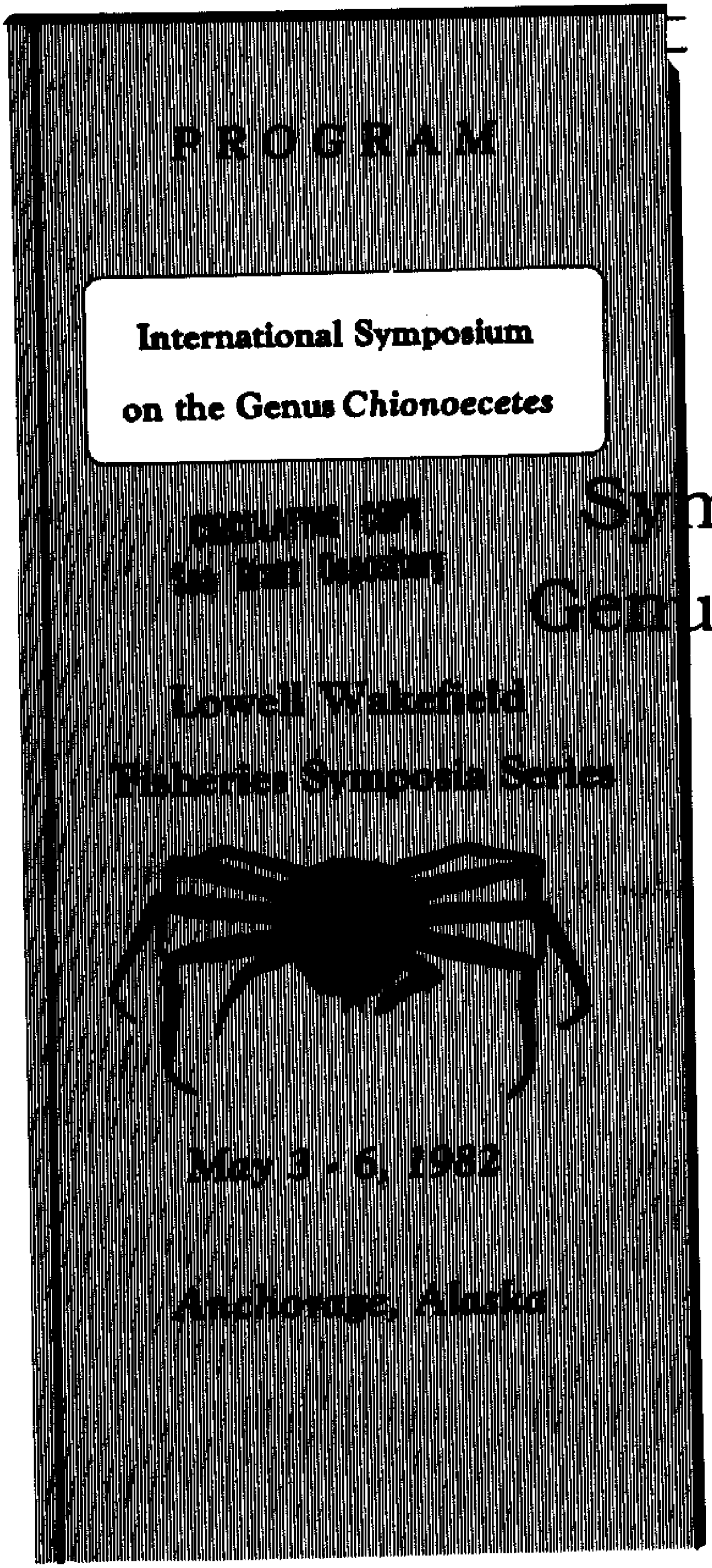
Proceedings of the International Symposium on the Genus *Chionoecetes*



PROGRAM

International Symposium on the Genus *Chionoecetes*

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Lowell Wakefield
Fisheries Symposia Series

May 3 - 6, 1982

Anchorage, Alaska

University of Alaska
December 1982
Alaska Sea Grant Report No. 82-10

Alaska Sea Grant College Program
University of Alaska
Fairbanks, Alaska 99701

Proceedings of the International Symposium on the Genus *Chionoecetes*

May 3-6, 1982
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Symposium Sponsors
Alaska Department of Fish and Game
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University of Alaska Sea Grant College Program

Brenda Melteff, Symposium Coordinator

December 1982
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ACKNOWLEDGMENT

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INTRODUCTION

Crab of the genus *Chionoecetes* support commercial fisheries in the northwest Atlantic, North Pacific, and the Bering Sea. Fisheries for the genus are regulated and managed by Canada, Japan, the United States and the Soviet Union. Within the jurisdiction of each country exist localized fisheries administered by regional agencies. Thus, on a worldwide basis there are many unrelated research and management programs which localize the focus of their efforts. Communication between individuals associated with management of regional fisheries is impeded by geographic separation, differences in languages, and the tendency of agencies to record research information in reports with limited circulation. To facilitate the information exchange between individuals involved with research and management of the resource this international symposium on the genus *Chionoecetes* was convened 3-6 May 1982 in Anchorage, Alaska. There were four major objectives of the symposium: 1) to facilitate the meeting of individuals associated with the *Chionoecetes* fisheries, 2) to provide a forum where researchers and fishery managers could formally describe their current programs and concurrently receive comments from persons attending the syposium, 3) utilizing a workshop approach to identify the types of research necessary to better manage the resource, and 4) to document both the papers presented at the symposium and the results of the workshop on research needs.

It is hoped that this symposium will set a precedent and in the future years similar symposia on the genus *Chionoecetes* will be convened.

Members of the symposium planning committee were:

Name	Agency
A.J. Paul	University of Alaska, Seward
Fred Gaffney	Alaska Department of Fish and Game, Juneau
Dennis Haanpaa	Alaska Department of Fish and Game, Anchorage
Jerry Reeves	National Marine Fisheries Service, Seattle
Ray Baglin	National Marine Fisheries Service, Kodiak
Steven K. Davis	North Pacific Fishery Management Council, Anchorage

WELCOME

Donald H. Rosenberg
Director
Alaska Sea Grant College Program
University of Alaska

On behalf of the University of Alaska, welcome to the first Lowell Wakefield Fisheries Symposium. Dr. Jay Barton, president of the University of Alaska, sends his apology. He had hoped to be here this morning but was called away at the last minute to a meeting on the educational needs in rural Alaska. Dr. Barton particularly wished to welcome our colleagues from Canada and Japan who have joined us to participate in this symposium. We hope that your stay in our country and in Alaska will be pleasant and the meeting profitable to you.

This symposia series is named in honor of Lowell A. Wakefield, the pioneer of the Alaska king crab industry. During the years of development, Lowell recognized that two major ingredients were necessary if the king crab fishery was to survive. First, it was necessary to insure that a quality product was available to the consumer. This ingredient was handled through his work with the state toward establishing the Alaska King Crab Quality Control Board. It is interesting to note that this need for quality in other Alaska seafood products has only recently been recognized, resulting in the establishment of the Alaska Seafood Marketing Institute.

The second important ingredient which Lowell recognized was the role of sound management programs in the maintenance of a viable fishery. Here he worked closely with both the federal and state governments, encouraging establishment of management programs which would not only insure that the king crab resource would remain viable but that the regulations would also encourage the establishment of the domestic fishery. Throughout Lowell's long and productive life, he recognized the need for sound management based upon the best scientific data available. In his later years, Lowell joined the faculty of the University of Alaska as an adjunct professor of fisheries. In this capacity, he influenced the direction of the university's then-infant Sea Grant Program. His influence results today in the nation's 16th Sea Grant College.

In recognition of these many years of effort on behalf of Alaska fisheries, the University of Alaska has established this series of fisheries symposia named in honor of Lowell Wakefield. The symposia are designed to provide the interaction and information exchange necessary to insure that our resources are managed based upon the best available scientific data. This symposium is specifically directed at furthering the information and scientific base of the tanner or snow crab resources.

Alaska's tanner crab resources have recently gained importance to our domestic industry. Tanner crab were first harvested, incidentally, in the king crab fishery. A limited, directed fishery was established in the early 1960s, increasing rapidly, especially as a foreign fishery in the late '60s. This increase was the result of a reduction in the foreign production of king crab. With the implementation, in 1977, of the Magnuson Fishery Conservation and Management Act, the foreign harvest of tanner crab was reduced. Meanwhile, the domestic industry was growing. At this time, our domestic industry was harvesting approximately 45 million pounds while the foreign industry was harvesting approximately 35 million pounds.

Today the resource is fully utilized by the domestic industry. The need for sound and effective management and understanding of the resource is critical. During the last two years, we have witnessed a substantial decrease in the crab available for harvest. The cause of this decline is unknown. Many of us speculate that it is a combination of natural variation coupled with mortality associated with a very high fishing effort.

The reduced availability of the resource and the high level of fishing effort make it imperative that future management of this resource be based upon the best available scientific information. Over the next three days, a series of papers are scheduled, providing a full range of scientific data on the world's tanner crab resource.

On Thursday morning an important workshop is scheduled. I encourage all of you to participate. This workshop is specifically designed to provide a forum where the data needs and management criteria can be discussed and debated. The results of this workshop will be used by the various scientific and management agencies to develop management plans and future research programs.

In closing, I would like to congratulate the planning committee on putting together such a full and complete program. This symposium will be setting the example to be followed in future Lowell Wakefield symposia. I am sure that future symposia planning committees will find this act a hard one to follow.

Overview Papers

Overview of the Snow Crab *Chionoecetes Opilio* Fishery in Atlantic Canada

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INTRODUCTION

The crab fishery in Canadian Atlantic waters is based almost entirely on the snow crab, *Chionoecetes opilio* (O. Fabricius). To date, only sporadic exploitation of other Atlantic crabs with commercial potential (Jonah crab, *Cancer borealis*; rock crab, *Cancer irroratus*; deep-sea red crab, *Geryon quinquedens*) has occurred. The landings of all crab species taken in Canadian waters during 1979 are shown in Table 1.

Canadian snow crab landings have risen rapidly since the inception of the directed fishery in 1966 after exploratory vessels found abundant stocks in the Gulf of St. Lawrence (Table 2). In 1978, 21,936 MT, representing 20% of the world catch of *Chionoecetes*, was landed. In 1979 and 1981, landings were worth over $20 million to the fishermen (Table 2) and are currently ranked sixth in value on the Atlantic coast behind cod, lobster, scallops, herring, and flatfishes. Snow crab landings in 1981 of 36,191 MT were the highest recorded and exceeded the forecasted sustainable yield of 20,000-32,000 MT.

The following overview summarizes biological knowledge on the Atlantic snow crab *resource*, the present and historical *harvesting* levels and methods, the *management* strategies employed to optimize yields, and the *research* problems currently being probed.

THE RESOURCE

In Atlantic Canada principal commercial snow crab grounds lie between 26-220 fathoms and are located in the St. Lawrence estuary and Gulf, around Cape Breton, and off the east coast of Newfoundland (Fig. 1). Any new exploitable areas will probably lie off the coasts of Newfoundland and Labrador. Adult snow crabs are most commonly found on mud substrates where the water temperature is between 0 and +5°C throughout the year. Aggregations of juvenile snow crabs may be found on gravel bottom at shallower depths (Miller 1975). However, high densities of early stage juveniles have also been found evenly distributed over mudbottom commercial grounds (R.W. Elner, unpubl. data). Field observations indicate that mature females may be highly aggregated, whereas larger males (70 mm carapace width) approach a random distribution (Miller 1975). Tagging experiments off Newfoundland

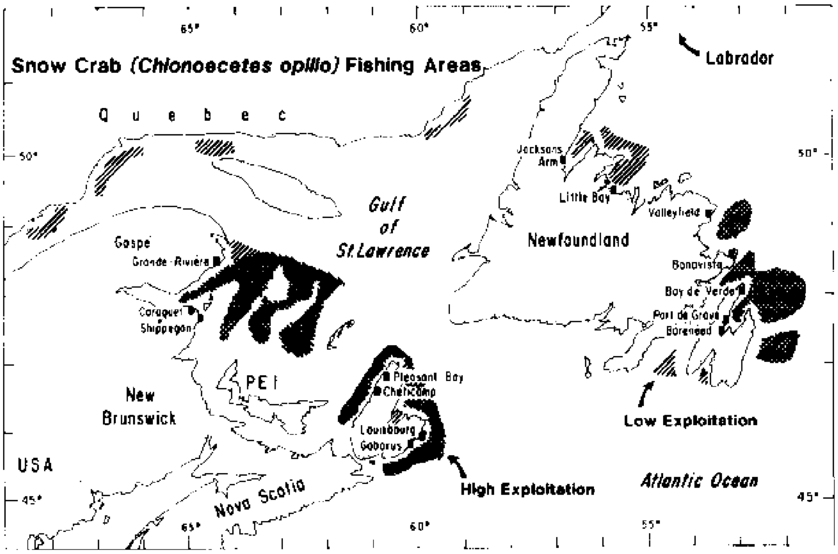
Table 1. 1979 Canadian crab landings, all Atlantic and Pacific species.

Location	Species	Landings (MT)
Atlantic Maritime Provinces (including Quebec)	Snow	19,486
Newfoundland	Snow	11,195
Pacific	Dungeness	1,179
Atlantic	Rock	31
Atlantic	Jonah	16
Canada total crabs	All species	31,907

Table 2. Snow crab landings and landed values for the Atlantic coast of Canada, 1966-81.

Year	Gulf of St. Lawrence (P.E.I., N.B., Quebec) (kg)	Cape Breton Island (N.S.) (kg)	Newfoundland (kg)	Atlantic Canada total (kg)	Landed values ($000)	Average price to fishermen (¢/kg)
1966	30,098	-	-	30,098	5	17
1967	255,508	240,934	-	496,442	84	17
1968	4,223,190	712,882	93,000	5,029,072	1,005	20
1969	7,805,782	98,120	319,000	8,222,902	1,664	20
1970	6,552,539	90,488	891,000	7,534,027	1,582	21
1971	5,405,510	-	1,380,000	6,785,510	1,221	18
1972	5,182,047	51,456	1,484,000	6,717,503	1,948	29
1973	6,804,416	121,881	2,622,370	9,548,667	3,724	39
1974	6,725,221	216,907	3,103,434	10,045,562	3,817	38
1975	4,650,429	378,883	1,820,099	6,849,411	2,397	35
1976	7,603,795	489,490	2,406,343	10,499,628	4,619	44
1977	9,411,948	936,297	3,750,806	14,099,051	7,331	52
1978	11,319,594	3,189,061	7,427,591	21,936,246	12,503	57
1979	16,260,927	3,224,849	11,195,000	30,680,776	20,556	67
1980	16,727,872	2,499,533	9,311,230	28,538,635	16,838	59
1981	21,967,499	1,615,406	12,607,710	36,190,615	20,991	58

Figure 1. Distribution of snow crab stocks exploited in Atlantic Canada.



(D. M. Taylor[1], pers. comm.) and Cape Breton Island (Elner and Robichaud 1980, 1981) have not revealed either extensive or clear patterns of movement by adult male snow crabs. In tagging experiments in the Gulf of St. Lawrence (Watson and Wells 1972), the majority of recaptures (80-90%) have occurred within 25 km of the point of release, but a few crabs had relocated up to 56 km in less than a year. Although it is unlikely that there are exchanges of adult males between the major fishing areas, the fact that larvae are pelagic for approximately 12 weeks and subject to dispersion by surface currents, makes long-distance recruitment relationships possible. Indeed, results of a preliminary electrophoretic survey of 12 enzyme systems in the snow crab infer that crabs from the western Gulf of St. Lawrence and Cape Breton Island are similar in genetic structure. However, crabs from northeastern Newfoundland appear genetically distinct from both the Cape Breton Island and western Gulf crabs. These results appear to be supported by morphometric and meristic analyses (K. Davidson and R. W. Elner, unpubl. data). The preliminary conclusions, in concurrence with our limited knowledge of larval duration and surface current patterns, support the hypothesis that there are two separate snow crab populations in Atlantic Canada.

A distinctive feature of the Atlantic snow crab resource is that under present conditions larval recruitment does not appear to be affected by exploitation. The fishery is regulated to land only male crabs of 95 mm carapace width (CW) and above. This size is well above the 57-mm CW size of 50% male maturity (Watson 1970) which allows most mature males at least 1-2 years to mate before entering the fishery. Female crabs are effectively excluded from the fishery as they undergo a terminal molt to maturity below legal size. The fact that practically all mature females examined over recent years have been 'berried' (carrying eggs) indicates that a high reproductive potential is being maintained.

Our present knowledge of growth and, hence, recruitment, and its controlling factors is deficient. Studies suggest that growth is not necessarily an annual event. Elner (unpubl. data) recaptured five male crabs of between 79-110 mm CW that had been tagged three years previously and had not grown. In both the Gulf of St. Lawrence (R. J. Bailey[2], unpubl. data) and around Cape Breton Island (Elner 1982) large variations commonly occur in both the time of recruitment and the magnitude of recruitment.

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[1] D.M. Taylor, Biologist, Department of Fisheries and Oceans, St. John's, Newfoundland, Canada.

[2] R. J. Bailey, Biologist, Department of Fisheries and Oceans, Quebec City, Quebec, Canada.

Annual monitoring of fishing effort, landings, catch rates, soft-shell incidence, and population structure in the Cape Breton Island fishery since 1977 has allowed a 4-year time-series of commercial biomass, growth and recruitment, and exploitation rate estimates to be made (Elner 1982). Similar monitoring of the Newfoundland fishery since 1979 has generated commercial biomass and exploitation rate estimates for most of the management areas (Taylor and O'Keefe 1981; D. M. Taylor, unpubl. data). The snow crab fishery in the Gulf of St. Lawrence has been monitored at varying intensities since 1966 but, due to the large area involved and the nature of the fishery, only limited assessments have been practical (Bailey 1978b; Lamoureux 1981). Based on research and fisheries data, the historical and forecasted resource situation for each major region is given below.

Gulf of St. Lawrence

The fishery in the Gulf of St. Lawrence started in 1966 and rapidly reached a level of 4,000-7,000 MT which was maintained from 1968-75. During this period, the effort (number of traps) increased considerably while catch per unit of effort (kg per trap haul) declined. In the period 1976-79, the increase in effort continued although catch per trap haul remained constant after a slight increase in 1976. The catches increased to over 16,000 MT in 1979. Crabs were abundant in 1980 but market problems curtailed landings which finished close to 1979 levels. In 1981, with catch rates as high or higher than the previous year, landings attained an all-time high of approximately 22,000 MT. The exploitation rate in the Gulf of St. Lawrence is high and the fishery is heavily dependent on new recruits. Thus, the recent increase in landings and the reduction in mean size appears to be the result of a significant improvement in the level of recruitment. Based on historical catch trends, maximum sustainable landings have been projected at between 10,000-15,000 MT per annum.

Cape Breton Island

In 1980, landings for Cape Breton Island were down to 2,500 MT, a drop from a peak of 3,225 MT in 1979. The 1981 landings have accelerated the decline. Although buyer-imposed and management controls probably contributed to landing reductions in 1980 and 1981, only marginal growth and recruitment levels have been observed in stocks on the Atlantic side of the Island since 1979. In contrast, biomass additions to the stocks on the Gulf side of the Island have been sustained. In general, the Cape Breton Island fishery appears fully to overexploited, with the Gulf-side fishery becoming increasingly dependent on new recruitment and the Atlantic-side fishery collapsing in the absence of recruitment (Elner 1982). In the long term, landings may be expected to stabilize at approximately 2,000 MT per annum.

Newfoundland

The Newfoundland snow crab fishery began in 1968 and expanded rapidly to attain peak landings of 12,608 MT in 1981. At present, the fishery is concentrated off the east coast but continues to expand offshore and along the NE coast. Preliminary estimates of maximum sustainable yield are in the 8,000-15,000 MT per annum range, although the possibility that new areas will become exploited dictates that these estimates be viewed with caution.

HARVESTING

Harvesting of the Atlantic snow crab is through a directed single-species fishery prosecuted by approximately 388 licensed vessels with traps as their sole gear type. Landing snow crab bycatch taken by all other gear types is prohibited.

On commercial grounds close to the coast, the fishery is carried out by boats under 13.7 m in length. Such boats fish the inshore areas of the north shore of the Gulf of St. Lawrence, Chaleur Bay and around Cape Breton Island where 1-day trips are feasible. These boats engage in other fisheries, particularly the lobster fishery, depending on season and earnings. The majority of landings are made by vessels ranging in size from 13.7-21.3 m in length, with the capability of making up to 3-day trips on offshore grounds. The composition of the snow crab fleet for 1979 is shown in Table 3 and is similar to the present fleet.

Trap numbers are more reliable indicators of fishing effort than the number of participating vessels. While no accurate information on traps is available for the entire Atlantic fishery, approximate total trap numbers for each region can be estimated by multiplication of the maximum trap numbers by the number of licensed vessels (Table 3). Effort comparisons are confounded because there are differences in trap sizes between regions. Traps most frequently used in the Gulf and Cape Breton Island

Table 3. Structure of the snow crab fishing fleet for the Atlantic Atlantic coast of Canada in 1979 - by province, vessel length, and total traps.

Vessel length (m)	New Brunswick	Quebec	Nova Scotia	Newfoundland	Total
Less than 13.7 m	-	42	178	5	225
13.7-15.2	14	25	-	8	47
15.2-18.3	13	11	-	30	54
18.3-21.3	47	2	-	8	57
21.3 and over	2	3	-	-	5
	76	83	178	51	388
Estimated total traps	12,200	6,600	5,340	40,800	64,940

fisheries are rectangular steel frames, 1.5 x 1.5 x 0.6 m, covered in polypropylene netting, with two entrances on opposite sides. Such traps are generally set singly and baited with frozen herring or mackerel. In Newfoundland, as well as small sectors of eastern Cape Breton Island and the Gulf, conical traps are used. Most are 1.2 m across the base and 0.65 m high, covered with polypropylene netting and have a plastic entrance at the top. In Newfoundland the traps are set in strings of 35-75 and are baited with frozen squid or mackerel. Trap soak time is usually 2 days in the Newfoundland fishery and 2-3 days in the main Gulf fishery. Inshore boats around Cape Breton Island and in the Gulf generally haul all traps daily.

The snow crab season in the Gulf of St. Lawrence is approximately 6 months, extending from the ice breakup in April to the onset of adverse weather in November. Off Cape Breton Island, regulations limit the season to approximately 2 months. Given favorable ice conditions, crab fishing may continue almost year round off Newfoundland, except for a legal closure in January.

After capture, crabs are stored live on ice in the hold of the fishing vessel. Off-loaded crabs are transported to the processing plants and are processed within a few hours of delivery. The illegal landing of soft-shelled, recently molted ("white") crabs has been a quality problem at various times in some Gulf and Cape Breton Island fishing areas. "White" crabs do not keep well, are difficult to process, return a low meat yield, and produce an inferior product. The problem arises from high exploitation rates on the various affected grounds and, hence, a high dependence by fishermen on freshly recruited crabs. In the affected area of Cape Breton Island, a delay in season dates appears to have improved crab quality considerably. Various management measures to improve quality are being considered for the fishery.

MANAGEMENT

The Atlantic snow crab resource is under the jurisdiction of the Federal Government of Canada and is managed through the Department of Fisheries and Oceans. When the snow crab fishery started in the 1960's, there were no restrictions on effort or gear. Regulations for the Atlantic snow crab fishery were drafted by the Gulf of St. Lawrence Snow Crab Advisory Committee in 1976. Resource management involves both biological and economic parameters.

The aim of biological measures is to ensure the renewal of the resource by protecting female and sublegal size male crabs. This is done by:

1) Regulations that state all females caught in traps must be returned to the water.

2) Regulations, enforced in the Gulf and Cape Breton Island fisheries, that state at least one side panel of each trap must be covered with netting of at least 131 mm mesh size. In Newfoundland mesh size must be at least 114 mm.

3) Regulations that prohibit possession of any crab of less than 95 mm CW.

The major purpose of the economic measures imposed on the snow crab fishery has been to control fishing effort. In addition to preventing depletion of crab stocks and an overreliance on new recruits, the effort controls have restricted overcapitalization and have, thus, assisted all participants in attaining a reasonable income from the fishery. Current economic measures are summarized as follows:

1) Control of the size and number of vessels participating by strictly limiting the number and type of snow crab licenses issued.

2) Control of the amount of fishing gear by imposing maximum trap number per vessel limits. Presently, the limit in Newfoundland is 800 traps, 150 traps for most of the Gulf of St. Lawrence and 30 traps for nearshore fishermen around Cape Breton Island and in the St. Lawrence estuary.

3) Control of the amount of crab landed by imposition of a total allowable catch (TAC) with distribution of the TAC into sector, fleet, or boat quotas. Around sections of Cape Breton Island, the management strategy has been to maintain stability in the commercially available stock by permitting harvest of TAC's equivalent to the estimated annual biomass increases resulting from growth and recruitment. In Newfoundland, where estimates of annual growth and recruitment have been less practical, management has attempted to confine exploitation rates to 50-60% in order to maintain high catch rates, stability in landings, and avoid a "white" crab problem.

4) Control of the number of vessels in a given area by establishing fishing zones. Such zones are enforced around Cape Breton Island and Newfoundland to help better distribute the resource among the local fishermen.

5) Control of the period in which fishing takes place by the imposition of seasons. As discussed in the Harvesting section of this paper, various natural and management-imposed controls on fishing period exist. In Cape Breton Island the relatively short season is in accord with developing this particular fishery as a supplementary fishery with a large number of participants. Manipulation of seasons also has been used to successfully avoid "white" crab quality problems.

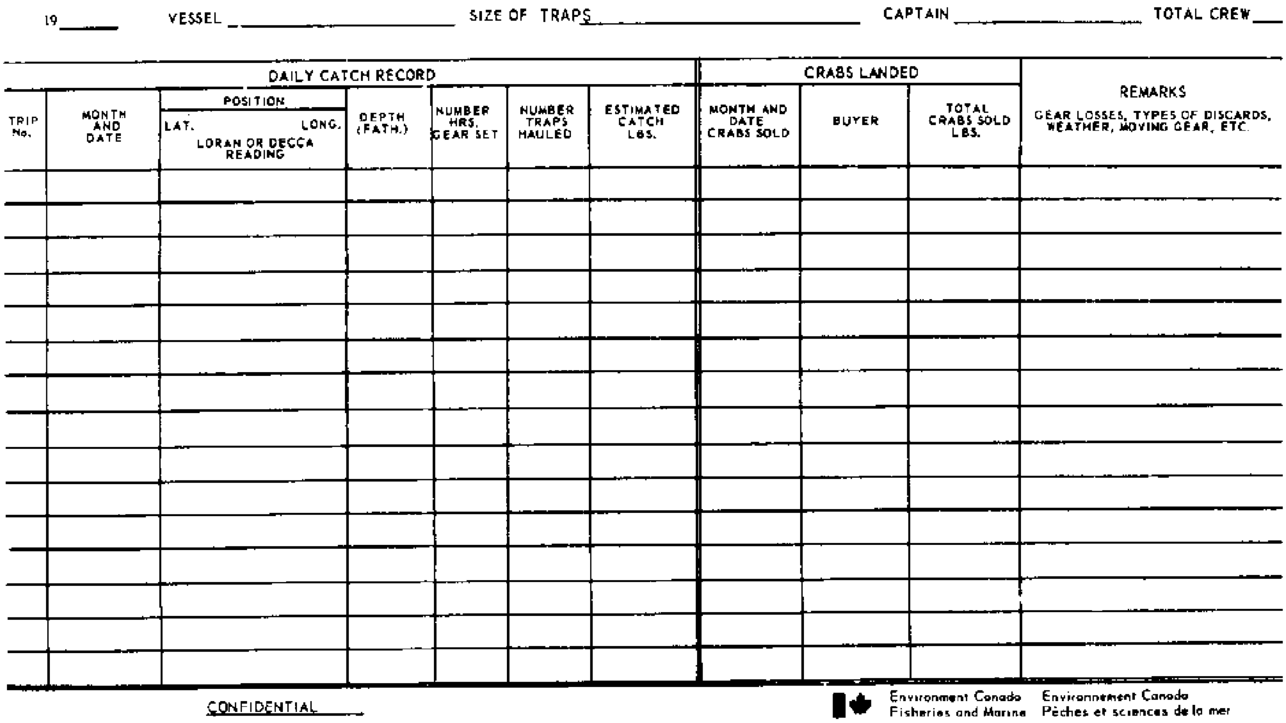
To aid stock assessments, all licensed fishermen in Atlantic Canada are required, as a condition of licensing, to keep detailed logbooks (Fig. 2). Annual assessments are carried out by biologists on the basis of logbook, tagging, research cruise, and commercial sampling data. Assessments are subject to peer review and scrutiny through two levels of the Canadian Atlantic Fisheries Advisory Committee (CAFSAC). Management considers CAFSAC-generated advice in context with socio-economic factors before making recommendations for possible enactment at senior management level. Regional snow crab advisory committees, made up of representatives for fishermen, processors, and the provincial and federal governments, serve as a link between industry and government and may debate or propose management recommendations. There are advisory committees for both the Gulf of St. Lawrence and Newfoundland fisheries. The Gulf committee has a subcommittee responsible for Cape Breton Island.

RESEARCH

A major research thrust is being made because effective management of the resource is hampered by a lack of understanding of the crab's biology.

Around Cape Breton Island, in the estuary of the Gulf and off Newfoundland, stock biomass assessments have been carried out both by Leslie analysis of logbook data and tagging studies (Bailey 1978a, Elner 1982). However, both methods, being dependent on commercial fisheries data, are subject to bias. Research into independent biomass assessment techniques using traps and trawls in conjunction with underwater photography is underway. Tagging techniques have been refined to produce apparently reliable anchor-tags that will be retained when a crab

Figure 2. Logbook page as currently utilized by snow crab fishermen in Atlantic Canada.



19_____ VESSEL __________ SIZE OF TRAPS __________ CAPTAIN __________ TOTAL CREW _____

DAILY CATCH RECORD								CRABS LANDED			REMARKS
TRIP No.	MONTH AND DATE	POSITION LAT. LONG. LORAN OR DECCA READING	DEPTH (FATH.)	NUMBER HRS. GEAR SET	NUMBER TRAPS HAULED	ESTIMATED CATCH LBS.		MONTH AND DATE CRABS SOLD	BUYER	TOTAL CRABS SOLD LBS.	GEAR LOSSES, TYPES OF DISCARDS, WEATHER, MOVING GEAR, ETC.

CONFIDENTIAL

Environment Canada Fisheries and Marine — Environnement Canada Pêches et sciences de la mer molts (R. W. Elner, unpubl. data; Taylor 1982). Such molt-retained tags are expected to supply valuable information on biomass levels, exploitation and growth rates, as well as long-term movements. Hitherto, such data have been suspect or unobtainable with vinyl body and anchor-tags.

The ecology and population dynamics of juvenile snow crab are being investigated through beam trawl surveys off NW Cape Breton. Stomach analyses of groundfish, which feed on juvenile crab, are providing an alternative survey mechanism as well as elucidating crab natural mortality.

Overall, if the fishery is to be managed on a long-term basis, it will be critical that biological production models for the various crab populations be developed. However, a more thorough knowledge of growth and recruitment mechanisms is needed before such models can be described and used to optimize yields.

ACKNOWLEDGEMENTS

R. J. Bailey, T. H. Butler, J. D. Pringle and D. M. Taylor provided critical reviews of early drafts of this manuscript.

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ABSTRACT

Since the inception of a directed fishery for snow crab off Canada's Atlantic coast in 1966, landings and effort have increased considerably. Currently, snow crab is the most important crab species (value and tonnage) fished in Canadian waters. Landings of 36,191 MT in 1981 were worth $21 million to Canadian fishermen. This ranked sixth in value for all commercial species on the Atlantic coast. Most known grounds are considered fully to overexploited and landings are increasingly dependent on new recruits. Annual biomass additions from growth and recruitment vary considerably, thus, future landings will fluctuate accordingly. Annual sustainable yields from the three major Atlantic snow crab areas, Newfoundland, the western Gulf of St. Lawrence, and Cape Breton Island, have been projected at 8,000-15,000 MT tons, 10,000-15,000 MT, and 2,000 MT, respectively.

The minimum legal size of 95 mm carapace width confines the fishery to mature males. The reproductive potential of the stocks appears unaffected by exploitation. Other regulations and management controls deal with the number of licensed fishermen, the maximum number of traps per boat, trap mesh size, vessel size, quotas, fishing zones and seasons. Stocks are monitored by port and at-sea sampling, tagging, trapping, trawling and photography. Stock assessments are conducted annually and recommendations enacted after peer review, management scrutiny and industry consultation through advisory committees.

Fisheries for the Genus *Chionoecetes* in Southwest Japan Sea

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INTRODUCTION

According to historical documents and literary works, one-boat trawling in waters along the southwest coast of the Japan Sea began as early as 1087 for flat fishes. This type of gear predominated in shallow and deep waters and was modernized between 1913 and 1917 to the seiner of the hot-bulb type engine. Between 1915 and 1930 one-boat trawls continued developing operations with the introduction of modern conveniences, improvements, and intensification of technical installations. The one-boat seine fishery has expanded the fishing grounds to the continental shelf and westward across the Japan Sea trench to the grounds adjacent to China and to the coast of U.S.S.R. between 1935 and 1941. In early years seiners did not fish for crab. After World War II, however, a strong interest developed in the crab fishery following reduction of the fishing area.

The main crab fishing grounds in the Japan Sea are situated along the 200 m to 1,500 m contours. Fishing for _C. opilio_ is confined to shallow water of less than 350 m depth and _C. japonicus_ to deep water of more than 800 m depth. (See Figure 1.) Water of less than 100 m depth is restricted to Danish seiners. By agreement among the fishery cooperatives in this region, the fishing grounds are segregated by gross tonnage with small seiners of less than 14.9 gross tonnage and offshore seiners of more than 15 gross tonnage. Traps are used mainly to catch _C. japonicus_. About 13 boats belonging to Shimane Prefecture are licensed for fishing _C. opilio_.

The grounds off Hyogo, Tottori, and Shimane Prefectures support a large population of both species and landings at the three prefectures, although the landings from the area do not exceed those at any other port of Japan. Namely, the other demersal fish keep the crab fishery active. In the northern part of the area, from Echizen Peninsula to Kyoga Head, development of the crab fishery does not compare with that in the southern part, due mainly to small fishing grounds off each prefecture.

A new method of fishing _C. japonicus_ with a baited trap was begun in 1959 in Toyama Bay and off Niigata Prefecture. About 65 boats each carrying 30 traps landed 1,400 tons in 1965, mainly from the sea around Toyama Bay, and the crab has since extended rapidly in the southern Japan Sea. Of the 33,000 tons of _C. japonicus_ landed in 1980 from the Japan Sea, 66 percent were landed at Tottori and Shimane Prefectures, 9 percent at Hyogo, and 8 percent at Niigata. From initially developed waters in the Toyama Bay, the catch has declined by 344 tons (25 percent) from 1965 to 1980.

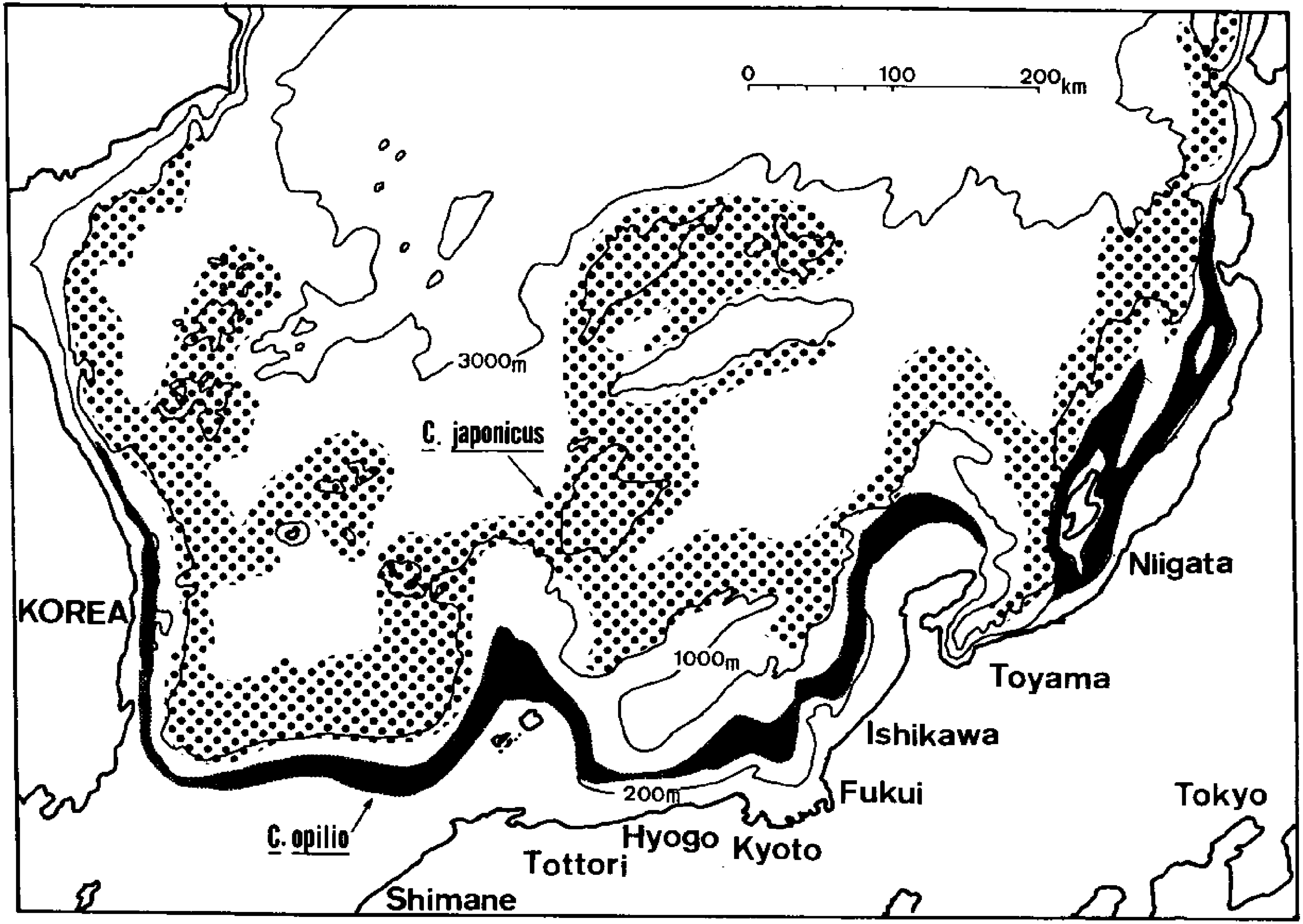

Figure 1. The distribution of Chionoecetes opilio and C. japonicus in the Japan Sea.

In early years the main grounds of this species were confined to 900 to 1,500 m depths off each prefecture. Recent catches of crab have been in waters of 1,200 to 1,500 m depth where crabs are numerous, extending to the central part of the southwest Japan Sea.

CRAB FISHING BOATS

In the statistical records, Danish seiners are classified into two categories based on the gross tonnage as mentioned previously--small seiners of less than 14.9 gross tonnage and offshore seiners of greater than 15.0 gross tonnage. Various factors govern the types of boats, the most important being the harbor facilities and the distance from the port to the grounds. With the decreased catch, larger boats having a powerful engine were required for good catches within a given time. The present day Danish seiners install a variety of horsepower engines averaging 20 to 80 horsepower in small seiners and 130 to 304 horsepower in offshore seiners, and are fitted with depth-sounders and other modern navigational aids. A boat is crewed by seven to eight men; and when crab fishing on a one-night trip, it can haul from seven to eight seines. The numbers of boats that engaged in the crab fishery since 1953 are shown in Figure 2.

It is generally expected that the increased horsepower of the engine brings about better results in the increase of areas swept by the net and warp and in the development of new grounds in the offshore area. Assuming that crabs are gathered from the ground swept by sweep line and that the area of it is equal to that enclosed by sweep line and warp, the total swept area is approximately 1.302 km^2 on the average (Sinoda, 1969), though there is no conclusive evidence for behavior of sweep line while being towed. Since the crabs in the area swept by net may be more catchable than those in the area swept by sweep line, both areas are not considered to have the same catchability. Probably the net is able to catch various sizes of crabs present in front of the mouth, but the sweep line permits the crabs to escape by leaping over the rope or burrowing into the ground. A schematic diagram of Danish seining and radar observation are shown in Figure 3.

During the early 1970s the "crab trap boats" were used in Tyama Bay and introduced at Tottori and Shimane Prefectures following the decline of C. opilio landings. In 1974 the 340 licensed boats (about 220 engaged in crab fishing) in the Japan Sea were rearranged so that the numbers in 1980 were about 280 boats; of which about 130 boats took part in the crab fishery as shown in Figure 4. Although there are two classes of crab trap boats, small boats of less than

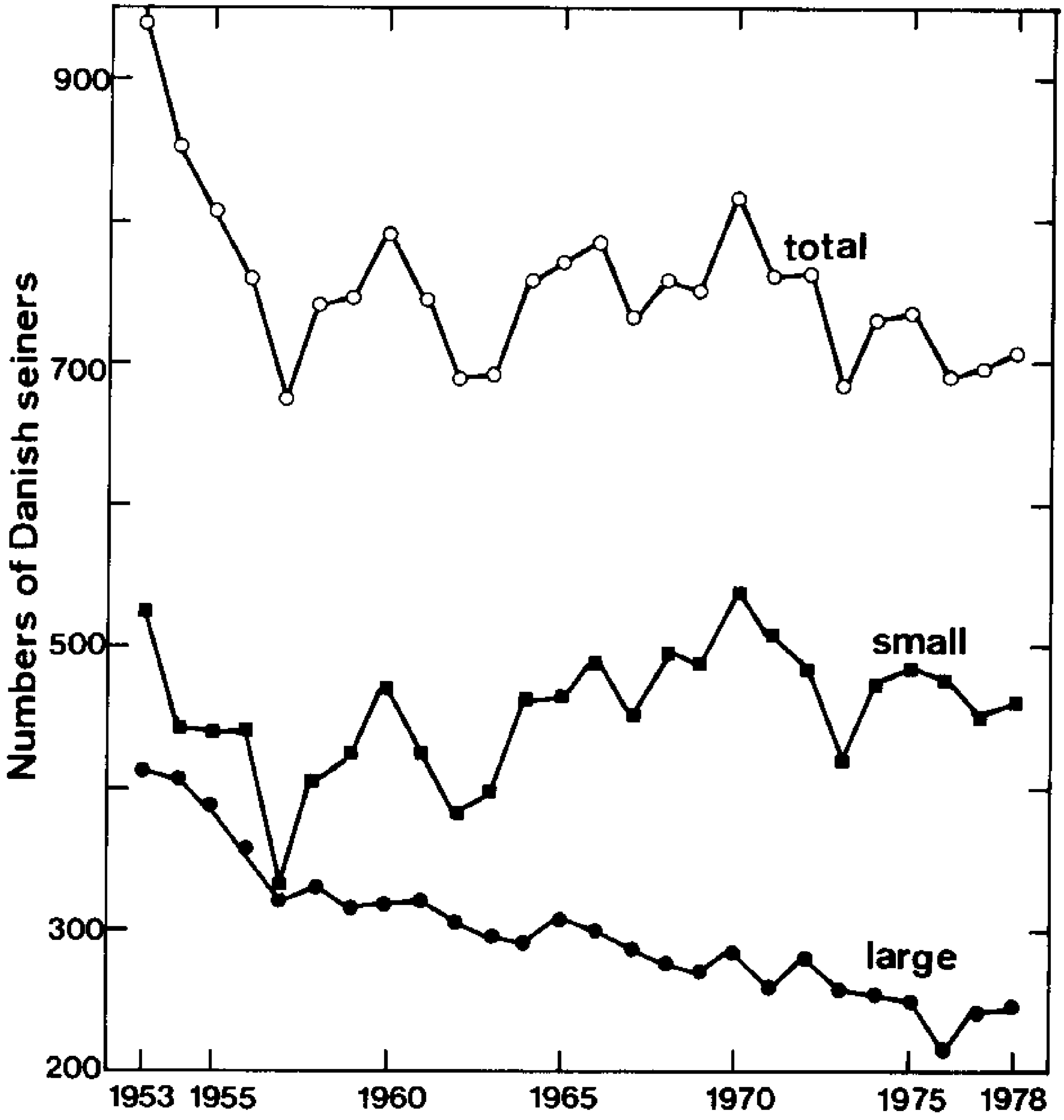

Figure 2. Number of Danish seiners fished in the southwest Japan Sea.

