated with this symposium dealt with identifying areas of research needed to better understand the basic biology of high latitude crab species and the impacts of fisheries on the resources. The international workshop was attended by the international group of scientists who attended the Wakefield symposia. The Alaska interagency workshop, held prior to the symposium, focused on Alaskan crab resources and research needs specific to the region. The Alaska workshop was attended by Alaska Department of Fish and Game staff, National Marine Fisheries Service staff, and University of Alaska staff who attended the Wakefield meeting (see Kruse, Crab Research in Alaska: An Interagency Long-term Plan, this volume).

The lists of research topics are not all-inclusive, nor are the topics listed in order of importance. Their purpose is to serve as thought-provoking guides to the research community and agencies that support research or regulate the resources.

The following list of research topics was generated by all the attendees of the Wakefield symposium. The list was compiled by A.J. Paul and Judy McDonald Paul.

1. What are the stocks and stock structure?
2. How abundant are the target species and what methodology is appropriate for estimating population size?
3. What factors regulate the productivity of a stock?
4. How should the resource be extracted; what are the criteria for deciding harvest levels?
5. Determine the prevalence of spawning grounds or incubation areas, nursery areas, and their importance to larval recruitment. What is

the interannual variation in the location of female pods during reproduction in species where spawning females aggregate?

6. What role do climatic events play in modifying food web structure?
7. Are there indicator species that can be used to show the existences of climatic changes?
8. What is the molting frequency of target species and what methodologies need to be developed to measure it?
9. Undertake life history studies on noncommercial crab species to gain insight into biology at the family level.
10. What are the appropriate size limits for harvested crabs? What criteria should be used in determining what the size limit should be?
11. What is the importance of carapace age or condition in reproduction and other behaviors?
12. What roles do genetics and environment play in determining growth?
13. What mechanisms cause pulses of recruitment (strong year classes), e.g., environment, sex ratio, population abundance?
14. What role do ocean currents have in effecting recruitment at the local level and on larger scales? Develop hydrological programs that are carried out by crab biologists themselves. Examine coastal processes and expanded use of satellite technology, include oceanographers in crab meetings.
15. Explore the role of female choice in reproductive strategy. Determine the importance of male size and shell condition.
16. Develop and deploy over vast areas artificial collectors that measure settlement and early recruitment in king crabs and other species that settle in collectors.
17. Carry out a genetic analysis of parasites and disease organisms.
18. Study the role and distribution of intermediate hosts of parasites.
19. Develop tests and field kits that measure shell condition and disease.
20. Improve genetic techniques to differentiate stocks or hybrids, and begin an international catalog of genetic profiles.
21. Examine hybrid viability.
22. Determine the consequences of female harvest.

23. Determine the habitat requirements of different life stages, particularly juveniles. Initiate studies of multispecies interactions.
24. Measure mortality rates due to predation for different life stages.
25. Improve the understanding of processes that allow populations to rebuild from low population levels.
26. Observe long-term mortality rates due to fishing and handling.
27. Develop more effective harvesting gear that minimizes the capture of nontargeted animals.
28. Track the effects of the moratorium on cod harvest in eastern Canada, and closure of Alaskan king crab fisheries on crab stocks.
29. Improve the estimates of catchability coefficients and exploitation rate values.
30. Improve communication between fishermen and biologists and clarify goals of the management program. What are the social and economic tradeoffs of pulse fishing versus lower, more constant harvests.
31. Determine the consequences of fishery alterations of size and sex structure in crab population.
32. Develop cost-effective Remote Operated Vehicles (ROV) to use in the study of life history.
33. What role might refuges and reserves play in attracting and propagating crabs?
34. Initiate life history studies on deepwater species that are not currently harvested but probably will be in the future.
35. What challenges could be made to existing assumptions on reproductive biology?
36. How efficient are trawls as sampling devices? Do they sample all sizes? What are crab reactions to their presence? What are trawl openings? How deep do they dig? What is the mortality and injury rates of crab due to trawl fishing?
37. What is the fate of bycatch discards on the benthic ecosystem?
38. For species whose life history is fairly well described, begin synopsis profiles that are continually updated.
39. Improve understanding of population dynamics. Investigate stock–recruitment relations for more stocks.

Discussion Summary

A.J. PAUL: Historically the task we've undertaken in the Wakefield symposium series is to create a laundry list of research needs for the taxa we're interested in. This serves to guide individual scientists as they put proposals and work schedules together.

The first Wakefield symposium that dealt with crab was in 1982 on Tanner crabs. The sheet of research topics we handed out was compiled from the lists produced by the first and subsequent crab symposia and material put together by Gordon Kruse and the ADF&G group who are doing a similar task.

Our first task is to take a look at the list and see if anything needs to be added. Additions can be made now or as they come up in discussion. You could write things down and send them to me. I will accept written materials to go into the list until the middle of next month.

I want to update the list and see if any topics can come off the list. Are there things that we have dealt so that the knowledge level is now sufficient to lessen priority or remove it from the list? I would also like to see if there are some topics that might be the focus of a synthesis meeting where a small group with pertinent data might put together a report. I envision a highly focused report with Alaska Sea Grant being the vehicle to get it into circulation.

I would also like to put some mechanism in place to identify the types of ongoing research we're involved in and those we might plan to get involved in. Glen Jamieson's *Crab Newsletter* might be the vehicle to do that. Glen, would you stand up and speak briefly about it?

G. JAMIESON: For those of you that don't receive the *Crab Newsletter*, Lee Armstrong and I are the editors. We try to produce two issues a year, March and October, and we need more submissions. If this newsletter is going to be useful, submissions need to come in regularly. One of the problems now is that I feel like I'm hounding people. There are regional coordinators scattered around, and about two or three months before each issue I send a memo asking them to please send me something. Sometimes they do, but I think even they have problems getting material.

Unless I get the cooperation of the crab community, it's going to slowly die. Anyone who wants to summarize briefly what they've done here at the workshop, can give it to me. It's best to e-mail it to me so that I don't have to retype it, which saves me a lot of time.

I'd welcome anything from book reviews to descriptions of fisheries, problems that you've having, anything that's related to crab. We've gotten information requests from Eastern Europe, Africa, and India. They didn't know anything about these other fisheries; they don't come to meetings like this. As crabbers, we're sort of unique to the rest of the world. We're so fortunate in the Pacific Northwest to have meetings like this.

I really welcome contributions, in fact I need them desperately, so if you can submit something, that's great. If the *Crab Newsletter* can help to coordinate and plan research initiatives, that'd be super. I'd certainly consider anything along that line.

A.J. PAUL: Thank you very much, Glen. Another topic I have on my list is scheduling of future meetings. I'm sure that we're all aware of the decreased funding situation in our respective countries and governments, and the effect it may have on our ability to attend meetings, so perhaps we must look to the electronic media and the print media such as the *Crab Newsletter* to be the glue between these meetings.

So this is an open forum for discussion that can go on as long as there are ideas; it's up to you. The floor is open.