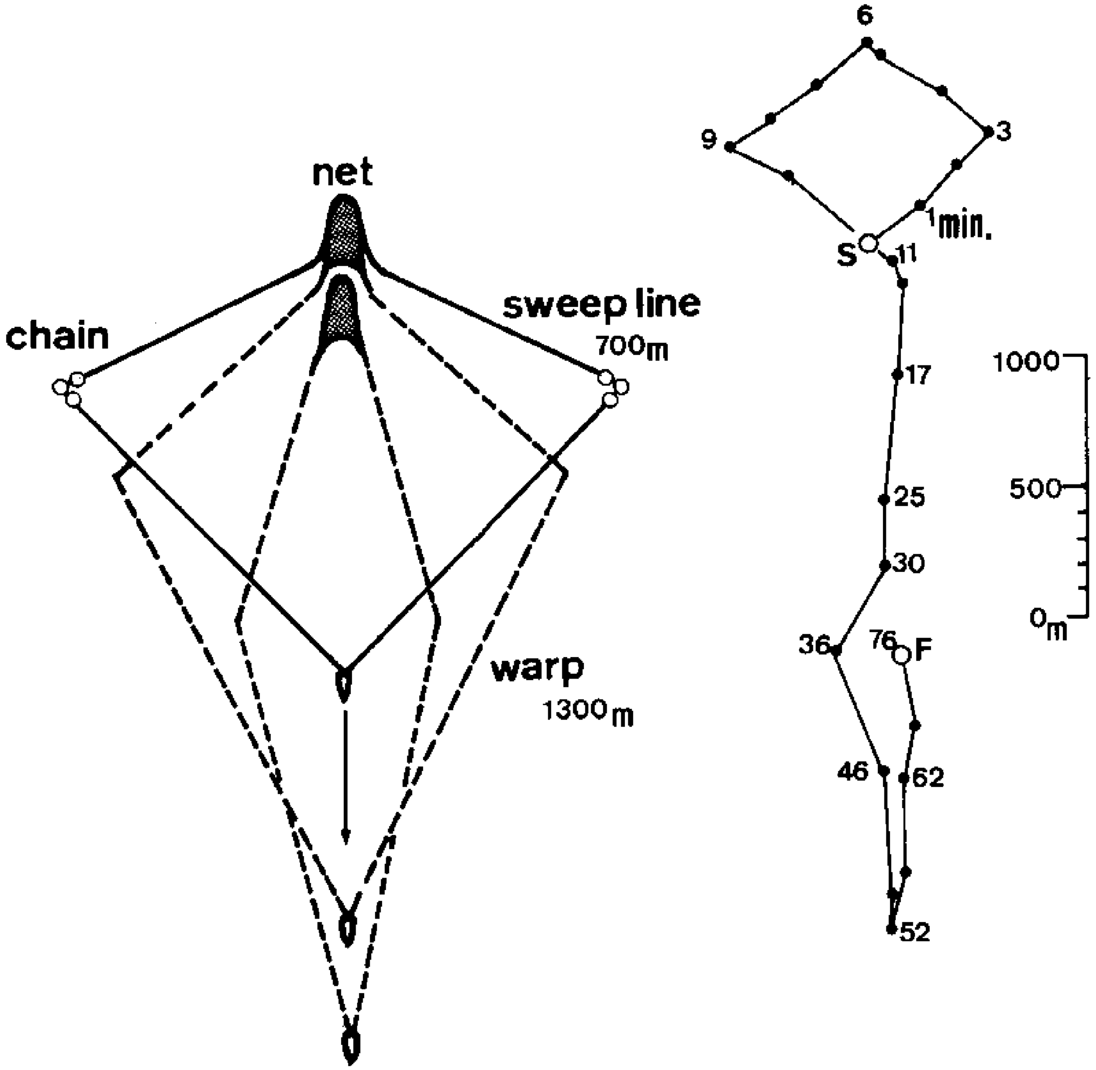

Figure 3. Schematic diagram of Danish seining and rada observation of seiner, S and F represent the starting and finishing points, respectively, and the total time elapsed in the process of towing (affixed number).

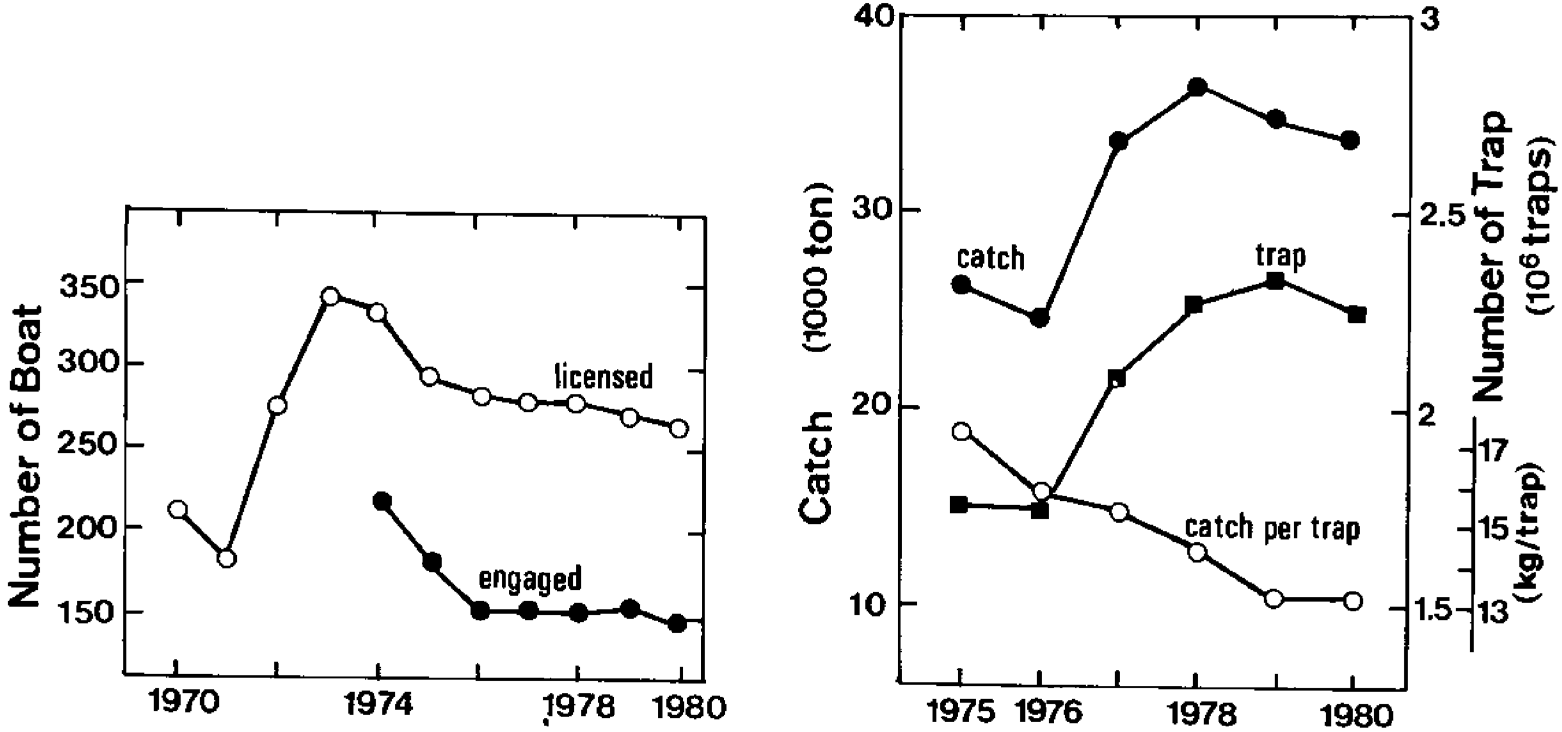

Figure 4. Numbers of crab-trap boat and traps used, and catch of <u>Chionoecetes bairdi</u>.

19.9 gross tonnage and boats larger than 20 gross tonnage, the types of boats are various. As compared to Danish seiners, the intensity of work on crab trap boats is less. A boat is crewed by four or seven men, some of which are the older former crewmen of Danish seiners.

The number of traps worked by a boat depends upon the gross tonnage; a small boat can work about 200 traps, while a large boat can handle up to 450 traps. The trap of the pudding-type is 80 cm in diameter on the upper surface, 120 cm on the lower surface, and 75 cm high. It has an opening 40 cm in diameter on the top. Iron rods about 9 to 12 mm in diameter are used for framing, and the entrance tunnel is a cylinder of polyethylene, which is said to be more effective for capturing crabs than an iron cylinder and easily obtainable. The largest numbers of crabs per trap can be obtained when the distances between two traps is about 40 to 56 m because the low catch per trap may be caused by overlapping of the area of bait attraction between neighboring traps (Sinoda, 1968a, 1968b, 1976). Most of the bait is caught locally. The mackeral, Pneumatophorus japonicus japonicus, is commonly used because it is relatively inexpensive.

LANDINGS

Records of the annual landings of Zuwai crab, C. opilio, are available from the 1920s when a total landing from the Japan Sea was approximately 800 to 1,500 tons as extracted from Statistics and Survey Division, Ministry of Agriculture and Forestry, Japanese Government.

In common with other fisheries resources which were not exploited during World War II, there was an upward trend in the crab catch from 1948 (about 6,800 tons) to 1964 (more than 15,500 tons). As shown in Figure 5, however, landings from 1964 to 1967 sharply declined, and during 1968 to 1972 increased. From 1973 to 1975 there was further downward trend, and the total landings since 1975 have been fairly stable at the lowest level in the 32-year period of the fishery.

Following the drastic decline of Zuwai crab landings, the C. japonicus catch has progressively increased. The shape of catch curve of C. japonicus, known locally as Beni-zuwai gani, represents a slow increase during the period of 1959 to 1971. After the introduction of trap fishing to the southwest prefectures, where there are a large number of offshore boats available, landings of this species have gone upward, surpassing the Zuwai crab catch in 1973. This increased landing may be due to the development of new

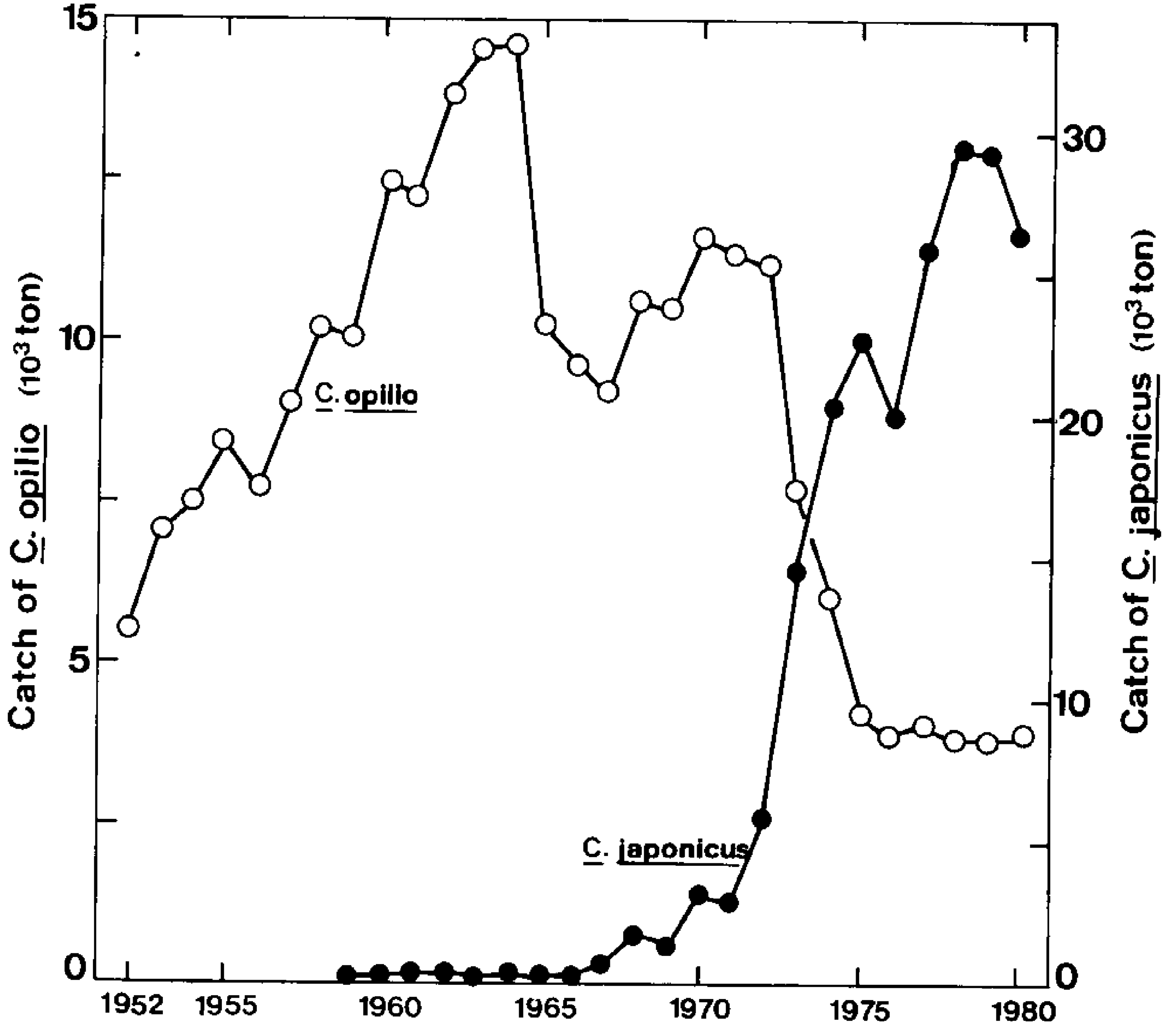

Figure 5. Annual catches of C. opilio and C. japonicus in the southwest Japan Sea.

grounds on offshore banks and in deeper waters. In 1980 a total of 33,000 tons of crabs were landed at all the prefectures along the Japan Sea coast. About 90 percent was landed at the southwestern ports, with 66 percent of the catch going to Tottori and Shimane Prefectures.

CATCH IN RELATION TO HORSEPOWER OF DANISH SEINER AND NUMBERS OF TRAPS USED

The reason for the increases and decreases in catch by Danish seiners and crab trap boats would be better understood if the number of seinings by the size of gear used and the numbers of traps hauled in a specific ground had been known. Unfortunately, accurate data on the fishing efforts and the amount of catch is only available in the captain's log book. The fishing effort is summarized in each Fisheries Cooperative Office based on the captains' reports. Due to the variety of methods used for compiling fishing effort data, we are obliged to fall back on the log books to have accurate statistics on crab fishery.

Information on the changing abundance of crabs on the grounds can be obtained by relating the weight of the catch to the numbers of traps and of seiners by horsepower. This is one useful guide to outline the state of the crab stock over a long period. Figure 6 shows an example for _C. opilio_ off Hyogo Prefecture. The shape of the catch curve has two predominant peaks from 1963 to 1964 and 1970 to 1972 which are similar to total landings from all the southwest Japan Sea because the landings at Hyogo have accounted for about 34 to 44 percent of all landings since 1953. Figure 6 indicates that catch variations after the initial peak can be smoothed when the catches are standardized by numbers of boats and horsepower. Although there was a large increase in horsepower during the 10-year period of 1965 to 1974, poor landings occurred as shown in Figure 7.

The change in abundance of _C. japonicus_ can be obtained by relating the weight of the crab to the number of traps used. Catch per unit of trap during the six-year period is shown in Figure 4 and has gradually decreased with the increase of the numbers of traps fished. As mentioned previously, the number of crab trap boats were changed in 1974, since the total landings from grounds along the coast of the southwest Japan Sea have shown a downward trend. Catch per trap in the recent years is apparently stable. It is probable that there are higher catches from developing grounds in the offshore and smaller landings from the developed grounds.

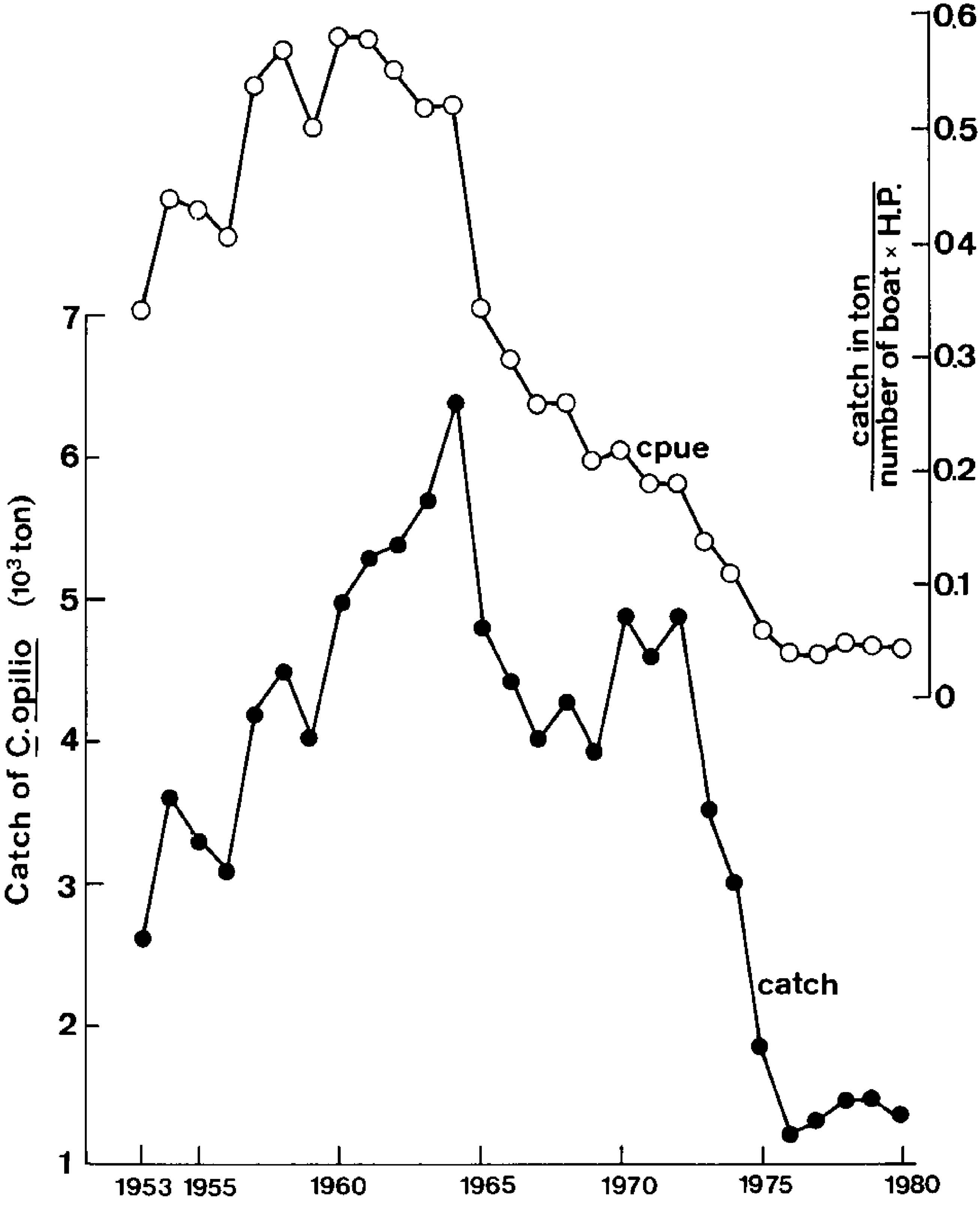

Figure 6. Catch of C. opilio and standardized catch by number of boat and average horsepower (H.P.) in Hyogo Prefecture.

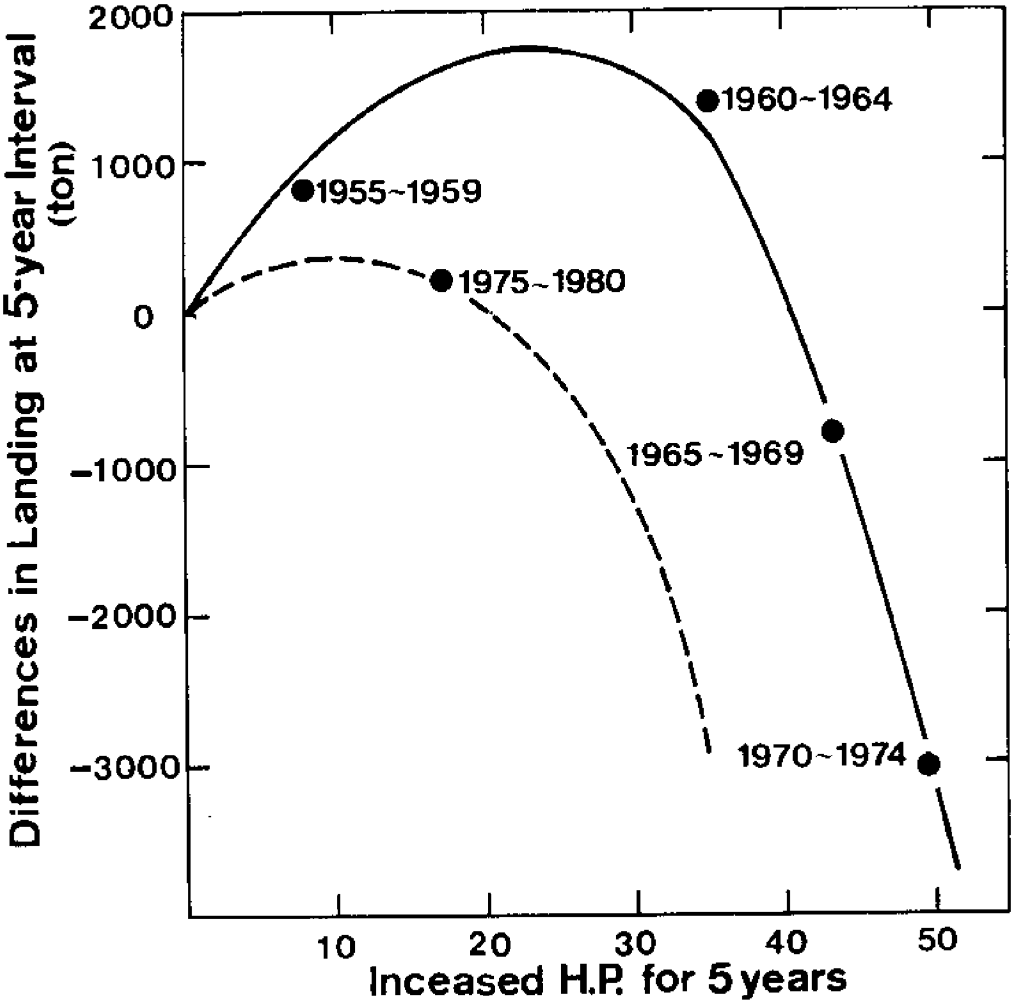

Figure 7. Relationship between increased H.P. for 5 years and differences in landing at 5-year interval.

REGULATIONS OF CRAB FISHERY

The difficulty in application of fishery biology to management of the crab fishery is well known. Fishery biologists have provided significant understanding of the important crab populations of the Japan Sea. The success and failure of the management was left in the hands of fishermen. The stock of *C. opilio* has been irreparably damaged, it is believed, due to heavy exploitation with nonselective gear on crab size.

The management items of crab fisheries are authorized as follows:

A. Danish seine (*C. opilio*)

1. Maximum amount of catch per trip

	Female crab	Soft crab
< 24 hrs./trip:	15 boxes*	15 boxes*
24-48 hrs. trip:	25 "	30 "
> 48 hrs./trip:	60 "	70 "

*One box = 15 kg.

2. Prohibited crab

Immature females and males of less than 9 cm in carapace width

3. Fishing season

Male crab	Soft male crab	Female crab
11 Nov. - 31 Mar.	16 Dec. - 31 Mar.	11 Nov. - 31 Jan.

4. Fishing ground

In waters of more than 100 m depth and restricted waters in accordance with agreement among fishermen

B. Crab trap (*C. japonicus*) in the case of Hyogo Prefecture

1. Prohibited crab

Females, and males of less than 9 cm carapace width

2. Numbers of trap

> 20 gross tonnage boat:	450 traps
< 20 gross tonnage boat:	200 traps

3. Net mesh size

   > 15 cm in stretched size

4. Fishing season

   From 1 September to 31 May of next year

5. Fishing ground

   In waters of more than 800 m depth off Hyogo Prefecture

6. Boat

   Boats of less than 100 gross tonnage boats based in Hyogo Prefecture

Based on stock information before opening the fishing season, the preceding items may be changed in the annual meeting which consists of the ministry and prefectual officers, fishermen, and scientists.

In view of the biology of the crab, population control, increased fishing intensity and nonselective or indiscriminate exploitation of crabs of various sizes and age groups are the important factors contributing to the decline of landings. The eumetric fishing curves show that the selectivity of gear is at its best when crab is exploited at a particular age or size at which the population attains its maximum weight. As the optimum age or size of exploitable crabs are important parameters for the management of fishery resources, it must be determined whether the minimum landing size of 9 cm has a biological basis.

The optimum age (t_m) of exploitation is that age at which the total weight of recruits attains its maximum, and at which the increase in weight due to growth (W_t) and the decrease in weight due to total mortality (Z) are at equilibrium. Therefore, t_m can be calculated by finding the age (t) when the following equation holds:

$$\frac{d(N_t W_t)}{dt} = W_t \frac{d_{Nt}}{dt} + N_t \frac{dW_t}{dt} = 0 \qquad (1)$$

where N_t is the number of individuals at time (t), and W_t the weight at time (t) given by the von Bertalanffy equation for growth, by which the growth of C. opilio could be estimated (Sinoda, 1968a and b; Ito, 1970). The length l_m at t_m is given by:

$$l_m = l_\infty \left(\frac{3}{Z/K + 3} \right), \qquad (2)$$

and substituting l_m for the length in growth equation, we get the relationship (Sinoda, 1976):

$$t_m = t_o \; \frac{1}{K} \log_e \left(1 - \frac{3}{Z/K + 3}\right), \qquad (3)$$

where t_o and K are the parameters in the growth equation. Figure 8 shows the variation in t_m and l_m/l_∞ with Z=0.1 - 3.0 and K=0.05 - 0.80 $year^{-1}$ under conditions computed from equations (2) and (3) putting t_o=0. Using this figure it is possible to describe the propriety of the landing size of 9 cm in carapace width, when K=0.097 - 0.165 $year^{-1}$, l_∞=164 - 180.4 mm and Z=0.98 $year^{-1}$ (Sinoda, 1968a and b; Ito, 1970). Since the value of l_m/l_∞ can be evaluated as less than 0.5 in the case of Z=0.98 $year^{-1}$ and K=0.097 - 0.165 $year^{-1}$, it is implied that the minimum landing size of 9 cm in carapace width does not conflict with biological viewpoints on C. opilio.

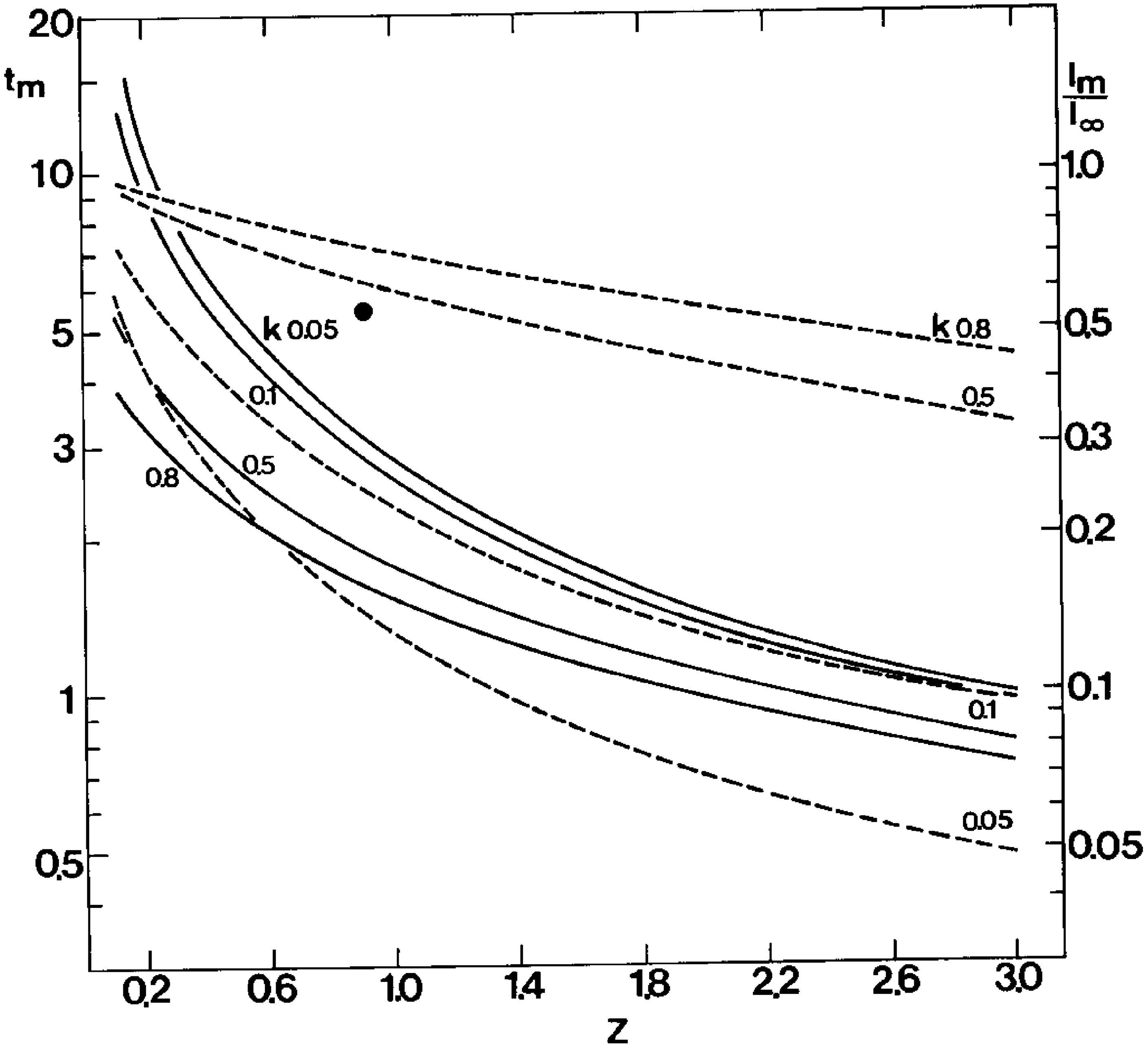

Figure 8. Relationship between total mortality (Z) and $l_m/l_{m\infty}$, t_m in equations (2) and (3).

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ABSTRACT

The species fished commercially in the Japan Sea are *C. opilio* and *C. japonicus*. The former, known locally as *Zuwai Gani*, is caught mainly by Danish seining vessels of 14 to 70 gross tons and some pots are used for the latter.

A large fishery is centered in the southwest Japan Sea off Fukui, Kyoto, Hyogo, Tottori, and Shimane Prefectures (total landings of *C. opilio* 3,060 tons in 1980, *C. japonicus* 33,000 tons in 1980). A sharp rise in landings of *C. opilio* reached two peaks of 15,500 tons in 1963 to 1964 and 12,500 tons in 1970. The large landings of *C. japonicus*, more than 35,000 tons in 1978, have shown a relatively slow downward trend over the next two years.

The fishing season for *C. opilio* opens on 11 November and closes on 31 January (females) and 31 March (males). The minimum legal size is 90 mm carapace width and the soft crab capture is restricted in season, 11 November to 16 December. Catches of female crabs are restricted to the berried group, and the small ones are prohibited from being landed. These regulations are enforced to allow mating, breeding, and molting to proceed.

Both males and females of *C. japonicus* are trapped in deeper waters more than 800 m deep, from 1 September to 31 May of the following year. For *C. opilio* the minimum legal size is 90 mm carapace width, and numbers of traps used by a boat are restricted to 200 for boats less than 20 gross tons and 450 for boats more than 20 gross tons.

In 1980 the total number of Danish seiners was approximately 1,893 in the southwest Japan Sea. Prior to 1971, the total number of trap-vessels was about 200, and in 1973 the number showed a further decrease with an increase in the number of traps used. With the decrease of *C. opilio*, the percentage occurrence of soft female crabs in landings have shown an upward trend, especially in the main fishing area off Kyoto, Hyogo, and Tottori Prefectures.

A Review of the Gulf of Alaska Tanner Crab, *Chionoecetes Bairdi*, Fishery and Management Related Research

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Introduction

In the North Pacific Ocean crabs of the genus *Chionoecetes* are found in commercial quantities in a number of areas. They have been exploited as a food resource for almost a century in Asiatic waters, particularly in Japan (Cahn 1948). As crab stocks in the Sea of Japan declined in the middle 1960's (Sinoda 1968) attention was turned toward finding supplementary stocks which might be suitable for exploitation. Exploratory fishing was conducted in the eastern Bering Sea by Japan and a fishery for Tanner crab soon developed in that region. In the Gulf of Alaska (GOA) domestic fishing effort on the Tanner crab was negligible due to the fact that a large scale effort to exploit the red king crab, *Paralithodes camtschatica*, resource kept the fleet busy for most of the year. The severe decline in king crab catches after 1967 (Brown 1971) spurred interest in harvesting the Tanner crab as a means of supplementing income. The highlights of the Tanner crab fishery, management related research and regulatory scheme used to manage the commercial fishery in the GOA is reviewed in the balance of this paper.

Geography

The area of the northern Pacific Ocean which is considered herein includes the continental shelf and upper slope waters of southeast Alaska west along the GOA coastal rim through the Aleutian Archipelago. This ocean region generally extends from 130° W. longitude west to the 172° E. longitude and 51° N. latitude north through Prince William Sound and Cook Inlet to approximately 61° N. latitude (Figure 1). Within this region, representing approximately 250,000 km^2 of shelf and upper slope bottom area, the shelf is divided by numerous troughs and varies in width from about 2-176 km. It is narrow off of many of the islands in the Aleutian Archipelago and broadest in the region northeast of the Kodiak Archipelago. Bottom substrate composition consists of rock, gravel, sand or mud and changes rapidly within short distances (Ronholt et al. 1977).

Distribution (North Pacific)

Five species of the genus *Chionoecetes* have been described from the North Pacific region (Table 1) (Garth 1958). One of these, *C. opilio*, is subdivided into two subspecies, *C. opilio opilio* and *C. opilio elongatus*. The latter along with *C. japonicus* is found only in the western North Pacific along the coast of Asia. Of the remaining species, *C. opilio opilio* is restricted in the Pacific portion of its nearly circum-arctic range to the Bering Sea while *C. bairdi*, *C. angulatus* and *C. tanneri* are more widespread in the eastern North Pacific (Table 1). *Chionoecetes angulatus* and *C. tanneri* are predominantly abyssal forms and little interest has been shown to date in developing a commercial fishery on either species. Brown (1971) reported that *C. bairdi* was the only Tanner crab exploited commercially south or east of the Aleutian Islands. This is still the case in 1982. The balance of this review deals solely with this commercially important species.

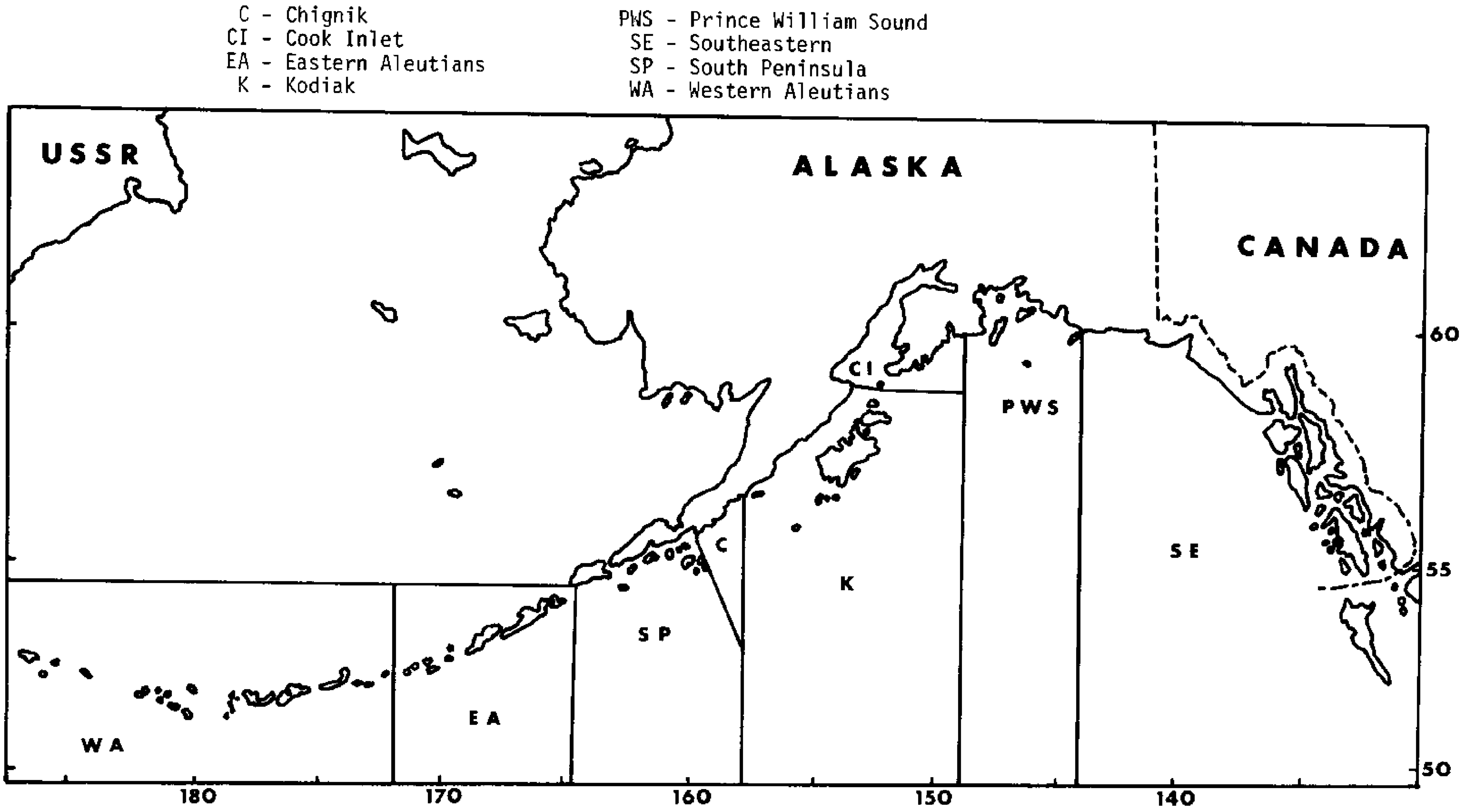

Figure 1.--Geographic areas of the Gulf of Alaska region which form the basis of Tanner crab management districts.

Table 1.--*Chionoecetes* spp. and their distribution

Species of *Chionoecetes*	Depth Meters	Location
C. opilio (O. Fabricius)	13-155	Bering Sea, Arctic Ocean, N. Atlantic Ocean from west coast Greenland to Casco Bay, Maine.
C.o. elongatus Rathbun	to 2222	Sea of Japan, Okhotsk Sea
C. bairdi Rathbun	shoalwater to 473	Bering Sea to California (Hosie and Gaumer 1974).
C. tanneri Rathbun	53-1942	Bering Sea to lower California (E. Monk, personal communication)
C. angulatus Rathbun	90-2972	Bering Sea to Oregon
C. japonicus Rathbun	411-2103	Sea of Japan (Watson 1969a; Fukataki 1965).

Catch History

On seasons

Fishing seasons in the GOA frequently last from late one year to spring the following year. Correctly stated each season would be referred to by both years comprising the season (example: the 1979-80 and 1980-81 seasons produced......). Since this tends to be cumbersome, I will refer to fishing seasons by the second year which generally encompasses the period of greatest fishing effort (the example above becomes: the 1980 and 1981 fishing seasons produced......).

The Tanner crab is by no means a new food resource. Cahn (1948) reported that Tanner crabs have been exploited in Asiatic waters since the late 19th century. Although the Japanese had been harvesting king crab in the Bering Sea since 1930, Japanese king crab fleets did not begin to process the readily available Tanner crab until 1953 (Zahn 1970). Production remained at experimental levels until the 1965 U.S.-Japan King Crab Agreement established a quota on the Japanese king crab harvest. This quota, in conjunction with declining king crab catches caused king crab prices to become exhorbitant for the Japanese consumer which generated greater interest in the Tanner crab resource. The Japanese Tanner crab catch in the eastern Bering Sea jumped from 1.5 million crabs in 1965 to 12.0 million crabs by 1968 (INPFC 1970). During the 1968 commercial season the GOA Tanner crab harvest exceeded 453.6 mt (or 1 million pounds) for the first time. The total GOA harvest that season reached 1,450.4 mt (Figure 2 and Table 2) considerably higher than the previous season's catch of 53.8 mt. Interestingly, the almost 27 fold increase in the GOA harvest during the 1968 season was not directly related to the increased interest shown by the Japanese in the Bering Sea Tanner crab resource. It was related to the widespread and significant declines in king crab harvests after 1966 (Figure 3). Catches of Tanner crab up to 1968 had been incidental to the king crab harvest. With the declines in king crab catches, fishermen turned to Tanner crab to supplement declining income from the king crab fishery.

During the early years of the GOA Tanner crab fishery, 1968-1971, effort remained relatively low due to poor marketing conditions. According to Brown (1971) these conditions stemmed from, "1) uneconomical extraction of meat from the shell; 2) relatively low consumer acceptance; 3) competition on the U.S. marked from imported *Chionoecetes* crab meat; and 4) a black encrustment on crab shells" (Black Mat Syndrome). Market conditions improved somewhat as the king crab harvest declined which resulted in a major increase in the GOA Tanner crab catch from the 4,898.8 mt landed during the 1971 season to the historic high of 29,667.8 mt landed during the 1974 season (Table 2).

Three major increases in industry interest in the GOA Tanner crab seem to have occurred (from the standpoint of the number of vessels fishing) since its inception (Figure 4). Two of these increases, one in 1968 and 1969, and another in 1978 and 1979 resulted from declines in king crab catches while the third increase, 1973 and 1974, occurred as a result of improved marketing conditions.

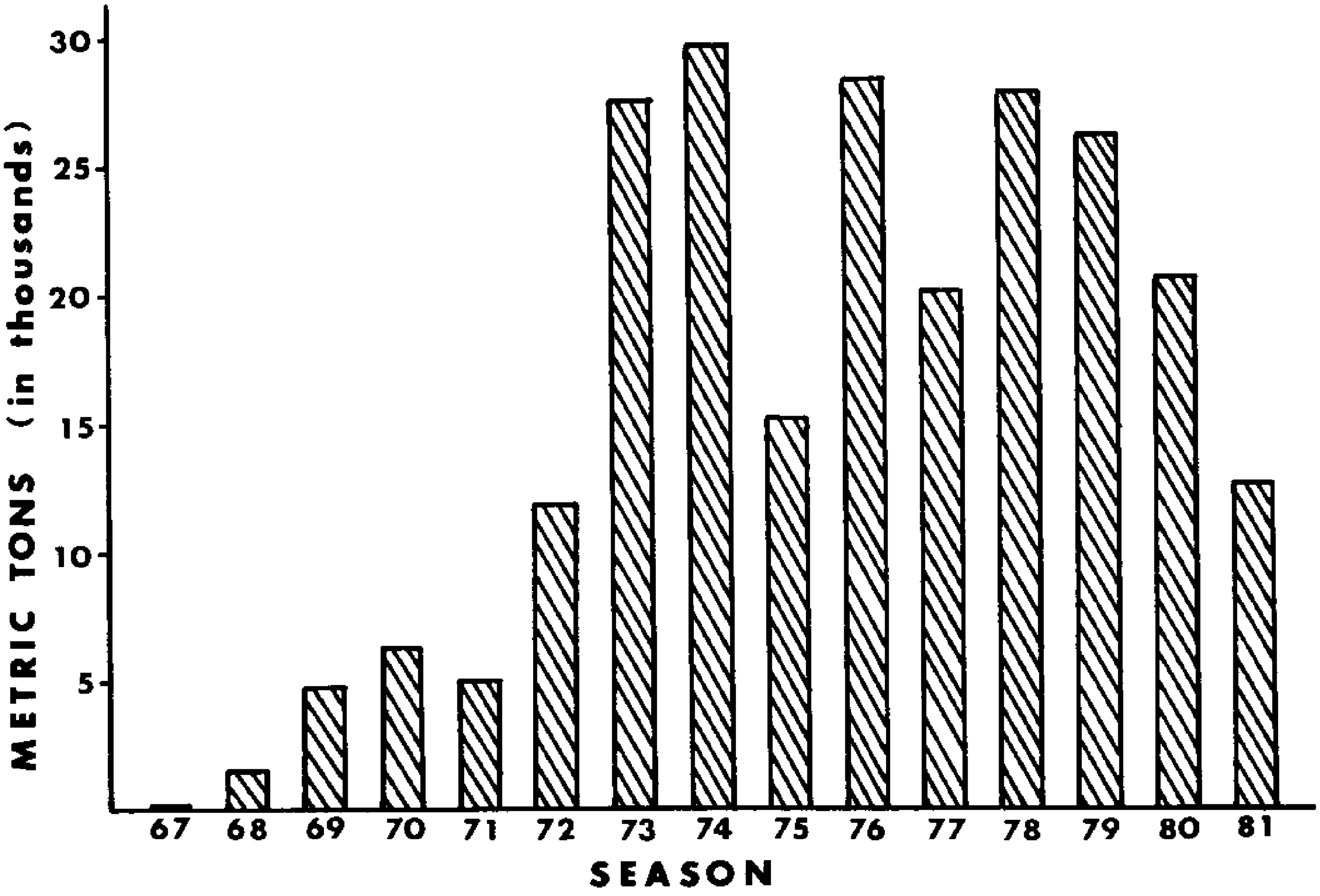

Figure 2.--Total Gulf of Alaska Tanner crab, *Chionoecetes bairdi*, commercial catch, 1967 through 1981 commercial seasons.