B. STEVENS: I'm with National Marine Fisheries Service. I want to bring up something that I've seen and worked on which is aggregation of crabs. When we've tried to do larval recruitment studies we've taken a shotgun approach, with plankton tows all over the ocean. In Chiniak Bay, we have a population of crabs that's very concentrated in space and we know they're hatching at a very concentrated point in time. A good next step would be to look at larval recruitment of a population with a known hatching time to see the radiation of larvae out from a spreading center where crabs aggregate.

UNIDENTIFIED: I was talking to Debbie Schultz about her paper on behavior of ovigerous females, and in other pods you find that movement of ovigerous females is quite restricted, and they seek refuge. If the ovigerous female lives in a featureless environment on a silty substrate, there are two ways to get refuge. One is to dig a hole; the other is to sit under another female. It may very well be that this podding behavior is a refuge-seeking behavior. We don't catch buried freshwater crayfish females with traps, because they don't move. What we do is drop artificial refuges into the lakes and ponds and the crayfish all come in seeking refuge.

By exploring this behavior, maybe we can develop a different type of sampler or pick up ovigerous females rather than finding pods.

G. JAMIESON: I'm from Nanaimo. Following up on those points, I think a number of species tend to move into areas where there's topography suitable to hiding. If it is sediment-related or substrate-related, maybe there are special incubation areas where these females go. This might be particularly important from a habitat conservation point of view. This may not be too important in Alaska where there is lots of open space, but around Vancouver, Puget Sound, and the George's Strait area, there are a lot of urban developments occurring. The last thing we want to do is have a big container pier, or something like that, where all our females go to incubate their eggs. I know this was an issue in Everett, Washington, where they were building a port for their aircraft carrier. Dave Armstrong surveyed it and found an incubation area and they had to do mitigation. If we are trying to conserve our stocks, areas of urban development have to be looked at.

G. CONAN: I'm going in the same direction. It seems from our prolific information that pods come up year after year in the same location. If you have a trawl fishery which picks up everything at once and kills it by bringing it to the surface, you might be doing considerable damage to your fishery without knowing it. It would be interesting to know where the pod formations are, if they are always in the same location, and why. This is interesting research which should be done, and it is potentially important for management of the stocks.

A. LEVINGS: I'm with Deakin University, Australia, and have a background of 20 years as a fisherman. One of the things that I find very useful is time series of data; and as a fisherman, to look at major climatic events and the consequences of those events as they flow through the food chain. We target newly molted lobster as they come out, and the timing in the autumn of the emergence of that new molt is a couple of months after all the squid aggregate and mate. We fisherman think the crayfish and crabs are the beneficiaries of that fallout.

We find that squid are a very good indicator of those major climatic events. This year we had a major southern event which resulted in strange things happening in the food chain. For example, instead of catching two to three ton of squid a night, they were catching eight ton of squid a night. Instead of getting our normal run of crabs a couple of months after that, we didn't catch any. But in the processors' tanks, the lobsters that had been caught molted continually. We believe that there was such a large fallout of food that there was no need for them to go into the traps for bait.

In my role as a scientist, I'm very conscious of opportunities in a time series of data to take advantage of these natural events. You've got an indicator that you can work from, with a number of good implications in terms of growth of adult classes, the food chain relationships, and recruitment.

T. SHIRLEY: I'm with University of Alaska Fairbanks. One of the things that's impressed me is how much we learn by observation rather than by remote sampling. Brad certainly pointed this out with the sub work. When we use ROVs, we see spatial relationships, but lots of different kinds of life history phenomena become more apparent. I would urge that we continue with either more direct observation or using instrumentation that allows us to do the same sort of thing with various kinds of locators, transponders, and other things like that.

B. DONALDSON: I'm with Alaska Fish and Game. Quite a few of us have different levels of involvement dealing with *Chionoecetes*, we have Bering Sea snow crab and snow crab in Japan. I think we need to try and find some way for the scientists in the different areas to work closely together. We have a paucity of information on *C. opilio* in the Bering Sea because of the location. If we can determine whether populations are closely related or not so closely related, we could borrow data that's been developed from the other areas. Somehow we need to find a modus operandi to work closely together as scientists in this field.

R. OTTO: I'm with National Marine Fisheries Service. Virtually all of the shallower water and conventional crab resources available in the world are now exploited or fully exploited. We no longer have opportunities to exploit new resources at depths below the shelf rim, something on the order of 200 meters or so. We talked about exploiting things like *Hyas coarctatus*. It probably can be exploited, but it's not as desirable.

I want to suggest that what happened in trawl fisheries worldwide due to the 200-mile limit, full exploitation, and allocation schemes resulted in almost all groundfish fisheries worldwide into deep water. Future crab fisheries will not involve shallow water resources. I advise us to collectively consider life below the shelf break.

G. JAMIESON: Because of large fisheries being established, a lot of us got involved in doing stock surveys. Regulations were set and we asked after the fact if they were appropriate. One of the concerns I have, which is driven home by the work on the Majids and Dungeness crab, is that we have to start being more critical about assumptions behind our understanding of reproductive procedures. I think it's very easy to build models—we assume that models will do everything—but you need to have a proper survey approach. As Brad points out with his aggregations, you've got to have an understanding of what's going on for it to mean anything. Tom's comment about how you have to go out and observe things in order to have an idea of what's going on is also really important.

Don't assume that because everyone's been doing it for years, that it's necessarily right. There's a lot of environmental change happening, we're seeing a lot of populations becoming larger or smaller for no apparent reason and we have to try and understand it. The only way to do this is through experimental management or we make more observations.

G. CONAN: I'd like to bring up the difficulty in extrapolating from surveys to predicting fishable biomass. We don't know how to predict who is going to molt and whether it's going to be a terminal or a regular molt. This goes beyond finding out if it's a premolt stage, it goes to finding out what is restricting or creating the possibility to molt, and there's little work on this.

D. HANKIN: I'm with Humboldt State University. One thing that would be valuable are comparison studies of fisheries performance for, say, *Chionoecetes* species throughout the world. There does seem to be a similarity in their performance. There's sufficient variation in management regimes throughout the world that perhaps it's something to be learned from. Too many of us get buried in our fishery and resource and no one takes a global perspective. There are enough people here working on *Chionoecetes* to make it a good model. However, I'm afraid that throughout the world we're all trapped in the same three-S management: size, sex, season.

When I started teaching fishery management I'd ask my students what's the real justification for protection of females. It's because we can identify the difference between a male and a female. If we couldn't do that, we wouldn't worry about it. And that's true with every other population of fish I've worked on.

A.J. PAUL: Maybe it's not *Chionoecetes*, but the family Majidae, then you could add noncommercial species that are not being manipulated. Our Japanese colleagues are starting to study species that have previously not been studied. If we go up one level from the genus to the family, maybe we have a powerful tool.

G. CONAN: Maybe you have the tool already. There is an international majid working group that changes its task each time and convenes in a different country. The last meeting took place in Paris at the Museum of Natural History. There is a report on it. We would be pleased to give you all the list of participants so that it can continue.

B. STEVENS: I'd like to talk about challenging assumptions. One assumption is that we have to stick with a tried and true management technique, taking crabs larger than a specific size limit. Maybe it works well for Dungeness crab, but for the majids we have crabs which mature over a large spectrum of sizes and it doesn't make sense to catch animals larger than a given size. We ought to be harvesting across the whole size frequency of mature crabs, or those with large claws. I believe there was some Canadian experimentation with a claw ring.

Now we're finding that shell condition of males is very important in the mating activity. Work that we did in Kodiak looking at mating pairs showed that 90% of these animals mating with oviparous females were oldshell crabs. Work that A.J. just published supports that oldshell males win competitions the majority of the time, so there may be some effect of selecting shells in the fishery. Mikio (Moriyasu) showed us a picture earlier of nice, pretty, clean *Chionoecetes opilio*, whose shell the fishermen preferred, yet that crab may not be one whose shell is old enough to allow him to participate in mating. At this point I can't advocate whether we should leave newshell crabs to become oldshell, or catch them and let the oldshells left do the mating. I think it's something that should be considered in management.

H. LAUFER: I'm with the University of Connecticut. If you remove the largest members of the stock, you're soon going to select for small reproducers and bias the species. This is true for any species. I think the best thing to do is to put a moratorium on taking the largest animals. I think there is a restriction on taking the largest lobsters.

S. OLSEN: I'm from Norway. I think there is good reason to challenge the assumption about the trawl catching coefficient being 1.0. That is certainly not true with regard to fish and I will be very surprised if this is so with crustaceans. The Russians have some evidence from the Bering Sea that in trawling for shrimp it was considerably less than 1.0. The Canadians are starting to use a *Nephrops* trawl, assuming that this will catch everything.

There has been a continuous development of *Nephrops* trawls over the last 20, 30 years, and a few years from now our Canadian friends may find that if they used the last model they may have to assume a catching coefficient of 1.2. This proves that no trawl is perfect, it's always being improved.

G. JAMIESON: Going back to the point Mikio raised about population pulses, I think there are different types. For some populations of Dungeness crab off Washington there seems to be cycling every five or ten years. On the East Coast there seems to be very sporadic recruitment. What may be happening in the Gulf of St. Lawrence is also happening in the outer coast off Newfoundland; perhaps there's some sort of global North Atlantic pattern that's occurring.

We've seen this with salmon in recent years off Vancouver Island, and my presentation at this symposium talks about pulses near Hecate Strait.

Local oceanographic conditions are a lot more dynamic than we appreciate. In this meeting of mostly crab biologists we talk about temperature, maybe about salinity, and a bit about substrate, but no one's really talked about the dynamics of currents. I think a lot of the settlement patterns and other phenomena that we see is related to weather. There are lots of larvae, but do the currents bring them in, put them in the right spot at the right time? There may be global changes on a regional scale that we should have some understanding of. There's a real need to work a little more closely with oceanographers. They tend not to work in coastal situations, they like to work in the central Pacific. In British Columbia as money dries up they are having to rationalize their work and they're more than happy to start working with coastal fisheries. I think we have to try and bring them to meetings like this. It's not as productive to talk about what's going on without understanding the environment.

G. CONAN: I'd like to respond to two things that were brought up. The first is the *Nephrops* trawl. It's a trawl that digs into the bottom; that's what it was built for. I believe that the future in surveys lies much more in direct estimates rather than virtual population analysis (VPA). Considerable progress has been made in this area; the Global Positioning System (GPS) is one example. We now have exact locations when we start the trawl and where we end up. Great progress was also made with SCANMAR, which allows us to get an exact measurement of the trawl opening.

We have extensive observations via videocamera showing that very small snow crab do react to trawls, but they don't go very far and their reaction is extremely intermittent. The big ones don't seem to react very much, they just stay there and are picked up on the way.

I think it's very important to look at the hydrography, particularly water masses. Oceanographers are sometimes not very useful for coastal processes because they deal with great oceanic gyres and things of that type. We have to be our own oceanographers. We found that *Chionoecetes* get below the mixing layer. There they avoid drifts due to tides or anything random, and navigate pretty well.

B. SAINTE-MARIE: I'm from Quebec. I have two comments on Gerard's comments. We had a diver out on a tow board 10, 20 meters in front of the trawl and we saw important escape reactions from larger crab. Apparently they can feel something, it might be mechanoreception, but they moved out of the way on sandy bottoms.

The other comment is regarding larval dispersal. I think the oceanographic characteristics are important. We've been monitoring genetic composition of successive cohorts that settle in one spot for six years. For two to three years they were very similar which suggests that the larvae were coming from a common pool. Then suddenly after one or two years there was a bizarre pulse which had nothing to do with the previous year classes. We don't yet know whether that was infection from other production areas or reflects something going on in the population. There can be considerable genetic variation among year classes and we need to understand what that represents in terms of larval mixing or oceanographic processes.

G. JAMIESON: That brings up a good point. The technology developed in the last four or five years of mitochondrial DNA analysis and RNA analysis is at a stage where you can process a lot of samples relatively cheaply and quickly. This really would lend itself to understanding the dynamics of what's happening. Do you get survival of certain genotypes in certain places or are different populations being factored? A lot of work is being done with salmon and I think we should try to get in on it.

We never really understand what's going on by trying to predict where larvae go with the currents.

T. SHIRLEY: One of the biases we labor under is chauvinism, and we often fail to consider the role of female crabs in mate selection and other aspects of the reproductive process. Conversely, we often fail to consider the importance of large males in population size, structure, or other aspects of population maintenance. Perhaps some of these things will change as our own sex ratio changes over the years. Our population has been one primarily dominated by males and I think we carry with us these biases.

F. BLAU: I'm with ADF&G in Kodiak. I've been involved with using artificial collectors to collect larval stage settlings of red king crabs. The project was trying to predict recruitment for about five years and it is a fairly economical way of telling where crabs settle and at what depths. We're trying to relate this to the adult populations so many years later. Our populations of red king crab in Kodiak as a whole are declining. Collectors are a good way to find out where these things are occurring, and you can go back through time.

D. LOVE: I'm with National Marine Fisheries Service in Juneau. I've been studying bitter crab diseases. Bitter crab disease impacts about 5% of the commercial harvest of *Chionoecetes bairdi* in Southeast Alaska. It has been found in *opilio* and we don't know if it occurs in the Japanese or the Canadian stocks. This group of parasites is found in at least six different commercially important decapod species worldwide, and the potential to be in some of these other species has not been determined.

We need to work on the genetics of the different parasite species and try to develop a DNA probe that we can use as a field test to get a more accurate culling procedure. I think culling has been effective in Southeast Alaska and should be developed for some of the other areas. There is a risk of overharvest because there's a strong correlation with disease and shell condition. The new molt crabs have a higher percentage of disease. In some areas of Southeast Alaska, 90% of the new molt animals are infected. If we lose those animals, we're going to have recruitment failure. If we overharvest on top of that recruitment failure, we're going to have fishery failure.