Table 2.--Tanner crab, *Chionoecetes bairdi*, catches (in metric tons, mt) from the Gulf of Alaska, by area, 1961 through 1981 commercial seasons.

Commercial Season	AREA						Gulf of Alaska Totals
	Southeastern	Prince William Sound	Cook Inlet	Kodiak	South Peninsula Chignik/Aleutians		
1961	3.1	-	-	-	-		3.1
1962	3.5	-	1.5	-	-		5.0
1963	-	-	-	-	-		-
1964	6.3	-	-	-	-		6.3
1965	-	-	-	-	-		-
1966	-	-	-	-	-		-
1967	1.2	-	-	50.3	2.3		53.8
1968	49.5	111.2	68.5	1,161.5	59.7		1,450.4
1969	101.2	560.5	635.5	3,096.8	292.3		4,686.3
1970	299.5	582.7	600.1	3,817.8	950.0		6,251.1
1971	75.9	1.9	721.7	3,059.1	1,040.1		4,898.8
1972	297.9	3,532.8	1,924.6	4,290.1	1,653.5		11,707.1
1973	853.0	6,317.6	3,431.0	13,925.3	2,886.4		27,413.4
1974	1,443.4	4,607.6	3,614.3	13,526.7	6,217.0	258.9	29,667.8
1975	1,286.6	1,748.2	1,867.9	6,191.6	4,012.2	34.1	15,140.6
1976	1,761.0	3,235.4	2,481.6	12,399.9	8,222.9	270.6	28,371.4
1977	1,214.8	1,053.0	2,107.2	9,398.6	5,645.8	590.4	20,009.8
1978	1,398.8	2,180.3	2,424.5	15,096.4	5,506.7	1,209.8	27,816.4
1979	1,431.0	3,198.1	2,595.8	13,233.2	5,089.6	670.1	26,217.8
1980	1,909.6	2,718.3	2,299.4	8.447.7	4,753.3	555.1	20,683.5
1981	1,125.6	1,259.1	1,543.7	5,329.1	3,001.2	396.7	12,655.5

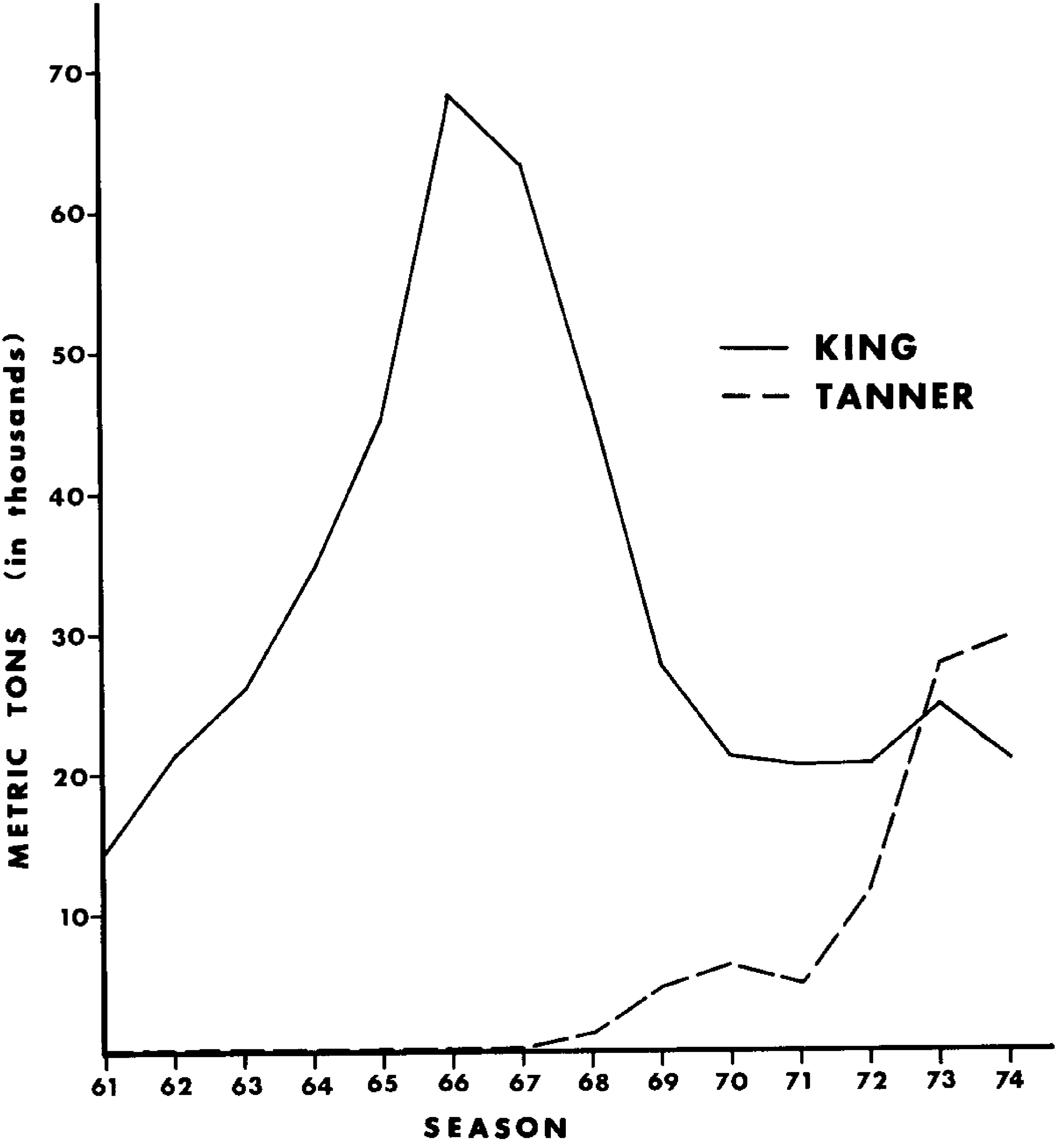

Figure 3.--Relationship between king crab, *Paralithodes camtschatica*, and Tanner crab, *Chionoecetes bairdi*, in Gulf of Alaska during early development of the Tanner crab fishery, 1961 through 1974 commercial seasons.

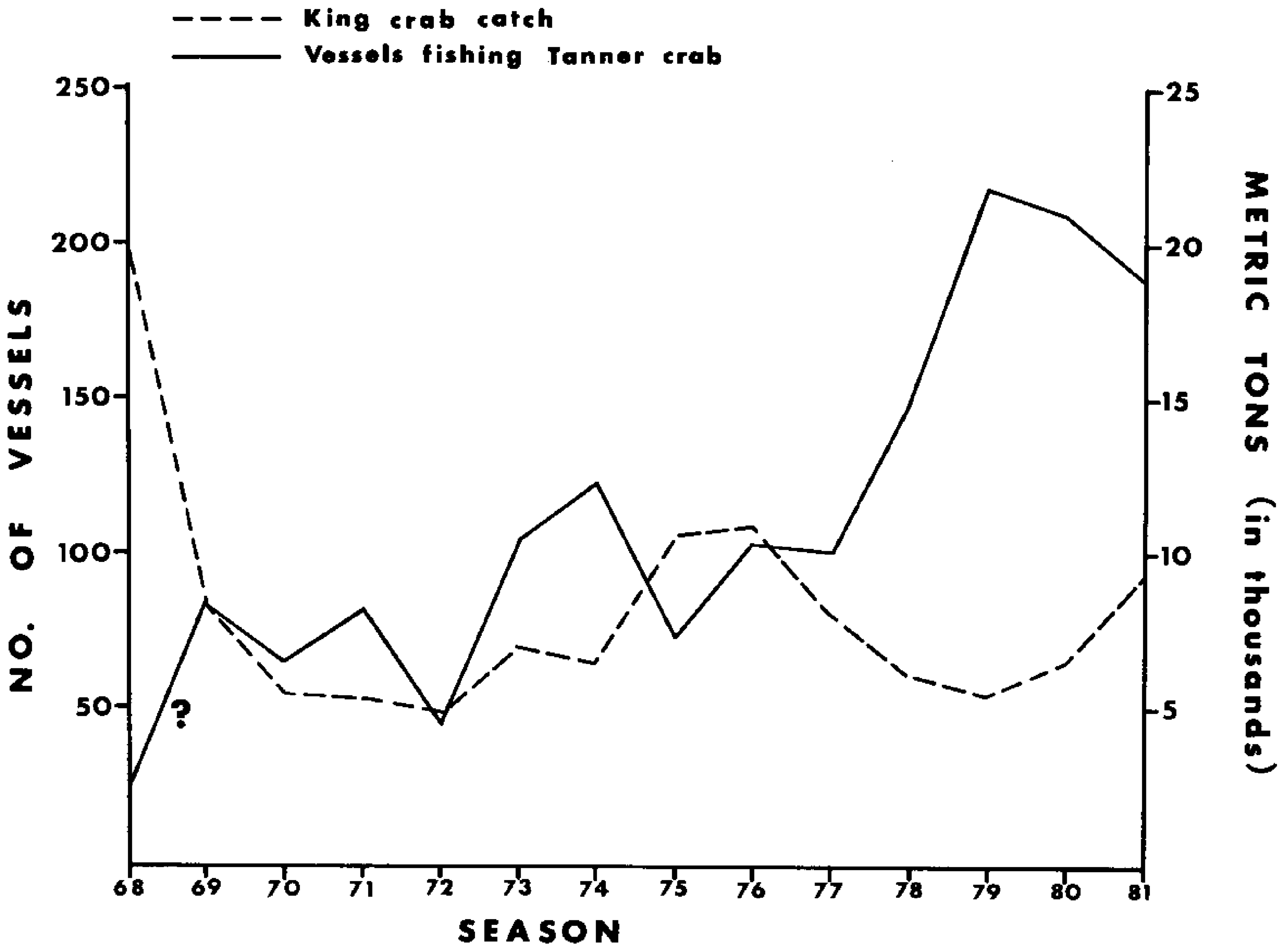

Figure 4.--Relationship between king crab, *Paralithodes camtschatica*, catch and number of vessels fishing for Tanner crab, *Chionoecetes bairdi*, in the Kodiak area, 1968 through 1981 commercial seasons.

Another way of looking at the increases in fishing effort is by examining the number of vessels fishing, the number of deliveries and the number of pot lifts during the commercial seasons. In the Kodiak area, data on the number of vessels and pot lifts for 1967 are not available. However, we do know that the 50.3 mt of Tanner crab delivered that season (Table 2) were the result of 83 vessel landings. The first major increase in fishing effort occurred the following season, 1968, when 817 vessel landings produced 1,161.5 mt of crab. From 1969 through the 1972 fishing seasons, the number of vessel landings and the resulting production averaged 686 and 3,566.0 mt of crab respectively. During this same period an average of 70 vessels fished lifting an average of 69,472 pots each season.

The next major increase in fishing effort occurred during the 1973 fishing season as market conditions improved for Tanner crab. The number of vessels fishing increased to 105, a 67% increase over the 70 average of the previous four seasons (Figure 4). The number of pot lifts also rose dramatically to 188,158, a 171% increase over the previous four season average. The 1,466 vessel landings were more than double the previous four season average, an increase of 114%.

The third major increase in fishing effort spanned two commercial fishing seasons, 1978 and 1979. In 1979 the number of vessels fishing in the Kodiak area reached the historic high of 218 (Figure 4). The number of pot lifts was 275,455, the second highest on record. Vessel landings decreased to 1,225 which was actually lower than the landings during the 1973 season.

This three step increase in effort on the Tanner crab resource observed in the Kodiak area seems to have occurred in most of the other areas of the GOA. Southeastern, Prince William Sound, Cook Inlet, South Peninsula-Chignik and the Aleutians (seasonal catch records for the last three areas were combined until the 1974 season when the Aleutians were recorded separately) recorded their first significant catches of Tanner crab in 1968 with subsequent catch increases during the 1969 season. In terms of catch the 1973 fishing season showed the most pronounced harvest increases in each of the GOA areas (Figure 5).

Taking a closer look at the catch histories of the GOA areas (Figure 5 and Table 2) shows several with erratic harvest patterns. This is particularly true of the Kodiak, Prince William Sound and South Peninsula-Chignik areas. Cook Inlet, Southeastern and the Aleutians seem to experience less fluctuation in Tanner crab harvests. These fisheries are local in nature and less fishing pressure on the available stocks in Southeastern and the Aleutians areas may be partially responsible for the relative stability of the catches, particularly since the 1975 season. Cook Inlet has experienced considerable fishing activity and certain management practices may be responsible for the relatively stable catches since the 1975 season.

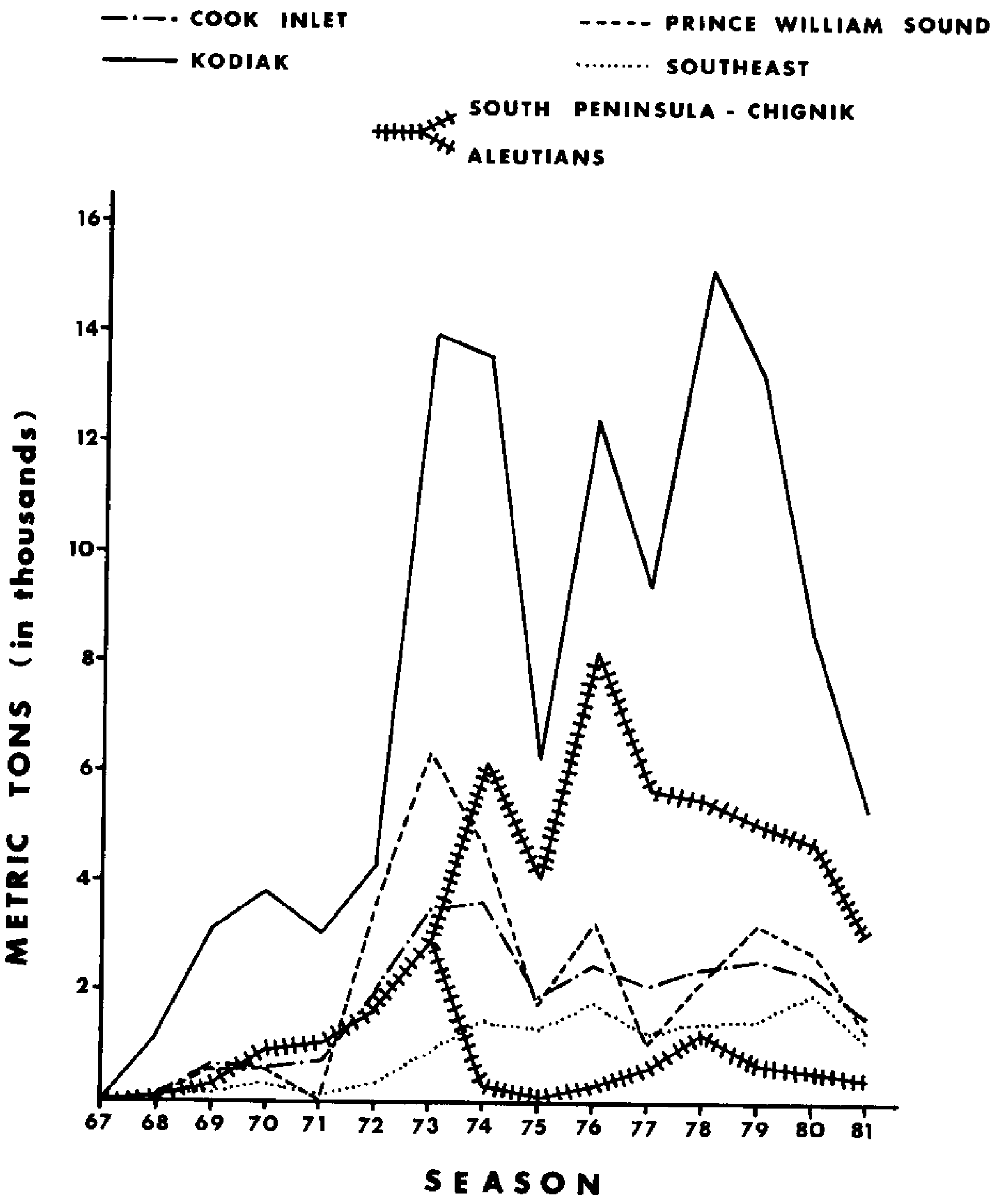

Figure 5.--Tanner crab, *Chionoecetes bairdi*, catch in the Gulf of Alaska by area, 1967 through 1981 commercial seasons.

A few other points should be mentioned with regard to the catch histories of the GOA areas (Figure 5). The dramatic decline experienced in all areas in 1975 was due to the prolonged price negotiation (strike) which delayed the start of the season in all areas. Also, with the exception of the Aleutians area, Tanner crab harvests declined in 1977 due to the imposition of a size limit by the Alaska Board of Fisheries. Lastly, with the exception of the Southeastern area, all GOA areas experienced declining catches in 1980 and 1981. These declines probably reflect actual declines in the available stocks of Tanner crabs.

Research

General

Research on the genus *Chionoecetes* has developed, primarily, in areas where the fisheries began. Prior to 1970 the Tanner crab fishery in Japan stimulated research on *C. opilio* (Yoshida 1971; Ito 1963, 1967, 1968; Kon 1969; Kon et al. 1968; Yosuda 1967; and others) and *C. japonicus* (Fukataki 1965). Similarly the development of a fishery for Tanner crab in maritime Canada stimulated research on *C. opilio* in the northwest Atlantic (Brunel 1960; Deveau and Aucoin 1966; Powles 1966, 1968; Watson 1969). In the eastern North Pacific area, including the Bering Sea, aside from the early taxonomic and distributional studies of the genus (Rathbun 1925; Slipp 1952; MacGintie 1955; Garth 1958), work was done on *C. tanneri* off the coast of Oregon/Washington (Pereyra 1965, 1966) and preliminary research began on *C. opilio* and *C. bairdi* in the Bering Sea (Karinen 1969; Takeshita et al. 1969). Very little work was conducted on *C. bairdi* in the GOA before Bright's (1967) study of the natural history of the king crab, *Paralithodes camtschatica*, and the Tanner crab, *C. bairdi*, in lower Cook Inlet. Some distributional survey data which included *C. bairdi* had been published earlier (IPHC 1964; Hitz and Rathjen 1965) for the northern GOA.

As the Tanner crab fishery in the GOA became established (by 1970) it became apparent that little was known about the biology and behavior of *C. bairdi* that would be of value to fishery managers. Preliminary work began in the Kodiak area on defining the size at maturity and the size of mating males (Brown and Powell 1972). Using morphometric measurements, reproductive tract weights and size of pre-copulatory males, Brown and Powell concluded that 50% of the males are mature at about 110 mm carapace width (CW). With regard to mating males, they found that all grasping males (they observed 48 mating pairs over a five year period) were at least 14 mm larger than their female partners. Preliminary work on *C. bairdi* growth began in the Prince William Sound area by analyzing width-frequency distributions of crabs captured by various means and times of the year (Van Hyning and Cooney 1972). They found distinct size groupings among the juvenile crabs while crabs above 100 mm CW tended to be lumped together in one mode (due to the effects of skip molting in mature crabs).

The first major work on female *C. bairdi* was undertaken by Hilsinger in 1973. The study emphasized reproductive biology using crabs captured off

Prince William Sound and some of his results laid to rest a number of erroneous conclusions on Cook Inlet Tanner crabs drawn by Bright (1967) which conflicted with the findings of investigations on other members of the genus (Hilsinger 1976). He found that while a few adult females may molt, for the most part the female molt to maturity in *C. bairdi* is a terminal molt. He also determined that the female reproductive cycle in *C. bairdi* was five or six months longer than that reported by Bright (1967).

The Alaska Department of Fish and Game (ADF&G) began the first long term study of *C. bairdi* in the GOA in 1973. Partial federal funding for this study was provided by the Commercial Fisheries Research and Development Act (Public Law 88-309 as amended). The main objectives of the project included, 1) determining growth and age at size; 2) describing the frequency of the molt; 3) describing the reproductive biology; 4) determining the distribution and relative abundance of Tanner crab with respect to size and sex; 5) assessing the effects of the commercial fishery upon the population; and, 6) observing inter-relationships between Tanner crabs and other marine organisms (Donaldson and Dick 1977). Federal funding for this research ended in 1981.

Since it is not within the scope of this review to give a detailed description of the research conducted over the past decade, I will mention the highlights of the program and, hopefully, give the reader some sense of where we are in terms of the program objectives stated above. It should be noted that unless stated otherwise the research covered was conducted in the Kodiak area. I, in no way mean to slight work done in other areas of the GOA; however, since the bulk of the Tanner crab harvest from the GOA has been landed from the Kodiak region it was a logical place to conduct most of the research work.

Growth and age at size

Describing the growth rate of a commercially important species is important information to fishery managers. In 1973, a joint ADF&G-University of Alaska effort to develop estimates of growth, age at size and size at sexual maturity of *C. bairdi* from the northern GOA was initiated (Donaldson et al. 1981). Growth, size and age and size at sexual maturity estimates were derived from observations on molting crabs and from modal groups evident in width-frequency distributions of crabs captured by various means and in differing locations at various times of the year. In summary, among juvenile crabs, growth per molt is not significantly different; growth ranged from 25% to 36% for the first to sixth molts preceding the molt to maturity; in mature male crabs growth ranged from 14% to 22% over five molts. Size at 50% maturity for females was determined to be 83 mm CW; these crabs would be 97 mm CW after the molt to maturity. Among males, 90 mm CW seems to be the size at which the puberty molt occurs; these individuals would be 112 mm CW after the molt was complete.

Frequency of the molt

Information on the frequency of the molt was obtained from the same research work (Donaldson et al. 1981). When crabs hatch at a particular time of the year it is possible to follow the discrete width-frequency modes over time. Comparing growth information with observed size frequency modes sampled from the population at various times will give a good idea of the frequency of molting for juveniles. As the inter-molt period becomes less well defined (after reaching maturity) determination of the frequency of molting increasingly becomes a matter of guesswork. Formulating a growth model for male crabs from the size-age relationship of small crabs suggests a gradually increasing intermolt period with crabs < 35 mm CW molting more than twice per year and large crabs (about 150 mm CW) molting every 18 months. It should be noted that male *C. bairdi* may undergo a terminal molt at a size which has not been determined. Few males larger than 180 mm CW are captured in the Kodiak area commercial catch.

Reproductive biology

In 1979 another joint ADF&G-University of Alaska project was initiated to study *C. bairdi* reproductive biology in more detail than previously. Utilizing crabs from the Kodiak Island area the Institute of Marine Science was to conduct work for three years. Some of the objectives were 1) determine the length of time prior to and following molting that a female will attract adult males for the purpose of mating, 2) determine whether oldshell females are capable of mating and will they choose to mate or will they prefer to produce egg clutches using sperm stored in their spermathecae, 3) determine the number of viable egg clutches and the number of eggs extruded by a female relying on stored sperm compared to females which have recently mated, 4) determine how much sperm is stored and how many eggs are produced by females after they have mated with various size males, 5) determine what percent of a random sample of oldshell females are barren due to senescence, and 6) determine if males mate more than once in the breeding season. Answers to all these questions could have management implications if a population of crabs becomes reproductively stressed through fishing pressure or some other means. The third and final year's work is currently underway in Seward. Results of this study are reported elsewhere in these proceedings.

Reproductive potential as a function of egg clutch size has been measured on the population indexing surveys in most north central and western GOA areas since 1976 (Table 3). Adult female crabs which were not carrying egg clutches at the time of capture were classified as barren. The highest incidence of barren female *C. bairdi* has consistently been recorded in the Kodiak area. Even there, however, the percent of barren females has not exceeded 10% of the adult females captured.

Distribution and relative abundance

In 1973 the ADF&G initiated an experimental survey program which used king crab pots as the means of capture. Although the program was designed to assess red king crab populations (Powell et al. 1974), Tanner crab work was included due to the fact that they would readily enter king crab pots. The primary goals of these surveys was to estimate the annual relative

Table 3.--Percent of female Tanner crabs, *Chionoecetes bairdi*, that were not carrying eggs at the time of capture, 1977 through 1981 population index surveys.

Area	1977	1978	1979	1980	1981	$\overline{X}$ All years
Kodiak	4.4	9.5[1]	6.7	8.5	3.4	6.5
Eastern Aleutians	1.0	-	2.6	3.5	2.1	2.3
Sand Point	1.3	3.3	2.7	3.0	7.9	3.6
Cook Inlet	2.0	1.9	1.5	4.3	7.6	3.5

[1] only south end of Kodiak Island surveyed.

abundance of legal size males and predict recruitment trends 2-4 years in advance of crabs attaining commercial size. These estimates would allow the ADF&G to establish annual harvest levels and recommend harvesting strategies in order to obtain the optimum yield under certain management policies established by the Alaska Board of Fisheries and the North Pacific Fisheries Management Council.

The ninth year of the Kodiak crab pot indexing survey was completed in 1981. Similar surveys were initiated in lower Cook Inlet, Prince William Sound and the South Peninsula areas in 1974, and the Eastern Aleutians in 1975. In the Western Aleutians area surveys were conducted in 1975, 1976 and 1977. An example of the type of information the ADF&G obtains from the surveys using pots is numbers of male crabs captured by size group (i.e. Kodiak area) (Table 4) (Donaldson and Hicks 1980; Colgate and Hicks 1982). It is evident from the variations in pot lifts between surveys that the numbers of crabs captured are not necessarily comparable. More importantly small Tanner crabs ($\leq$ 114 mm CW) do not seem to enter pots in predictable numbers from survey to survey; thus little can be determined regarding future recruitment trends. Problems in the pot survey data are compounded by the fact that the total area fished changes frequently due to fluctuations in funding or changes in priorities. We do use changes in the relative abundance of legal size crabs at stations fished consistently for several years as our primary management tool along with in season catch data. The smallest Kodiak area population unit we have confidence managing on this basis is crab "stocks" which have been estiblished primarily as a result of migration information (Table 5 and Figure 6) (Donaldson 1980a).

Due to problems in acquiring data on Tanner crab necessary to meet our management objectives from the pot survey, interest has been generated in the use of trawls to survey the Tanner crab resource in the GOA as has been done by the National Marine Fisheries Service in the Bering Sea. An experimental program to test this possibility began in 1980 and is continuing. The preliminary results of the trawl survey program are presented in another paper in these proceedings.

Since intelligent management of the *C. bairdi* resource depends on accurate knowledge of the species growth, frequency of molting, migration and population abundance, a tagging method which is practical, permanent and identifies specific individuals is highly desirable. A number of attempts to develop such a tag using a basic T-bar design have been disappointing. Tag placement is critical in that tags easily hang up in the old exoskeleton during ecdysis which effectively prohibits the successful completion of the molt (Colgate and Hicks 1982). Vessel hold studies in 1979 with similar tags showed a significant amount of tag clipping and removal by other crabs (Donaldson 1980b). Work is continuing on the development of an acceptable tag.

In order to obtain information on fishing mortality, migration and, to some extent shell aging, the ADF&G has utilized a non-permanent carapace dart tag on legal sized crabs captured during the Department's surveys. Tag recoveries have generally been poor in the Kodiak, South Peninsula and

Table 4.--Number of male Tanner crabs, *Chionoecetes bairdi*, captured by size group and percent total catch, 1973-1981 Kodiak area pot surveys. Catches are standardized to a 24-hour soak period.

Group (mm)	1973		1974		1975		1976		1977		1978*		1979		1980		1981	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
≥ Fours ≤ 69	52	.2	41	.1	7	.0	6	.0	4	.0	1	.0	5	.0	26	.2	11	.1
Threes, 70-91	179	.8	947	2.8	122	.4	185	.6	36	.0	4	.0	70	.5	179	1.5	83	.8
Twos, 92-114	1,252	5.9	4,064	12.2	1,836	6.2	2,195	6.6	561	2.6	281	3.5	813	6.2	1,317	11.4	947	9.1
Ones, 115-139	4,934	23.3	9,510	28.7	8,829	29.7	10,088	30.1	6,135	27.9	3,053	37.2	4,782	36.2	4,814	41.6	4,316	41.6
Recruits, Newshell 140-164	5,822	27.4	7,035	21.2	5,288	17.8	6,931	20.7	7,293	33.1	3,184	26.6	2,409	18.2	2,390	20.6	3,873	37.3
Postrecruit 1's Oldshell and Very Oldshell 140-164	4,614	21.7	6,209	18.7	9,499	31.9	9,394	28.0	4,826	21.9	1,920	23.4	3,180	24.1	1,786	15.4	394	3.8
Postrecruit 2's ≥ 165	4,354	20.5	5,368	16.1	4,065	13.7	4,703	14.0	3,142	14.3	742	9.1	1,935	14.6	1,062	9.2	752	7.2
Total Legals ≥	14,790	69.7	18,612	56.0	18,852	63.3	21,028	62.8	15,261	63.3	4,846	59.1	7,524	57.0	5,238	45.3	5,019	48.4
Total crabs	21,207		33,170		29,734		33,504		22,009		8,194		13,193		11,572		10,376	
Pot Lifts	1,990		2,017			1,895		1,946		1,646		895		1,709		2,339		1,793

Table 5.--Mean catch/pot of legal ($\geq$ 140 mm CW) male Tanner crab, *Chionoecetes bairdi*, in the Kodiak area, by stock, 1973 through 1981 population index surveys.

	Kodiak Surveys								
Stock[1]	1973	1974	1975	1976	1977	1978	1979	1980	1981
A	11.9	10.3	9.2	6.8	4.7	-	4.7	2.2	1.2
B	10.7	24.8	10.0	4.4	6.3	-	6.7	2.8	3.8
C	11.0	11.2	16.1	11.9	15.7	5.2	2.0	2.0	0.7
D	8.0	18.9	6.1	14.6	12.4	4.6	2.3	4.1	6.6
F	1.0	3.3	14.1	23.1	7.1	-	6.0	3.2	8.7

[1] See Figure 6 for stock locations. Stocks E, G and H have not been surveyed consistently and are not included.

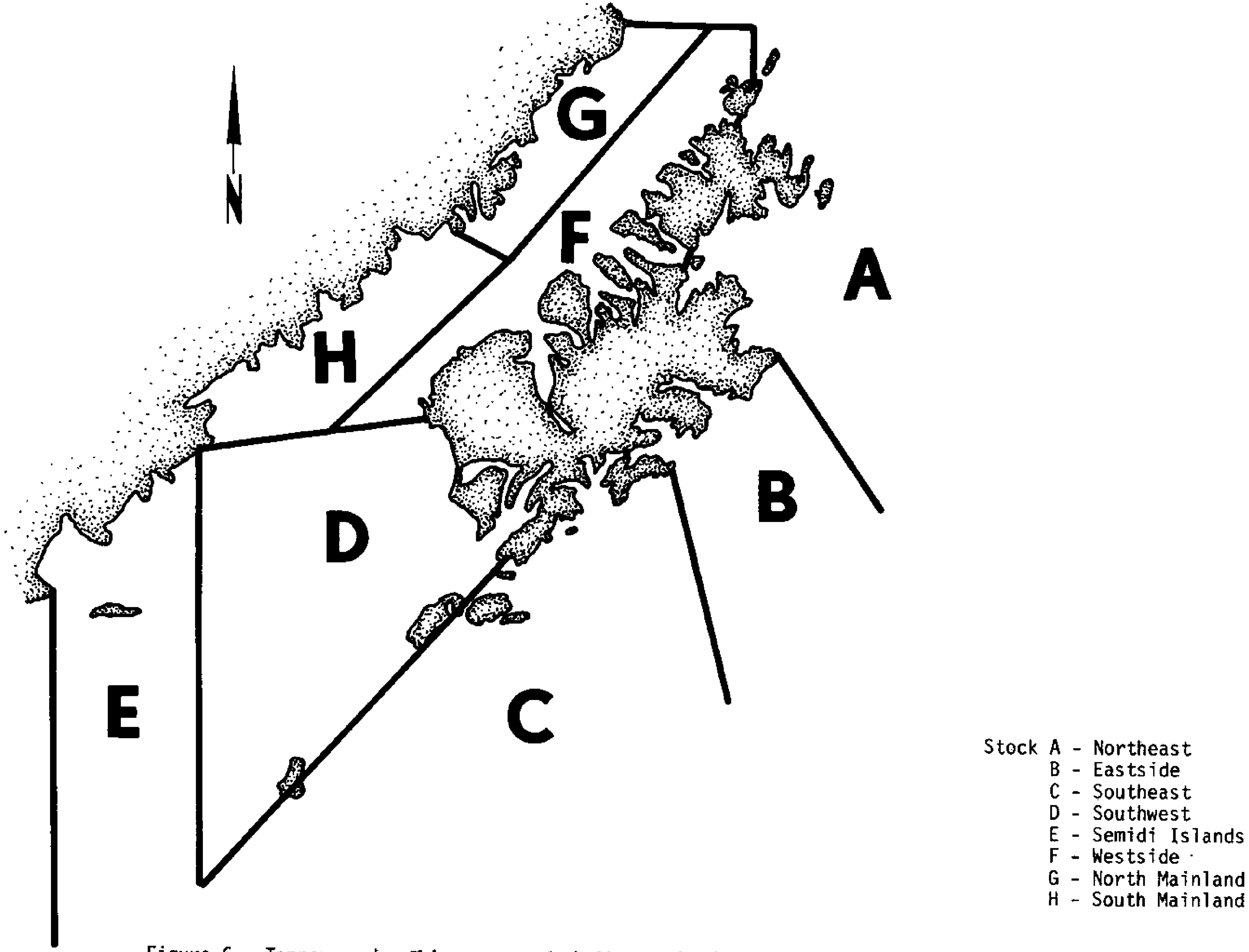

Figure 6.--Tanner crab, *Chionoecetes bairdi*, stocks in the Kodiak area.

Aleutians areas (Table 6) and we have not been able to use them for in season fishing mortality with any confidence. In Cook Inlet tag recoveries increased dramatically when the tagging operation was moved from about June (1974 and 1975) to November (1976 through 1981) (Table 6) (Davis 1980 and personal communication). Tagging crabs soon after the peak molting period (May) when the exoskeleton was relatively soft may have resulted in large numbers of tags being lost or high tagging mortalities. Tagging in the Kodiak, South Peninsula and Aleutians areas has frequently been conducted in July. This may partially explain the low tag recovery rates in those areas.

Important data on *C. bairdi* migration has been obtained from the non-permanent tagging program in the Kodiak area. A migration study was done using 1973 through 1979 recaptures with accurate recovery data (Donaldson 1980a). The data was analyzed by "CRABWALK", a series of computer programs designed to assist in the analysis of crab migration data. Some of the conclusions of the investigations were that mature male *C. bairdi* tagged in bay areas tended to move to deeper offshore waters while mature males tagged in offshore areas tended to remain there wandering randomly within certain geographic areas (particularly gullies). Individuals may range widely in a particular area though the average movement during the course of the study was only 24 km. No correlation was found between the length of time crabs were free and the distance migrated upon recapture. More work will be necessary to determine if there are seasonal migrations. In terms of management, it seems that relatively independent stocks of mature male *C. bairdi* are definable, at least in the Kodiak area.

Monitoring the commercial fishery

During the 1974 commercial fishing season a fisherman logbook program was initiated by the ADF&G to gather data on the catch per unit of effort for various pot types, soak times and gear locations and to delineate fishing grounds (Donaldson and Dick 1977). Data from the program was of value with respect to in-season evaluation of the catch; however, voluntary participation in the program was not great and it soon became apparent that until a method for standardization of fishing effort is developed, effort related information must be regarded as suspect.

Most GOA areas have dockside sampling programs during Tanner crab season which collect data similar to logbooks by interviewing the fishermen. In addition, samples of 50 randomly selected crabs are collected from many of the catches. Data is taken on size frequency and shell age. In the Kodiak area information on the presence of Black Mat Syndrome is also gathered from commercial catch samples.

Interrelationships with other species and other research

A number of studies dealing with species interrelationships have been conducted in the GOA. One such study described the summer food of the Pacific cod, *Gadus macrocephalus*, off Kodiak Island from stomach analysis (Jewett 1978). The results of this investigation are included in another

Table 6.--Number of tagged Tanner crabs, *Chionoecetes bairdi*, released and percent recovered in the subsequent commercial fishery, 1974 through 1981 commercial seasons.

Area	1974		1975		1976		1977		1978		1979		1980		1981	
	Number Released	% Recovered	Number Released	% Recovered	Number Released	% Recovered	Number Released	% Recovered	Number Released	% Recovered	Number Released	% Recovered	Number Released	% Recovered	Number Released	% Recovered
Kodiak	2,267	16	1,816	10	926	14	2,285	14	1,651[1]	10	665	10	1,338	25	789	18
South Peninsula	NS[2]	-	NT[3]	-	NT	-	1,144	5	1,072	4	1,086	22	322	20	376	14
Eastern Aleutians	NS	-	NS	-	NT	-	98	5	NS	-	145	8	113	11	128	-
Cook Inlet[4]	2,289[5]	5	1,500[6]	8	1,000[7]	8	497[7]	45	438[7]	54	362[7]	29	442[7]	49	500[7]	36

[1] not carapace dart tags
[2] NS = no survey
[3] NT = survey conducted, but no tagging
[4] Southern district only
[5] tagged in early June
[6] tagged in late May
[7] tagged in November

paper herein and will not be discussed here. A similar study was conducted in 1977 in Southeastern Alaska using cod from offshore and inshore areas (Clausen 1981). *Chionoecetes bairdi* was the most common invertebrate encountered in the stomachs and the second most common species in stomachs from all areas combined. It was considerably less frequently encountered in cod from the protected inshore areas - though still quite common.

A study of the epifauna associated with *C. bairdi* in the Kodiak area was done in 1977 (Donaldson and Dick 1977). One hundred five crabs captured during the commercial season were used. So as to be more certain about shell age, 98 of the crabs used were tag recaptures. Of the 40-50 epifaunal forms identified, a bryozoan, *Alcyonidium* sp., was most prevalent (83% of the crabs). Significant differences seemed to exist in the incidence and relative abundance of some epifaunal forms on crabs from different areas within the region. As one would expect, the incidence as well as individual number of epifaunal forms per crab increased with increasing shell age.

Another study of interest is the ongoing Black Mat Syndrome research in the western GOA (Colgate and Hicks 1982). This fungal disease was reported by Brown (1971) as one of the causes of poor market conditions for Tanner crab during the early development of the fishery. The ADF&G began looking at the incidence and distribution of the disease in the Kodiak area in 1979 and the results of that work are presented elsewhere in these proceedings.

Regulations

In an attempt to avoid the pitfalls of overfishing the Tanner crab resource off Alaska, the North Pacific Fishery Management Council in response to provisions of the Magnusen Fisheries Conservation and Management Act of 1976 (U.S. Public Law 94-265) developed a Fishery Management Plan (FMP) for Tanner crab. The plan was adopted in May 1978 and federal regulations went into effect in December 1978. The management plan has three basic objectives:

"1. Minimize fluctuations in stock abundance due to harvest by maintaining the full reproductive potential of the Tanner crab stocks.

2. Insofar as possible, prevent industry overcapitalization and minimize economic distress due to extreme fluctuations in harvest based on naturally fluctuating stock abundance; and

3. Integrate management of Tanner crab stocks with those of other fisheries to maximize economic returns and minimize adverse impact on other stocks." (NPFMC 1978).

Technically, the State of Alaska has jurisdiction over all inland waters and those coastal waters from shore out to 4.8 km while the United States federal government has jurisdiction over the Fishery Conservation Zone which essentially extends from 4.8 km out to 321.8 km. The FMP for Tanner crab has been amended as conditions changed and better information became available.

Hopefully, the plan will evolve into a framework plan similar to that developing for king crab. This would allow flexibility in management depending on stock and industry status and would eliminate the necessity of annually updating the FMP.

According to the FMP, the State of Alaska's regulatory goal emphasizes three primary objectives and procedures to accomplish them:

"1. Maximize yield from harvestable surpluses: This is accomplished by seasons and gear restrictions to increase meat yield per individual crab and reduce mortality on sublegal crab.

2. Maximize reproductive potential of the Tanner crab stocks by: a) imposing seasons, gear restriction, size and sex limits and harvest levels to protect crab during reproduction; b) minimizing mortality on female crab due to handling or harvest; and c) assuring full female fertilization by providing adequate numbers of males of all sizes for breeding.

3. Seek economic stability in the Tanner crab industry. Avoiding overcapitalization based on levels of population abundance which may not be sustained over time by; a) regulating annual harvest to discourage too rapid expansion of harvesting and processing capability until the resource potential can be better evaluated and; b) by stabilizing harvest levels within the range of natural recruitment fluctuation if not precluded by excessive natural mortality beyond the first year at maturity." (NPFMC 1978).

Six main regulatory categories are utilized by the State of Alaska to meet these objectives. Briefly described, they are:

Fishing seasons

In order to sustain optimum levels of Tanner crab production seasonal closures are required which encompass peak molting periods as well as the egg hatching and breeding seasons. Season opening dates are set long enough after the peak molting period to insure maximum weight gain for a high quality product.

Sex limitation

The combination of a prohibition against harvesting female crabs and the maintenance of an adequate mature male population for breeding purposes should (under "normal" environmental conditions) result in full female fertilization which would protect the reproductive potential of the Tanner crab.

Size limit

Chionoecetes bairdi could be commercially harvested at the size of maturity (about 112 mm CW). In order to provide a large population of breeding males to insure the reproductive viability of the population a certain portion of the desirable size mature male crabs must be saved from harvesting for reproductive purposes. Since nearly all *C. bairdi* males are mature at 135 mm CW a size limit of 140 mm CW has been imposed statewide with the exception of Prince William Sound where the limit is 134.6 mm CW (for economic reasons). Of course it is possible that full female fertilization might be attained with less than 100% of the mature male population being allowed to mate for at least one breeding season before being exposed to the commercial fishing effort; however, data on the size of the male and female populations along with a knowledge of male breeding efficiency will have to be defined before adopting a less restrictive size limit policy.

Harvest levels

The Tanner crab harvest expanded rapidly during the 1970's and the expansion occurred before adequate biological assessment of the stocks, particularly with regard to reproductive requirements and the development of acceptable predictive capabilities for future recruitment. In order to avoid the possibility of overexploitation of some stocks and the underutilization of others guideline harvest levels have been used to distribute fishing effort among the various crab stocks in the state. They have also served to inform the industry that unrestricted harvest expansion may not be desirable. The harvest guidelines are defined as ranges so as to allow managers flexibility in an area's harvest based on annual population assessment data and to allow adjustments in the harvest based on fishery performance or crab condition. The Alaska Board of Fisheries recently (1982) repealed the use of harvest guidelines as regulation for much of the state since the time frame for proposed changes and resultant fisheries precluded their usefulness.

Fishing area restrictions

Exclusive registration areas have been defined in certain regions in order to help reduce the rate of harvest and prevent economic dislocation of local participants in the industry. In the Gulf of Alaska, exclusive registration areas have been established for Prince William Sound and Cook Inlet.

Gear restrictions

In order to protect non-legal Tanner crab, that is females and undersized males, allowable gear types for capturing crabs are restricted to pots, ring nets and scuba. All are selective in that they permit the safe return of small males and females unharmed. Other types of gear such as trawls and tangle nets can cause high mortalities of non-legal crab.

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ABSTRACT

Although catches of the Tanner crab, *Chionoecetes bairdi*, have been recorded from the Gulf of Alaska since 1961, landings were incidental to king crab catches until 1967. Fishing effort and catches increased fairly consistently from 1967 through 1974 when the record harvest was landed from the Gulf of Alaska. Catches have fluctuated considerably since 1974 and have consistently declined since 1978. In order to obtain the data necessary for adequate management of the Tanner crab fishery in the Gulf of Alaska research is being conducted on the distribution and relative abundance of the Tanner crab with respect to size and sex; assessment of the effects of the commercial fishery upon the population; growth and age at size; frequency of molting; reproductive biology; migration; and documentation of interrelationships between the Tanner crab and other marine organisms. The knowledge gained from the program is necessary in order to accomplish the goals for the management of this resource as stated by the State of Alaska. The federal and state governments share responsibility in the management of the resource. A Fishery Management Plan for Tanner crab has been developed by the North Pacific Fishery Management Council in cooperation with the Alaska Board of Fisheries. The plan is currently under review with the goal of developing a framework for Tanner crab similar to the plan being developed for king crab. The Tanner crab fishery is currently controlled by a number of regulations concerning fishing seasons, types of gear, sex limitations, size limits, fishing area restrictions and harvest levels.

History of Tanner Crab Management off Alaska and the Role of the North Pacific Fishery Management Council

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ABSTRACT

Prior to 1964 the harvest of Tanner crab *Chionoecetes sp.* was incidental to the Alaskan king crab fishery. As bilateral agreements between the United States and foreign nations placed restrictions on the foreign king crab harvest, foreign interest and effort shifted to Tanner crab with catches eventually reaching a high of 57 million pounds in 1969. Management of the foreign Tanner crab fishery off Alaska began in 1969 as a result of additional bilateral agreements. The U.S. fleet first targeted on Tanner crab in 1969, with catches increasing dramatically from a low of 6,800 pounds to over 131,381,000 pounds by 1979. The rapid expansion of the U.S. fleet was primarily due to a decline in king crab stocks, increased markets for domestic harvest, increases in prices, and the eventual elimination of the foreign Tanner crab fishery in 1980.