Some of the population pulsing we see long term could be due to symbiotic relationships, such as parasitism. There are articles, pieces of information in the literature that suggest that copepod populations may be controlled by the dinoflagellates.

S. MERKOURIS: I'm with the Alaska Department of Fish and Game. I've just completed a statewide stock ID study based on allozymes of *Chionoecetes bairdi* and *opilio*, and have a manuscript being reviewed. We found a relatively low level of variation and made a commitment to take this a bit further. We have some developmental work with Dr. Benson at the University of Washington to develop some primer markers for both mitochondrial and total genomic DNA approaches. So far we've not had a great deal of luck in finding within-species variation with *Chionoecetes*, but we've found some very good between-species variations.

A secondary objective of this study included looking at a possible genetic basis for a difference between old- and newshell crab. The initial collection was 50 individuals of each shell class from the Pribilof and St. Matthew Island area. This was an allozyme study which had relatively low levels of variation, but there was enough to give us an indication that there is a significant difference between old- and newshell, with the oldshell crab having a higher heterozygosity.

The sample sizes were relatively small so we did not further subdivide them by cohort or age class. However, there may be some cohort effect there that Bernard Sainte-Marie is addressing. This probably merits further investigation.

We also expanded that analysis into the *bairdi* populations where we had shell age data on the individuals we analyzed, and did not see the same correlation. This could be a sampling problem, or maybe it just doesn't exist. We don't really know yet.

We've been involved in the genetic investigation of hybrids between *Chionoecetes bairdi* and *opilio* and we found some level of hybrid fertility. We found some back-crossed individuals and we're going to be looking further into this with some of the mitochondrial species markers.

I should also mention that we are working with Dr. Benson to investigate the utility of microsatellite DNA variation of red king crab. We had one paper in the 1989 king and Tanner crab symposium showing evidence of stock stratification based on allozymes.

I'm coming away from this meeting knowing that I'm not the only one interested in the shell age and genetics. I'd like to develop a project on it.

Dr. Kon and I talked about the possibility of getting some tissues to my lab from Japan. We're interested in looking at *japonicus* and *opilio elongatus* and comparing them to the crab we have here. I would like to use the mitochondrial markers that we've developed to do some sort of a systemic review of the genus.

B. SAINTE-MARIE: We don't know a lot about the first early benthic stages of *Chionoecetes* in terms of distribution, biology, requirements for growth or stock recruitment relationships. We don't know how many eggs or what spawning biomass are needed to ensure production. Most of our crab fisheries are conducted on a male-only basis, and we consider touching females is very bad. Compare this to the lobster fishery where they let the females breed once before they take lots of them.

Maybe we need to refine our understanding of these relationships to make progress on how we manage the resources.

Collectors would be a good starting point to look at some of the relationships between the spawning biomass and production levels.

R. OTTO: A theme through this meeting has been the differences in distribution of various life stages, between multiparous and primiparous females, and between juveniles, contrasted with large adult males. There's usually a substantial component of the adult male population removed from concentrations of females during part of the year. Females are more likely associated with juveniles. There seem to be critical habitats for very early stages. It means that they play very different ecological roles at these different stages. If there's something that's been missing here, it's really a consideration of what those roles are and what things in the ecosystem.

S. FRUSHER: I'm from the Department of Primary Industry and Fisheries, Hobart, Tasmania. I'd like to talk about the lobster collectors we use. We've got collectors around the state for monitoring the settlement stage of the rock lobster, and we've now got a few years' data. We've gotten together with New Zealand and other Australian states, including Western Australia, where there is a totally different species. Once we put all this information together, we really started to get some very interesting trends. This sort of collaboration at the international level is something very positive.

Due to many of the satellites that have been put up, oceanographers are getting a lot more resolution in their information. A lot of it's still surface information, but on some of the coastal processes they're telling us that they can come up with some really tight information about where currents are going to and coming from.

It appears that the people who have been looking at southern bluefin tuna have a lot of oceanographic information. They've also done a lot of work on larval collection for tuna, and fortunately they'd kept all their samples. We're going back and look at all the other information that is around.

B. MITCHELL: I'm wondering if there are any fishing industry reps here and what the industry's perspective on research priorities might be.

D. WITHERELL: I'm with the North Pacific Fishery Management Council. It's obvious to me that king crab stocks are depressed around the world. In some cases fisheries are still occurring on these stocks, maybe they are above threshold or below threshold. The ones I'm concerned about may be just above threshold and there is still a fishery. We need to find out whether or not it's biologically possible to bring these stocks up to higher levels. If it is, we need to convince the management agencies, the government, and the fishermen that it's worthwhile to bring stocks up.

J. NELSON: I'm with Baranof Fisheries, Courageous Seafoods. We have operated a couple of crab catcher/processors since 1978. The question was asked, "what does industry need?" I have a couple of perspectives.

In Alaska, the Bering Sea crab fishermen are competing with groundfish fishermen and probably impact each other greatly. We desperately need some research on the effects of trawl fishing on unobserved mortality. Work has been done on crab mortality in the laboratory. It needs to be expanded to the crab fleet during actual fishing operations.

The predator-prey relationship between groundfish and crab is vital. This may affect fishing strategies in the future. The environmental groups have taken an interest in what we dump back in the ocean and studies should be done on what happens to bycatch discarded in the ocean and whether or not it provides a food source.

S. OLSEN: I want to emphasize that bycatch is probably one of the greatest future problems for fishing in the world. I propose that we should do more than to try to find out what happens. In many cases it's possible if you want to invest in research and development of fish capture to reduce non-target species catch.

B. SAINTE-MARIE: Canada has a moratorium on ground fishing in the Gulf of St. Lawrence. If it is long enough, we might see some response in the crab population. There is historical data from the southern Gulf crab survey with some fishing, and now we'll see what happened with no fishing. There may be an impact from trawling on female crab aggregations, and also on males, which in some seasons tend to concentrate for molting.

G. CONAN: Trawl surveys allow you to visualize where the males and females of different categories are. It gives you a picture of what's occurring on the bottom. The difficulty in the past was to measure the surface you were trawling on. The difference between the distance on bottom measured by GPS and as estimated by time can vary from one to four. Using old data is not good, but we are heading toward something which is quite good.

I don't think very many snow crab are escaping in front of the trawl. Mikio's (Moriyasu) estimates have been consistent since 1984; they pretty well follow the catch.

B. STEVENS: We have a 30-year experiment in Alaska called management. We don't yet know what the effect of it is. Consider a top-down approach: Managers sit on the top and try to draw conclusions that say if we manipulate the fishery or fishermen that way, it will have a certain result on the population. I don't know how effective that is; nature may be the greatest manipulator.

I find that crabs are extremely resilient, they have a great amount of behavior plasticity, they can respond behaviorally, genetically, and physiologically to an extreme array of conditions. Before we might have considered them to be just passive particles in the ocean, but they're not. This means that we may not be having as great an impact on their populations as we think; that oceanography may play a big role.