With the enactment of the Magnuson Fishery Conservation and Management Act in 1976, a new era of fishery management off the United States was begun. By 1977 a Preliminary Management Plan was implemented for the foreign Tanner crab fishery and a Fishery Management Plan developed by the North Pacific Fishery Management Council soon thereafter. Since 1978 the Council has worked in concert with the State of Alaska and the fishing industry to manage the Tanner crab fishery. The Council process and the Tanner Crab Fishery Management Plan have evolved over the last six years into a successful management system. However, some obstacles to proper management have arisen and the Council, in its continuing role as a manager of this fishery, is currently making great strides towards improvement and increased efficiency in Tanner crab management.

THE TANNER CRAB FISHERY

Tanner Crab (*Chionoecetes sp.*) in Alaskan waters are located on the continental shelf from Southeastern Alaska to the Bering Sea. There are two commercially important species of Tanner crab in Alaskan waters, *C. bairdi* and *C. opilio*. Both species are found to a depth of 473 meters and often share their habitat with king crab (*Paralithodes sp.* and *Lithodes sp.*).

The commercial fishery for Tanner crab off Alaska has only recently developed, initiated as a result of changes within the long-established king crab fishery. King crab have been exploited commercially in Alaska since the 1920's and, except for fishing by the Japanese during the 1930's, there were no major fisheries for king crab prior to World War II. Commercial fishing for king crab was revived in 1948 by domestic fishermen. Later both the Japanese and the Soviets entered the post-war fishery for king crab off Alaska, targeting specifically on crab stocks in the Bering Sea. Tanner crab harvest was incidental to the king crab fishery until 1964, when both Japan and the U.S.S.R. increased their effort on this resource. The shift to Tanner crab was largely due to bilateral restrictions by the U.S. on foreign king crab harvest in 1964 and ultimately led to complete closure of the foreign king crab fishery as the U.S. fishery expanded.

The combined Japanese-Soviet Tanner crab catch increased rapidly to about 57 million pounds (25,862 mt) in 1969 and 1970 (Table 1). Since 1970 quotas for Tanner crab sharply reduced foreign landings, eventually forcing the Soviets to leave the fishery in 1971. The quota was again reduced to 16,530,000 pounds (7,500 mt) before the decline in the resource and the increasing domestic fishery completely eliminated all foreign Tanner crab fishing in 1980.

The Tanner crab resource off Alaska was first utilized by the U.S. fleet in 1961, with a total harvest of 6,800 pounds (3.1 mt) valued at $680. Like the foreign fishery, the Tanner crab catch was incidental to the domestic king crab fishery until 1964 when fishermen began to specifically fish for Tanner crab. The harvest rapidly increased to 11,206,720 pounds (5,085 mt) in 1969, 63,906,037 pounds (28,995 mt) in 1974, and continued to increase to an all-time high of 131,381,085 pounds (59,610 mt) in 1979 (Table 2). In 1981 the total Tanner crab harvest was 105,083,460 pounds (47,678 mt) valued at approximately $45 million.

Several factors contributed to the rapid development of the domestic fishery. The king crab (*P. camtschatica*) harvest suffered a steady four-year decline from a peak of 160 million pounds (72,595 mt) in 1966 to about 50 million pounds (22,686 mt) in 1970. During this same period the Tanner crab harvest increased more than one hundred-fold. As observed with the foreign fishery in the early 1960's, this increase was attributed to a change in fishing effort from one fishery to another, in this case from king crab and salmon to Tanner crab.

Another factor was that over the short history of the domestic fishery, the harvest of Tanner crab from the Bering Sea had contributed an increasingly larger share of the total Alaska harvest. Table 2 shows that the percentage contribution of the Bering Sea catch increased from 0.5 percent in 1968 to 76.2 percent of the total harvest in 1981. This was due, in part, to the commercial acceptance of the smaller Tanner crab, *C. opilio*, and the apparent abundance of both *C. bairdi* and *C. opilio* in the Bering Sea in relation to the declining abundance of king crab. In recent years *C. opilio* Tanner crab have made up the largest proportion of the total Tanner crab harvest (Table 2).

Development of Management Regime

Prior to 1964 there were no U.S. regulations for the foreign or domestic crab fisheries. In 1964 the United States ratified the 1958 Continental Shelf Convention and declared king and Tanner crab (among other species) as "creatures of the Continental Shelf." In that same year bilateral arrangements were concluded with both Japan and the U.S.S.R. Quotas and a minimum size limit were applied to their king crab catches. Catch quotas were first applied to the foreign Tanner crab fisheries in 1969 and the use of tangle net

Table 1. FOREIGN AND U.S. CATCH OF TANNER CRAB IN EASTERN BERING SEA 1965 TO 1976[1]
(In Millions of Pounds)[2]

	JAPAN			USSR	U.S.	TOTAL CATCH
	Tangle nets	Pots	Total	Tangle nets	Pots	
1965	2.482	...	2.482	1.603[3]	...	4.085
1966	3.591	...	3.591	1.603[3]	...	5.194
1967	20.051	.699	20.750	8.170[3]	...	28.920
1968	24.341	4.531	28.872	8.411[3]	.014	37.297
1969	23.464	18.931	42.394	15.046	.851	58.291
1970	18.506	25.332	43.838	13.795	1.162	58.794
1971	2.051	35.880	37.931	10.132	.147	48.210
1972	.930	36.649	37.579	...[4]	.104	37.683
1973[5]	...	33.603	33.603	...	.321	33.923
1974[6]	...	33.706	33.706	...	6.102	39.808
1975[7]	...	22.239	22.239	...	6.683	28.922
1976[8]	...	23.240	23.240	...	22.341[9]	44.824
1977		27.562[10]	27.562	...	51.876[9]	79.438

Source: International North Pacific Fisheries Commission.

[1] Chionoecetes bairdi and C. opilio.

[2] The number of crab was converted to number of pounds by using a factor of 2.41 pounds/crab, the weight per crab used by NMFS in their Bering Sea stock estimation (1977).

[3] Estimated by applying number of pounds per case in 1969 to case pack figure in indicated year.

[4] No USSR fishery after 1971.

[5] Japanese catch in 1973 was 14.441 million pounds in Area A and 19.162 million pounds in Area B. Areas are those defined in the 1972 bilateral agreement.

[6] Japanese catch in 1974 was 14.458 million pounds in Area A and 19.249 million pounds in Area B. Areas are those defined in the 1972 bilateral agreement.

[7] Japanese catch in 1975 was 5.256 million pounds in Area A and 16.983 million pounds in Area B. Areas are those defined in the 1974 bilateral agreement.

[8] Japanese catch in 1976 was 5.873 million pounds in Area A and 17.366 million pounds in Area B. Areas are those defined in the 1974 bilateral agreement.

[9] U.S. catch through September only; no further effort expected.

[10] The Japanese quota for the Eastern Bering Sea in 1977 was 12,500 mt. It is assumed that the entire quota was harvested.

Note: Statistics for the USSR fishery provided to the United States by the USSR.

Table 2. Alaska Catch of Tanner Crab[1/] 1967-1981 (units in pounds)

Year	Alaska Total	Bering Sea	Bering Sea % of Total	Bering Sea *C. opilio* only	Bering Sea *C. opilio* as % of Total
1967	118,932	0	0	0	0
1968	3,247,575	17,900	.5	0	0
1969	11,206,720	1,008,900	9.0	0	0
1970	14,473,228	1,487,161	10.3	0	0
1971	12,880,124	166,100	1.3	0	0
1972	30,135,404	119,200	.4	0	0
1973	61,719,396	301,348	.5	0	0
1974	63,906,037	5,044,197	7.9	0	0
1975	46,857,047	7,028,378	15.0	0	0
1976	80,770,981	22,341,475	27.7	0	0
1977	98,475,995	51,876,235	52.7	0	0
1978	130,625,764	67,831,257	51.9	1,715,636	2.5
1979	131,381,085	74,705,265	56.9	32,187,039	43.1
1980	118,988,000	75,883,218	63.8	39,570,668	52.1
1981	105,083,460	80,083,517	76.2	50,483,909	63.0

Source: Alaska Dept. of Fish & Game, *Catch and Production Commercial Fisheries Statistics, Statistical Leaflets Nos. 21-29*
Alaska Dept. of Fish & Game, "Monthly Cumulative Shellfish Catch"
Alaska Dept. of Fish & Game, "Westward Regional Shellfish Management Office Board Report" January 1981

[1/] *C. bairdi* and *C. opilio*

gear was restricted in later bilaterals. These aforementioned bilateral agreements were modified biannually, resulting in progressively lower foreign quotas for both king and Tanner crabs.

Though the U.S. fleet had been harvesting Tanner crab incidental to the king crab fishery since 1961, it was not until 1969 that the first conservation and management regulations were employed in the domestic fishery. The State of Alaska, through the Alaska Board of Fisheries (the Board) and the Alaska Department of Fish and Game (ADF&G), established seasons, required registration, and claimed in-season adjustment power, primarily to control the rapidly expanding domestic fishery. Regulations have been expanded and changed to some degree each year since 1969 to reflect conditions in separate areas.

In March 1977 the Magnuson Fishery Conservation and Management Act of 1976 (the Magnuson Act) became effective, extending U.S. jurisdiction over offshore fisheries within 200 miles of its coast and possessions (the Fishery Conservation Zone) and making it the policy of the land to use some of the most advanced ideas available to manage marine fisheries. Implementation of this law necessitated a level of understanding of fishery resources and the fishing industry that had never before been attempted by the U.S. Government. It required development of methods to balance biological, economic, and social factors relating to fisheries to best serve the national interest. Much of the information necessary for this process still does not exist.

The Magnuson Act established eight Regional Councils to set standards, develop plans, and prepare regulations for management of the fisheries in each region. The North Pacific Fishery Management Council is unique because it works with only one state and possesses the largest geographic area of authority, which includes the fisheries in the Fishery Conservation Zone (FCZ) of the Arctic Ocean, Bering and Chukchi Seas, and the Pacific Ocean seaward of Alaska (Figure 1).

The primary purpose of the Council is to recommend fishery management plans (FMP) to the Secretary of Commerce for approval and implementation. The management plans which the Council develops must, under law, take into consideration domestic, foreign, and recreational fishing. Once it is determined what portion of the allowable catch can be harvested by U.S. fishermen, the remainder must, by law, be allocated as foreign catch. In preparing these FMPs, the Council relies on the most recent biological, social and economic information available, in addition to advice from a variety of committees and the public. When possible the Council identifies and supports research programs to supplement available information.

When the Magnuson Act became effective in March 1977, a requirement for its implementation was the preparation and adoption by the National Marine Fisheries Service of preliminary management plans (PMP) for each individual fishery in which foreign participation might occur. Since there had been a foreign fishery on king and Tanner crab off Alaska, NMFS prepared the Preliminary Fishery Management Plan for King and Tanner Crabs of the Eastern Bering Sea. Unlike an FMP, a PMP focuses solely on foreign fisheries, leaving domestic fisheries unregulated in the FCZ. The development of an FMP that would regulate all Tanner crab fisheries in the FCZ off Alaska became one of the highest priorities of the Council. As development of the FMP progressed,

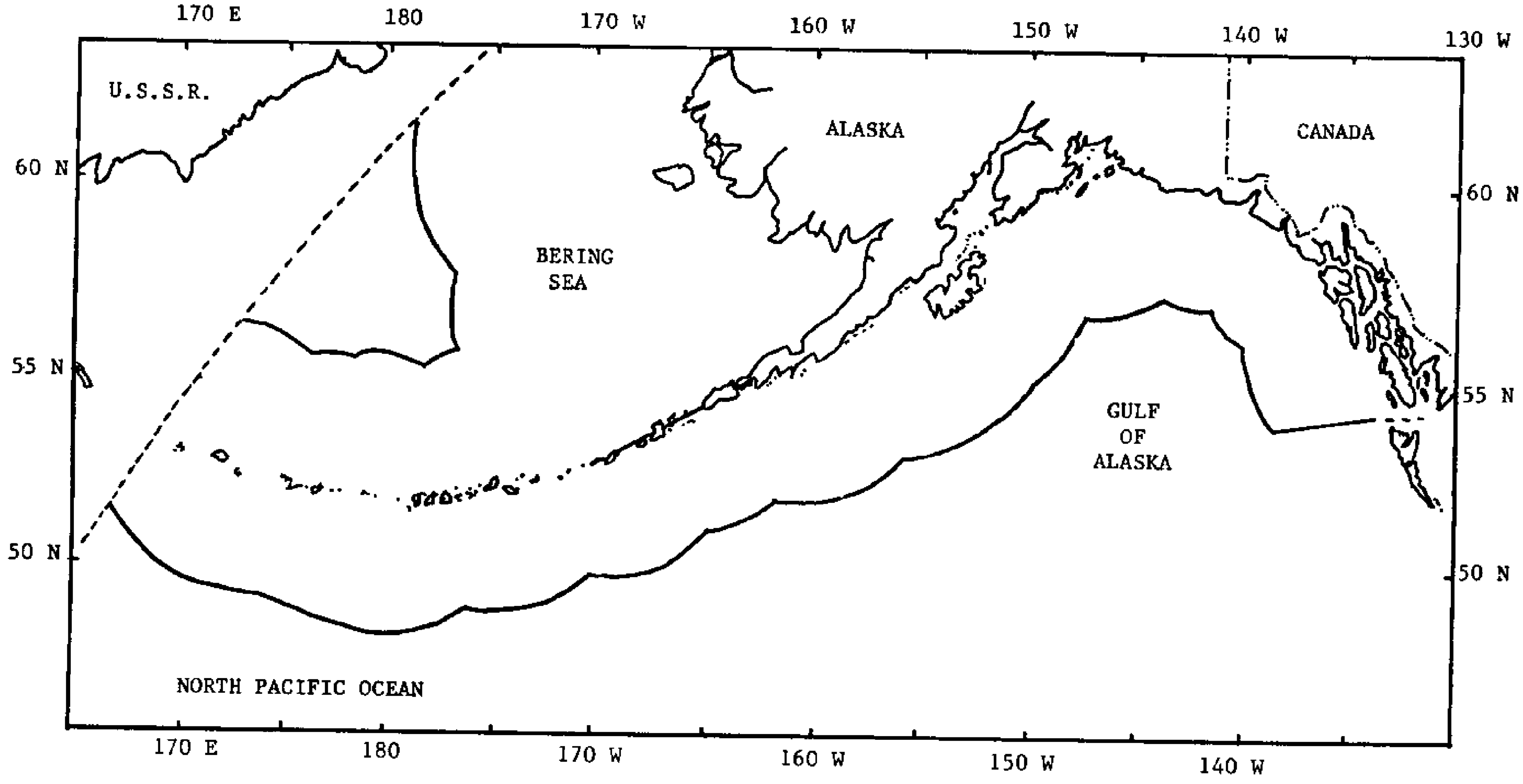

Figure 1. The Fishery Conservation Zone off Alaska.

so did ADF&G's management regime for Tanner crab. The Council worked closely with the Board, ADF&G, and NMFS to develop a management strategy that would be acceptable to all the agencies. The result of this effort was the Fishery Management Plan for Tanner Crab off Alaska, which was implemented by the Secretary of Commerce in May 1978. The management measures adopted by the Secretary mirrored those developed by the State of Alaska. The FMP was designed as a one-year plan; amendments were submitted annually, if necessary, as the Council and the State gained further experience in the fishery.

During the six-year history of the Magnuson Act, the Tanner crab fishery has undergone major change. Since 1976 the U.S. crab fleet has more than doubled in size in response to increased king crab abundance, increased U.S. proportions of the total allowable Tanner crab harvest, increased king and Tanner crab markets, and higher prices. The Council responded to these factors by amending the FMP six times, which led to increases in *C. opilio* optimum yield, decreases in *C. bairdi* optimum yield due to declines in *C. bairdi* stocks, and further restrictions on the Japanese Tanner crab harvest. More recently, sharp declines in *C. opilio* stocks and continued growth of the U.S. fishing fleet have required another plan amendment whereby the total domestic harvest will equal the total available biological catch, thus eliminating all foreign fishing for Tanner crab.

It has been during this period that the Council has discovered its greatest obstacles to effective management. First, like with any fishery, the quality of its management is strongly dependent on the quality of its fishery information. When comparing what is known about Tanner crab to a historical, well-developed fishery such as salmon it is apparent that Tanner crab information is limited. In fact, like the fishery itself, Tanner crab research programs have only recently been conducted and until an acceptable data base is collected, the Council must be conservative in its decisions. Even though this management approach protects the biological integrity of the crab stocks, it may not produce the greatest return to the fishing industry.

A second problem is the FMP and amendment review process. Due to administrative changes the time required for amending a plan has been significantly lengthened. This severely limits the Council's effectiveness. Plans now become gravely out of date with the fishery and lose all usefulness as a management tool. Major modifications to both the FMP and amendment review process must be made if the Council is to function at all.

Future Outlook

Since the enactment of the Magnuson Act and the creation of the Regional Councils, much has been learned about how we may best manage the fishery resources within the FCZ. The North Pacific Council has developed five FMPs in addition to the Tanner crab plan. From this experience and the relationship established with the State of Alaska and the fishing industry, it is clear that the North Pacific Council and the Council forum provide one of the most successful and frequently used processes for fisheries management. Only under the auspices of the Magnuson Act can fisheries issues be routinely examined, discussed, and acted upon. However, the Council recognizes that the current management process and the Tanner crab plan do have their weaknesses, and they are currently attempting to make improvements wherever necessary. Administratively the future outlook for the Council's Tanner crab FMP is to create a more flexible plan, one that will enable the Council and NMFS to respond more rapidly to changes within the fishery without requiring a plan amendment.

It is also apparent that with the observed fluctuations in Tanner crab stocks and the lack of scientific information to explain them, further research is desparately needed. In an economic environment that is rapidly eliminating some very important studies, the Council is continuing its efforts to direct available funds to these programs.

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An Overview of the Eastern Bering Sea Tanner Crab Fisheries

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INTRODUCTION

The development of eastern Bering Sea tanner (snow) crab fisheries for *Chionoecetes bairdi* and *C. opilio* proceeded in three phases. At first, tanner crab catches were small and taken incidentally. During the second phase, directed fisheries were established by Japanese and, to a lesser extent, Soviet fishermen. The third phase was the development of domestic fisheries that culminated in the prohibition of foreign fishing within the 200 mile U.S. Fisheries Conservation Zone.

As is frequently true, fisheries for less valued species developed as incidental catches in more lucrative fisheries. Foreign and domestic fisheries for *C. bairdi* developed as offshoots of king crab (*Paralithodes camtschatica* and *P. platypus*) fishing, and *C. opilio* fisheries developed from efforts directed at *C. bairdi*. Declining abundance of the more valued species and more stringent management measures catalyzed transitions from incidental to directed fisheries.

Available data from commercial fisheries and surveys conducted by the National Marine Fisheries Service (NMFS) provide an index to fluctuations in stock abundance for the last 15 years. Unfortunately, neither source provided complete coverage of commercially exploitable portions of tanner crab stocks until recently. A complete and continuous record of abundance is available only from 1978 onward. Consquently, estimates of average yields that can be expected from tanner crabs in the eastern Bering Sea fisheries are rudimentary. Record high catches of both species have been taken within the past 5 years. Fishery and research data, however, indicated declining stock abundance for both species since 1975. Current catch rates in domestic fisheries are the lowest on record. While the significance of these trends is not clear relative to long-term expectations, it is obvious that declines in commercial stocks of *C. bairdi* and *C. opilio* have been severe.

Eastern Bering Sea tanner crab fisheries are fully developed. While some changes in management might increase potential yields, these increases would be largely dependent upon the feasibility of harvesting, processing, and marketing smaller crabs. Other species of *Chionoecetes* (*C. tanneri* and *C. angulatus*) that are found in the area are not currently marketable and fishery development is improbable. The future of EBS tanner crab fisheries is, hence, related to variations in stock abundance, and dependent on economic factors or technological innovations rather than expansion of fleets or processing capability.

FLEETS, VESSELS, AND GEAR

Four separate fleets have participated in eastern Bering Sea tanner crab fisheries over the past 30 years. Chronologically these fleets entered the fishery as follows: Japanese mothership fleets, Soviet mothership fleets, U.S. crab vessels, and Japanese independent crab vessels.

The earliest tanner crab fishing was tangle netting from Japanese king crab motherships (factory ships). Each mothership (about 122 m or 5,000 tons) had an associated fleet of small (13-14 m) deck-loaded boats and several scouting vessels. The small boats (kawasaki boats) were used for hauling tangle nets. Scouting vessels were usually trawlers of about 27 m (60-70 tons) and were used to set tangle nets as well as for trawling. A tangle net is simply a large mesh (about 23 cm bar-measure) bottom gill net hung about seven meshes deep. The standard unit of gear was the "tan", which was about 40 m of net. According to Miyahara (1954) about 200 tans were tied end-to-end for each set and each set was fished 5 to 10 days. Aside from substitution of synthetic fibers for cotton twine, methods remained about the same until pot fishing was instituted in 1967. The Soviet fishery was similar to that of the Japanese in that one mothership served a fleet of net-hauling boats.

When pot fishing was instituted, each mothership served four to seven catcher boats that were about 27 m in length (100 tons). The two most recently used motherships were the Keiko Maru (7,519 tons) and the Koyo Maru (7,500 tons). Both were about 137 m in length. Japanese fishermen used top-loading, steel framed, mesh covered pots that were in the shape of a truncated cone. A plastic collar was inserted in the top to prevent crabs from escaping. Pots were about 1.5 m in basal diameter. About 130 pots were fished on a groundline and 15 to 18 lines were fished by each catcher boat. Gear was fished for 3 to 4 days and then pulled with a hydraulic longline puller (gurdy). Crabs were stored in sacks and delivered daily to the mothership. Most mothership operations were conducted in outer Bristol Bay or the Pribilof Island area until the last years of the fishery.

The Japanese independent (land-based) fishery was conducted in the area bounded by 55°30'N lat., the U.S.-USSR convention line, and 175°00'W long. (often called the "triangle area") until 1978. Some fishing occurred east of 175°W long. after 1978. In most years, the catch came largely from grounds situated near the 183 m isobath northwest of the Pribilofs. Japan licensed 28 vessels to fish in the triangle area in 1975 and 31 vessels in 1976 (Beardsley, 1975, 1976). The vessels were larger (40-50 m) than the catcher vessels used in conjunction with mothership operations, and processed their catch aboard. Frozen product was periodically transferred to a supply ship (freighter). Pot fishing operations were similar to those described above.

The U.S. crab fleet consists of steel-hulled vessels that currently average 33 m in length or about 140 tons (Alaska Department of Fish and Game 1982). Vessels in the fishery have ranged from 14 to 45 m over the past 5 years. These vessels have tanks equipped with circulating sea water pumps that allow the catch to be delivered live to shore-based processors. There are, however, about 10 catcher-processor vessels currently participating in the fishery. Many Bering Sea crab vessels are capable of holding 90-100 t of tanner crab but average landings usually do not exceed 36 t per delivery. Hydraulic blocks are used to pull pots, decks are frequently equipped with articulating cranes for stacking or loading gear. Crab vessels have ample deck space and many can carry 200 pots on deck. More than 300 pots are generally fished. Crab pots are constructed of steel frames (often concrete reinforcing bar) and nylon web. The most common dimensions are 2.1 x 2.1 x 0.9 m with an average weight of about 300 kg. Pots are fished singly and each is equipped with its own buoy line.

HISTORICAL TRENDS IN TANNER CRAB FISHERIES

The Early Years (1953-65)

It seems probable that substantial stocks of tanner crabs were detected during Japanese fishing for king crab and yellowfin sole (*Limanda aspera*) during the 1930's. Similary, one would expect that U.S. exploratory trawling in 1940 (Harrison et al. 1942) would have found them. There is, however, little mention of tanner crab until Miyahara (1954) went aboard the *Tokei Maru* to observe the Japanese mothership fishery in 1953. Miyahara reported as follows:

> "The expedition encountered a large population of tanner crabs (*Chionoecetes* sp.), especially in the vicinity of Amak Island. This population was thought to be considerably larger than previously observed."

He also notes that "areas of king-crab abundance were sometimes avoided when large numbers of tanner crab (*Chionoecetes* sp.) or other undesirable forms were present".

While Japanese crab fishing during the 1950's was primarily directed at red king crab (*P. camtschatica*), a small amount of tanner crab fishing occurred. Processing of tanner crabs was reported by Japan for 1953, 1954, 1955, 1958, and 1959 in International North Pacific Fishery Commission (INPFC) Annual Reports (INPFC 1956; Fisheries Agency of Japan 1959, 1960). The largest pack for these years was 3,457 cases of 48 one-half pound (0.23 kg) cans and the total pack for the above 5 years was 7,754 cases. According to the 1970 INPFC Statistical Yearbook (INPFC 1972), 176 tanner crabs are required for one case and the total reported catch during the 1950's was about 1.4 million crabs on this basis. The annual average catch would have been less than 300,000 crabs and, judging from the areas fished, almost all of the catch was *C. bairdi*.

Although there was little directed fishing for tanner crabs, scouting vessel catch records indicated interest in their abundance. Part of this interest was a matter of avoiding heavy concentrations of tanner crabs that interfered with king crabbing. The abundance of tanner crabs in scouting vessel catches, however, undoubtedly influenced the development of directed fisheries. The Fisheries Agency of Japan (1967) noted that: "In 1961, tanner crabs replaced hard-shelled male king crabs as the most numerous category, and since then the proportion of this category in the catch has continued to be overwhelmingly greater than that of any other, without any conspicuous trend of increase or decrease." The trend toward increasing relative abundance of tanner crab as well as the sharp transition in tangle net catch rates that accompanied development of a directed fishery is shown in Fig. 1.

Development of Directed Fisheries (1966-73)

The earliest development of directed fisheries involved redeployment of tangle net fishing. The effectiveness of this tactic is shown by an increase in the Japanese catch rate from 3.3 crab per tan-lift in 1966 to 18.9 crab per lift in 1967. Similarly, Soviet catch rates increased from 5.5 crab per lift in 1967 to 14.4 crab per lift in 1968. Since effort statistics (Table 1) are only available for combined king and tanner crab fisheries, catch rates in portions of Japanese and Soviet fisheries devoted to tanner crabs must have been considerably higher. Japanese fishermen soon developed a pot fishery that was specifically directed at tanner crabs but Soviet fishermen did not.

Most of the development of Japanese and Soviet tanner crab fisheries occurred from 1965 to 1970. Quotas were established in 1969 through U.S.-Japan and U.S.-USSR bilateral negotiations (Table 2). Quotas were met from the beginning. From 1970 to 1972 tangle nets were phased out of the fishery and by 1973 only pots were used. It is apparent that the Japanese fishing industry was committed to developing tanner crab as a substitute for king crab fisheries. The USSR did not make a very strong commitment in this direction. When king crab quotas were severely reduced and it became evident that tangle nets were going to be prohibited, Soviet effort was discontinued. Despite having been allocated quotas in each subsequent year until 1976, the Soviets left the grounds in 1971.

United States fishermen began to harvest tanner crabs in the eastern Bering Sea in 1968 and have harvested them continually ever since. Catches were, however, sporadic during this period and taken incidentally to king crab fishing. A catch of 482,000 tanner crabs in 1970 was not exceeded until 1974.

In summary, the developmental period of directed fisheries was characterized by the redirection of fishing effort, increasingly restrictive king crab quotas, cessation of tangle net fisheries, establishment of the Japanese pot fishery, imposition of the first quotas, and the early beginnings of the U.S. fishery.

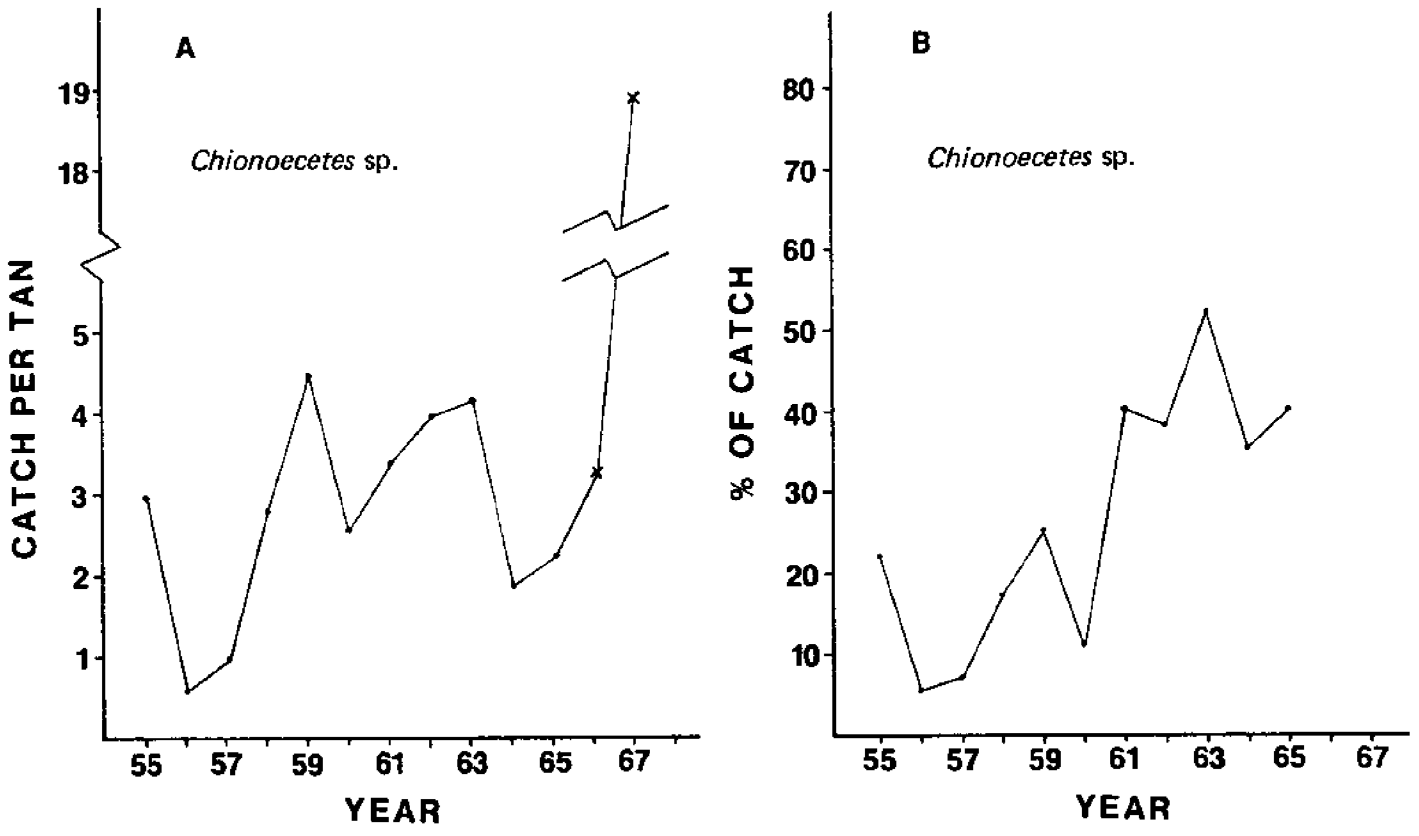

Figure 1. (A) Catch per unit effort by Japanese scouting vessels (points) and early commercial efforts (X's) in the eastern Bering Sea; (B) proportion of tanner crab in all crabs taken by scouting vessels.

Table 1 -- Catch and effort for eastern Bering Sea tanner crab (<u>Chionoecetes bairdi</u> and <u>C. opilio</u>) by various countries.

(catch in millions of crab, effort in thousands of tan or pot lifts) 1/

	Japan 2/				USSR		United States		
	Tangle nets		Pots		Tangle nets 3/		Pots 4/		
Year	Catch	Effort	Catch	Effort	Catch	Effort	Catch	Effort	Total catch
1965	1.030	452.1	-----	------	0.665	616.7	-----	------	1.695
1966	1.490	447.3	-----	------	0.665	617.2	-----	------	2.155
1967	8.320	440.5	0.290	35.3	3.390	657.0	-----	------	12.000
1968	10.100	484.7	1.880	151.6	3.490	242.0	0.006	1.4	15.476
1969	9.736	271.9	7.855	615.1	6.243	248.1	0.353	29.9	24.187
1970	7.679	252.3	10.511	797.1	5.724	228.9	0.482	16.4	24.396
1971	0.871	27.5	14.888	1,111.0	4.204	205.5	0.061	7.3	20.004
1972	0.386	12.1	15.207	1,104.1	-----	-----	0.043	6.7	15.635
1973	-----	-----	13.943	1,023.2	-----	-----	0.133	16.5	14.076
1974	-----	-----	13.986	852.2	-----	-----	2.532	22.0	16.518
1975	-----	-----	9.228	541.0	-----	-----	2.774	38.5	12.001
1976	-----	-----	9.640	563.7	-----	-----	8.950	141.2	18.590
1977	-----	-----	11.932	704.3	-----	-----	20.413	305.1	32.345
1978	-----	-----	20.339	1,872.2	-----	-----	27.456	521.9	47.794
1979	-----	-----	22.919	2,246.2	-----	-----	38.830	584.5	61.749
1980	-----	-----	11.699	1,753.8	-----	-----	40.446	760.5	52.145
1981	-----	-----	------	-------	-----	-----	46.290	994.4	46.290

1/ One tan is approximately 40 m of tangle net. U.S. pots differ substantially from Japanese pots.

2/ From information provided to International North Pacific Fisheries Commission, Japanese catch subject to various area quotas and closures, 1973-79 (see text).

3/ From information provided in bilateral negotiations, catch in 1965-68 estimated from packing statistics.

4/ U.S. catch incidental to king crab fishing until 1974; statistics are from Alaska Department of Fish and Game (1982).

Table 2 -- Quotas established under bilateral crab agreements with Japan and the USSR and under the Magnuson Fishery Conservation and Management Act of 1976 (MFCMA).

Years	Japan		USSR	
	King crab	Tanner crab	King crab	Tanner crab
	(cases) 1/	(number)	(cases)	(cases)
1965-66	185,000		185,000	
1967-68	163,000		100,000	
1969-70	85,000	16,000,000 2/	53,000	40,000
1971-72	37,500	15,000,000 3/	23,000	35,000
---------- Number ----------				
1973-74				
(Area A)	270,000	6,000,000	100,000	1,800,000
(Area B)	430,000	8,000,000	160,000	2,400,000
---------- Metric tons ----------				
1975-76				
(Area A)	0	2,500	0	750
(Area B)	953	7,700	256	2,310
1977 4/				
(Area A)	0	2,500	0	0
(Area A & B)	0	8,100	0	0
(Area A, B & C)	0	12,500	0	0
1978 5/				
North of 58° lat.	0	15,000	0	0
1979 5/				
North of 58° lat.	0	15,000	0	0
1980				
North of 58° lat.	0	7,500	0	0
1981				
Prohibited	0	0	0	0

1/ One case is equal to 48 1/2-pound cans. In producing frozen meat Japan considers 29.3 pounds of king crab meat equivalent to one case. Retention of female crab prohibited in all years.

2/ Plus an allowance of 15%.

3/ Plus an allowance of 10%.

4/ Under MFCMA 1977-81.

5/ Japanese fishing was allowed south of 58°N lat. and west of 173°W long. during a portion of the season. Catches were small and retention of *C. bairdi* was prohibited.

Full Development (1974-82)

This period is characterized by the development of U.S., and phasing out of Japanese, fisheries. Throughout this period, Japanese quotas existed both by catch and area (Fig. 2). United States fisheries developed in the southeastern Bering Sea (Bristol Bay) and in the Pribilof Islands. Imposition of smaller quotas and gradual changes in quota areas resulted in diminished competition between U.S. and Japanese fleets. Changes in fishing areas also caused drastic reductions in the proportion of *C. bairdi* in Japanese mothership catches (Table 3). Mothership fleets were largely excluded from the *C. bairdi* grounds by 1977 and almost completely excluded by 1978. Species composition in Japanese mothership catches came to resemble that of the Japanese independent fleet (Table 4) as the areas fished became more similar and finally identical. Regulations promulgated under the Magnuson Fishery Conservation and Management Act (MFCMA) of 1976 prohibited foreign crab fishing within the FCZ in 1981 and thus ended an era of Japanese crab fishing in the eastern Bering Sea that began 28 years earlier.

Development of U.S. tanner crab fisheries was extremely rapid and was soon accompanied by various management measures (Fig. 3 and Table 5). The catch of *C. bairdi* increased more than 8-fold in numbers and 10-fold in weight from 1974 to 1977 (Table 6). Catches of *C. bairdi* peaked in 1978 at 26.2 million crab or 30,400 t. Small amounts of *C. opilio* were included in the *C. bairdi* catch prior to the first directed efforts for *C. opilio* in 1978. By 1979 the number of *C. opilio* taken exceeded that of *C. bairdi* and had increased more than 17-fold in that year. By 1980 the catch of *C. opilio* exceeded that of *C. bairdi* both in number and weight. The *C. opilio* catch in 1981 again exceeded that of *C. bairdi*. Due to sharp declines in abundance of red king crab, *C. opilio* became the dominant species in the U.S. crab catches in the eastern Bering Sea. The 1981 *C. opilio* catch of 34.4 million crab or 23,900 t established a U.S. record. This catch had, however, been exceeded by combined U.S.-Japanese catches of 47.6 million and 35.5 million crab in 1979 and 1980.

The 1982 tanner crab fishery is now in progress and low catch rates of *C. bairdi* prevail (Table 7). As of 25 April it appeared that catch rates of *C. bairdi* are low enough (5 to 10 crab per pot) that they are being taken incidentally in a fishery targeting mostly on *C. opilio* (35 to 64 crab per pot) in spite of the lesser price ($1.77 for *C. opilio* versus $3.09-$3.53/kg for *C. bairdi*). Competition for *C. opilio* among U.S. vessels is extremely high at present and, for the first time, the U.S. fishery is active north of 58°N lat. In the short space of 4 years, the least-valued, last-developed resource has become first in volume and may even become first in value.

Tanner crab fisheries in the eastern Bering Sea could be considered as fully developed from 1977 onward in that either U.S. or Japanese fishermen were exploiting the entire area where commercial-size crabs

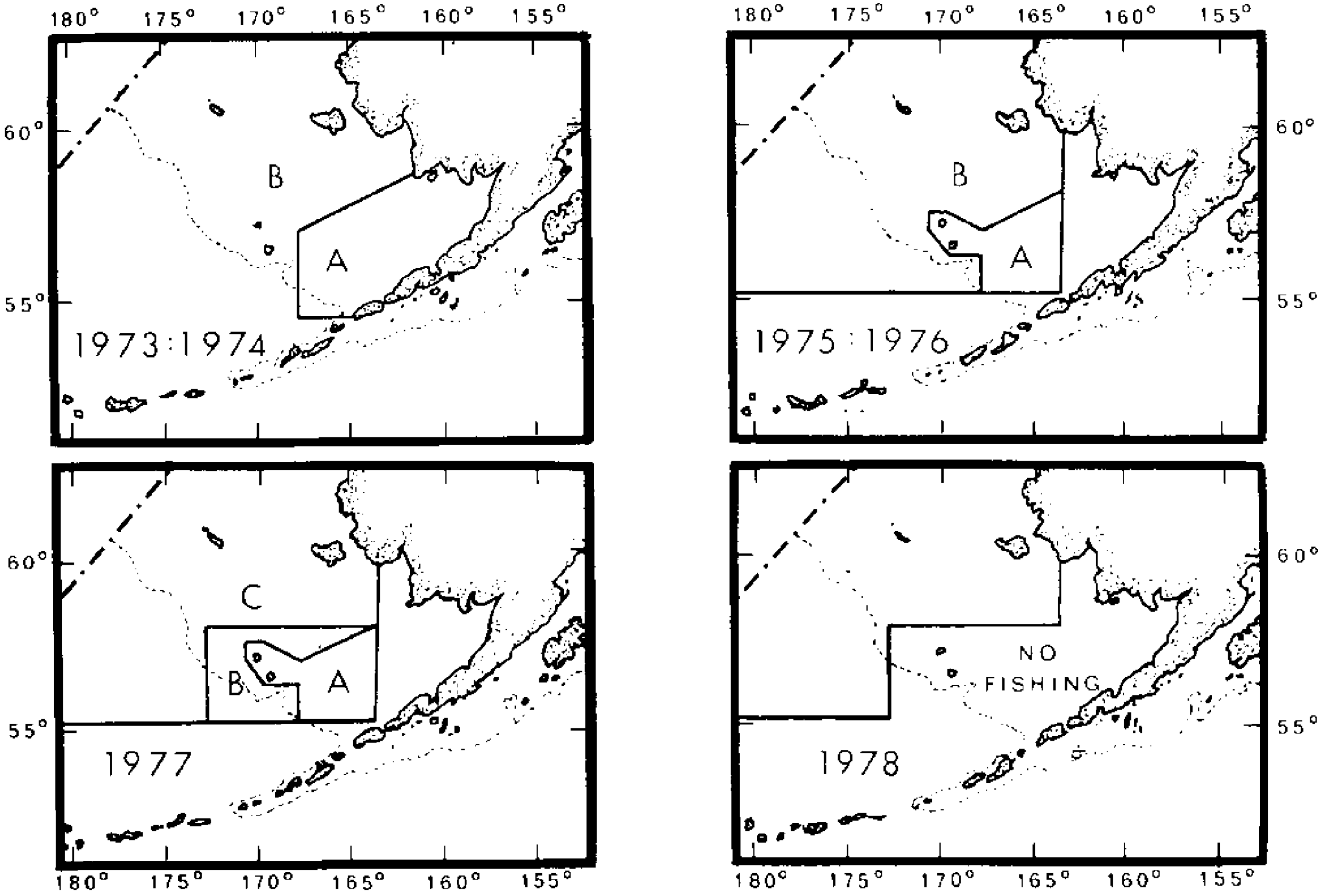

Figure 2. Quota areas for Japanese and Soviet crab fisheries in the eastern Bering Sea. Areas from 1973 to 1976 were negotiated through bilateral agreements; 1977 areas result from the Preliminary Management Plan for king and tanner crab fisheries, and the 1978 area is from the North Pacific Fishery Management Council fishery management plan for tanner crab.

Table 3 -- Estimated species composition of Japanese mothership catches of eastern Bering Sea tanner crabs. 1/

		Catch (1,000's of crab)			Percentage of
Year	Area	*C. opilio*	*C. opilio*	Total	*C. opilio*
1970	A	15,880	836	16,716	5
	B	811	663	1,474	45
	Total	16,691	1,499	18,190	8
1971	A	12,731	670	13,401	5
	B	1,286	1,052	2,338	45
	Total	14,017	1,722	15,739	11
1972	A	13,828	728	14,556	5
	B	986	52	1,038	45
	Total	14,814	780	15,594	5
1973	A	5,812	180	5,992	3
	B	3,657	4,294	7,951	54
	Total	9,469	4,474	13,943	32
1974	A	5,519	480	5,999	8
	B	5,112	2,875	7.987	36
	Total	10,631	3,355	13,986	24
1975	A	2,209	192	2,401	8
	B	4,438	2,389	6,827	35
	Total	6,647	2,581	9,228	28
1976	A	2,410	24	2,434	1
	B	3,459	3,747	7,206	52
	Total	5,869	3,771	9,640	39
1977	A	2,354	98	2,452	4
	B	2,221	4,945	7,166	69
	C	112	2,136	2,248	95
	Total	4,687	7,179	11,866	61
1978	S. of 58° lat.	0	1,578	1,578	100
	N. of 58° lat.	1,600	12,662	14,262	89
	Total	1,600	14,240	15,840	90
1979	S. of 58° lat.	0	1,715	1,715	100
	N. of 58° lat.	1,569	15,355	16,924	91
	Total	1,569	17,070	18,639	92
1980	N. of 58° lat.	1,084	4,414	5,448	81

1/ Japanese catch sampling data used for species composition in 1970-76; U.S. observer data used in 1977; data from International North Pacific Fisheries Commission Annual Proceedings used in 1978-80.

Table 4 -- Fishery statistics from the Japanese independent vessel (land-based) fleet. 1/

	Vessels	Vessel days	Catch		% C. opilio		Catch per day	
			t	1,000's	t	1,000's	t	1,000's
1975	28	1,115	2,100	2,919	----	-------	1.9	2.5
1976	31	1,477	2,109	2,929	----	------	1.4	2.0
1977	11	620	2,721	3,677	N/A	98.5	4.4	6.2
1978	11	832	3,271	4,462	83.0	86.3	3.9	5.1
1979	11	1,026	3,200	4,273	92.0	92.0	3.1	4.2
1980	14	1,497	4,200	6,251	91.0	98.4	2.8	4.1

1/ Provided by Japan during bilateral negotiations (1975-77); U.S. observer estimates (1978-80).