I'm sorry we don't have more participants from the University of Washington where they've done a lot of work with Dungeness crab. They have shown that oceanography is important in bringing larvae to shore which allows for a large year class. A large year class doesn't materialize and establish itself until it's on the ground for the first couple of days because predation during the first 24 to 48 hours is really what establishes it. A large pulse of larvae can come in and be totally consumed by fish and virtually disappear. We need good oceanographic conditions, but it may be the first couple of days of benthic life that really determine whether or not those animals survive. This points out the importance of knowing more about the predator-prey interactions and the juvenile habitat.

We know red king crabs require a very specific habitat during the first year of life, a live bottom, hydroids, bryozoans, or stalked ascidians. We also know that this kind of habitat is very sparse in the Bering Sea; it's near shore, but it's scattered. The hypothesis I put forth is that king crab as a species is probably not very well adapted to the Bering Sea. This may be one of the reasons why populations aren't very large in the Bering Sea. Crabs are probably better adapted to the Gulf of Alaska where there's a lot of rocky shoreline, a lot of rocky habitat, a lot of structure for them to hide in, and things to grow on. In the Bering Sea, on its flat sand bottom, they probably just don't survive very well unless they can find those little habitats. So why are they in the Bering Sea? It could be that the temperatures there are good for them now and they're not so good in the gulf. But they may not be able to sustain themselves at high levels.

M. WARD: I'm with Alaska Department of Fish and Game. There is a conflict in management in Alaska. The National Marine Fisheries Service (NMFS) manages the groundfish stocks and the state of Alaska manages the shellfish. NMFS is currently doing a good job in maintaining fish stocks at extremely high levels in the Bering Sea. A lot of people think that high fish stocks and high crab stocks are incompatible. That's a political problem. There is a big factory trawler fleet and also shore-based processors that are politically very powerful. They are not going to want to reduce the groundfish stocks in the Bering Sea and the Gulf of Alaska to benefit crab stocks. That's something the politicians will have to figure out.

D. TRACY: I'm with the Alaska Department of Fish and Game. One of the most challenging research issues for any commercially exploited crab stock is the question of exactly what the exploitation rate is.

Brad just got finished saying that he didn't know how well suited red king crab were to the Bering Sea. Well, the biggest commercial harvest of red king crab in the history has come out of the Bering Sea. If you can field-validate an exploitation rate, you can work backward to just about any other assessment problem or goal. Some great modeling has been done by Gordon Kruse and Jie Zheng. If we can actually validate what the exploitation rate on this stock is, we can work backward and validate the population estimates and models for those estimates. The only way to solve this problem may be through some type of marked recapture, but that's been real problematic with shellfish.

We have used tagging employing an internal integrated transponder. It worked well and seemed to eliminate a lot of the problems with visual tags. The biggest obstacle is the cost, and some developmental problems in terms of trying to come up with a prototype that could be applied to a variety of commercial processing or delivery environments.

I think that's one of the biggest challenges for a research biologist in government. With the amount of resources and staffing we have available, it may be more prudent to answer some of the research questions imminently related to management and try to work backward from there. We can establish all the life history characteristics and population dynamics for a species, but if we don't know the exploitation rate, we're still not going to be able to answer all the management questions.

M. MORIYASU: We should also look at the management target instead of the optimal exploitation rate. How you exploit a fishery is most important. We can set the harvest at lower levels for a long term, or higher levels for a short term. We need to have better relationships with fishermen to determine what their goal is and how we can accommodate it based on population dynamics and biology. I don't think that there's only one optimal exploitation rate. We should have a meeting of biologists and fishermen and set the real target we are looking for.

C. LEAN: I'm with Alaska Department of Fish and Game. From a manager's standpoint, I think we concentrate on immediate gratification. In the past we tended to harvest our recruitment within a few years of its occurrence. A rhetorical question I'd like to ask is, should we attempt to stabilize fisheries at a set exploitation level or a set harvest level over time, to create a more stable market situation and increase the value and predictability of the fishery?

A. LEVINGS: The idea of providing artificial habitat for the crab is excellent. We look at it as crab biologists, but you might look at it as a fish refuge. An emerging issue in Australia is the interaction between the groundfishing fleet and the crab fishing fleet. Now, it is of concern to the groundfishing fleet that habitat is being degraded, and they are looking at reserving fish refuge areas. Refuges provide the opportunity to ameliorate the resource sharing conflict and also to enhance habitat.

G. CONAN: Stabilization may not be a reachable goal, we've seen fluctuations in the snow crab stocks that we can't manage. We don't know its origin. Maybe it's a natural phenomenon that exists in unharvested populations. Maybe it's best to follow what is going on and as a function of your prediction for the next year and decide whether or not you're going to fish. For instance, if there's a good wave coming in, you must decide between taking everything the first year or leaving some of it knowing that the quality is going to vary. Then you have to discuss that with the harvesters and buyers to find out the correct level of TAC for that particular year. That is the approach being used now in the Gulf of St. Lawrence.

S. FRUSHER: Rock lobster is one of western Australia's best studied fisheries. We have a fairly good correlation between settlement and the future fishery. We're fortunate enough to have a fairly long-term theory to guide us. What the fishermen have actually done here is very similar to what Gerard Conan was saying. Because of this long history of data, the fishermen sort of know what's happening year in and year out. They've decided to set a de facto TAC lower than many of their peak catches. One reason has to do with marketing. If they catch a lot, they get a lower price. They also get a lot of dips in recruitment, and they can ride this out successfully by having a lower TAC. This is acceptable because they have money flowing in fairly evenly year in and year out. This is a very good example of what Gerard Conan was saying.

J. ARMSTRONG: I'm from the University of Washington. On the idea of refuges and providing refuges for crab and fish, the University of Washington was involved in a dredge mitigation project over the last few years. We had some very interesting results.

The oyster industry puts out shell, and it does serve as refuge for newly settled crab. Crabs are cannibalistic and there are other species of crab in the estuary that are competitors. You get very unpredictable movement of crab and settlement into these areas. We've seen early settling cohorts cannibalize later settling cohorts of juvenile Dungeness crab. We've seen a competing species totally take over what was supposed to be juvenile Dungeness crab habitat. We've seen wild fluctuations in the numbers of juveniles in the shell plots. Putting out material that is well-established prime crab habitat doesn't necessarily give the anticipated result.

B. STEVENS: I agree with Gerard Conan in that these populations are inherently unstable. Maybe instead of trying to flatten out the peaks and curves, which would stabilize the market and the fishery, we ought to learn to work with instability and incorporate it into our management.

We see peaks of recruitment spaced at intervals from five to 10 years in Alaska and eastern Canada. We've seen about three of them in the last three decades. In at least one case we can identify this as a single year class that came from the lowest population on record. So you know there's not a stock recruitment pattern there.

One way we might be able to use this is to change the exploitation rate as a cohort comes in. For instance, in Alaska we use a constant exploitation rate on *opilio* stocks, we catch about 58% of whatever is there. However, when you have a group of males recruiting to the legal size, it might make sense to lower the exploitation rate during the first year to allow those males to become hardshells that will eventually mate. Then as those animals get older, increase the exploitation rate on them.