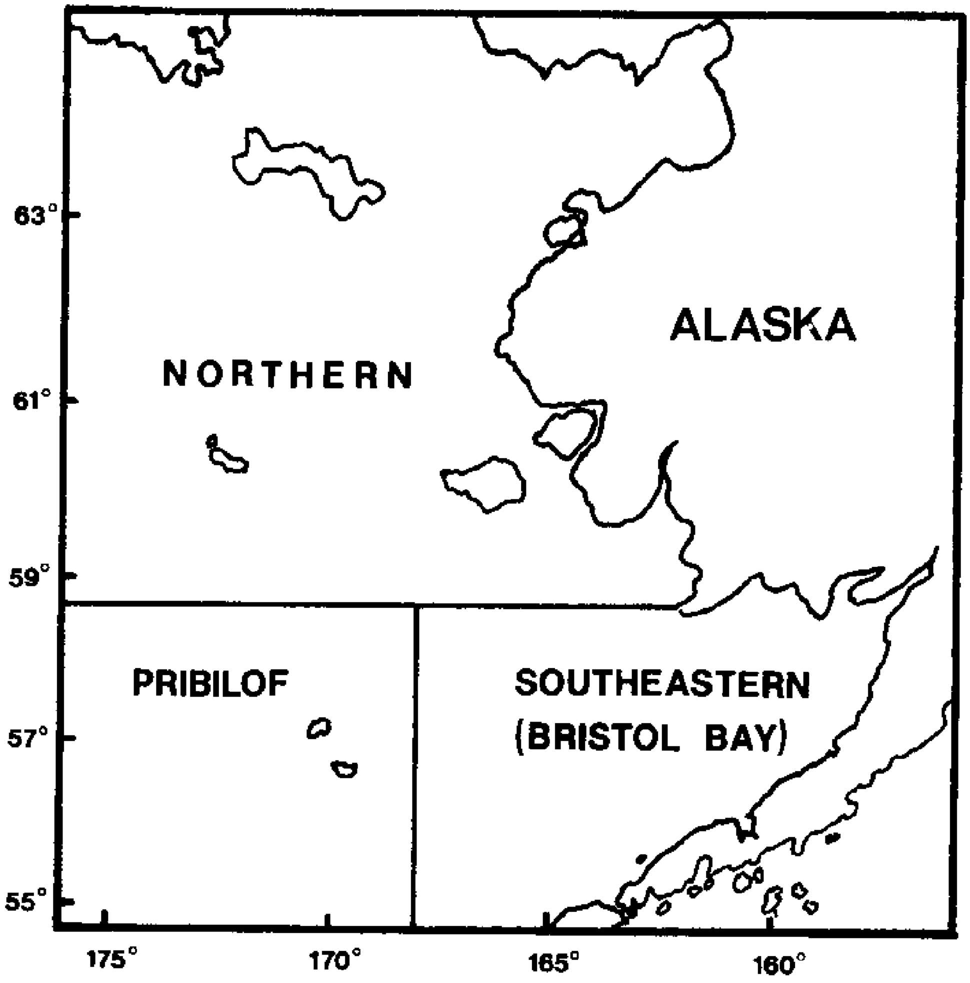

Figure 3. Statistical districts for U.S. tanner crab fisheries in the eastern Bering Sea (modified from Alaska Department of Fish and Game 1982).

Table 5 -- Development of U.S. regulatory measures for Bering Sea tanner crabs. 1/

Year	Season 2/	Guideline harvest level	Size	Gear
C. bairdi				
1973-74	None	None	None	Pots, ring nets, diving gear and pot tunnel limited to 157 mm height
1974-75	7/01-6/15 3/	None	None	Same except pot tunnel limited to 197 mm
1975-76	7/01-6/15	None	None	Same
1976-77	7/01-6/15	None	140 mm	Same
1977-78	11/01-6/15	29-43,000 t	140 mm	Same
1978-79	11/01-6/15	18-32,000 t	140 mm	Same
1979-80	11/01-6/15	13-16,000 t	140 mm	Same
1980-81	1/15-6/15	13-16,000 t	140 mm	Same
1981-82	2/15-6/15	13-16,000 t	140 mm	Same
1982-83 4/	2/15-6/15	Not Available	140 mm	Same
C. opilio				
1977-78	11/01-8/15	16-27,000 t	None	Same
1978-79	11/01-8/15	16-27,000 t	None	Same
1979-80	11/01-8/15	59,000 t	None	Same
1980-81	1/15-9/3 5/	18-41,000 t	None	Same
1981-82	2/15-9/3	18-41,000 t	None	Same
1982-83 4/	2/15-9/3	Not Available	78 mm	Same

1/ From: Fishery Management Plan for the Commercial Tanner Crab Fishery the Coast of Alaska, North Pacific Fisheries Management Council (1979) for 1973-76; Alaska Department of Fish and Game (1978, 1979a) for 1977 onward. Guideline harvest levels are similar to quota ranges, all are given to the nearest 1,000 t. Retention of females prohibited.

2/ Seasons usually closed prematurely by emergency order.

3/ Season opened by emergency order sometime after 7/1.

4/ Proposed.

5/ Alaska regulations close season on 8/15.

Table 6 -- Recent fishery statistics for U.S. Tanner crab fisheries in the eastern Bering Sea (Data from Eaton 1981). 1/

Year	Number of vessels	Number of landings	Catch		Number of pot lifts	Average weight (kg)	Average crab per pot	Price per kg ($)
			Number of crab	Metric tons				
1974	18	69	2,531,825	2,288	22,014	0.9	115	0.29
1975	27	80	2,773,770	3,188	38,462	1.1	72	0.29
1976	66	305	8,949,886	10,134	141,179	1.1	63	0.41
1977	83	580	20,412,566	23,531	305,052	1.1	67	0.60
1978								
C. bairdi	119	823	26,188,543	30,041	508,776	1.1	51	0.84
C. opilio	15	38	1,267,196	778	13,177	0.6	96	0.66
Total	134	861	27,455,739	30,819	521,953	1.1	53	
1979								
C. bairdi	138	801	16,711,455	19,286	393,788	1.1	42	1.15
C. opilio	101	490	22,118,498	14,600	190,746	0.7	116	0.66
Total	239	1,291	38,829,953	33,886	584,534	0.9	66	0.93
1980								
C. bairdi	154	804	14,739,611	16,608	488,434	1.1	30	1.15
C. opilio	141	603	25,706,262	17,935	272,065	0.7	94	0.46
Total	295	1,407	40,445,873	34,543	760,499	0.9	53	0.79
1981								
C. bairdi	169	759	11,873,513	13,473	588,621	1.1	21	1.27
C. opilio	155	867	34,416,334	23,929	435,762	0.7	79	0.57
Total	324	1,626	46,289,847	34,401	994,383	0.8	47	0.82

1/ A small portion of the catch prior to 1978 was *C. opilio*, catches of hybrids are largely included with *C. opilio*.

Table 7 -- Preliminary catch data for U.S. eastern Bering Sea tanner crab fisheries for the week ending 25 April. (Data courtesy of Alaska Department of Fish and Game).

Species and District	Weekly catch 1981	Weekly catch 1982	(t) ±%	Cumulative catch 1981	Cumulative catch 1982	(t) ±%
C. bairdi:						
Southeastern	1,134	195	-83	10,956	2,614	-76
Pribilof	181	53	-71	1,132	776	-31
Total	1,315	248	-81	12,088	3,395	-72
C. opilio:						
Southeastern	1,814	308	-83	10,240	3,710	-64
Pribilof	363	590	+63	1,420	3,583	+152
Total	2,177	898	-59	11,660	7,293	-37
Grand Total	3,493	1,146	-67	23,748	10,687	-55

are available. The importance of these fisheries can be measured by the fact that this area provided 33,292 t or 42% of the 1977 world tanner crab catch of 79,200 t (Food and Agriculture Organization, 1979). The combined U.S. and Japanese catch reached 44,402 t or 42% of the world catch again in 1978. Aggregate catches remained high through 1981 and it is probable that eastern Bering Sea tanner crabs have provided at least 40% of world landings for the last 5 years.

STATUS OF TANNER CRAB STOCKS

Stocks

Four species of tanner crabs are known in the eastern Bering Sea. C. bairdi and C. opilio are widely distributed and are exploited by commercial fisheries (Fig. 4). C. angulatus and C. tanneri are not fished in U.S. waters, but are found in deep water along the continental slope. In addition, C. bairdi-C. opilio hybrids make up a small percentage of eastern Bering Sea stocks.

The distribution of C. bairdi is strongly associated with the coast of the Alaska Peninsula, continental slope areas, and the Pribilof Islands (Fig. 4). Most of the commercially important stock has generally been found north of the Alaska Peninsula or around the Pribilof Islands. The two centers of abundance are connected by a region where C. bairdi, although lower in abundance, are certainly not rare. Surveys from 1974 onward showed that the size-frequency distributions of C. bairdi in the Pribilof Islands were different from those in the area north of the Peninsula. As NMFS surveys were expanded, it became evident that crabs in the Pribilof area were larger in size compared to those along the continental slope north and west of the islands. Somerton (1981a) has shown differences in the average size at sexual maturity between populations east and west of 167°W long. It is not yet clear whether these differences are caused by genetic or environmental factors. Substantial and consistent differences between the size-frequency distributions of C. bairdi (Fig. 5) found in different subdistricts (Fig. 3) do, however, exist even though the species is considered a single stock for management purposes.

The population of C. opilio inhabits an immense area but the fishery has been confined to a small portion of the range (Fig. 4). The areal distribution of the fishery reflects that of commercial-size male crab. As one goes northward along any given meridian the average size of C. opilio tends to decrease. By consequence, northern and central areas of the continental shelf are characterized by concentrations of small crab that have no current commercial value. Frequent changes in localized abundance of commercial size crab have occurred and required changes in the distribution of fishing effort. It is probable that there is one extremely large population of C. opilio that displays localized areas of commercial abundance that are geographically unstable with time. At present C. opilio are managed as a single stock.

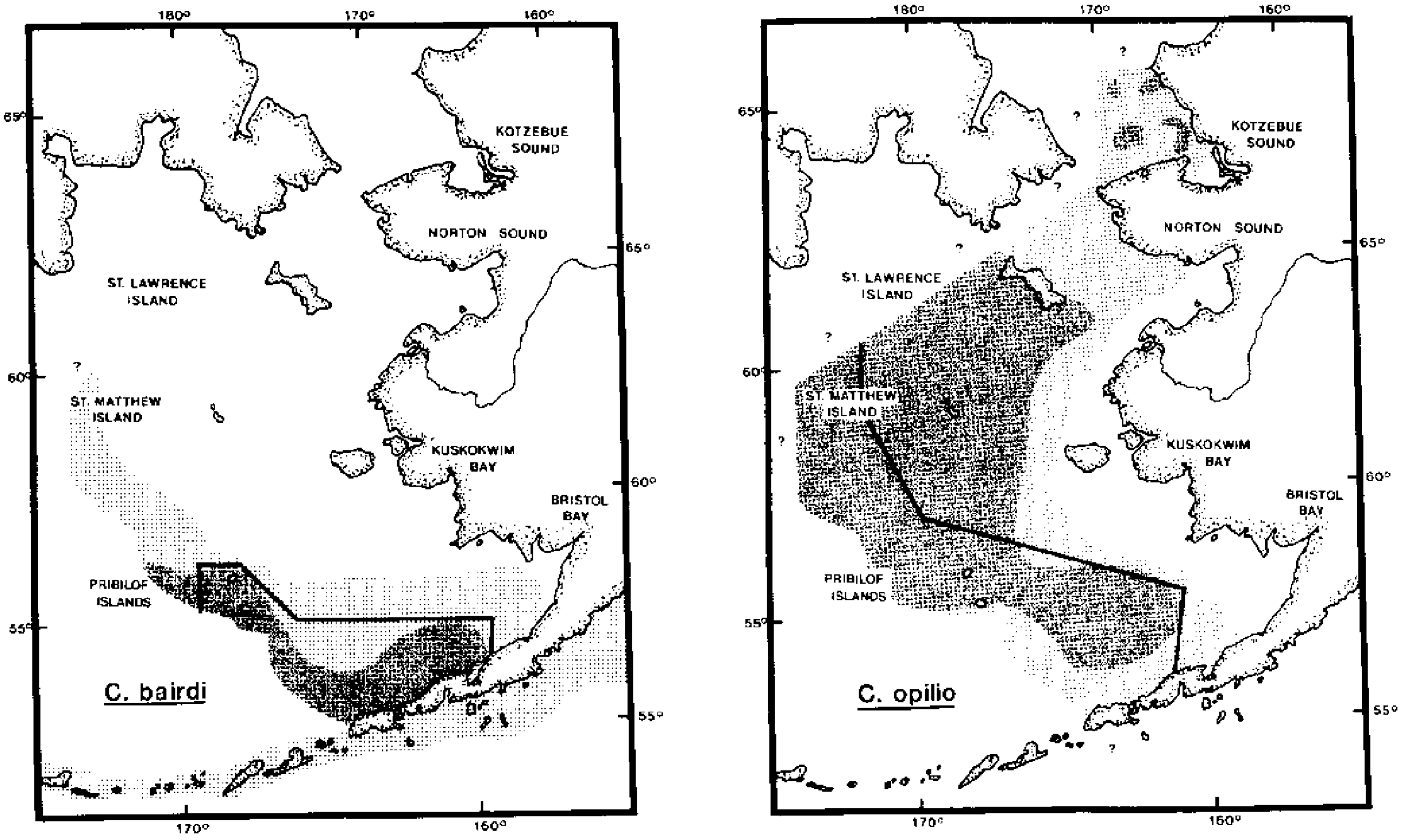

Figure 4. Distribution of tanner crabs in the eastern Bering Sea. Darkly shaded portions indicate areas of consistantly high abundance. Fisheries occur to the south or west of solid lines.

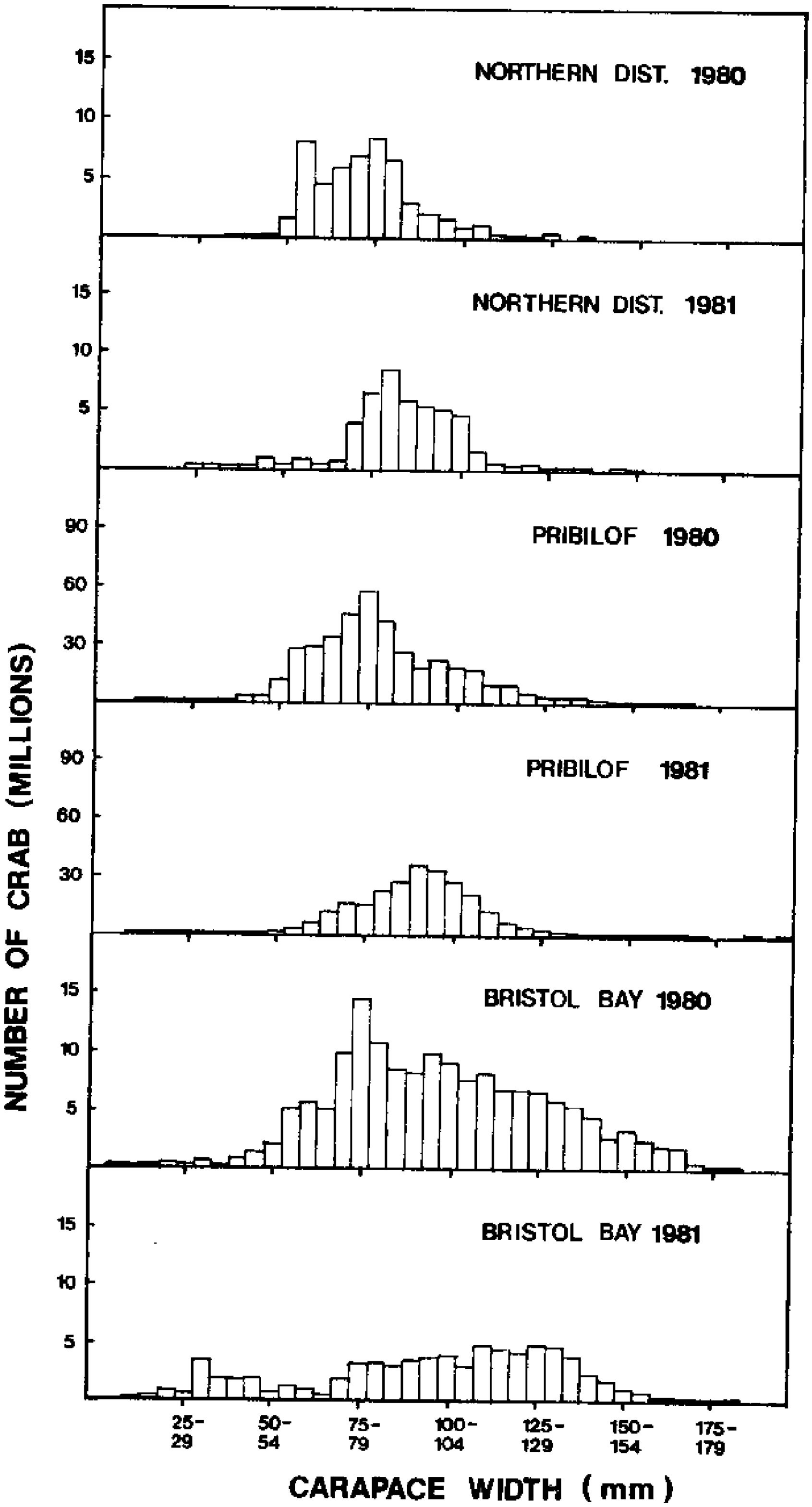

Figure 5. Size frequency distributions for C. bairdi in various statistical districts derived from NMFS trawl surveys of the eastern Bering Sea.

Trends in Abundance from Fishery Data

Interpreting trends in tanner crab stock abundance from commercial fisheries is difficult because of various developmental phases, shifting grounds, changes in management measures, and the lack of precise species composition data. Trends in nominal catch per unit effort (CPUE) do not show large variations over most of the history of Japanese and Soviet fisheries (Fig. 6). If one accepts that part of early increases in tangle net CPUE reflect increased abundance of _C. bairdi_, then a peak of abundance was probably present in the _late 1960's._ This interpretation is consistent with catch reports of Japanese scouting vessels (Fig. 1). The stability of CPUE in Japanese pot fisheries is puzzling. Changing area definitions and reduced quotas during the 1970's may have stabilized catch rates by ensuring that new grounds were fished.

In the area north of 58°N lat., mothership catch rates increased slightly in the last years of the fishery. Mothership catch rates were maintained, however, only at the expense of decreasing the average size of crabs in the catch (Fig. 7). Catch rates of the independent fleet (Table 4) generally decreased from 1977 onward and average size was more stable.

Catch rates of _C. bairdi_ in U.S. pots decreased steadily from the onset of _directed fishing_ in 1974 (Fig. 6). The precipitous decrease in CPUE from 1974 to 1975 is partially explained by an increase in the average size of crab taken (Fig. 8 and Table 6). Mean size was, however, remarkably constant from 1975 onward while stock abundance was declining. A legal size limit of 140 mm carapace width was imposed late in 1975 (Table 5). As _C. bairdi_ abundance declined and competition for available _resources increased_, the size-frequency distribution of the catch became progressively more skewed (Fig. 8). Skewness probably reflects increasing fishery dependence on recruitment as well as keener sorting of the catch in response to competition and lower catch rates.

Catch rates in the U.S. _C. opilio_ fishery increased in the second year of directed _fishing and have_ decreased since (Fig. 6, Table 6). Decreases in catch rates may partially reflect a trend toward the harvest of larger crab (Fig. 9). I suspect, however, that decreases in abundance are the main cause. There has been no minimum legal size in the fishery and the size of crab landed simply reflects market conditions. A minimum size of 78 mm is currently in the process of being implemented, but it is not yet clear that market conditions will allow harvesting of crab this small.

Research Surveys

Summer trawl surveys conducted annually by NMFS have provided a continuous series of crab abundance estimates since 1969. Early

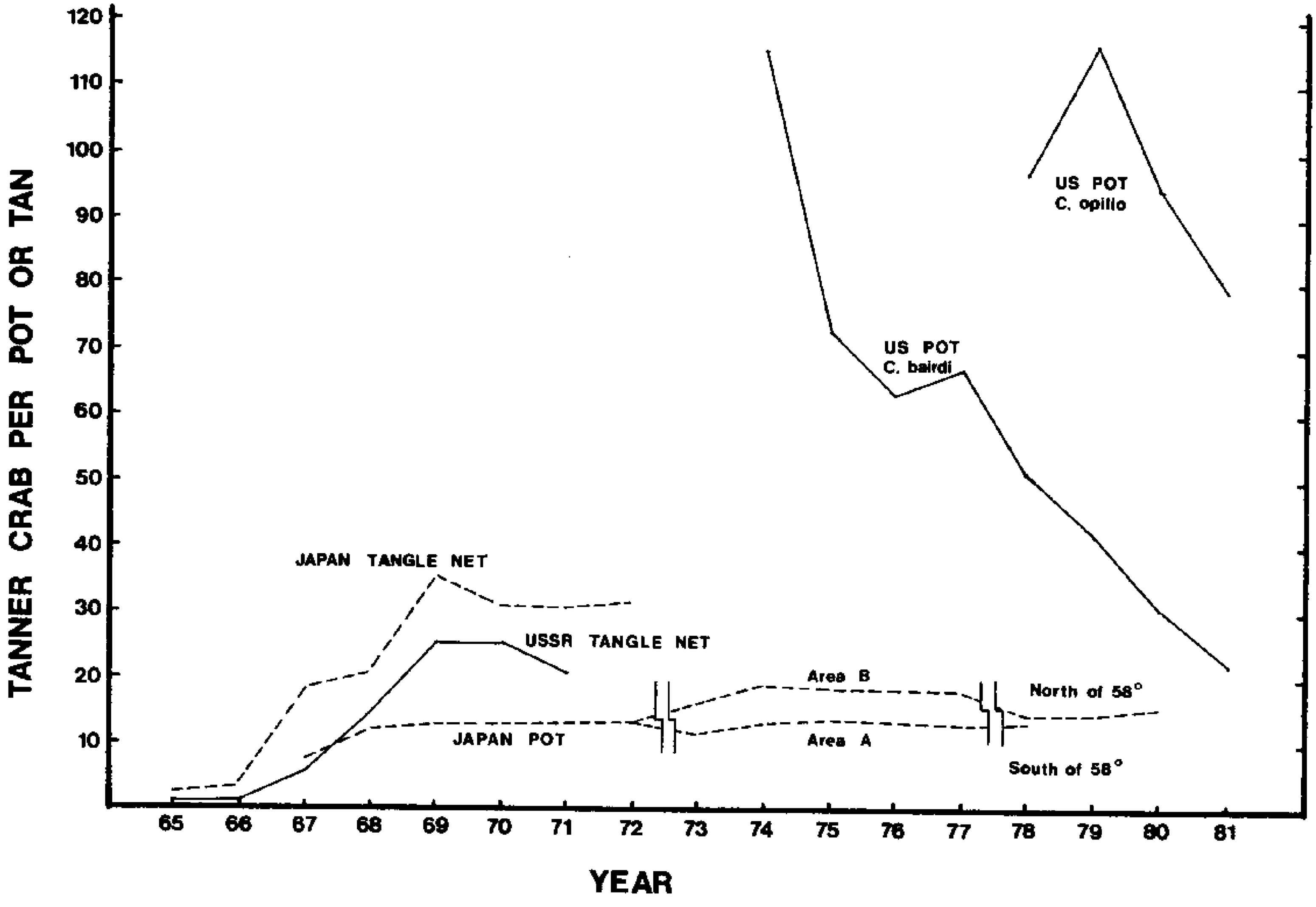

Figure 6. Nominal catch per unit effort in Japanese, Soviet and U.S. tanner crab fisheries.

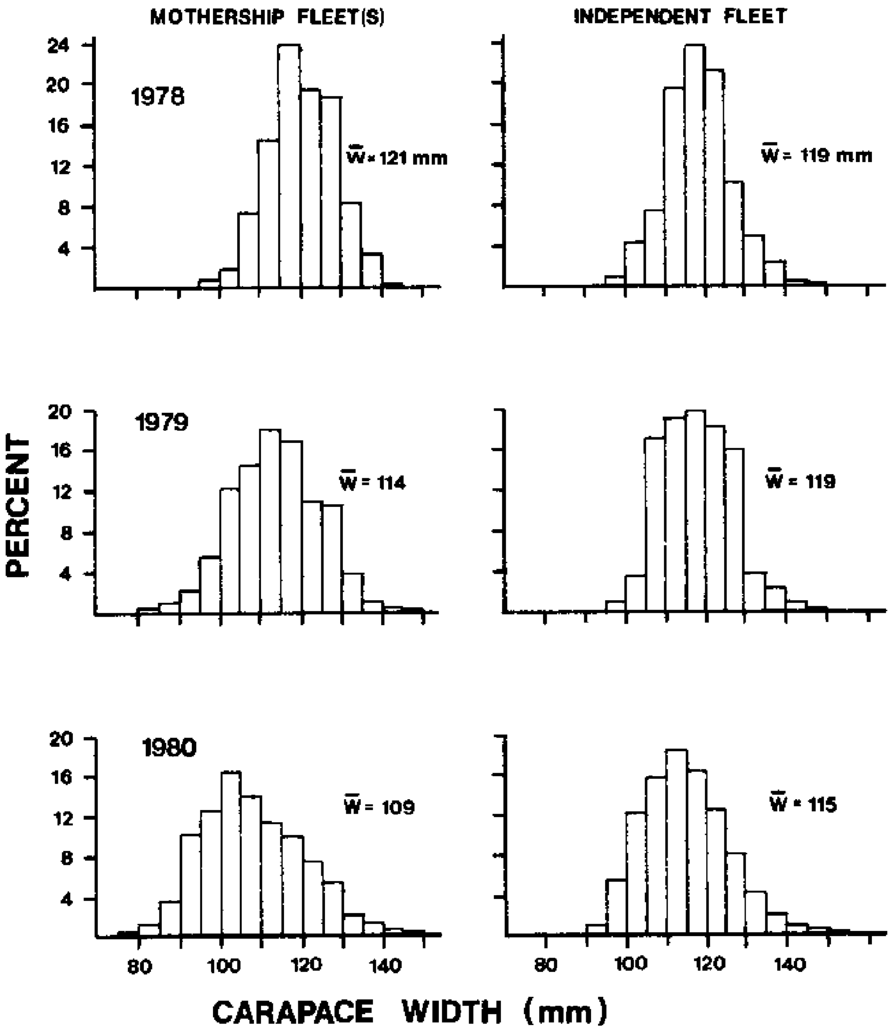

Figure 7. Size composition by fleet and year for tanner crab harvested by Japan in the eastern Bering Sea (from Wolotira and Armetta 1980).

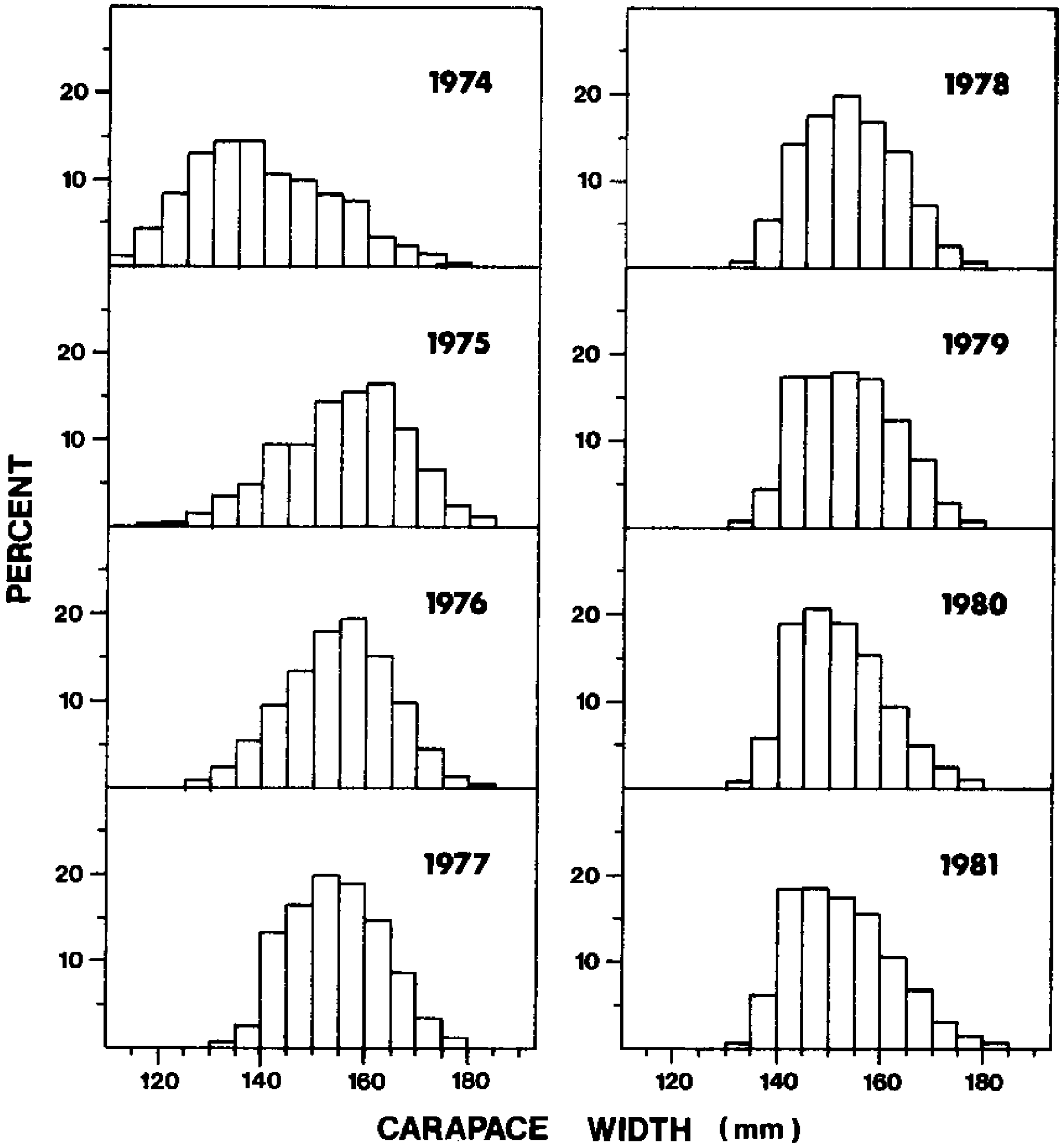

Figure 8. Size frequency distributions for *C. bairdi* taken in the U.S. eastern Bering Sea fishery.

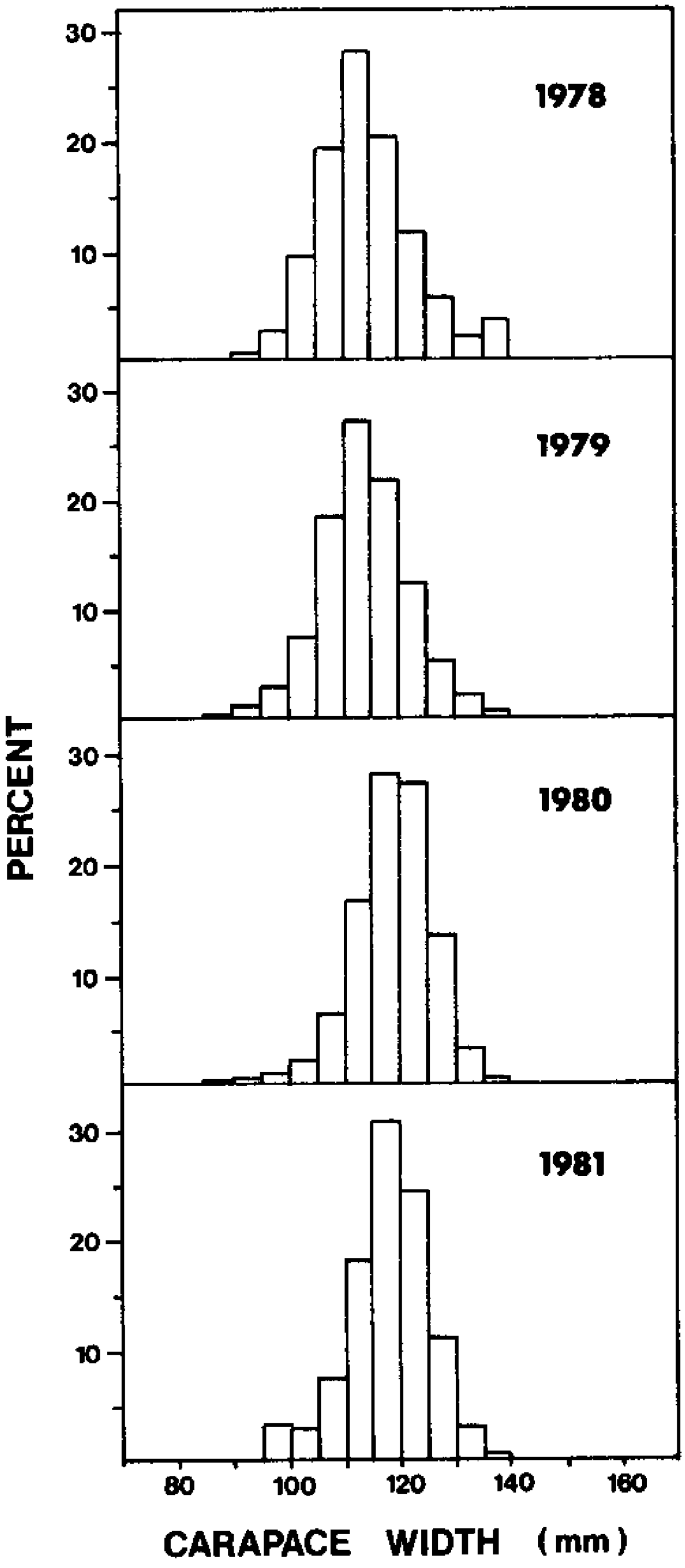

Figure 9. Size-frequency distributions for *C. opilio* taken in the U.S. eastern Bering Sea fishery.

efforts concentrated on red king crab north of the Alaska Peninsula. In 1973, the Pribilof Islands were included in the survey and almost all tanner crab habitat south of 58°N lat. has been surveyed ever since. The entire eastern Bering Sea shelf was first surveyed in 1975 as part of energy-related environmental research (Pereyra et al., 1976) and all commercial tanner crab grounds have been surveyed annually since 1978.

Catch rates from selected survey stations (Fig. 10) suggest high *C. bairdi* stock abundance south of 58°N lat. in the late 1960's and rapid declines by the early 1970's. Later data (Fig. 11) show a rapid rise in stock abundance of both species from 1972 to 1975. Sharp declines in stock abundance of both species have occurred since 1975. Survey estimates and commercial fishery data show identical trends in population abundance. Given 1982 fishery performance (Table 7), it appears that stocks of both species are continuing to decline in the area south of 58°N lat. North of 58°N lat., survey data show declining abundance from 1978 to 1979 and stable abundance thereafter.

In summary, it appears that *C. bairdi* populations were at relatively high levels in the periods 1959-63 (Fig. 1), 1968-69 and 1974-76. Available data are too limited to evaluate population trends of *C. opilio* before 1973. Populations of *C. opilio* have followed the same trends as those of *C. bairdi* since 1973.

FUTURE OF THE U.S. FISHERY

Short term prospects for the fishery are not good. The problem of low stock abundance is compounded by high interest rates on outstanding vessel loans, increased fuel costs, and intense competition among vessels of a large fleet. A decline in the Bristol Bay red king crab catch from 58,944 t in 1980 to 15,237 t in 1981 was also an extremely severe economic blow to fishermen and processors. Declining economic viability of crabbing has led many vessels to enter groundfish fisheries (particularly joint ventures) or seek cannery tending charters. It is unlikely, however, that these other activities will be able to fully occupy the large fleet that was built during the late 1970's when stocks of both king and tanner crabs were abundant.

Past population trends suggest that several years are required for stocks to recover from periods of low abundance. Size-frequency data for *C. bairdi* (Fig. 5) do not suggest rapid increases in recruitment. Recruitment patterns in *C. opilio* are not well elucidated by size-frequency information because there are little data available on regional differences in growth and migration. Somerton (1981b) shows that recruitment of *C. opilio* has been intermittent on most of the grounds south of 58°N lat. The relationship between large populations of small *C. opilio* in central portions of the eastern Bering Sea shelf and recruitment to the fishery is not understood. The persistence of areas where no large crab are found from year to year suggests slow growth rates and little migration to other areas. It appears that most *C. opilio* in the will never be exploited unless smaller

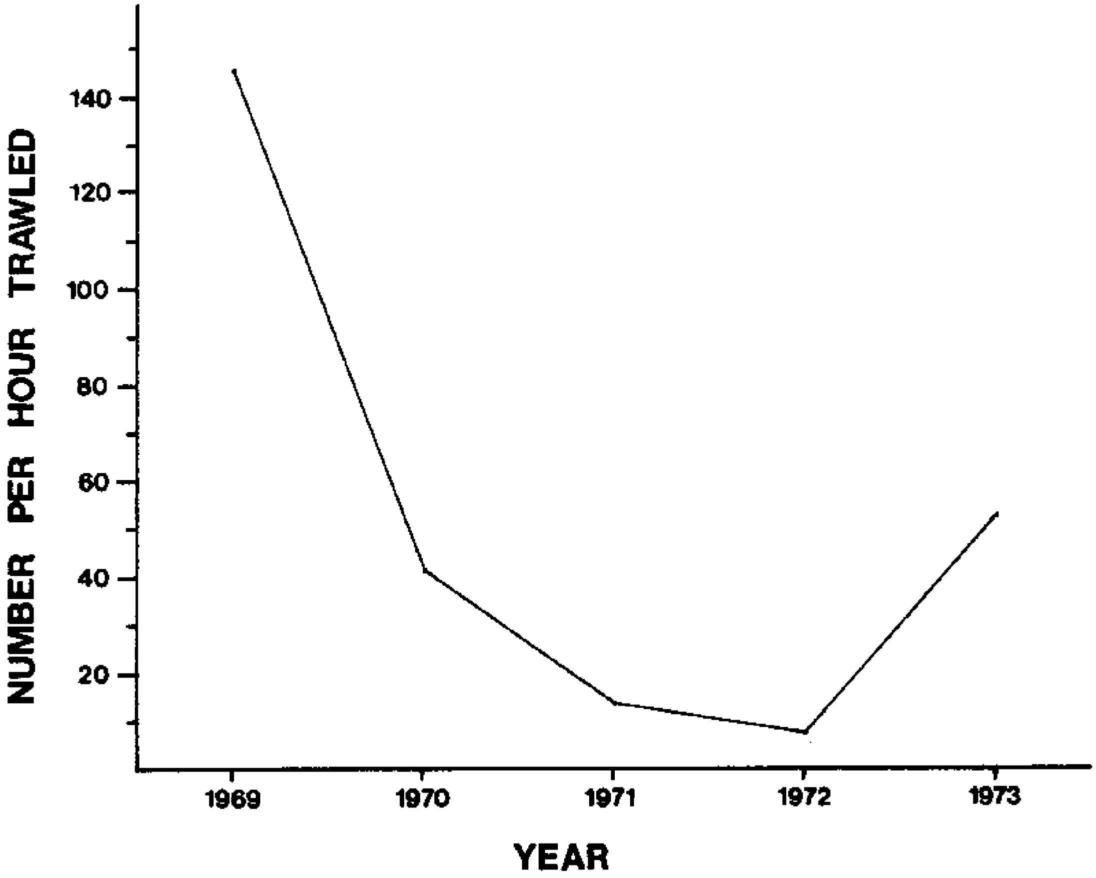

Figure 10. Catch rates of C. bairdi taken in early National Marine Fisheries Service trawl surveys (data from Hayes and Reid 1975).

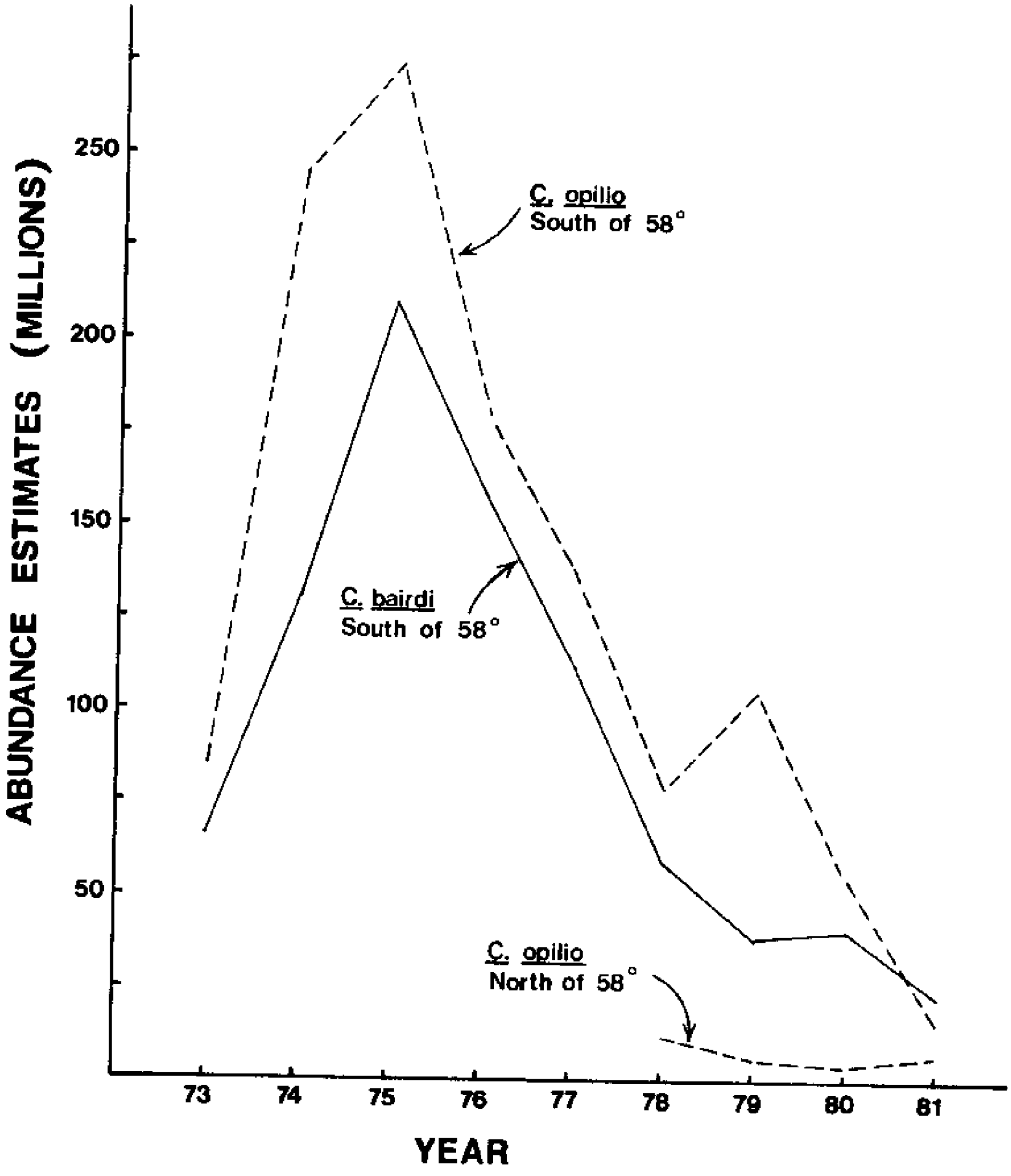

Figure 11. Abundance estimates of tanner crabs derived from recent National Marine Fisheries Service trawl surveys.

crab are harvested. There is also the possibility that smaller *C. bairdi* could be harvested, particularly in the Northern District (Fig. 8).

Because there are large numbers of small *C. opilio* available, decreasing the size of entry into the fishery by a small amount, greatly increases potential yields (Table 8). For example, decreasing the size at entry from 110 to 90 mm (18%) increases the exploitable stock from 15,500 to 67,500 t (435%). Since a 78 mm size limit was proposed on biological grounds, this sort of decrease does not pose problems.

The marketability of smaller crab remains in question. The size frequency of crab taken by Japanese motherships in 1980 suggests that a market exists. Currently most tanner crabs are marketed as cooked sections. Improvements in technology may, however, allow economical processing of picked frozen meat in the future. In any case, harvesting smaller crab is necessary if production is to be stabilized and maintained.

Table 8 -- Biomass of *C. opilio* estimated from the 1981 trawl survey.

			Cumulative > lower size limit		
Size (mm)	Number (millions)	t (thousands)	Number (millions)	t (thousands)	Average weight per crab (kg)
80-84	40.4	25.5	337.0	112.9	0.33
85-89	73.0	19.9	227.0	87.4	0.39
90-94	52.0	17.2	154.0	67.5	0.44
95-99	36.2	14.1	102.0	50.3	0.49
100-104	28.3	12.7	65.8	36.2	0.55
105-109	15.3	8.0	37.5	23.5	0.63
110-114	10.2	6.2	22.2	15.5	0.70
115-119	5.8	4.0	12.0	9.4	0.79
120-124	3.2	2.5	6.2	5.4	0.89
125-129	1.5	1.3	3.0	2.9	1.00
130-134	0.7	0.7	1.5	1.6	1.12
135-139	0.6	0.7	0.8	0.9	1.19
140-144	0.1	0.1	0.2	0.2	1.36
145-149	0.1	0.1	0.1	0.1	1.36

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Abstract

Eastern Bering Sea tanner (snow) crab (*Chionoecetes bairdi* and *C. opilio*) fisheries developed as an outgrowth of Japanese and Soviet king crab (*Paralithodes* spp.) operations. Some landings of tanner crabs were reported as early as 1953, but major development did not begin until 1965. Development of Japanese and Soviet fisheries was spurred by progressively smaller king crab quotas and relatively high tanner crab abundance. The United States entered the fishery in 1968 but almost all catches were incidental to king crabbing until 1974. The USSR discontinued tanner crab fishing in 1971. The Secretary of Commerce, at the suggestion of the North Pacific Fishery Management Council, eliminated annual quotas for Japan in 1981. Currently, the United States is the only country participating in directed fisheries. Eastern Bering Sea fisheries are fully developed and production has probably exceeded 40% of the world total catch of tanner crabs over the past 5 years. Various trends in tanner crab populations and fisheries are presented and their probable future discussed.