F. BLAU: Most of us deal with some kind of ongoing fisheries, but for the last 12 years in Alaska a number of red king stocks have not come back and the fisheries have been closed for that long. What do you do with a closed fishery? Other fisheries that have been going on out at Adak have been minimal for 20 years, even though some low level of fishing was occurring. If we're in a fishery that's low, perhaps we need to look at enhancement. The Japanese weren't able to do this for red king crab. I'm wondering how long we will watch the decline of crab stocks, with basically no input of money in any form. Yet our salmon stocks continue to get money for rehabilitation or enhancement at record levels. So, how do we manage stocks which have historically been very valuable but are now depressed?

G. KRUSE: I'm with Alaska Department of Fish and Game. I'd like to see continued emphasis on the potential importance of size structure. We've seen some reproductive work in terms of the potential importance of size in mating pairs, as well as shell condition. One common thing among crab fisheries is the size limits that we have. In Alaska we have run an experiment called management, which historically has seen a fairly high exploitation rate resulting in recruit-only fisheries. What happens is you truncate the size structure by half. That's a very major change for a population to withstand. Given the monitoring exercises that show recruitment can vary substantially, we might need to face the fact that size structure is a built-in population characteristic to withstand those oscillations. I think that's something we need to understand better.

A.J. PAUL: Early on I brought up the topic of getting together a process that lists the ongoing projects, especially in the international community. We all know that we have topics that overlap at some level, but we don't have a good mechanism, other than these meetings, to get together and sort out that information. We've discussed the *Crab Newsletter*, but if anybody has any other ideas let us know.

Our Japanese colleagues and our Canadian colleagues seem to agree that some sort of synthesis on *Chionoecetes* biology would be worthwhile.

G. CONAN: It would be nice if you include that as a recommendation because we might be able to use it with our management to indicate somebody should put that together.

A.J. PAUL: Yes. I've discussed it with Brenda Baxter and she's agreed that Sea Grant could be the vehicle for creating the documents. I don't think it'll be in this symposium, but it's a new task. I'm wondering if, as we go to our home countries, we can identify at least one contact person to see if we can develop a *C. opilio* synthesis report. We'll meet telephonically and electronically initially to keep costs down. I envision this to be something with several author contributions; many subchapters, some of them fine scale, some of them broad brush; a living document that changes with time which would be very valuable to us.

High Latitude Crabs: Biology, Management, and Economics
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Crab Research in Alaska: An Interagency Long-term Plan

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Introduction

This paper describes a long-term research plan for king, Tanner, and snow crabs in Alaska. It is intended to foster ongoing dialogue about research needs and to improve coordination of studies among agencies and universities. This research plan reflects the accumulated submissions of many contributors. Concomitant with congressional funding of a budget initiative for crab research in 1992, staffs of Alaska Department of Fish and Game (ADF&G), National Marine Fisheries Service (NMFS), and some Pacific Northwest universities have since met annually to discuss king and Tanner crab research (e.g., Kruse 1994b). Murphy et al. (1994) conducted a 1991 survey of crab researchers who were asked to prioritize crab research topics. Based on questionnaire results and discussions with crab scientists, a long-term research plan was drafted for review at the first interagency meeting in August 1993, and was subsequently published (Kruse 1994a). Progress on a number of research topics since autumn 1993 prompted a reevaluation of the plan at the annual interagency meeting in October 1995 and this revision of the original Kruse (1994a) plan.

Rationale for Long-term Research Plan and List of Research Needs

Overview

Waters of the Gulf of Alaska, Aleutian Islands, and Bering Sea have supported large commercial fisheries on red king crab (*Paralithodes camtschaticus*), blue king crab (*P. platypus*), golden king crab (*Lithodes aequispinus*), Tanner crab (*Chionoecetes bairdi*), and snow crab (*C. opil-*

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io). Significant changes occurred in stocks and landings since the development of Bering Sea crab fisheries by the Japanese in the 1930s: many stocks crashed in the 1980s, and over a dozen fisheries now remain closed due to low abundance. Crab fisheries have not been sustained over the long term, begging a critical evaluation of our understanding of crab biology, ecosystem dynamics, and fishery management strategies in Alaska. Unfortunately, our knowledge of these species is limited. In addition, fisheries for Korean hair crab (*Erimacrus isenbeckii*) and grooved Tanner crab (*C. tanneri*) have emerged in recent years as fishers seek new resources to replace dwindling stocks of king, Tanner, and snow crabs. This expansion portends yet another iteration of stock demise unless effective management plans grounded by research precede extensive harvesting.

The long-term crab research plan is based on the idea that wise management of any fishery can only be accomplished by providing answers to four basic questions: (1) what are the stocks, (2) how abundant are they, (3) what features drive their productivity, and (4) how should this productivity be extracted? To answer these pivotal questions, investigations are pursuing four broad areas: (1) stock structure, (2) population estimation, (3) stock productivity, and (4) harvest strategies. The rationale for these four broad topics and a list of specific research needs follow.

Stock structure

Ideally, management units should align with stock boundaries. In some cases, crab management units have been established from mark-recapture data, but more commonly such units have been established from information about geographical distribution. Although the distribution of some stocks is geographically discrete (e.g., Norton Sound red king crabs), questions remain about the structure of other stocks. Some of the most important questions concern Tanner and snow crabs and their hybrids and golden king crabs, although uncertainties exist concerning stock boundaries for some red king crabs as well. Better definition of stock boundaries would improve the alignment of fishery management units to coincide with individual stocks. Ultimately, a stock should be managed to reflect its individual productivity characteristics. Research needs follow.

King crabs:

1. Conclude ongoing genetic stock identification (GSI) studies (allozymes) for red king crabs.
2. Investigate DNA-based methods, including microsatellites, as tools to separate red king crab stocks, particularly in areas of Kodiak Island and Southeast Alaska where the potential for multiple stocks is highest.

3. Conduct a pilot GSI study of golden king crabs to begin to delineate management units in the Aleutian Islands and Southeast Alaska. Alternative sampling sites are Pribilof Islands and Bowers Ridge in the Bering Sea.
4. Investigate genetic differences among blue king crabs off St. Matthew, Pribilof Islands, and King Island.

Tanner/snow crabs:

5. Conclude ongoing GSI studies (allozymes) for Tanner and snow crabs.
6. Conclude ongoing genetic studies of hybridization among Tanner and snow crabs.
7. Pending success with king crabs, consider investigating the utility of mitochondrial DNA- (mtDNA) and nuclear DNA-based methods for separation of stocks of Tanner and snow crabs. If they are promising, apply them to archived samples.

Other:

8. Analyze crabs for enforcement cases of time/area closures, as needed.
9. Consider documenting baseline levels of detectable genetic variability in newly exploited stocks to define management areas and to permit future studies of genetic selection.
10. Publish a paper on the utility of morphometric characters and computer imagery to measure and classify individual crabs to stock and species (e.g., *Chionoecetes*) and develop a weatherproof system for field work.
11. Develop a tag release and recapture program for investigating relationships of snow crabs in the northern Bering Sea to snow crabs on the fishing grounds.