Early Life History

The Larval Stages of the Genus *Chionoecetes*: *C. Opilio* and *C. Japonicus* Reared in the Laboratory

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INTRODUCTION

Two species of edible crabs of the genus *Chionoecetes*, *C. opilio* (O. Fabricius) and *C. japonicus* Rathbun, occur in the Sea of Japan. The former species, called Zuwai-gani in Japan, are caught by the Danish Seine fishery at a depth of 200 to 350 m; and the latter, Benizuwai-gani, are captured by the basket fishery (a kind of basket trap called Kanikago in Japan) at a depth of 700 to 1,500 m.

Of the two species, *C. opilio* is of more commercial importance than *C. japonicus* because of its greater commercial abundance, more economical fishing operation, and its more palatable flavor.

The objective of this paper is to give a detailed description of and to summarize similarities and differences between *C. opilio* and *C. japonicus*, providing a basis and method for future identification of the larvae of all species belonging to the genus *Chionoecetes*.

MATERIALS AND METHODS

Ovigerous females of the two species were caught by commercial seine (*C. opilio*) or by commercial basket trap (*C. japonicus*) during the winter seasons in 1968 and 1973 in the middle of the Sea of Japan. They were placed in the wooden tanks of the fishing boats and were transported within three days to the laboratory of the Marine Culture Station of Ishikawa Prefecture.

The sea water used for both ovigerous females and the larvae was pumped up to the laboratory and filtered with 60µ-sized nylon mesh, then held in a dark, cool room. The temperature of the sea water ranged between 4.5 and 13.0°C and the specific gravity varied from 1.022 to 1.025 ($\sigma 15$).

Hatching usually occurred within three weeks after capture. By using a strong light and a large-bore pipette, some 200 photopositive zoeae were collected and distributed equally in 10 plastic 500 ml finger bowls. Daily or every other day the larvae were transferred into clean finger bowls with a new supply of filtered sea water. Recently-hatched nauplii of the brine shrimp, *Artemia salina*, were added for zoeae and young brine shrimp were provided for magalopae. Heavy mortality was observed during the stages of the second zoea and megalopa.

The larvae were preserved in a 5 percent neutralized formalin solution. Appendages were dissected out from larvae, mounted on a slide with a small amount of lactic acid with diluted formalin, and drawn by free hand under a stereo microscope. All the measurements were taken under a microscope with the aid of an ocular eyepiece.

The description of the present paper consists of those of Motoh (1973, 1976) and additional materials laboratory-reared during the winter of 1980 by Mr. Y. Suzuki of the Fukui Prefectural Fisheries Experimental Station.

The larval forms of the two species are so similar that their descriptions are made as one.

DESCRIPTION OF LARVAE OF C. OPILIO AND C. JAPONICUS

All larvae hatched as prezoeal stage and they molted to the first zoea in about one hour. Hereafter, there are two zoeal and one magalopa stages in the larval development.

Prezoea: The whole body is covered with an embryonic cuticle without any spines or processes on the carapace. The distance between outer margins of eyes is 0.78 to 0.85 mm. Antennule each have long and short projections. Antenna has a small endopodite and large exopodite. The abdomen consists of five segments and a bifurcate telson having seven spines each.

First zoea (Figure 1): The carapace has four spines: a dorsal and a rostral spine approximately equal in length and a pair of lateral spines. The eyes are not stalked. The length of the larva from the tip of the rostral to the tip of the dorsal spine is 4.85 to 5.52 mm, and the width including both lateral spines is 3.30 to 3.98 mm. The distance between outer margins of the eyes is 0.85 to 1.20 mm. The abdomen consists of five segments and the telson which is bifurcated. The second and third segments bear a pair of lateral knobs or hooks. Each furca of the telson bears three setae on the inner side and a small spine each on the lateral and the dorsal sides, respectively. The postero-lateral margins of the third, fourth, and fifth abdominal segments terminate as a pair of long lateral spines. The antennule bears three terminal processes: two or three broad, flat aesthetes and one or two smaller setae. The antenna is almost as long as the rostral spine, and its peduncle tapers to a point with several rows of setules. The exopodite has three setae, approximately 1:2:3 in proportion of their length. The mandible is small with an irregular cutting edge. The endopodite of the maxillule bears six spines of equal length arranged in pairs, and one more spine is present at the base of the endopodite, which later becomes an apparently separate segment. The basipodite and coxopodite each have six or seven setules. The scaphognathite of

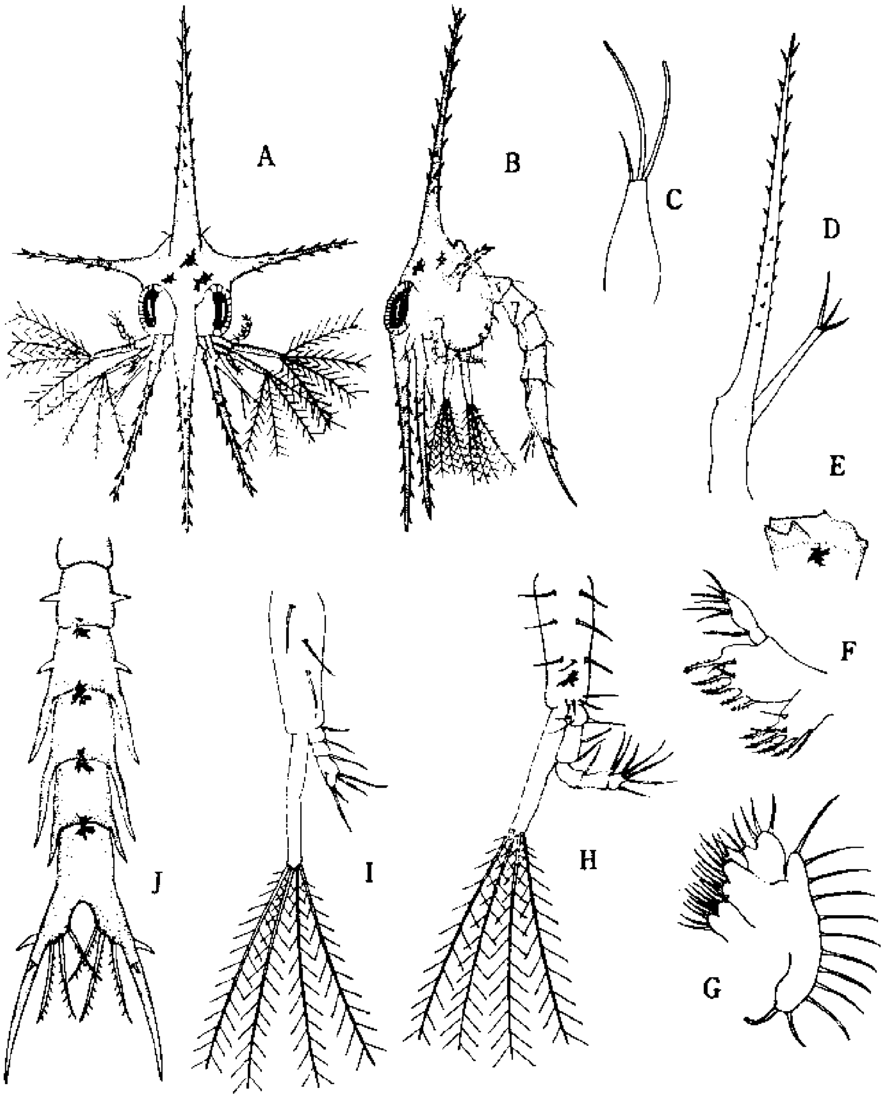

Fig.1a . *Chionoecetes opilio* (O. Fabricius). First zoea. A, dorsal view; B, lateral view; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, abdomen in ventral view. A, B, ×30; C, E, F, G, ×150; D, H, I, ×75; J, ×60. (after Motoh, 1973)

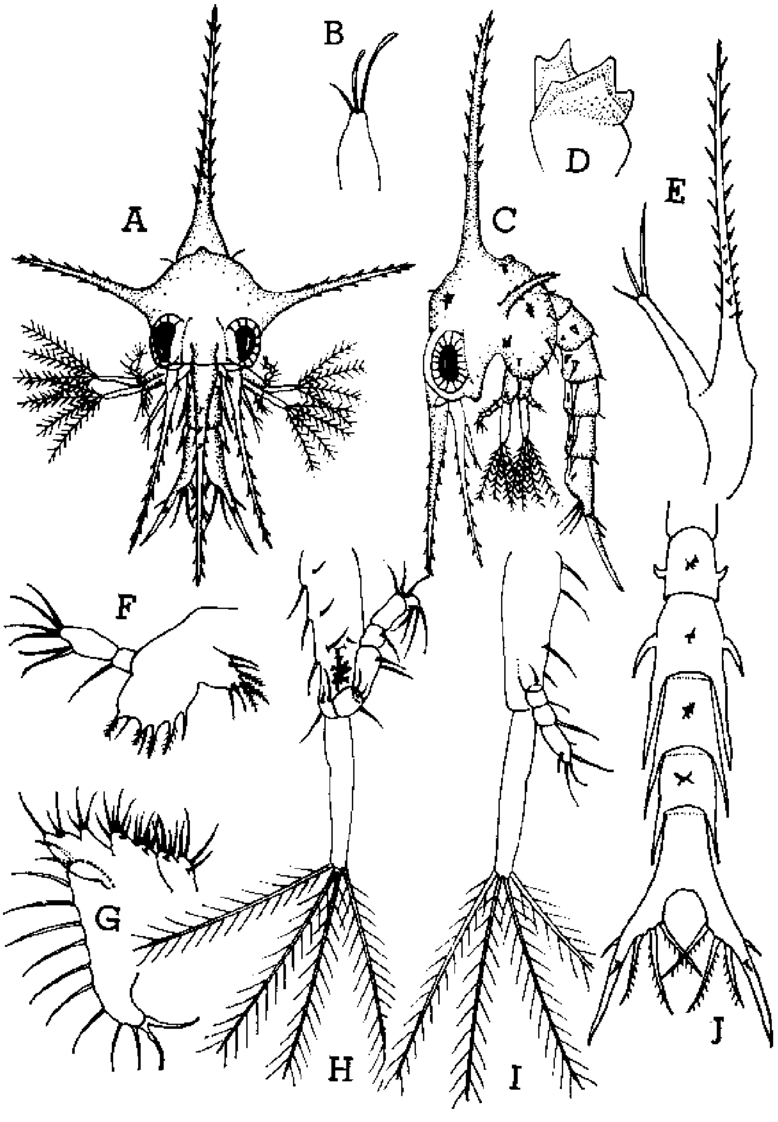

Fig.1b .*Chionoecetes japonicus* Rathbun. First zoea. A, dorsal view; B, antennule; C, lateral view; D, mandible; E, antenna; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, abdomen in ventral view. A, C, ×20; B, D, F, G, ×150; E, H, I, ×75; J, ×40. (after Motoh, 1976) the maxilla has 12 to 15 (usually 12 or 13) long soft plumose hairs including one, two, or three thick ones, and the bifurcate endopodite bears three spines on each lobe. The basipodite and coxopodite are also bifurcated and have the spinal arrangement of 5-5 and 4-4, respectively, with a slight variation.

The endopodite of the first maxilliped has five segments with a spinal arrangement of 3-2-1-2-5 from proximal to distal. Four natatory or swimming hairs are present on the distal end of the exopodite. The second maxilliped also has four natatory hairs and a 1-1-5 spinal arrangement on the three segments of the endopodite. One of the five spines on the distal is very minute.

Second zoea (Figure 2): The length of the larva from the tip of the rostral to the tip of the dorsal spine is 5.72 to 7.10 mm. The width including both lateral spines is 3.33 to 3.92 mm. The distance between outer margins of the eyes is 1.32 to 1.51 mm in C. opilio and 1.56 to 1.87 mm in C. japonicus. The second zoea appears with the eyes stalked. Aesthetes on the antennule are increased to nine or ten and are divided into two tiers: one in the first tier and eight or nine in the terminal tier, which has six or seven large and two small sensory flagella. A club on the antenna represents the developing endopodite. The mandible has an unsegmented palp. The basipodite and coxopodite of the maxillule have eight to nine and six to eight spines, respectively. An additional plumose hair is located on the protopodite near the base of the endopodite. The endopodite of the maxillule now consists of two segments with a spinal arrangement of 1-6. The bilobate or trilobate endopodite of the maxilla bears six setae. The bilobate basipodite and coxopodite of the maxilla bear five and four spines on each lobe. The scaphognathite of the maxilla has 20 to 23 (mainly 22 or 23) in C. opilio and 23 to 27 (mainly 26 to 27) long soft plumose hairs including one, two, or three thick ones in C. japonicus.

The endopodite of the first maxilliped has five segments with a spinal arrangement of 3-2-1-2-5 from proximal to distal. Six natatory hairs are present on the distal end of the exopodite. The second maxilliped also has six natatory hairs and the endopodite with a spinal arrangement of 1-1-5 from proximal to distal segment, of which one of the five spines is very minute in the same manner as that in the first zoea. The inner margin of each prong of the furca of the telson bears one additional spine without setule.

Megalopa (Figures 3 and 4): The megalopa is 2.89 to 3.37 mm in carapace length including a rostral central process and 1.91 to 2.45 mm in carapace width. Seven heavy processes are on the carapace: three rostral processes of

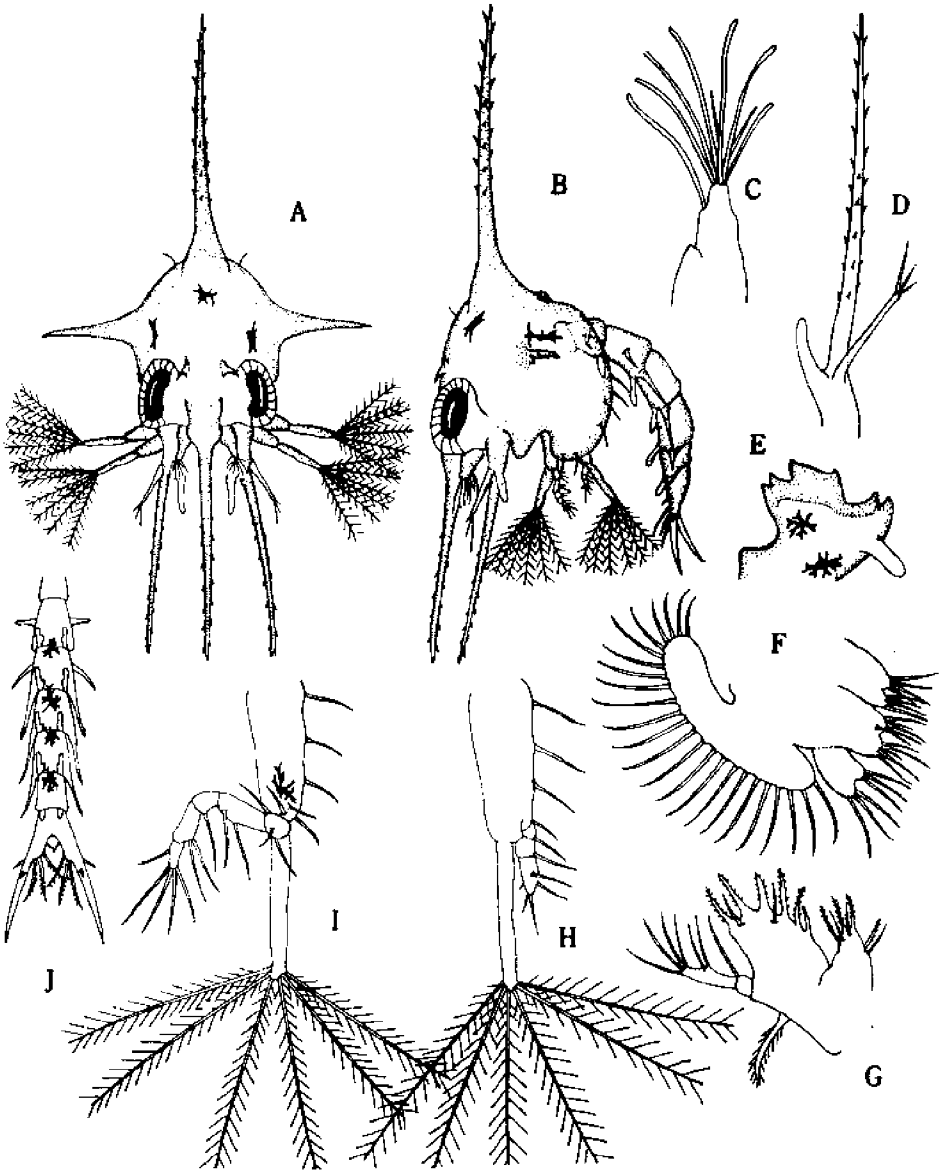

Fig.2a .*Chionoecetes opilio* (O. Fabricius). Second zoea. A, dorsal view; B, lateral view; C, antennule; D, antenna; E, mandible; F, maxilla; G, maxillule; H, second maxilliped; I, first maxilliped; J, abdomen in ventral view A, B, J, ×30; C, D, ×60; E, F, G, ×150; H, I, ×75. (after Motoh, 1973)

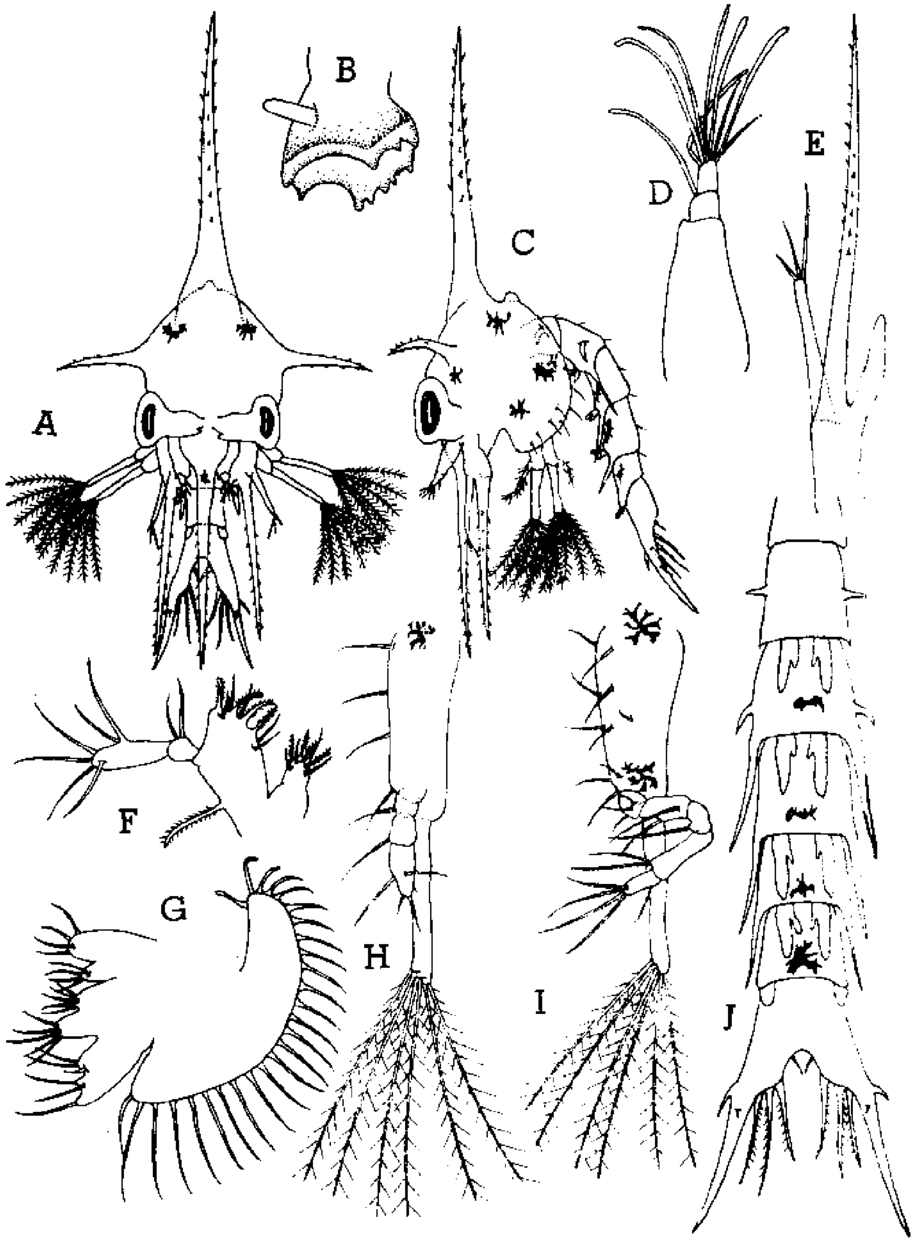

Fig.2b .*Chionoecetes japonicus* RATHBUN. Second zoea. A, dorsal view; B, mandible; C, lateral view; D, antennule; E, antenna; F, maxillule, G, maxilla; H, second maxilliped, I, first maxilliped; J, abdomen in ventral view. A, C, ×20; B, D, F ×150; F H, I, ×75; J, ×40. (after Motoh, 1976)

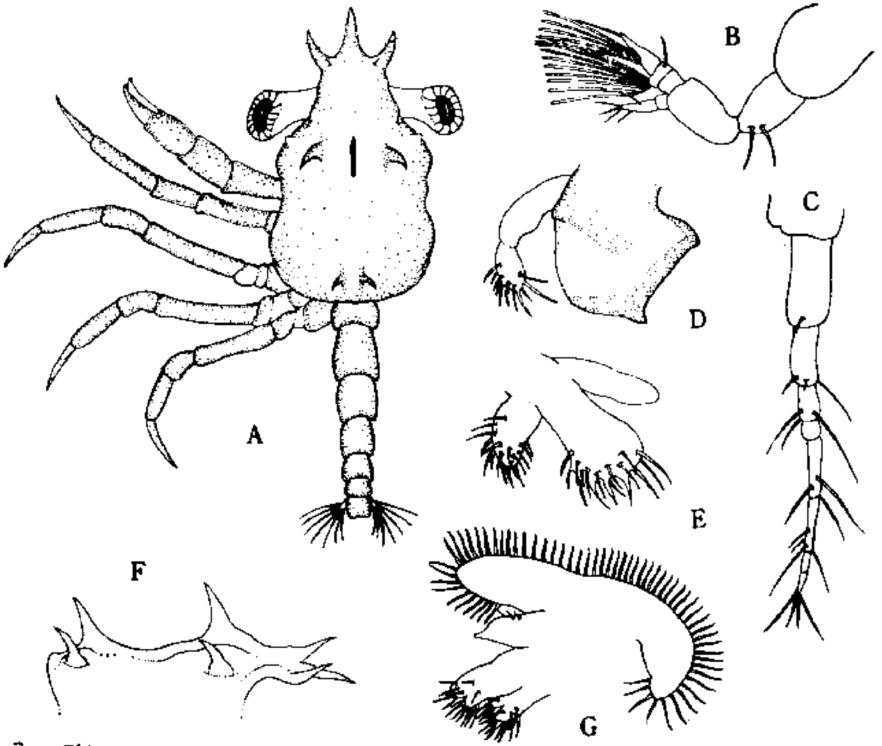

Fig.3 a .*Chionoecetes opilio* (O. Fabricius). Megalopa. A, dorsal view; B, antennule; C, antenna; D, mandible; E, maxillule; F, lateral view of carapace; G, maxilla. A, F, ×30; B, C, ×75; D, E, G, ×150. (after Motoh, 1973)

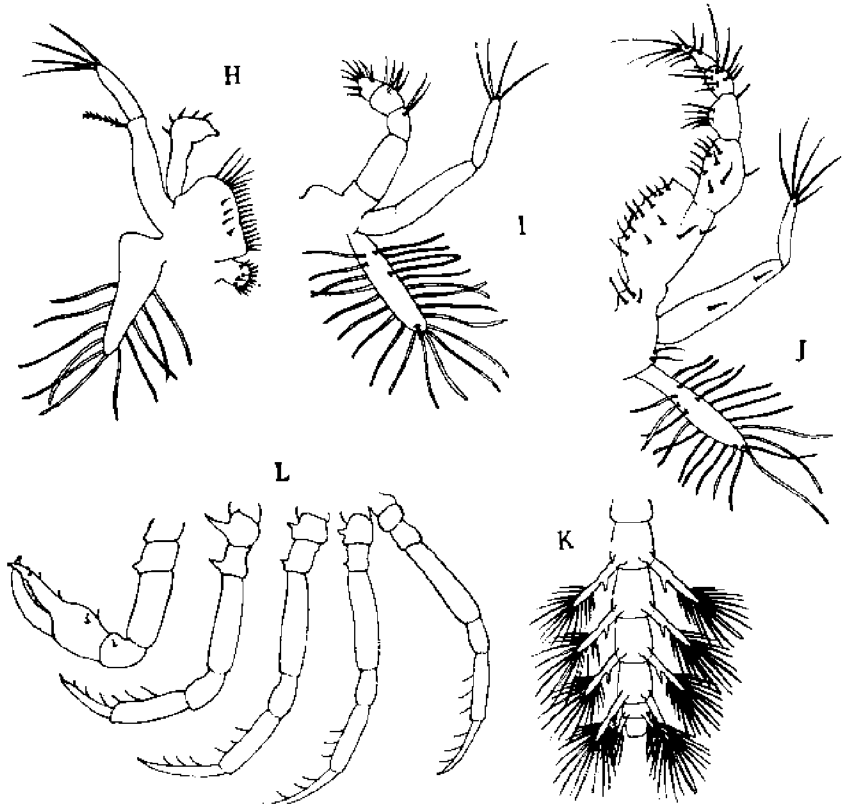

Fig.4 a .*Chionoecetes opilio* (O. Fabricius). Megalopa. H, first maxilliped; I, second maxilliped; J, third maxilliped; K, abdomen in ventral view; L, pereiopods 1st to 5th. H, I, J, ×150; K, L, ×30. (after Motoh, 1973)

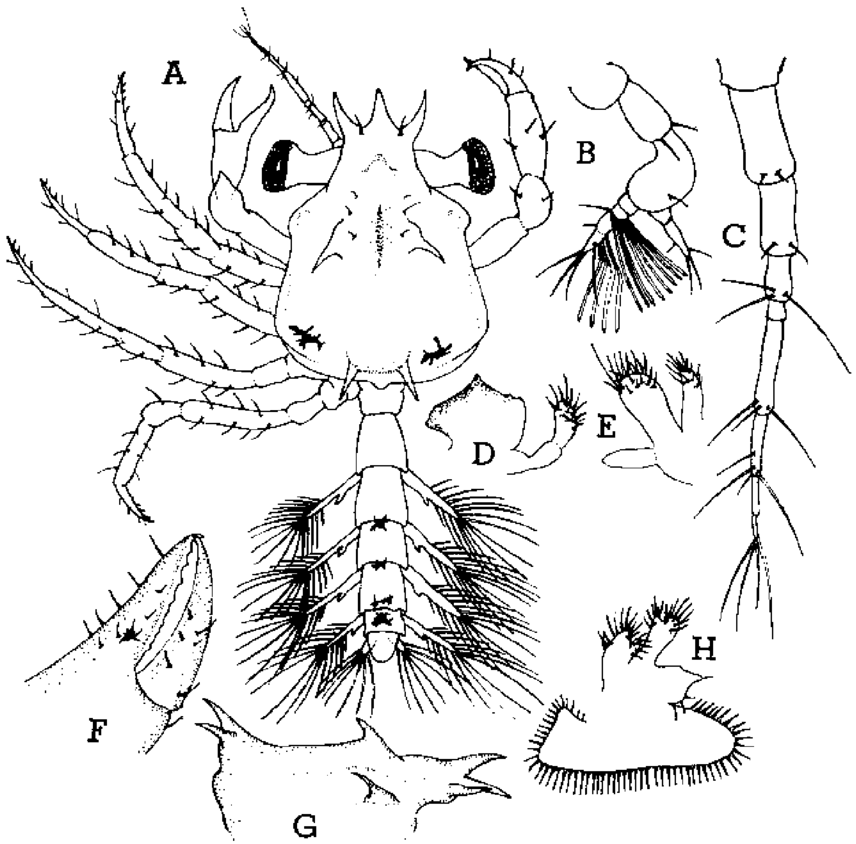

Fig.3b. *Chionoecetes japonicus* RATHBUN. Megalopa. A, dorsal view; B, antennule; C, antenna; D, mandible; E, maxillule; F, distal portion of chiliped; G, lateral view of carapace; H, maxilla. A, G, ×30; B, D, H, ×75; E, F, ×150. (after Motoh, 1976)

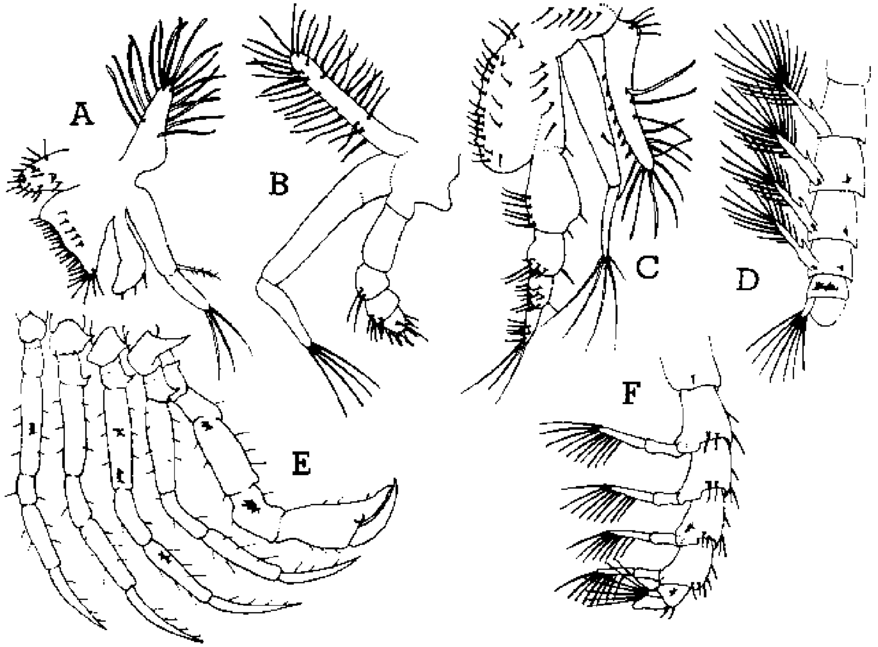

Fig.4b. *Chionoecetes japonicus* RATHBUN. Megalopa. A, first maxilliped; B, second maxilliped; C, third maxilliped; D, abdomen in ventral view; E, periopods 1st to 5th; F, abdomen in lateral view. A, B, C, ×75; D, E, F, ×30. (after Motoh, 1976)

which the central one is longer than the lateral two, a pair of anterior gastric lateral processes, and a pair of cardiac dorsolateral processes. The eyes are stalked.

The inflated peduncle of the antennule is followed by two segments. The antenna consists of eight segments with a spinal arrangement of 1-2-3-0-3-4-0-4 from proximal to distal segment with a slight variation in number. The palp of the mandible is well developed and bears approximately 11 spines. The endopodite of the maxillule has no spine. The scaphognathite of the maxilla is much broader with 60 to 64 soft plumose hairs in *C. opilio* and 69 to 71 in *C. japonicus*. The number of spines on the coxopodite has increased to 11 on one lobe of bifurcation and five or six on the other. The basipodite has five spines on one lobe and usually eight on the other. Usually, the endopodite has only three spines on its basal portion.

The first maxilliped has a well-developed epipodite with 11 to 17 soft hairs. The broad endopodite has three to five spines on the distal end and numerous spines on the basal end. One plumose and four terminal hairs are present on the exopodite. The endopodite of the second maxilliped has four segments with a spinal arrangement from proximal to distal of 0-2-5-7 (or 8). Four natatory hairs are still present on the terminal end of the exopodite. A well-developed epipodite is also present with some 20 soft plumose hairs with a heavy variation. The third maxilliped has developed tremendously at metamorphosis from the second zoea to megalopa. The endopodite has become quite massive and consists of four segments with numerous spines. The epipodite is well developed with about 20 soft nonplumose hairs.

The basi-ischiopodites of the first, second, and third walking legs have spines projecting ventrally. Furthermore, in *C. opilio* the spines are present on the cheliped, but in *C. japonicus* there is only one spine on the basipodite. The fourth walking leg has no conspicuous hairs projecting from the tip of the dactylopodite.

The abdomen consists of six segments and the telson. Pleopods are present on the second to fifth segments and bear about 16 long plumose hairs for locomotion, but a slight variation is noticed in the number of the hairs on each segment. There are seven (rarely six) plumose hairs on each side of the uropod.

DIFFERENCES IN LARVAL CHARACTER BETWEEN C. OPILIO AND C. JAPONICUS

The larval stages of *C. opilio* and *C. japonicus* are morphologically very similar. However, variations in the number of setae and in the shape of the appendages may be responsible for a substantial portion of the differences between them. In the case of the first and second zoeae, the differences between the two species within the present study are as follows:

1) The chromatophores are brown or reddishbrown in *C. opilio* and vermillion or crimson in *C. japonicus*. The same can be applied to the larvae of the prezoea and megalopa.

2) The length of the posterolateral spine on the third abdominal segment is more than 1.3 times the length of the fourth abdominal segment in *C. japonicus*, but is shorter than (and rarely equal to) that in *C. opilio* with a slight variation.

3) The length of the abdomen is, in general, clearly greater than the thickness in *C. opilio*, but is only slightly greater or more or less equal in *C. japonicus*.

In the second zoea, in addition to the three characters mentioned above, two differences become apparent as follows:

1) The distance between outer margins of eyes is 1.32 to 1.51 mm in *C. opilio*, but 1.56 to 1.87 mm in *C. japonicus* as mentioned previously.

2) The number of setae on the scaphognathite is mainly 22 or 23 in *C. opilio*, but it is usually 26 to 27 in *C. japonicus* also as mentioned previously.

In the megalopa, the ischiopodite of the cheliped has a spine in *C. opilio* but does not in *C. japonicus*.

DISCUSSION

In order to identify brachyuran zoeae, Aikawa (1929) proposed the following four characters: 1) spine on the carapace, 2) character of the second antenna, 3) character of the telson including its armature, and 4) grouping of chromatophores. According to his criteria, the characteristics of *C. opilio* and *C. japonicus* zoeae can be summarized as follows: all the spines present on carapace, second antenna B-type, telson A-type, chromatophores present on the second to fifth abdominal segments, protopodite of the first maxilliped, carapace, and on the mandible.

Five species of the genus Chionoecetes, namely, C. opilio (O. Fabricius), C. tanneri (Rathbun), C. bairdi Rathbun, C. angulatus Rathbun, and C. japonicus Rathbun, aside from the two subspecies (Kon, 1980), inhabit the colder and deeper waters of the world.

Regarding their larval stages, so far as the author is aware, Aikawa (1937), Kurata (1963, 1969), Kon (1967, 1980), Kuwatani et al. (1971, 1973), Motoh (1973), and Haynes (1973) described C. opilio; Motoh (1970, 1976) described C. japonicus; and Haynes (1973, 1981) and Jewett and Haight (1977) described C. bairdi.

To distinguish the zoeae of C. opilio from C. japonicus, Kurata (1969) provided the key showing the lengths of inner and outer exopodites on antenna in the ratio approximately 1:2 in C. opilio, while approximately 1:3 in C. japonicus. However, during the present study it was observed that this morphological characteristic sometimes overlapped due to the variation.

Kurata (1969) and Motoh (1976) described the presence of a spine on the ischiopodite of the cheliped of the megalopal C. opilio and the absence in C. japonicus. However, observing the present materials, it was noticed that the ischial spine of the C. opilio is sometimes very obscure.

Motoh (1976) proposed a difference between the species. The length of the posterior lateral spine on the third abdominal segment is more than 1.3 times the length of the fourth in C. japonicus, but is shorter than (or rarely equal to) that in C. opilio. While examining additional specimens of C. japonicus, it has appeared in rare cases that the length of the spine on the third segment was less than the 1.3 times the length of the fourth.

Haynes (1981) made the key for distinguishing the second zoeae as follows:

Lateral processes on the third abdominal segment reach the posterior margin of the segment in C. opilio, but they do not in C. japonicus. In addition to that, the posterolateral spines on the third to fourth abdominal segments barely reach the margin of the posterior segment in C. japonicus. During the present study it was observed that these differences are absorbed or become negligible with their morphological variations.

These morphological differences might be due to the phenotypic variation owing to the different environmental conditions in captivity and in the wild. Therefore, further study on the larval morphology and edaphic segregation of both species as well as other members of the genus Chionoecetes would be highly desirable.

Morphological differences between the species are summarized in Table 1.

ACKNOWLEDGEMENTS

Thanks are tendered to Mr. Y. Suzuki of the Fukui Prefectural Fisheries Experimental Station for providing additional larvae of the two species.

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TABLE 1

COMPARISON OF THE LARVAL CHARACTERS OF *CHIONOECETES OPILIO* AND *C. JAPONICUS*

	C. opilio						*C. japonicus*	
Larval Stage & Character	Kurata (1963,1969)	Kon (1967,1980)	Kuwatani *et al.* (1971,1973)	Motoh (1973)	Haynes (1973)	Present material	Motoh (1970,1976)	Present material
PREZOEA								
Short embryonic spine on antennule	*	Plumose	Plumose	*	Nonplumose	Nonplumose	*	Nonplumose
FIRST ZOEA								
Terminal process on antennule	*	5	5	3	5	3 to 5	3	3 to 5
Setae on endopodite of maxilla	3-2-1	3-2-1	3-2-1	3-3	3-3	3-3 or 3-2-1	3-2-1	3-3 or 3-2-1
Setae on scaphognathite	16	11 to 13	13	12 to 15	12 to 13	13 to 14	12 to 13	12 to 13
Spine on outer margin of telson	3(rarely 2)	3	2	2	3	2	2	2
SECOND ZOEA								
Setae on endopodite of maxilla	3-2-1	3-2-1	3-2-1	3-3	3-3	3-3 or 3-2-1	3-2-1	3-3 or 3-2-1
Setae on scaphognathite	*	*	*	20 to 23	*	22 to 23	23 to 27	25 to 27
Length of abdomen longer than thickness	*	*	*	*	Apparently	Apparently	*	Slightly or equal
MEGALOPA								
Setae on scaphognathite	*	65 to 69	*	60 to 62	*	61 to 64	70	69 to 71
Spine on ischiopodite of cheliped	Present	*	*	Present	*	Present (rarely obscure)	Absent	Absent

*Not given

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ABSTRACT

The larval stages of C. opilio and C. japonicus consist of one prezoea, two zoea, and one magalopa reared in the laboratory, and they are morphologically similar to each other as follows:

Prezoea - Covered with an embryonic cuticle; no spines on carapace.

First and second zoea - A dorsal, a rostral, and a pair of lateral spines on carapace; the abdomen consisting of five (in the first zoea) or six (in the second zoea) segments and the telson bifurcate; the endopodite of the first maxilliped having five segments with a spinal arrangement of 3-2-1-2-5 from proximal to distral segment, and the second maxilliped three segments with a 1-1-5 arrangement; the postero-lateral margin of the third, fourth, and fifth abdominal segments terminate in a pair of long lateral spines; telson bifurcate, long and slender; each furca of the telson bearing three setae on the inner side and small spine each on the lateral and dorsal sides, respectively; furthermore, there is a pair of additional internal setae in the second zoea.

Megalopa - Three rostral, a pair of antero-gastric, and a pair of cardiac dorso-lateral heavy processes; the first and second maxillipeds are well developed; the third one is tremendously developed with a massive endopodite consisting of four segments with numerous spines; the abdomen consists of six segments and the telson; pleopods present on the second to the fifth segments bear long plumose setae; the last pereiopod has no feelers at tip.

The larval stages of the two species, however, may be distinguished from each other by the following characters:

1) Chromatophores of prezoea, zoea, and megalopa are brown or reddish-brown in C. opilio and vermillion or crimson in C. japonicus; 2) Length of posterolateral spines on the third abdominal segment of the first and second zoea are shorter than (rarely equal to) the length of the fourth abdominal segment in C. opilio, but are more than 1.3 times the length in C. japonicus; Ischiopodite of the cheliped of the megalopa has a spine in C. opilio while no spine in C. japonicus.

On the Planktonic Larval Life of the Zuwai Crab, *Chionoecetes Opilio*, Occurring Along Coasts of the Central Japan Sea

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INTRODUCTION

The largest harvest of the zuwai crab, *Chionoecetes opilio*, from the Japan Sea was 15,604 tons in 1963. However, a rapid decrease in the landings of this crab occurred yearly, and at present the harvest is only 5,000 tons. The main factor for the decline in the size of the catch is directly dependent on the decrease in the resources affected by overfishing. One of the causes allowing overfishing is due to the lack of biological information in special reference to the life history of this species. Research into the ecology of the zuwai crab in the Japan Sea, therefore, began in 1967, and the results obtained were reported by many researchers, especially compiled by Ogata (1974) and Kon (1980). As a result of this ecological research, a few plans to protect the crab resource were carried out; however, so far there are no indications that show a definite recovery.

For that reason it is felt necessary to take more progressive action to propagate the zuwai crab resource. Like many coastal species--for example, the kuruma shrimp, *Penaeus japonicus*, the Japanese blue crab, *Portunus trituberculatus*, and the abalone, *Haliotis discus*--stocking artificially-reared young zuwai crabs is considered a promising possibility in the recovery of this resource. Fundamental studies for rearing the planktonic larvae of the zuwai crab were carried out by Kon (1970, 1973, 1979), and the techniques for mass productions of the seed are now being studied. At the same time, however, it is essential to know where and when and in what kind of water stocking planktonic larvae or young crab can be achieved.

Ecological studies of the planktonic larvae of the genus *Chionoecetes* in the Japan Sea were reported by Kurata (1963), Fukataki (1969), and Ito and Ikehara (1971). Furthermore, studies of young crabs just after settling on the sea bed were done by Ito (1968a) and Kon et al. (1968). However, even if these reports are compiled, it has not been possible to logically illustrate the changes in habitat and depths of larvae corresponding to larval stage or growth. This paper deals with the influence of oceanic environment on the life of the zuwai crab, from the prezoea to the first molting stage (first crawler), and hopes to show the relation between habitat and larval growth.

MATERIALS AND METHODS

Five voyages for plankton sampling were made at 18 stations in the waters of the zuwai crab fishing ground off Wakasa Bay in the Japan Sea during the period March to June 1978 (Figure 1). The depth of each station is in the range of 170 to 600 m. However, tows of nets in each station were

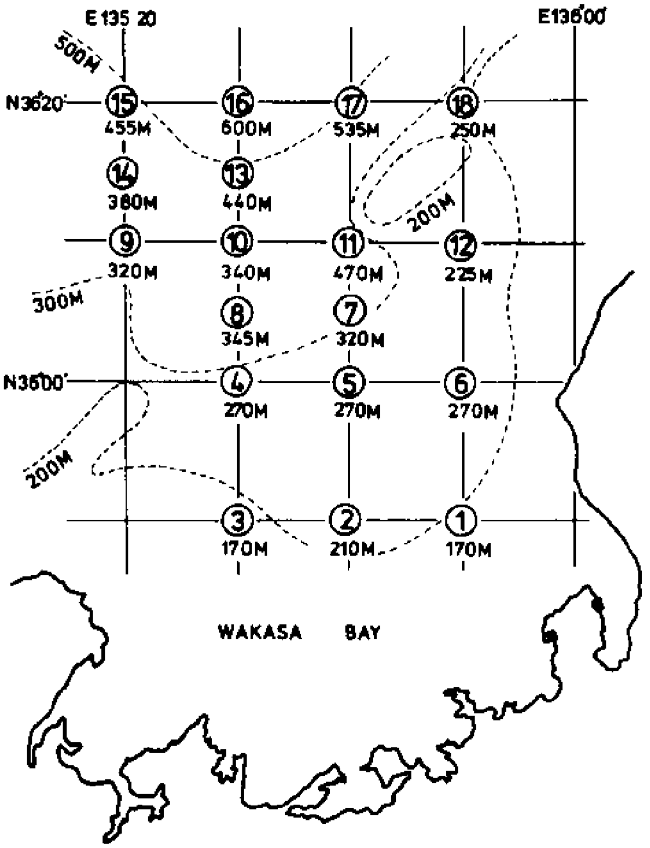


Figure 1. Location of the sampling station.

made in the six water depths ranging from 0 to 466 m. Six sampling nets having NGG 42 mesh, 1.3 m in diameter and 5 m in length were fixed on a wire which was lengthened to two or three times the depth of each station. The wire had an iron weight at the end, as shown in Figure 2. The wire was carefully hauled for 15 minutes at 1 to 2 knots so that the weight never left the sea bed. By using this method, simultaneous horizontal tows could also be made. As nets used for this study were not closed, it is impossible to avoid sampling in a shallower stratum than at an aimed depth. Water depths of some sampling nets were confirmed by a net recorder and a depth-distance recorder.