Population estimation

Maintenance of fisheries over the long term requires perpetuation of adequate spawning stock by allowing only a percentage of exploitable biomass to be harvested. Estimation of population size is typically based on assessment surveys. Whereas effective assessment programs exist for many crab stocks in Alaska, for some stocks (e.g., Bering Sea blue king crabs) the survey precision is low or survey costs are prohibitive (e.g., Adak golden king crabs). Although it may be neither practical nor prudent to expend more funds for additional surveys, some improvements in existing surveys may be achieved by changing the survey gear or by implementing new technologies. Effects of crab distribution and behavior on their catchability in surveys are unresolved. Also, population models are needed that integrate multiple years of diverse and sometimes conflicting information from survey and fishery performance into more precise estimates of abundance under a variety of situations. The following specific research needs were identified.

Surveys:

1. Implement rotational surveys among king crab stocks at Norton Sound, Adak, and the Pribilof and St. Matthew Islands. Seek ways to expand coverage to unsurveyed stocks (e.g., golden king crabs, grooved Tanner crabs) and stocks surveyed with low survey precision (e.g., blue king crabs, hair crabs), perhaps through multiple mark-recapture methods or expanded rotational surveys.
2. Improve enumeration of hybrid crabs with the aid of computer-based identification systems, and consider a new field project (or use of onboard observers) to estimate the geographic distribution of hybrids in the Bering Sea.
3. Investigate towed laser line scanning systems (LLSS) for crab stock assessments and studies on trawl catchability, trawl/dredge effects on benthic animals and habitats, and associations between crabs and their habitat.

Catchability:

4. Estimate crab pot catchability coefficients by a combination of tagging and fishing down the stock in a limited area.
5. Estimate relative catchability and selectivity of trawls. Possible methods of approach include depletion estimators, change in ratio estimators, visual estimates with trawl-mounted cameras, remote operated vehicles (ROVs), LLSS, and mark-recapture methods.
6. Conduct field experiments on catchability of various sizes and sexes of crabs at different times of the year. Highest priority are Tanner and snow crabs and female red king crabs.

Database management:

7. Consider a shellfish database manager to integrate survey, catch, at-sea, and port sampling databases for ease of use in research and management.
8. Complete historical data documentation and computer entry.

Alternative population estimation methods:

9. Apply recent advances in population estimation models to surveyed crab stocks. Potentially applicable models are catch-survey analysis (CSA), length-based analysis (LBA), and stock synthesis (SS).
10. Conclude evaluation of the use of Passive Integrated Transponder tags in estimating exploitation rates and population sizes.
11. Develop analytical methods to estimate abundance of unsurveyed stocks. Methods may include recently developed catch-length analysis (CLA), change in ratio estimators, and detailed analyses of fishery data with geographic information systems (GIS). The effects of individual fishing quotas on catch per unit effort should be considered in the applications.

Stock productivity

Ideally, harvest rates should be based on the biological characteristics that drive stock productivity, including growth, natural mortality (M), and recruitment. Unlike most groundfish, herring, and salmonids, for many crab species critical biological information is lacking about parameters that regulate productivity. For example, the absence of good estimates of M for most stocks brings into question the current harvest rates and definitions of overfishing. Growth of Tanner and snow crabs (including terminal molt of males) is poorly understood, and the lack of a tag that is retained through molting is problematic. Questions exist about size at maturity of snow crabs, which is important because of the direct bearing on size limits. Little is known about most life history traits of golden king crabs, grooved Tanner crabs, and hair crabs making them particularly vulnerable to management error. The following specific research needs on stock productivity characteristics were identified.

Natural mortality:

1. Estimate M of Alaskan crab species.
2. Investigate the relationship of M to molting and spawning.
3. Study potential relationship between shell condition and M.
4. Study the contributions of disease to M.
5. Estimate predation mortality and examine potential effects of male guarding on predation mortality of molting mature females.

Growth:

6. Consider radiometric aging and the durometer as tools to better estimate shell age and to assist studies of growth and M.

7. Develop a retainable tag for Tanner and snow crabs. Plastic injection methods may be possible.
8. Use external tags to study movements of mature females and skip-molt males.
9. Estimate growth of Tanner and snow crabs with respect to molting probability, growth increment, and terminal molt as affected by individual size, molting history, and cohort size.
10. Estimate temperature-related growth of juvenile Tanner and snow crabs. This includes continuing ongoing monitoring of Tanner crabs in Womens Bay, Kodiak Island, and new long-term laboratory studies of juveniles.
11. Estimate molting probabilities of golden and blue king crabs.

Reproduction:

12. Continue to study spawning geography, including geographic and temporal changes in fecundity, egg predation, and size at maturity.
13. Develop a better understanding of the effects of size, sex ratio (e.g., how many females can a male mate?), and shell condition on reproduction of red king, Tanner, and snow crabs.
14. Determine reproductive cycles and spatial distribution of egg-bearing blue and golden king crabs from laboratory studies and field data collected by observers and during surveys.
15. Estimate functional maturity of males as affected by size and shell condition.

Recruitment:

16. Estimate age of recruitment of juvenile Tanner crabs to the fishable stock.
17. Determine whether there is periodicity in the frequency of strong year classes.
18. Estimate effects of spawning biomass, sex ratio, and size structure on recruitment.
19. Estimate effects of oceanographic conditions on egg production, egg hatch, and larval survival.
20. Studies are needed on larval feeding, growth, mortality, and distribution.

21. Identify crab nursery areas and recruitment by deployment of crab collectors.

Habitat:

22. Develop better understanding of red king crab habitats as defined by the biological community (e.g., mussels, sea onions, etc.) and the effects of fishing on these habitats.

Diseases and parasites:

23. Continue to monitor bitter crab disease, black mat syndrome, rhizocephalan parasites, microsporidians, and viruses. Consider new studies on life histories of these organisms, modes of transmission, crab mortality, and possible density-dependent relations to stock size. Evaluate appropriate harvest strategies for infected populations.

Fishing-related effects:

24. Estimate bycatch (trawl and dredge), ghost fishing, and effects of handling on habitat displacement and predation mortality of Alaskan crab species.
25. Consider new studies, similar to those for red king crabs, on sublethal effects of handling on crabs returned to the sea.
26. Continue to collect observer data on crab injuries, and document handling methods used by the commercial fleet.
27. Document natural background levels of crab injuries in stocks for which new fisheries develop and in stocks that have not been fished for years.
28. Continue initiatives, such as in Chiniak Bay, to inventory the number and condition of lost pot gear on the sea floor.