The spawning season of the beni-zuwai crab, *C. japonicus*, which are numerous in the Japan Sea at a depth of 700 to 1,500 m, closely resemble that of zuwai crab (Ito 1976). Morpho logical differences of each larval stage in both species were reported by Kurata (1969) and Motoh (1973, 1976). As the differences reported are minute, it is difficult to discriminate larvae collected between *C. opilio* and *C. japonicus*. The results obtained in this study, therefore, are illustrated as the larvae belonging to the genus *Chionoecetes*.

RESULTS

Horizontal and Vertical Distribution of First Zoeae

Two hundred sixty-two first zoea and one second zoea of genus *Chionoecetes* were collected from two to six depths (0, 50, 100, 150, 200, 300 m) at each station on the 6th and 7th of March. Figure 3 illustrates the quantitative distribution of the first zoea per one net haul at each depth. The densest areas at the surface and 50 m depth were both the fifth station, and at the 100 m depth at the fourth station. The depths of these two stations are both 270 m. Like a concentric circle, the more the distance increased from the densest areas, the less sparse the density distribution became. Limits of the distribution in these three depths are almost equal to an iso-depth line of 200 m on the coastal areas. These phenomena might show that the depth exerts a large influence upon the density distribution of first zoeae. As the numbers of first zoeae collected at each depth other than 150 m are less than 5 individuals per net haul, most of them might be collected in shallower depths on the way to or from these depths.

There was a large upwelling in the waters off Wakasa Bay at the beginning of March, and in the coastal waters of its upwelling there was another small one at the center of which the temperature was 10.4°C at both 50 and 100 m depths but 2.0°C at 200 m depth (Figure 4). The distributing area of first zoeae was situated around a coastal part of the small upwelling area.

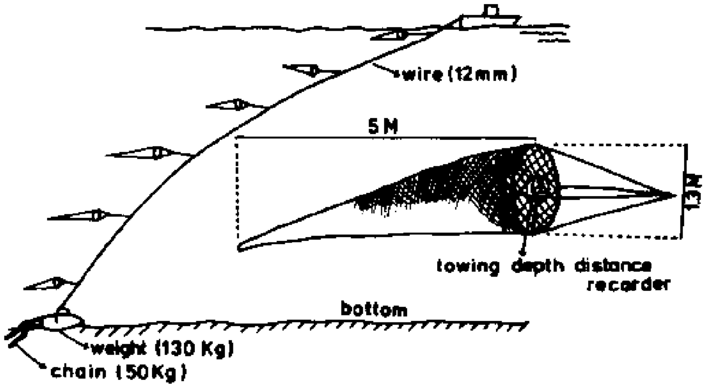


Figure 2. Structure and style of plankton net, and method of towing.

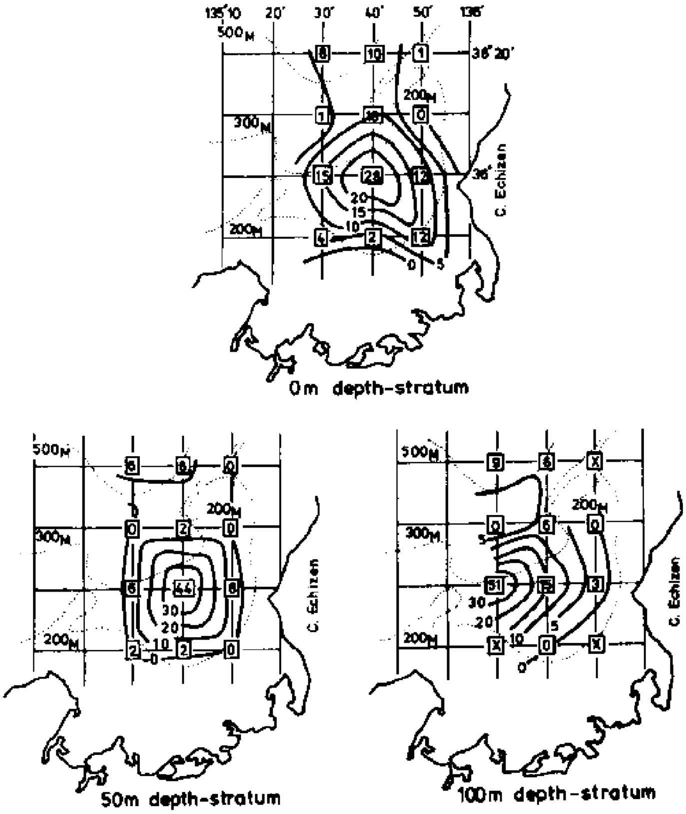
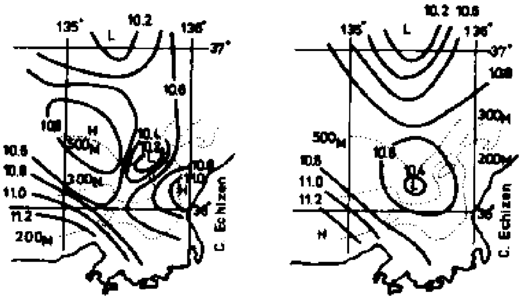
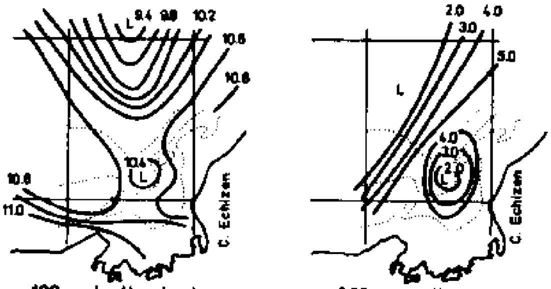


Figure 3. Density distribution of the first stage zoea per one net in the waters off Wakasa Bay in March 1978. :collected numbers, x: no towing.



0m depth-stratum 50m depth-stratum



100m depth-stratum 200m depth-stratum

Figure 4. Isotherms (°C) at each depth-stratum in the waters off Wakasa Bay in March 1978.

Horizontal Distribution of Megalopas

As a result of sampling made at depths ranging from 33 m to 466 m at 16 stations which were situated in waters deeper than the 200 m depth, 288 megalopas were collected in the middle of June. Figure 5 illustrates the quantitative distribution of these per one net at each station. The densest area of megalopas was found at the 10th station which was 340 m in depth. At this station eight individuals per net were collected. Like an ellipse, the more the distance increased from this densest area, the less sparse the density distribution became. It is thought that the depth exerts a large influence upon the density distribution of a megalopa as it does on the first zoea. Furthermore, it might be difficult to collect megalopas in waters shallower than 200 m during this season.

Seasonal Changes of Larval Quantity and Distributing Depths

As shown in Figure 6, first zoeae were collected during the period from early March, when sampling was tried for the first time, until early May. Almost all individuals collected in March were first zoeae, and mean numbers collected were 6.6 individuals per net. Eighty-one percent of all first zoeae collected in March were distributed vertically in the shallower depth than 100 m at an almost equal density. It also appears that alot of first zoeae were collected in 200 m and 300 m depths. As the plankton nets used were always open, it is difficult to deny the possibility that they were collected at a shallower depth on the way to or on the way back from these deeper depths. In early April the numbers of the first zoeae collected increased over those of the last month, and 10.5 individuals per net were gained as an average. About 77 percent of them were collected at depths shallower than 50 m, 27 percent of which were found at 25 m and 50 m, respectively, and 23.5 percent at the surface. The numbers collected in depths deeper than 50 m decreased gradually in accordance with depth. In early May the numbers of first zoeae collected decreased remarkably in all depths to less than three individuals per net. From the facts mentioned above, it may be concluded that a small number of first zoeae are dwelling as deep as 200 m, but most live in depths shallower than 100 m throughout all periods of this larval stage.

Second zoeae were collected during the period from early March to early May, but only one individual was collected in 39 nets in March. Numbers collected in early April, however, increased markedly to 745 individuals in 49 nets. Almost all of them were collected in depths from the surface to 100 m. As 13.4 percent of all second zoeae collected in

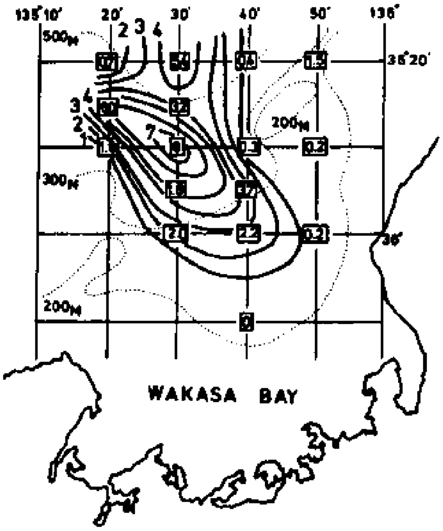


Figure 5. Density distribution of the megalopas per one net in the waters off Wakasa Bay in June, 1978.

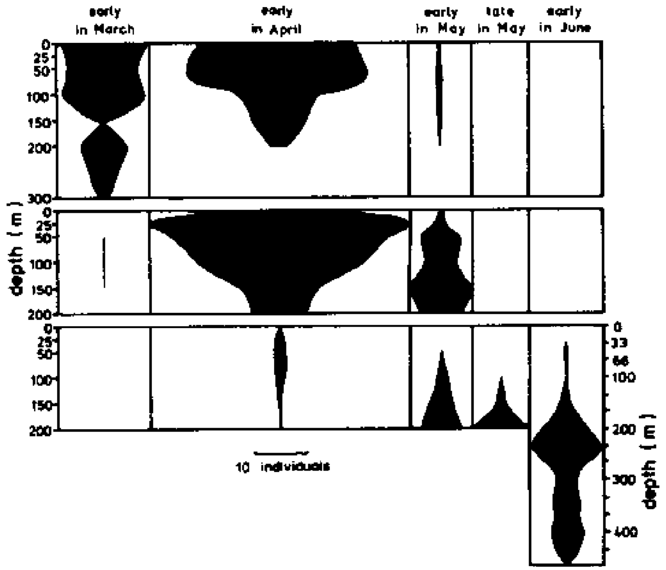


Figure 6. Monthly changes of distributional patterns of each larval stage. Upper tier: first zoea; middle tier: second stage zoea; lower tier: megalopa.

this month were gained at the surface, 29.2 percent in 25 m depth, 24.6 percent in 50 m depth, and 18.9 percent in 100 m depth, it is possible to say that except at the surface, the deeper the depth becomes, the less the distributional ratio changes in the range of these depths.

Most of the larvae of both first and second zoeae found in April were dwelling in the depths from the surface to 100 m, mostly from 25 m to 50 m. It looks as if they might have practically the same distributional pattern during this season. The second zoeae collected in May was the largest majority (66.5 percent) of all larvae collected. The numbers of second zoeae per net decreased sharply from 15.2 in April to 2.6 individuals in May with 93.6 percent of second zoeae collected at depths from 50 m to 200 m. The depth where they were collected most abundantly was 150 m, showing 33.9 percent. On the contrary, only 0.6 percent were at the surface and 5.8 percent in 25 m depth. These phenomena show that the concentrated depths of second zoeae changed from shallower in April to deeper in May. Furthermore, the second zoeae were distributed in deeper strata than the first zoeae in this month.

Megalopas were collected during the period from early April to early June when the last sampling was made. Numbers collected in April were only 0.5 individuals per net, and almost all of them were distributed vertically from 25 m to 100 m depths, especially at 50 m. In early May the numbers increased to 1.0 individual per net, but no megalopas were collected in the depths shallower than 50 m; and the deeper the depth became, the more the numbers increased. Most of them (54.2 percent) were gathered at the 200 m depth. The larvae collected in late May were only megalopas; however, the numbers per net were the same as early in this month. No megalopas were collected at depths shallower than 100 m. As earlier in this month, the deeper the depth became, the more the numbers increased. Most of them (85.5 percent) were found at the 200 m depth, which was the deepest stratum where nets were hauled at this time. In early June as well, only megalopas, 2.6 individuals per net, were collected. Many of them were obtained vertically in three lower depths--14.9 percent at 200 m, 23.4 percent at 233 m, and 11.5 percent at 266 m.

DISCUSSION

Distributional Patterns of First Zoeae

A distributional map of first zoeae in March shows the existence of a high distribution area like a concentric circle in the waters off Wakasa Bay. This corresponds to an area just above the sea bed at the depth of 225 to 275 m where a large school of adult female crabs dwell (Kon 1969). It is believed that larvae just after being hatched swim nearly straight upward to the surface waters without much scattering and remain in the neighboring waters. Yamamoto et al. (1978) reported that in the waters of the west coast of the Japan Sea, off the coast of Tottori Prefecture, first zoeae were collected in waters deeper than 50 m, not in waters where female adult crabs were dwelling. The differentiation of zoeal distributional patterns between Wakasa Bay and the coast of Tottori Prefecture may be related to an ocean current and/or a whirlpool. As the high density distributional area of first zoeae off Wakasa Bay is situated around the small upwelling area in early March, they may be able to remain in the nearby waters just above the sea bed where adult female crabs live. On the other hand, most of them off the coast of Tottoti Prefecture may be dispersed by the straight flow of the warm Tsushima Current.

The same phenomena as those mentioned above were also reported by some researchers investigating brachyuran larvae. Fukataki (1969) clarified that *Chionoecetes* larvae were collected much more often around an upwelling area in waters off the coast of Honshu in the Japan Sea. Ito and Ikehara (1971) reported that the distribution of the *Chionoecetes* larvae seemed to be closely associated with the upwelling, since the dense aggregation of larvae was found in the thermal trough around the upwelling area in the Japan Sea. Abe (1977) concluded that planktonic larvae of the horse crab, *Erimacrus isenbikii*, were gathered around the upwelling area in the way of a dispersal process and then migrated with its whirlpool.

From the facts described above, it is considered that the density distribution, aggregation, and migration of the *Chionoecetes* larvae are closely connected with a whirlpool. It is reasonable, therefore, to estimate that the number of the first molting stage crabs settling on commercial fishing grounds are determined by the oceanic environment of the planktonic larval seasons.

Changes of the Distributional Areas and Depths in Accordance with Larval Growth

The spawning season of the zuwai crab as reported by Kon and Honma (1970) corresponds closely to the appearance of the first zoeae in the waters off Wakasa Bay. Furthermore, the density distributional area of the first zoea clarified in this study corresponds also to just above the sea bed where a large school of the adult female zuwai crabs live (Kon 1969). Therefore, it can be considered that most of the larvae collected are zuwai crab, *C. opilio*.

Judging from the already known information and the facts obtained in this study, the distributional patterns of the zuwai crab larvae in the waters off Wakasa Bay are estimated as follows (Figure 7).

The spawning season is from January to April. The prezoeae just after hatching at a depth of 225 to 275 m swim and rise almost directly toward the sea surface after phototaxis (Kon 1967). However, as the duration of its stage in vitro is less than an hour (Kon 1967; Ito 1968b; Kuwatani et al. 1971), they may develop to the first zoeae before arriving at the surface.

Most of first zoeae that arrive near the surface are dwelling in depths ranging from the surface to 50 m. The first zoeae are collected until early May, but most of them are gathered from early March to early April. It is thought that the dispersion of the first zoeae is not very large because the area of their higher density distribution is situated around the upwelling area which arises near the zuwai crab fishing ground off Wakasa Bay almost every year.

The second zoeae are first collected from early March, but most of them range from early April to early May. In early April the center of their vertical distribution is located at the depth range of 25 m to 100 m, but early in May it changes to 150 m to 200 m. It is probable that the changes of their dwelling depths toward the deeper sea occur in accordance with elevated temperature near the sea surface.

Metamorphosis from a second zoea to a megalopa occurs in early April in the 150 to 200 m depth where the temperature is within the range of 6° to 12°C. After metamorphosis they go down to a deeper stratum beyond the large spring layer which is generated by the warm Tsushima Current and the cold Riman Current at the 200 to 250 m depth. The temperature under the spring layer is lower than 10°C all year round. The area of the high density distribution of megalopas is located further offshore and deeper than those of zoeal larvae. The depths showing the highest density distribution of megalopas changes to 355 m in early June, and almost no megalopas are collected in the waters shallower than 200 m in depth. Their dwelling water temperature in this season may be lower than 5°C. However, as there is no temperature zone lower than 5°C in waters shallower than 200 m in depth, almost no megalopas can live there.

Ito (1968a) reported that juvenile crabs up to the third molting stage had their habitats in the deep sea bed range from 300 to 350 m in depth. Furthermore, it was definitely shown by Kon (1969) that juvenile crabs up to the sixth molting stage were widely distributed in the regions deeper than 275 m in depth. The area of higher density

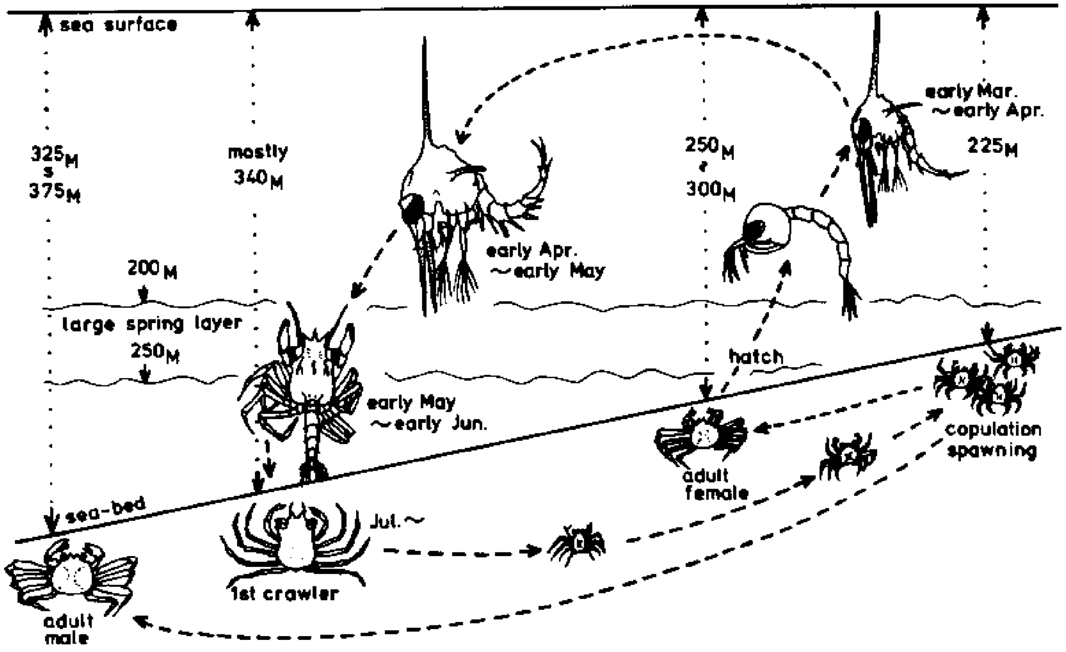


Figure 7. A supposed schematic presentation of the migration throughout its lifespan.

distribution of megalopas corresponds closely to the area reported for the juvenile crabs mentioned previously. This phenomenon supports the postulation that most larvae collected in this study belonged to the zuwai crab.

The spawning season of the zuwai crab occurs from January to April, mostly in February, in the waters off Wakasa Bay (Kon and Honma 1970). Furthermore, a small number of first molting stage crabs is collected in June, and the numbers of them increase dramatically in July (Tanabe and Suzuki 1981). Therefore, from these reports and the results obtained in this study, it is thought that the duration of the planktonic larval life may be about four to five months--about one month each for the first and second zoea stages and two to three months for the megalopa stage.

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ABSTRACT

The planktonic larval life of the zuwai crab occuring along the coasts of the central Japan Sea can be summarized as follows:

The prezoea just after hatching, from February to April, swim and rise toward the sea surface after phototaxis. However, as the duration of this stage is only about one hour, they may develop to the first zoea before arriving at the sea surface. The area of higher density distribution of the first zoea is located in the depth range from the sea surface to 50 m. That area corresponds to just above the sea bottom at the depth of 225 to 275 m where a large school of adult females were found. The area is also situated near an area of upwelling. Most of the first zoea are collected till early in May; however, most of them are from early March to early April.

The second zoea are collected from early March to early May; however, the greatest number are found from early April to early May. The depth stratum inhabited by the zoeal larvae moves toward the deeper sea in accordance with elevated temperature near the sea surface. Metamorphosis from the second zoea to the megalopa occurs from early April to mid-May in the 150 to 200 m depth.

The megalopa go down to the deeper stratum beyond the large spring layer at the 200 to 250 m depth. The area of higher density distribution of megalopa is located further off shore and deeper than for zoeal larvae. This area corresponds to the waters where previously reported crabs younger than sixth molting stage are found. Some first molting stage crabs (first crawlers) are collected in June, but most are collected in July. No larvae of any planktonic stage are collected in waters shallower than 150 to 200 m in depth.

Judging from these results, it is estimated that the duration of first planktonic larval life may be about four to five months; in other words, about one month each for the first and second zoea stages and about two to three months for the megalopa stage.

Effects of Sea Ice on the Distribution and Population Fluctuations of *C. Opilio* in the Eastern Bering Sea

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Chionoecetes opilio is distributed throughout most of the eastern Bering Sea (EBS), but its highest concentrations occur between the depths of 50-150 m in a region extending from St. Lawrence I. south to 55° N (Fig. 1). Areas of the continental shelf to the west and south of the high density areas, which superficially appear to be suitable habitats, contain relatively few *C. opilio*. Several factors could limit the abundance of *C. opilio* in these areas. Interspecific competition may be important because much of the western and southern region is occupied by *C. bairdi* (Fig. 1). Temperature may be important because the primary distributions of *C. opilio* and *C. bairdi* appear to be separated by a relatively strong thermal gradient (Somerton 1981a). In this paper, however, I examine evidence suggesting that sea ice, due to its probable effect upon primary production and larval survival, may be as important as either temperature or competition in determining the distribution of *C. opilio* in the EBS.

DATA AND METHODS OF COLLECTION

Chionoecetes opilio and *C. bairdi* were collected on EBS crab stock assessment surveys conducted by the National Marine Fisheries Service each year from 1969 to 1979. Sampling usually occured between May and August, but in 1969 and 1970 it occured two months earlier. The initial survey area included only Bristol Bay, but in subsequent years the area progressively expanded to the north and west (See Fig. 1 for the approximate size of the 1979 survey). Samples were collected using bottom trawls at stations located at the approximate centers of a 37 km grid. The catch was sorted to species and sex, then subsampled, if necessary. Carapace width was measured to the nearest 1 mm using calipers. Shell condition, a subjective index of relative postmolt age, was scored on a four point scale ranging from 1 (exoskeleton flexible) to 4 (exoskeleton scratched, discolored and typically covered with epifauna). Female maturity, based on abdominal width, was determined and the color of any attached eggs was noted.

SEA ICE, PRIMARY PRODUCTION AND LARVAL SURVIVAL

If sea ice influences the distribution of *C. opilio*, then it probably does so by influencing the food supply of *C. opilio* larvae. Although the diet of C. opilio larvae is not known with certainty (diatoms were the major gut component in a small sample of Stage I zoea examined at the University of Washington; D. Armstrong, Univ. Washington, per. comm.), the availability of suitable food is probably linked closely with the annual cycle of primary production.

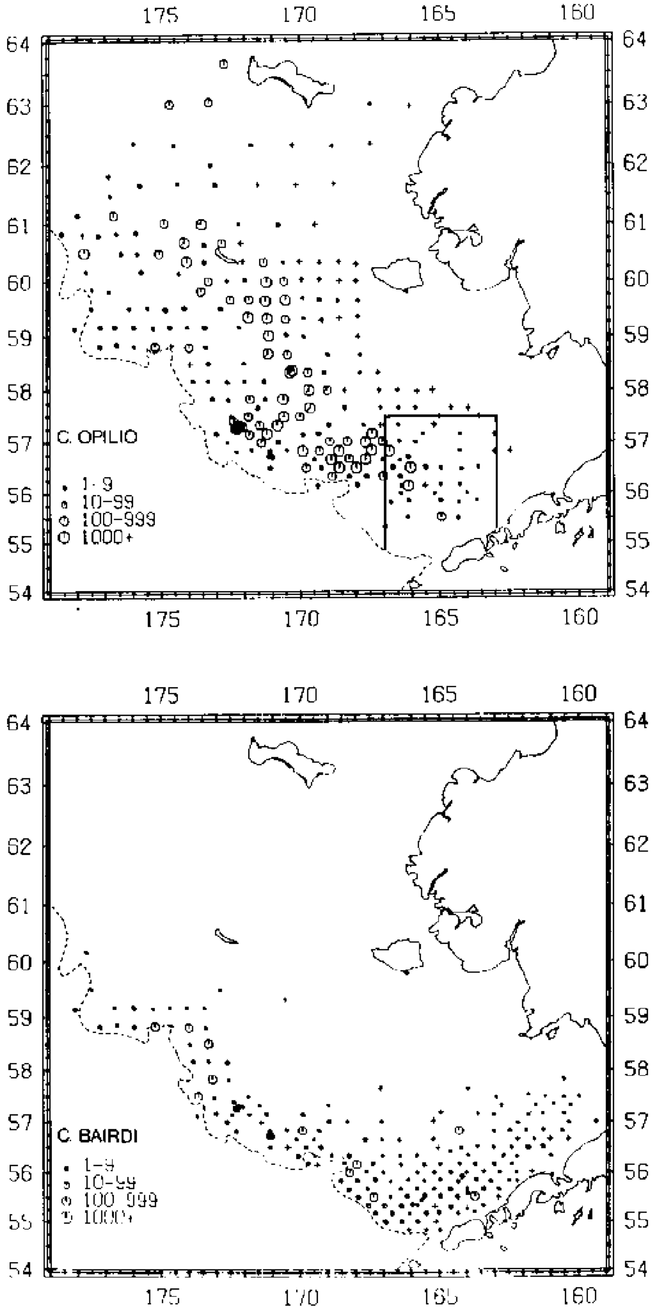

FIGURE 1

Distribution and abundance of adult female *C. opilio* (upper) and *C. bairdi* (lower) as depicted by the 1979 EBS crab survey. Catch per one half-hour trawl haul are indicated by symbol (circle) size. Pluses (+) indicate stations where juvenile but not adult females were caught. The dashed line indicates the 200 m isobath. The dark solid line on the upper figure delineates the study area defined in the text.

Within the EBS there are two distinct types of spring phytoplankton bloom. In ice covered areas, an intense but short ice edge bloom occurs when the ice begins to disintegrate and melt. This bloom is promoted by low salinity melt water which stabilizes the water column and by ice flows which inhibit wind mixing (McRoy and Goering 1974). In ice free areas, a normal bloom develops at two oceanic fronts and spreads across the shelf (Goering and Iverson 1981). This bloom is promoted by increased insolation which warms and stratifies the water column and by a shift in the storm tracks which reduces wind mixing (Goering and Iverson 1981). In most of the region inhabited by *C. opilio* the ice edge bloom is the only bloom and in most of the region inhabited by *C. bairdi*, the normal spring bloom is the only bloom (Alexander and Niebauer 1980).

Chionoecetes opilio and *C. bairdi* may each specialize on a different type of bloom, that is, *C. opilio* may be adapted to utilize the ice edge bloom and *C. bairdi* may be adapted to utilize the normal bloom. This specialization could involve a difference in the physiological tolerance of their larvae to the temperature and salinity regimes associated with each bloom, a difference in the ability of their larvae to forage on the various species of phytoplankton and zooplankton associated with each bloom or a difference in the time of larval hatch. Since most of the region each species inhabits experiences only one type of bloom, specialization probably does not represent a mechanism for resource partitioning, rather it represents an adaptation for maximizing larval survival in a particular environment.

If specialization does occur, then it should be most apparent in the major areas of sympatry, especially in the southern EBS, which are ice covered in some but not all years.

To determine if *C. opilio* and *C. bairdi* release their larvae at different times and thereby specialize on different blooms, the percent of adult females having recently hatched eggs was calculated for the months of April through July, 1976. The comparison was restricted to the region of the EBS south of 58° N. Egg color, which changes from orange to purple-brown during embryonic development, was used to separate females with new eggs from females with pre-hatching eggs. Some females with orange eggs, however, are primiparous and have not hatched a clutch. These females were identified by their new exoskeletons (shell conditions 1 and 2) and were excluded from the analysis. The percent of multiparous females with orange eggs (percent spawned) by month is shown for both species in Fig. 2. The percent spawned increased for both species from April to July when spawning appears to have been complete. But in April and May, *C. opilio* clearly had a higher percent

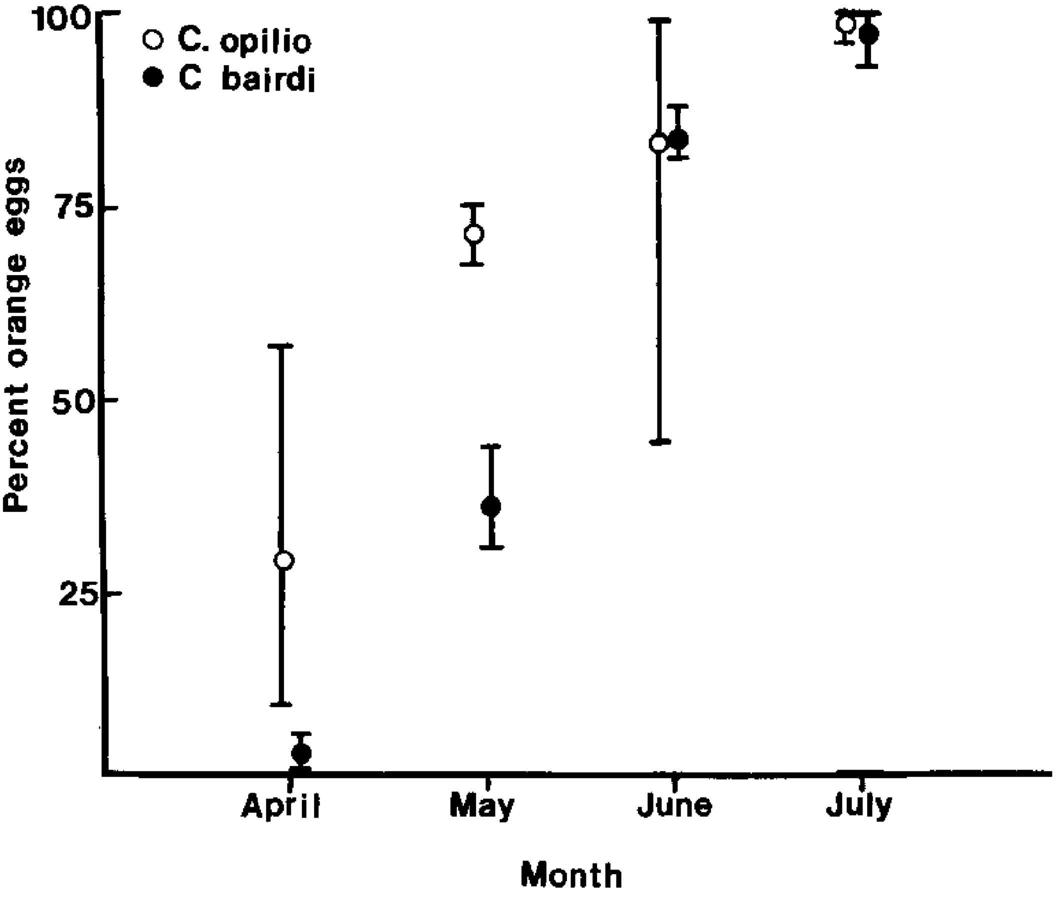

FIGURE 2

Percent of multiparous female *C. opilio* (circles) and *C. bairdi* (dots) carrying orange, recently extruded, eggs in each month from April to July, 1976. Vertical bars represent the 95% binomial confidence intervals. The presence of orange eggs indicates that a female has recently hatched a clutch of eggs.

spawned than *C. bairdi*. The general pattern of change in percent spawned suggests that, at least in 1976, *C. opilio* larvae started to enter the plankton earlier, possibly by as much as one month, than *C. bairdi* larvae.

Although *C. opilio* larvae appear to enter the plankton before *C. bairdi* larvae, it is not clear that the ice edge bloom preceeds the normal bloom. Both the ice edge bloom (McRoy and Goering 1974) and the normal bloom (Goering and Iverson 1981) are reported to begin in April. In years of extensive ice coverage, however, both blooms may occur sequentially at locations in the southern EBS (McRoy and Goering 1974). Of particular importance is whether, at locations which experience ice cover infrequently, primary production is advanced or retarded by the presence of ice. If it is advanced, then *C. opilio* could specialize on the ice edge bloom by releasing their larvae earlier than *C. bairdi*. Further research on the effect of ice on the timing of phytoplankton blooms is needed to answer this question.

SPATIAL AND TEMPORAL VARIABILITY IN *C. OPILIO* RECRUITMENT AND ITS RELATION TO ICE COVER

The extent of ice coverage in the EBS varies considerably between years. If the survival of *C. opilio* larvae depend upon the presence of ice, then larval survival and subsequent recruitment to the benthos should vary in a pattern consistent with the distribution of ice. This variability was examined in two different ways, spatially and temporally.

Since the frequency of ice cover, in the EBS, decreases with latitude (Webster 1979), the occurrence of *C. opilio* recruitment should also decrease with latitude. Recruitment was examined by constructing size frequency histograms, based on 1979 EBS data, for female *C. opilio* by intervals of 1° latitude (Fig. 3). If size frequency modes represent year classes, then these histograms indicate that there were two juvenile year classes in the population north of 60° N, one juvenile year class between 59° N and 60° N, and either no juveniles or low abundances of juveniles south of 58° N. The occurrence of recruitment, and therefore the occurrence of high larval survival, appears to decrease with latitude in the expected manner.

Temporal variability of *C. opilio* recruitment in the southern part of the EBS was examined by constructing a time series (1969-1979) of female size frequency histograms considering data only from a study area bounded by 163° W on the east, 167° W on the west, 57° 30' N on the north and the Alaska peninsula on the south (Fig. 1). This area was chosen because: 1) it was sampled in all survey years; 2) it is located at the south-

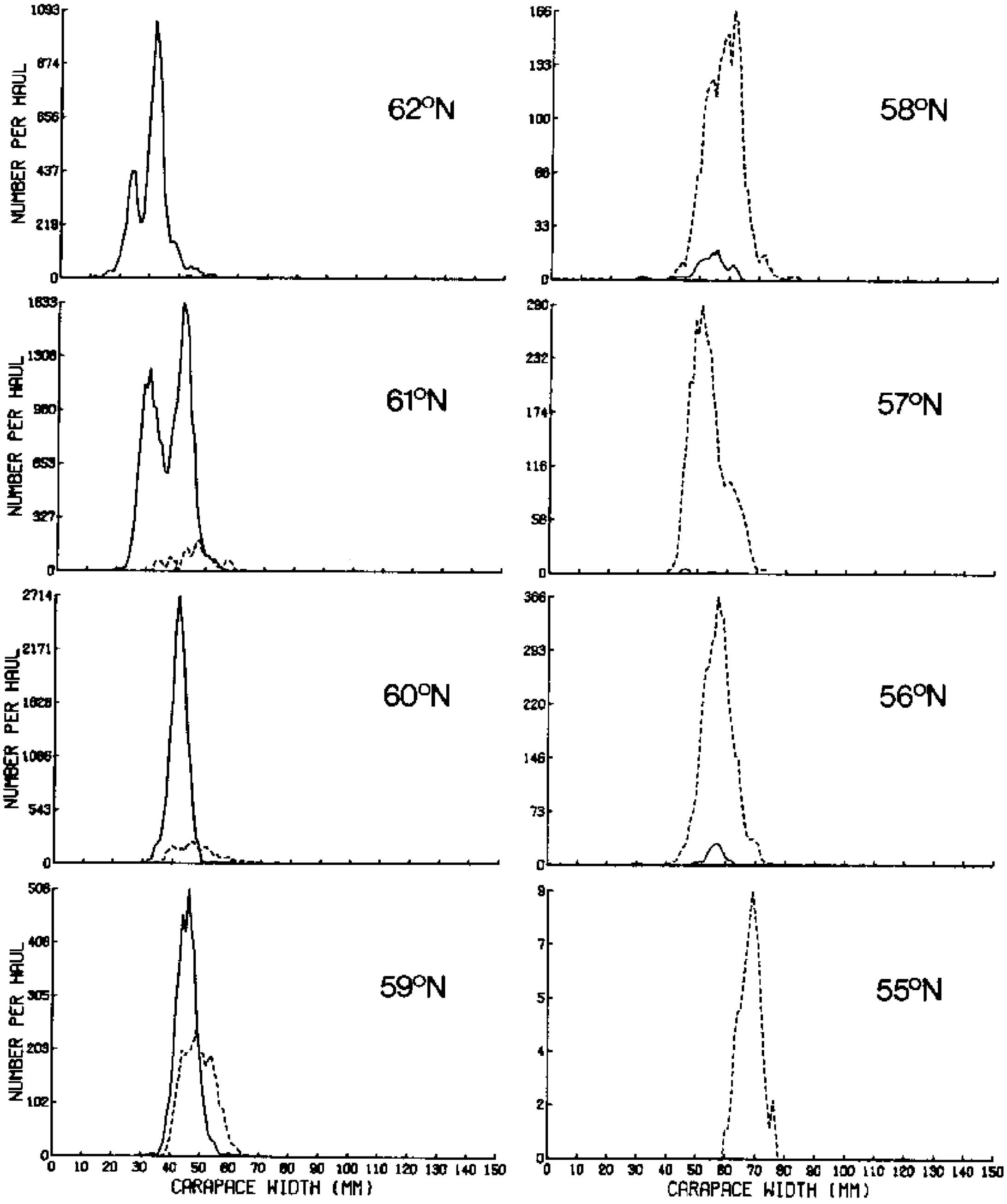

FIGURE 3

Size frequency histograms of juvenile (solid lines) and adult (dashed lines) female *C. opilio* by intervals of 1° latitude. Frequency (Y-axis) is represented by the average catch per one half-hour trawl haul. Note that the vertical scale changes with latitude.

ern extreme of the range of *C. opilio* and therefore should display considerable recruitment variability; and 3) it has weak and variable currents (Kinder and Schumacher 1981), therefore high recruitment should reflect high larval survival in the overlying water column.

This time series of histograms (Fig. 4) shows that, at the southern extreme of its distribution, *C. opilio* has infrequent recruitment. In 1969, the female population was dominated by a single cohort which had just reached maturity (91% of the adult females were recorded as recently molted or shell condition 1). In this, and every year until 1974, no juveniles were observed in the study area. In 1974, two year classes of juvenile females were first observed. One matured in 1975, the other matured in the following year. From 1976 to 1979, essentially no juvenile females were caught within the study area. If recruitment is defined as the maturation of a cohort, then significant recruitment occured in only 3 (1969, 1975, 1976) of the eleven years. Since female *C. opilio* probably mature at age 4 (Somerton 1981b), the apparent larval survival was high in 1965, 1971 and 1972.

To determine whether ice cover and year class strength are related, an index of the extent of sea ice within the study area during April was compared to the apparent larval survival. Ice data was obtained from a digitized arctic sea ice data base (Walsh and Johnson 1979), which consisted of the monthly percent ice cover, to the nearest 10%, within 1° latitude (60 nautical mile) squares for the years 1953-1977. An index of ice cover was constructed by summing the percent coverages at the six grid points that fell on or within the study area boundary. This index has the property of combining both the extent and density of ice within the study area, and could range from 600 if there were complete ice coverage at all six grid points to 0 is there were no ice in the study area. Apparent larval survival was scored as high (+) for 1965, 1971 and 1972, and as low (-) for all other years. The ice indexes and apparent larval survivals are shown in Table 1.

Of the three years with high larval survival, two (1971, 1972) correspond to years with extensive ice, but the third (1965) corresponds to a year without ice (Ice data before 1970 was obtained sporadically by airplane, but after 1970, ice data was obtained by satellite imagery. Thus, the apparent lack of ice in 1965 could be due to the inadequacy of the ice data. C. Pease, NOAA, Seattle, per. comm.). When all eleven years of ice cover and larval survival are considered, the ice cover in high survival years is significantly greater than the ice cover in low survival years at the 10% level (Mann-Whitney test, $.058<p<.092$).

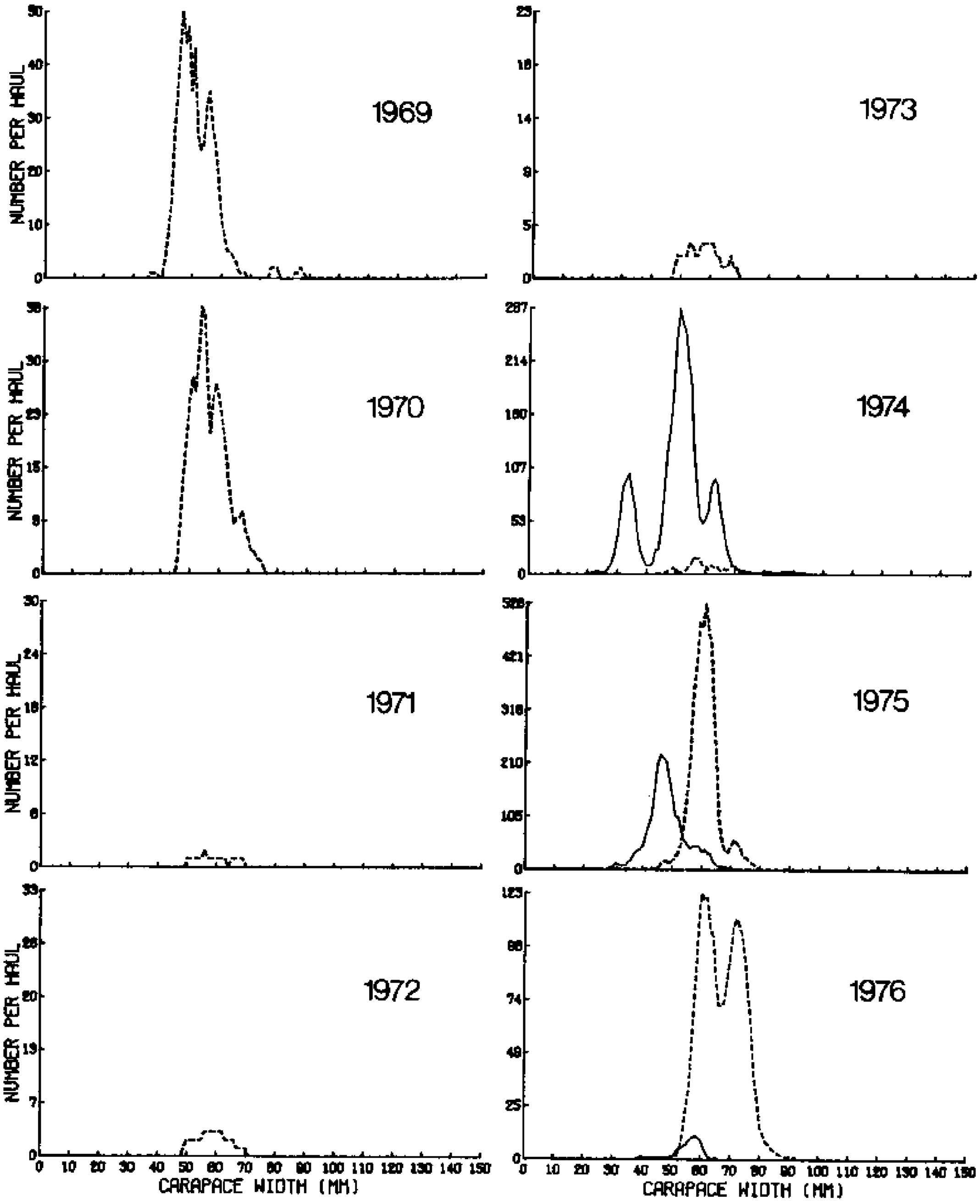

FIGURE 4

Size frequency histograms of juvenile (solid lines) and adult (dashed lines) female *C. opilio* by year (1969-1979) within the study area defined in the text. Frequency (Y-axis) is represented by the average catch per one half-hour trawl haul. Note that the vertical scale changes each year.