Harvest strategies

Crab harvest strategies may be flawed. Size limits, sex restrictions, and historical exploitation rates may adversely affect fishery productivity. In some instances, size limits are based on size of morphological maturity (i.e., males with large claws) rather than size of functional maturity (i.e., males that actually reproduce), which may be larger. Thus, in some cases high harvest rates may have eliminated breeding males from stocks managed by size-sex-season regulations. Size-sex restrictions coupled to gear designs may promote handling mortality that exacerbates stock declines. Lost gear results in additional unmeasured mortality through ghost fishing. Also, changes in other components of the ecosystem, such as predator-prey abundance and changes in oceanographic conditions, can have profound effects on crab stock dynamics. Ideally, optimal management strategies should be developed to recognize species- and stock-specific biological characteristics, such as growth, terminal molt, mortality, size of maturity, and recruitment dynamics driven by stock and environmental effects. To evaluate the implications of these factors on harvest strategies, the following research needs were identified.

Gear studies:

1. Continue studies on types of degradable devices (e.g., galvanic timed-release mechanisms, cotton twine) and their placement in pots.
2. Study pot degradation rates in situ.
3. Continue study of pot and trawl gear modifications (e.g., mesh size, escape panels and rings, Tanner boards, or sex-specific bait) to reduce bycatch.

Harvest policy:

4. Consider implementing an experimental management program whereby stocks are managed differently, such as alternative harvest rates or size limits to evaluate effects of male size distribution on female fertility.
5. Continue to develop simulation models to study population dynamics and management implications of alternative harvest strategies (e.g., threshold, exploitation rate, constant catch, escapement goal policy, female harvest, size limits, multi-species harvest policy).
6. Continue to estimate biological reference points for Alaskan crab stocks.
7. Consider development of a harvest strategy amenable to triennial surveys.
8. Develop new ways to manage unsurveyed stocks while preventing overfishing.
9. Estimate economic impacts of potential new management strategies.
10. Analyze the potential for genetic selection for stunted growth from size limits.

Roadmap to Conduct Future Research

A detailed year-by-year plan for specific research into the distant future cannot be projected, because the ability to conduct studies depends on numerous fiscal and personnel constraints that cannot be predicted. In addition, findings from ongoing studies may lead to new research avenues. Nonetheless, by periodically updating the plan for crab research, highest priority research projects can be specified to provide direction for selecting annual research endeavors.

Results from recent genetic studies help to delimit remaining research needs. GSI studies were conducted on red king, Tanner, and snow crabs, and their hybrids by ADF&G geneticists. Allozyme data indicates that stock structuring exists over broad geographic regions, but few allozymes are useful for discrimination due to low levels of heterozygosity. Despite this limitation, genetic data revealed regional differences, gave a better understanding of hybridization, and provided an enforcement tool for time/area closures. Under subcontract, geneticists at the University of Washington are now attempting to develop nuclear and mtDNA- and microsatellite-based methods that may yield higher discriminatory power. In addition to these genetic studies, ADF&G staff and subcontractors at the University of Minnesota developed a computer-based method for visual identification of Tanner and snow crabs and their hybrids.

Over the next year, results of allozyme studies for red king crabs and *Chionoecetes* are to be published. A study utilizing mtDNA species markers will be conducted on *C. bairdi*, *C. opilio*, and their hybrids to further investigate direction of hybridization and gene introgression. Pending ability to collect samples, a pilot allozyme study of golden king crabs will be conducted. Also, pilot studies of DNA-level markers, including microsatellites, will be conducted on red king crabs. Thus, the utility of all state-of-the-art genetics for red king crabs will be known soon and future research on stock structure can be planned accordingly. Success with DNA-level markers will allow research into finer-scale discrimination of red king crabs from archived samples. On the other hand, a lack of promise of DNA-level markers would suggest reevaluation of this line of research. Decisions regarding continuation of genetics studies of crabs will be conducted on a species-by-species basis. Computer-based visual classification systems warrant further development as a potentially useful tool for stock and species identification.

In terms of population estimation, exploitable biomass has been traditionally estimated by area-swept methods from trawl surveys and relative abundance indices from pot surveys. Recent research by agency staff has focused on improvements in electronic databases of survey and fishery data, detailed analyses of survey data using methods such as kriging and the delta distribution, and development of models for crab population estimation. A measurement error model (CSA) was developed to estimate survey catchability coefficients and abundance of legal-sized red king crabs. LBA models have been developed to estimate population size of male and female Tanner and red king crabs. And CLA has been developed for application to unsurveyed king crab stocks.

Over the next year, plans include publication of a number of scientific papers on development of CSA, LBA, and CLA methods and on expansion of this work to include sensitivity analysis. Analyses have been applied to red king crabs at Kodiak, Bristol Bay, and Southeast Alaska, and eastern Bering Sea Tanner crabs; these methods will be adapted to other stocks, such as Adak and Norton Sound red king crabs and Kodiak Tanner crabs. Over the long term, plans are to routinely apply such analyses in annual stock assessments. Future development of analytical methods should focus on GIS-type approaches that provide for fishery-based assessments of unsurveyed crab populations. A feasibility study of LLSS in stock assessments and studies of catchability is high priority pending funding.

With respect to stock productivity, recent research has focused on reproductive biology and handling studies. Agency research has included studies of Tanner crab aggregations in Chiniak Bay, Kodiak Island, by manned submersibles and ROVs. University of Washington researchers have examined spawning geography of snow crabs in the Bering Sea. University of Alaska Fairbanks researchers have examined effects of shell condition on the reproductive success of Tanner crabs, growth of reproductively mature Tanner crabs, conceptual models of year class formation of red king and Tanner crabs as related to oceanographic and other factors, and handling effects on red king crabs. NMFS conducted a similar handling study on Tanner crabs.

A daunting list of needed research remains in the area of stock productivity. In the next year, many of the ongoing research projects will be concluded and results will be published. The conceptual model of Tanner crab recruitment will be developed into a statistical study of potentially contributing oceanographic factors. A new study of mating success of legal-sized red king crabs is planned. Over the long term, studies on reproductive biology, sources of mortality, growth of *Chionoecetes*, critical habitat for young-of-the-year, and recruitment processes are priorities. The challenge is to make significant progress despite few laboratories with seawater systems and the high cost of at-sea research.

Recent analyses of harvest strategies by ADF&G include dynamic simulation analyses of strategies for Bristol Bay red king crabs, studies and calculation of biological reference points for red king crabs in Norton Sound, Bristol Bay, and Kodiak. Researchers at the University of Alaska Fairbanks have conducted pot gear studies in the laboratory to reduce red king crab bycatch. Both NMFS and ADF&G researchers have conducted field studies on Tanner crab gear.

Plans for next year include analyses of rebuilding strategies for the depressed stock of red king crabs in Bristol Bay. New field studies will be considered to test alternative gear designs for red king and Tanner crabs. In the future, promising designs should be tried in commercial fishery trials. The development of management strategies for unsurveyed stocks is a high priority in the near future. Progress in this area hinges upon successful development of fishery-based assessments from observer data. Over the long term, more radical changes to management need to be thoroughly evaluated. These include allowance of female harvest under some circumstances, consideration of "keep what you catch" harvest policies, and development of multi-species or ecosystem management approaches. Pursuit of these ideas will probably require improved understanding of crab reproductive biology, simulation modeling of population dynamics, socioeconomic impact analyses, and experimental management.

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