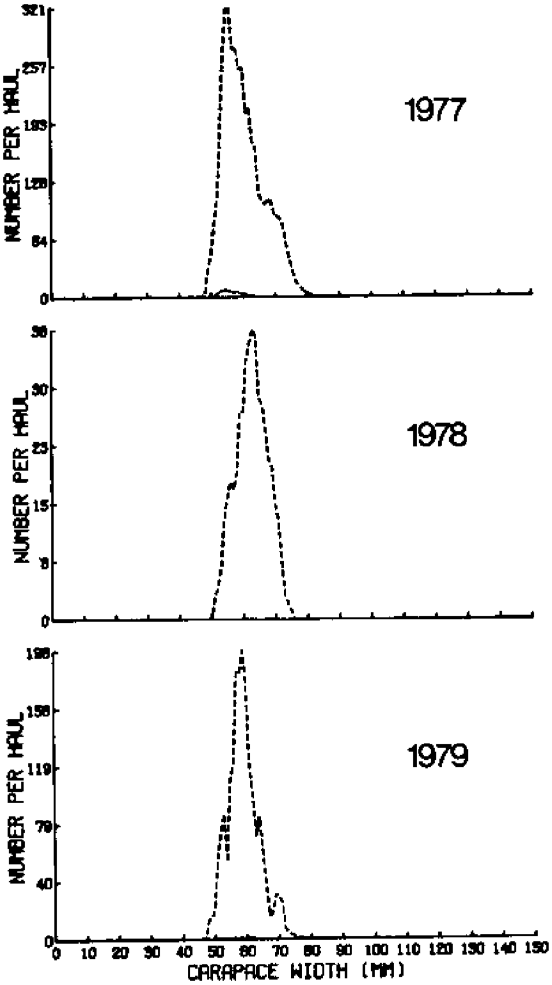

FIGURE 4 Continued

TABLE 1

Index of April ice cover and apparent larval survival of female *C. opilio* within a study area of the EBS defined in the text. Ice cover is the sum of the percent ice coverage at six locations within the study area. Ice cover index can range from 0 for no ice to 600 for complete ice coverage. Apparent larval survival was scored as high (+) if a strong year class of females subsequently matured four years later, and as low (-) if no subsequent recruitment occured.

Year	April ice cover index	Apparent larval survival
1965	0	+
1966	60	-
1967	0	-
1968	40	-
1969	0	-
1970	0	-
1971	360	+
1972	270	+
1973	70	-
1974	40	-
1975	60	-

DISCUSSION

The survival of *C. opilio* larvae appears to be related to a spring bloom of phytoplankton initiated by sea ice. Larvae may be adapted to enter the plankton at the usual time of the ice edge bloom, and when this bloom does not occur, either because ice is not present or because other conditions are unsuitable for initiation of a bloom, larval survival decreases. If this hypothesis is true, then the distribution of *C. opilio* is limited by the maximum extent of sea ice in April when the larvae enter the plankton.

Although the ice hypothesis was proposed to account for several aspects of the distribution and population fluctuations of *C. opilio* in the EBS, it may be applicable to other areas where *C. opilio* occurs. The northwest Atlantic is one such area. Figure 5 shows the average extent of ice in April, and the primary distribution of *C. opilio*, both in the EBS and in the northwest Atlantic. In both cases the southern extent of ice and the distribution of *C. opilio* are quite similar. In the northwest Pacific, however, the association between ice and a subspecies of *C. opilio*, *C. o. elongatus*, is not as clear. Although *C. o. elongatus* occurs in regions which are frequently ice covered, it also occurs in areas of the Sea of Japan (Watson 1969) which are always ice free.

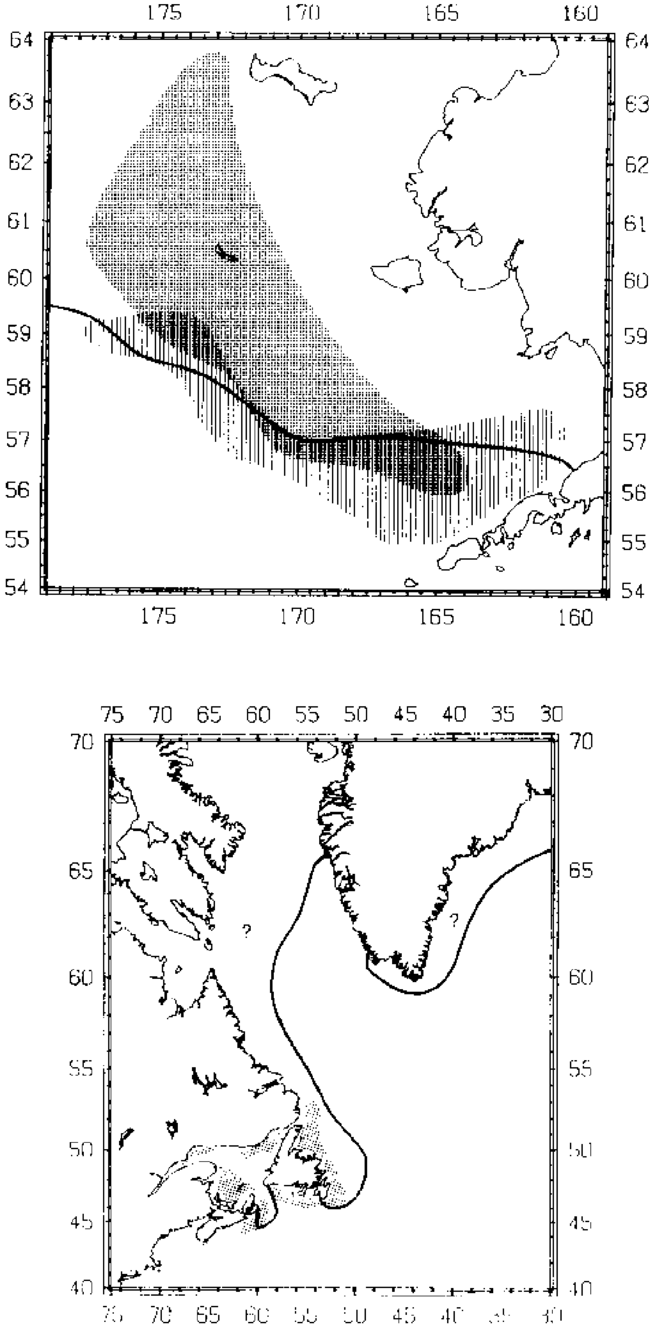

FIGURE 5

Average position of the ice edge in April (solid line) and the distribution of *C. opilio* and *C. bairdi*. The upper figure shows the distribution of adult female *C. opilio* (dots) and *C. bairdi* (stripes) in the EBS. The lower figure shows the distribution of commercial size *C. opilio* (dots) in the northwest Atlantic (R. Elner, per. comm.). Ice edge maps were obtained from the Naval Weather Service Attachment (1977) for the EBS and from Meserve (1974) for the northwest Atlantic.

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ABSTRACT

Evidence is examined which suggests that, in the eastern Bering Sea, *Chionoecetes opilio* may synchronize the release of its larvae with a spring phytoplankton bloom which is initiated by sea ice. When this ice edge bloom does not occur, either because ice is not present or because other conditions are not appropriate for initiation of a bloom, larval survival decreases. The distribution of *C. opilio* is therefore limited by the maximum extent of sea ice in April when *C. opilio* larvae enter the plankton.

Distribution of Juvenile *Chionoecetes Bairdi* in Cook Inlet

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INTRODUCTION

Tanner crab, Chionoecetes bairdi, support a small but locally important commercial fishery in Cook Inlet. Much of the fishing effort is concentrated in outer Cook Inlet or Kamishak Bay, near or within an area designated as a possible lease site for oil and gas development. As part of the Outer Continental Shelf Environmental Assessment Program, a preliminary examination of the distribution and abundance of Tanner crab was initiated (Feder and Paul, 1981). This report provides information on areas where Tanner crab less than 20 mm, and crab 21 to 80 mm, were observed during this survey.

METHODS

Sampling was accomplished with 3.6 m try-net fished on the bottom for ten minutes at a speed of 3 to 4 knots. The net contained a liner with a mesh of 9 mm^2. Carapace width of the crab were measured to the nearest millimeter with calipers. Station latitudes and longitudes are available in Feder and Paul (1981). A van veen grab sampled the infauna.

RESULTS AND DISCUSSION

The size distribution data for Tanner crabs (Table I) indicate that the areas within Cook Inlet that were sampled are inhabited primarily by large size individuals. Tanner crabs less than 20 mm carapace width were encountered primarily near the mouth of the Inlet and lower Kamishak Bay. Station 5 (Fig. 1) was the area where these crabs less than 20 mm were most abundant averaging 1,400 per km fished. Stations 8 (1,272 per km fished), 25 (377 per km fished) and 18 and 23 (290 per km fished) also had significant numbers of these young crabs (Table I). The size frequency of these small crab at Station 8 is presented in Table II.

Distribution of the zoeae of the commercially important crustaceans including Tanner crab has been determined by Dr. T. English (pers. comm. University of Washington) (Fig. 2). The distribution of Chionoecetes bairdi late zoeae are similar to the benthic stages less than 20 mm captured by trawls (Fig. 2). However, early zoeae are most abundant in Kachemak Bay near Station 40A where no benthic juveniles were captured in the trawls.

Early benthic stages were encountered mostly at depths exceeding 50 m. Stations 5 and 8 where small crab were most abundant were 166 and 150 m deep, respectively. Carlson and Straty (1981) reported encountering many Tanner crab less than 40 mm in the deepest part of Lisianski Strait, Southeast Alaska, at 230 m depth.

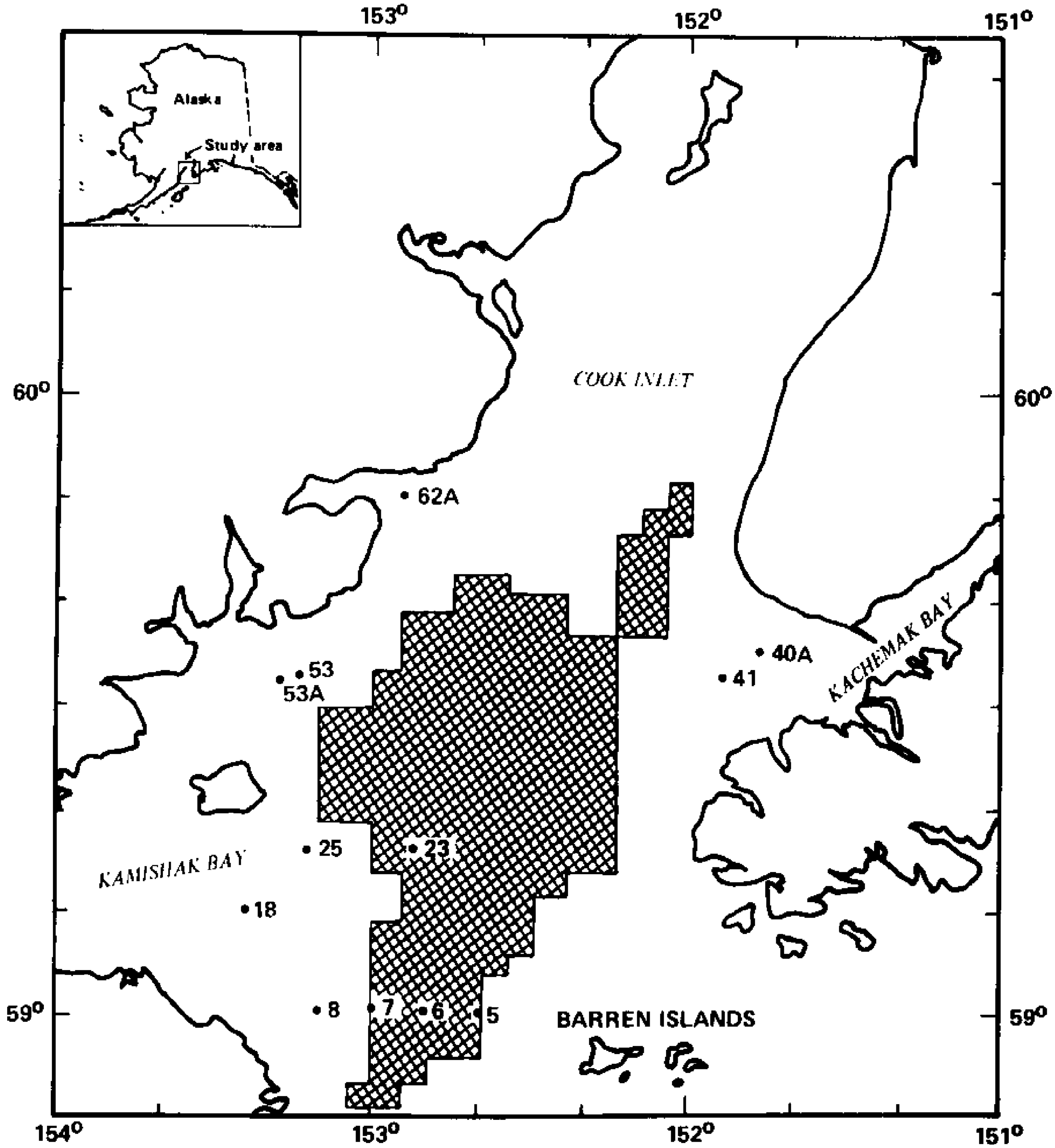

Figure 1. Lower Cook Inlet trawl stations. The possible oil and gas lease site is designated by hatch marks.

TABLE I.

SIZE DISTRIBUTION OF *CHIONOECETES BAIRDI* FROM SELECTED TRAWLS FROM COOK INLET STATIONS

Data recorded as numbers of crabs

Station	Depth (m)	No. Crab Raw Data 5-20 mm	21-80 mm	81+ mm	% less than 20 mm	Mean No. 5-20 mm crab per KM fished	No. Trawls
5	166	1469	16	27	97	1400	9
6	181	7	0	5	58	5	2
7	166	300	-	-	100	-	2
8	150	248	0	2	99	1272	3
18	44	44	0	14	76	290	4
23	91	22	0	3	88	290	3
25	59	396	-	2	99	377	3
40A	31	0	2	2	0	0	3
41	35	0	1	79	0	0	5
53	37	81	2	30	72	319	6
53A	40	92	0	13	88	-	2
62A	24	32	1	105	23	5	6

TABLE II.

JUVENILE TANNER CRAB CARAPACE WIDTHS, STATION 8, COOK INLET, ALASKA

10 May 1978		7 June 1978	
Width (mm)	Number	Width (mm)	Number
3	1	-	-
5	3	-	-
6	2	-	-
7	30	-	-
8	17	8	6
9	3	9	6
10	24	10	4
11	81	11	17
12	34	12	14
13	4	-	-
14	11	14	6
15	24	15	21
16	22	16	21
17	17	17	4
18	4	18	1
19	1	19	2
20	4	20	4
21	6	21	4
22	8	22	6
23	10	23	1
24	5	24	2
25	6	-	-

Total = 436

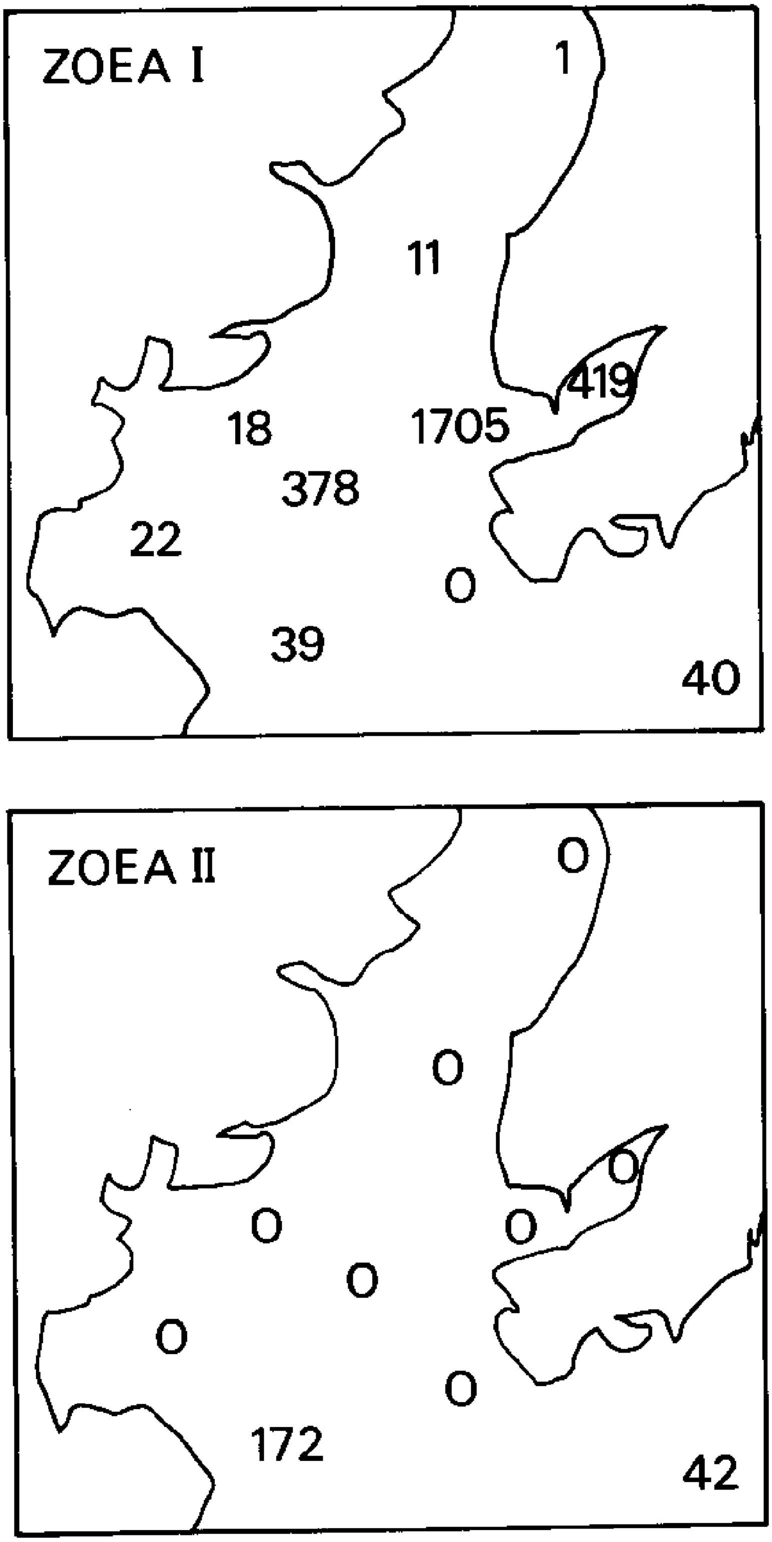

Figure 2. Distribution of zoea I and zoea II of *Chionoecetes bairdi* (data from Dr. T. English, University of Washington).

The size distribution data suggest the existence of a nursery area for Tanner crab that encompasses Stations 5, 6, 7, 8, 18, 23, 25, 53, 53A and other nearby areas not sampled. Stations 6 and 23 are in the lease area and the other stations, with the exception of 53 and 53A, are directly in the path of prevailing currents which flow southward over the lease area (Fig. 3).

The absence of Tanner crab less than 20 mm carapace width in the Kachemak Bay area is puzzling since the area supports a commercial fishery. Futhermore, the current gyre prevalent there (Fig. 3) should prevent the zoeae from being swept away. Their absence in Kachemak Bay may be due to recruitment failure, or perhaps crabs move from the nursery area described above or from other nursery areas not discovered, to Kachemak Bay and other parts of the Inlet. Further observations on the distribution of these small crabs are necessary to determine the importance of nursery areas as a source of recruitment to Cook Inlet and the adjacent Gulf of Alaska.

The trawl contents at Stations 5 through 8, where juvenile Tanner crab are most abundant (Table III), are dominated by small sponges intermixed with hydroid fragments, polychaete tubes, and crustacean and mollusc fragments. The most common polychaete tubes associated with the sponges are those of *Spiochaetopterus typicus*. After removing all motile organisms, the composition of the remaining material by per cent weight and volume is as follows:

	Wet Weight (%)	Volume (%)
Sponge	70	67
Hydroid and polychaete tubes	12	14
Hydroids	6	6
Crustaceans and mollusc fragments	12	13
Totals	100	100

Limited information is currently available concerning the food of Cook Inlet Tanner crab under 20 mm carapace width. Feder (1980) reported fragments of crustacean carapace in 60 percent of the stomachs of small *C. bairdi* they examined. The remains of brachyuran crabs, including *C. bairdi* and *Pinnixa schmitti*, were in 25 percent of the

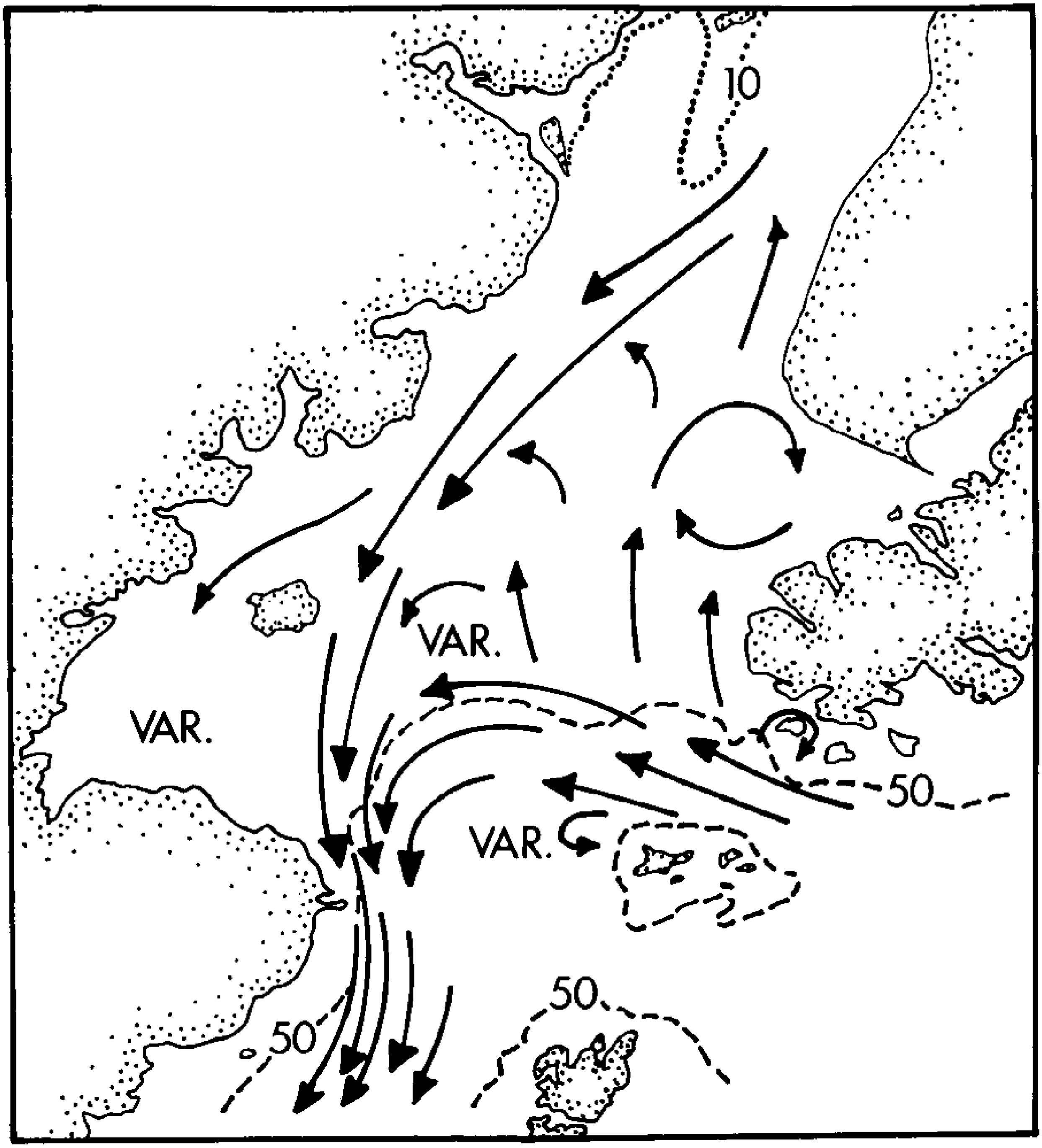

Figure 3. Diagram of spring and summer mean flow in lower Cook Inlet.

TABLE III.

EPIFAUNA ASSOCIATED WITH JUVENILE TANNER CRAB AT STATION 8, COOK INLET

Taxonomic Name	Counts per km	Counts per m^2	Weights (grams) per km	Weights (grams) per m^2
Eunephtya rubiformis	1.0	0.00028	5.2	0.00141
Eunoe depressa	1.0	0.00028	1.0	0.00028
Gattyana ciliata	22.7	0.00620	12.4	0.00338
Gattyana cirrosa	49.5	0.01353	1.0	0.00028
Anaitides mucosa	1.0	0.00028	2.1	0.00056
Typosyllis spp.	253.6	0.06933	1.0	0.00028
Potamilla neglecta	21.6	0.00592	1.0	0.00028
Sabella spp.	16.5	0.00451	1.0	0.00028
Crucigera zygophora	28.9	0.00789	2.1	0.00056
Chlamys rubida	12.4	0.00338	43.3	0.01184
Cyclocardia spp.	2.1	0.00056	1.0	0.00028
Hiatella arctica	2.1	0.00056	1.0	0.00028
Fusitriton oregonensis	43.3	0.01184	473.2	0.12936
Buccinum plectrum	13.4	0.00366	186.6	0.05101
Beringius kennicotti	3.1	0.00085	9.3	0.00254
Neptunea lyrata	23.7	0.00648	1087.6	0.29733
Gastropteron pacificum	2.1	0.00056	1.0	0.00028
Tritonia spp.	9.3	0.00254	1.0	0.00028
Nymphon grossipes	45.4	0.01240	1.0	0.00028
Cyclopoida				
Balanus hesperius	1.0	0.00028	2.1	0.00056
Balanus rostratus	13.4	0.00366	18.6	0.00507
Rocinela spp.	3.1	0.00085	1.0	0.00028
Ampelisca macrocephala	24.7	0.00676	2.1	0.00056
Ampelisca eschrichti	7.2	0.00197	1.0	0.00028
Anonyx nugax	35.1	0.00958	5.2	0.00141
Stegocephalus inflatus	20.6	0.00564	3.1	0.00085
Decapoda	103.1	0.02818	28.9	0.00789
Pandalus spp.	1.0	0.00028	2.1	0.00056
Pandalus borealis	34.0	0.00930	42.3	0.01155
Pandalus platyceros	150.5	0.04115	116.5	0.03185
Spirontocaris spina	9.3	0.00254	2.1	0.00056
Lebbeus groenlandica	2.1	0.00056	1.0	0.00028
Eualus barbata	4.1	0.00113	2.1	0.00056
Eualus suckleyi	2.1	0.00056	1.0	0.00028
Eualus townsendi	4.1	0.00113	1.0	0.00028
Eualus avina	143.3	0.03917	22.7	0.00620
Heptacarpus spp.	1.0	0.00028	1.0	0.00028
Crangon communis	2376.3	0.64961	918.6	0.25111
Argis dentata	23.7	0.00648	20.6	0.00564
Pagurus aleuticus	8.2	0.00225	187.6	0.05129
Labidochirus splendescens	24.7	0.00676	27.8	0.00761
Oregonia gracilis	106.2	0.02903	144.3	0.03946
Hyas lyratus	159.8	0.04368	479.4	0.13105

TABLE III.

CONTINUED

Taxonomic Name	Counts		Weights (grams)	
	per km	per m^2	per km	per m^2
Chionoecetes bairdi	449.4	0.12286	505.0	0.03824
Laqueus californianus	2.1	0.00056	1.0	0.00028
Terebratalia spp.	1.0	0.00028	1.0	0.00028
Synoicidae	24.7	0.00676	218.6	0.05975
Icelinus borealis	-	-	1.0	0.00028
Psychrolutes paradoxus	-	-	10.3	0.00282
*Asterotheca alascana**	-	-	7.2	0.00197

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*Many empty worm tubes of *Spiochaetopterus* and small sponges were also present but not counted. There was 0.5 kg sponge, hydroid and *Spiochaetopterus* present in the trawl.

stomachs. Small bivalves, polychaete and ophiuroid fragments were found in 38 percent, 11 percent and 9 percent of the stomachs, respectively (Feder, 1980). Paul, et al. (1979) reported hermit crabs, barnacles and small clams as important food of Cook Inlet *C. bairdi* less than 50 mm carapace width.

Small crabs (e.g., hermit crabs, *Oregonia*, *Hyas*) which are prey of juvenile Tanner crab, were numerically important in trawl samples at stations where young Tanner crab were abundant (see Table III for example). Likewise, polychaetes and small bivalves were dominant members of the infauna at these stations (see Tables IV and V). The protected habitat created by sponge and worm tubes at the stations where young Tanner crab were most abundant, may also provide a suitable environment for their preferred prey species. The concurrence of a habitat that protects small Tanner crab from predators and also harbors prey species may explain the observed distribution of juvenile Tanner crab in Cook Inlet.

Low numbers of sub-adult crab, 21 to 80 mm carapace widths, were encountered at all Tanner crab study stations (Table I). Perhaps Tanner crabs of this size range inhabit shallow waters not sampled. It is essential to know where this important size group of crab is located if the dynamics of this important species and its potential interaction with oil or recruitment to the fishery is to be comprehended.

A much larger sampling effort will be required to obtain a comprehensive understanding of critical habitats for planktonic and early benthic stages of Tanner crab in Cook Inlet. Such a survey may also provide information or factors regulating recruitment success in the species.

TABLE IV.

INFAUNA AT STATION 5, COOK INLET

Taxon Name	Mean No. per m^2	Mean Wet Wt. g/m^2
Sarcodina (Rhizopodea)	8.0	0.034
Rhynchocoela fragments	8.0	0.126
Rhynchocoela	2.0	0.030
Nematoda fragments	2.0	0.006
Polychaeta fragments	10.0	0.762
Polychaeta unidentified	2.0	0.004
Pholoe minuta	8.0	0.014
Eteone longa	0.0	0.002
Ancistrosyllis sp.	6.0	0.316
Syllidae	4.0	0.006
Nephtys fragments	2.0	0.070
Nephtys sp.	14.0	0.168
Nephtys longosetosa	8.0	0.082
Goniadidae unidentified	2.0	0.016
Glycera capitata	12.0	0.184
Goniada maculata	8.0	0.192
Lumbrineris sp.	74.0	0.828
L. latreilli	4.0	0.056
L. zonata	4.0	0.442
Ninoe gemmea	50.0	0.320
Haploscoloplos elongatus	36.0	0.114
Paraonidae unidentified	16.0	0.058
Aricidea sp.	20.0	0.258
Tauberia gracilis	28.0	0.070
Laonice cirrata	2.0	0.754
Prionospio sp.	4.0	0.014
P. malmgreni	4.0	0.024
Spiophanes sp.	2.0	0.008
Magelona sp.	308.0	1.582
Spiochaetopterus spp.	54.0	1.358
Cirratulidae unidentified	4.0	0.010
Tharyx sp.	2.0	0.000
Chaetozone setosa	2.0	0.000
Scalibregma inflatum fragments	2.0	0.016
Travisia brevis	2.0	0.022
T. forbesii	8.0	0.582
Capitellidae fragments	2.0	0.202
Capitellidae unidentified	142.0	0.328
Notomastus sp.	6.0	0.026
Maldanidae fragments	2.0	0.244
Rhodine sp. fragments	2.0	0.074
Myriochele fragments	6.0	0.554
Myriochele sp.	78.0	0.240

TABLE IV.

CONTINUED

Taxon Name	Mean No. per m^2	Mean Wet Wt. g/m^2
Ampharete sp.	6.0	0.306
A. arctica	2.0	0.032
Amphicteis gunneri	8.0	0.456
Pista cristata	12.0	0.324
Trichobranchidae unidentified	2.0	0.010
Terebellides stroemii	12.0	0.404
Chone sp.	10.0	0.254
C. cincta	2.0	0.074
Nucula tenuis	2.0	0.026
Nuculana fossa	2.0	1.582
Parvilucina tenuisculpta	6.0	0.380
Axinopsida serricata	160.0	0.168
Thyasira flexuosa	18.0	0.320
Odontogena borealis	38.0	0.160
Veneridae unidentified	2.0	0.008
Psephidia lordi	10.0	0.218
Macoma sp.	10.0	2.440
M. calcarea	72.0	15.398
Cardiomya planetica	2.0	0.012
Solariella sp.	2.0	0.022
S. obscura	4.0	0.178
S. varicosa	2.0	0.070
Natica clausa	2.0	0.050
Polinices pallida	2.0	0.050
Mitrella gouldi	2.0	0.242
Cylichna alba	2.0	0.018
Dentalium sp.	4.0	0.134
D. dalli	2.0	0.070
Ostracoda (Podocopa)	8.0	0.006
Leucon nasica	6.0	0.030
Eudorella emarginata	26.0	0.104
E. pacifica	2.0	0.006
Amphipoda unidentified	36.0	0.648
Ampeliscidae fragments	4.0	0.070
Ampelisca macrocephala	60.0	0.340
A. eschrichti	10.0	1.160
Byblis gaimardi	56.0	0.620
Haploops tubicola	2.0	0.012
Ischyrocerus sp.	2.0	0.004
Lysianassidae unidentified	2.0	0.004
Anonyx nugax	4.0	0.540
Phoxocephalidae unidentified	2.0	0.006
Heterophoxus oculatus	10.0	0.048
Pagurus sp.	2.0	0.044
Ophiopenia disacantha	10.0	0.218

TABLE V.

INFAUNA AT STATION 8, COOK INLET

Taxon Name	Mean No. per m^2	Mean Wet Wt. g/m^2
Hydrozoa	5.0	0.039
Rhynchocoela fragments	4.0	0.016
Rhynchocoela unidentified	1.0	0.005
Polychaeta fragments	6.0	0.164
Polychaeta unidentified	3.0	0.001
Pholoe minuta	3.0	0.030
Eteone longa	3.0	0.018
Syllis sp.	1.0	0.000
Nephtys fragments	3.0	0.293
Nephtys cornuta	3.0	0.005
Nephtys longosetosa	10.0	0.163
Glycera fragments	1.0	0.004
G. capitata	8.0	0.109
Glycinde picta	1.0	0.001
G. armigera	1.0	0.006
Goniada maculata	3.0	0.008
Eunicidae unidentified	3.0	0.210
Lumbrineris sp.	11.0	0.109
L. latreilli	3.0	0.065
Haploscoloplos elongatus	4.0	0.014
Scoloplos armiger	19.0	0.159
Paraonidae	3.0	0.006
Tauberia gracilis	1.0	0.001
Prionospio sp.	1.0	0.003
P. malmgreni	1.0	0.003
Spiophanes bombyx	13.0	0.101
Magelona sp.	13.0	0.034
Tharyx sp.	6.0	0.014
Chaetozone setosa	9.0	0.023
Capitellidae unidentified	6.0	0.009
Maldanidae fragments	5.0	0.079
Nichomache sp.	1.0	0.529
Praxillella gracilis	1.0	0.006
Rhodine gracilis	1.0	0.003
Owenia fusiformis	9.0	0.120
Myriochele fragments	5.0	0.264
Myriochele sp.	16.0	0.063
M. heeri fragments	1.0	0.223
Idanthyrsus ornatus	1.0	0.001
Ampharete sp.	4.0	0.060
Lysippe labiata	1.0	0.006
Terebellidae fragments	1.0	0.339
Pista cristata	18.0	0.315

TABLE V.

CONTINUED

Taxon Name	Mean No. per m^2	Mean Wet Wt. g/m^2
Procela emmi	1.0	0.001
Trichobranchidae	1.0	0.009
Nucula tenuis	6.0	0.023
Nuculana fossa	4.0	0.551
Musculus niger	1.0	0.004
Astarte esquimalti	4.0	0.840
Axinopsida serricata	1.0	0.003
Odontogena borealis	1.0	0.006
Psephidia lordi	30.0	0.375
Spisula polynyma	1.0	0.001
Macoma calcarea	13.0	1.470
Pandora filosa	4.5	0.045
Solariella obscura	4.0	0.019
S. varicosa	4.0	0.035
Natica clausa	1.0	1.641
Oenopota sp.	1.0	0.094
Ostracoda (Podocopa)	3.0	0.003
Leucon nasica	1.0	0.006
Eudorella emarginata	3.0	0.009
E. pacifica	6.0	0.006
Amphipoda unidentified	40.0	0.345
Ampelisca macrocephala	55.0	1.034
Byblis gaimardi	13.0	0.120
Ampelisca furcigera	1.0	0.094
Photis sp.	1.0	0.000
P. spasskii	3.0	0.004
Ischyrocerus sp.	1.0	0.009
I. anguipes	3.0	0.005
Anonyx nugax	1.0	0.185
Heterophoxus oculatus	4.0	0.015
Pagurus sp.	1.0	0.108
Chionoecetes bairdi	1.0	0.110
Pinnixia schmitti	1.0	0.019
Phoronida unidentified	3.0	0.006
Ophiuroidea fragments	1.0	0.156
Ophiuroidea unidentified	1.0	0.028

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ABSTRACT

A trawl survey was made in lower Cook Inlet to identify areas in which recently settled and juvenile stages of *Chionoecetes bairdi* are common. Young Tanner crab were observed primarily in outer Cook Inlet between the southern shore of Kamishak Bay and the Barren Islands. Small *C. bairdi* were also observed at several stations within Kamishak Bay. Young crab were most abundant at depths of 150 to 160 meters. Few Tanner crab less than 20 mm carapace width were observed in Kachemak Bay.

Tanner crab less than 20 mm were generally found in areas where sponges, hydroids and polychaete tubes were a major constituant of the material contained in the trawl.

Rates of Development and Growth of Larvae of *Chionoecetes Bairdi* and *C. Opilio* in the Southeastern Bering Sea

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ABSTRACT

Several aspects of the biology of larvae of *Chionoecetes bairdi* and *C. opilio* were investigated using zooplankton samples collected in the southeastern Bering Sea from 1978-1981. Large numbers of first stage zoeae of *C. bairdi* appeared in the plankton during late April and early May in the years sampled. The larvae of *C. opilio* appeared in significant numbers in the plankton at least two weeks prior to the major hatch-out of *C. bairdi* during two years and limited data from two other years indicates that this regularly occurs. Data on the timing of appearance of larvae in the plankton and on frequency of molting in larval populations of the two species indicate an approximate 30-day minimum to the duration of each zoeal stage and a 30 to 40-day hatch-out period. The duration of the magalops stage may be longer than 30 days for a significant proportion of the larvae of both species. A method for examining growth of the zoeae in the field is described and a growth rate of approximately 5% dry body weight zoea^{-1} day^{-1} calculated. The predicted ingestion rates necessary to satisfy growth requirements are briefly discussed.

INTRODUCTION

Most commercially harvested marine animals experience considerable fluctuations in abundance which are attributed in part to variations in recruitment. The term "recruitment" generally has been used in the field of fisheries to indicate entry of a year class into the size class legally harvested, but this term clearly involves a number of steps and interactions in nature. One step is recruitment from larval to post-larval stages, an event which is well defined for decapod crustaceans because it involves distinct changes in the organism. For most Brachyura, this recruitment step also involves leaving the planktonic environment for a benthonic one, providing a well-defined transition from one set of environmental conditions to another. The general "vulnerability" of plankton organisms and the well-defined period of direct planktonic influence on the survival of crab larvae make the larval stage a discrete and obviously fundamental place to search for causes contributing to fluctuations in commercial crab populations.

The purpose of this paper is to provide information necessary for further study on larvae of *Chionoecetes bairdi* and *C. opilio* in the southeastern Bering Sea. This paper addresses the timing of hatch-out of larvae of the two species, rates of larval development and preliminary information on growth.

MATERIALS AND METHODS

Sample Collection

Larvae of *Chionoecetes* spp. were removed from zooplankton samples collected throughout the southeastern Bering Sea during cruises conducted by the research vessels MILLER FREEMAN, THOMAS G. THOMPSON, ALPHA HELIX, DISCOVERER and ALASKA. The area of greatest concentration of sampling effort and dates of sample collection are shown in Fig. 1 and Table 1. Oceanographic features of the study area have been described by Kinder and Schumacker (1981). In keeping with their nomenclature, the region deeper than 100 m will be referred to as the outer shelf, from 50 m to 100 m depths as the middle shelf, and from 50 m to shallower depths as the coastal domain.

Zooplankton samples were collected with a variety of sampling gear and preserved in buffered formalin. The volume of water sampled was generally greater than 100 m^3 and the largest mesh size employed (505 μm) was small enough to retain virtually all *Chionoecetes* larvae entering the nets. Since this paper deals primarily with qualitative rather than quantitative aspects of the larval populations, comparison of larval concentration estimates provided by the various gear will not be discussed here. Mention will be made of sampling techniques as needed in the text.

Timing of Hatch-out

The timing of initial hatch-out of larvae of the two species was examined by plotting against time the mean larval densities estimated from samples collected during April and May of 1978, 1979 and 1981. Because crab larvae are relatively rare during these months, plankton samples were searched completely, not sub-sampled. The following criteria were used in selecting stations with data adequate for this analysis: (1) if a sample from a station contained larvae, the estimated density at that station was recorded for the corresponding date; (2) if a sample did not contain larvae but subsequent occupation of the sampling location showed that there were eventually larvae there, the "zero" density was recorded for

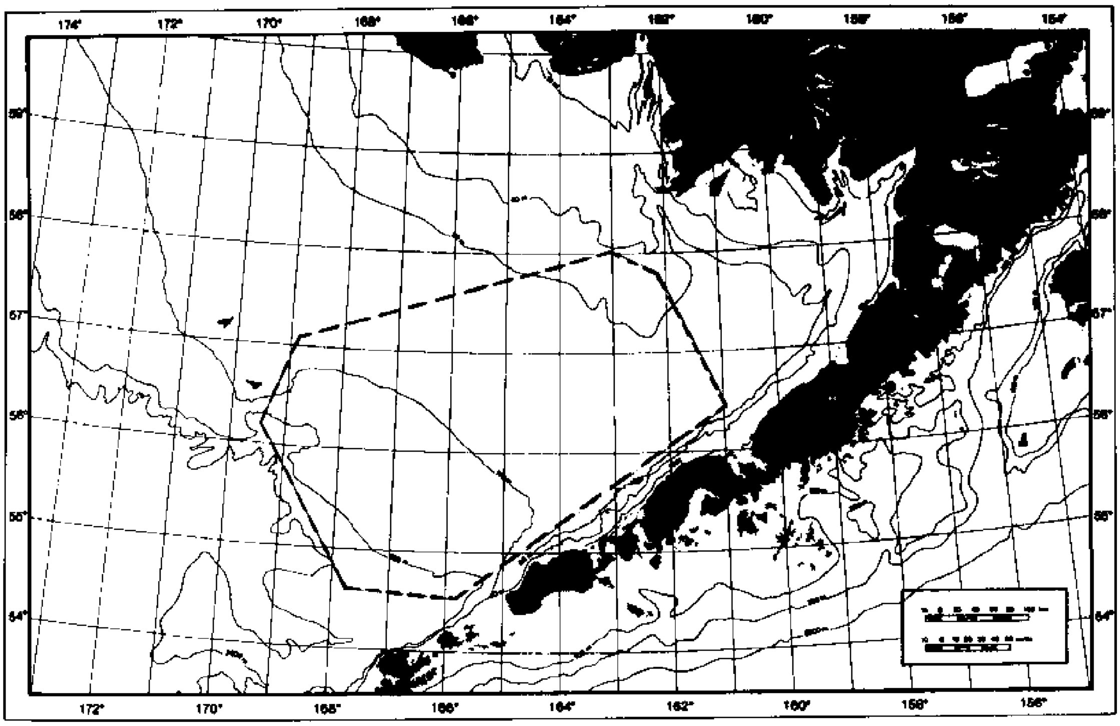

Fig. 1. Southeastern Bering Sea showing area covered by zooplankton samples examined in this study.

Table I

Zooplankton samples searched for larvae of *Chionoecetes bairdi* and *C. opilio*. in this study.

Year	Temporal Coverage of Zooplankton samples	Cruise	Cruise Sponsor*	Vessel	No. of Stations	No. of Samples
1976	26 April-31 May	MF-76A	NOAA	Miller Freeman	27	30
1977	16 April-17 May	RP-4-MF-77B	NOAA	Miller Freeman	80	112
1978	11 Feb-16 March	MF-78-1	NOAA	Miller Freeman	21	29
	11 April-29 June	TT-131	PROBES	T.G. Thompson	186	225
1979	1-27 June	3MF-79	NOAA	Miller Freeman	32	36
1980	6 April-8 June	TT-149	PROBES	T.G. Thompson	68	317
	4-5 October	AX9	PROBES	Alpha Helix	4	21
1981	16 April-20 July	TT 159	PROBES	T.G. Thompson	165	610
	14-31 May	RP-4-DI-81A	NOAA	Discoverer	16	16
	24 May-20 July	AL/811	NOAA	Alaska	23	23

* NOAA: National Oceanic and Atmospheric Administration
PROBES: National Science Foundation (Processes and Resources of the Bering Sea Shelf)

the earlier date; (3) if a station did not contain larvae and was not occupied again later, or was occupied and continued to show no larvae, the "zero" datum was not entered into the analysis. In this way, the period before any detectable hatch-out occurred could be identified without risk of biasing the analysis with data from sample locations not yielding zoeae of that species in that year. Sample coverage in the study area was not sufficient during any one year to enable a statistical comparison of initial hatch-out times for different sub-areas (middle shelf vs. outer shelf). Consequently, the data from all stations were pooled for various dates. The data presented here describe initial hatch-out periods of larvae primarily for areas where water depth exceeds 90 m.

Rates of Development

The rates of development of *C. bairdi* and *C. opilio* first stage (SI) zoeae in the southeastern Bering Sea were analyzed by examining the ratio of SI to total zoeae (SI:SI+SII) for each species at stations where at least six individuals of a species were examined in the sample or sub-sample. Using this low number of larvae increased the number of observations (stations) which could be included in the analysis and produced no obvious detrimental impact on the data variance, since a large variance existed even among stations with abundant larvae. The data were grouped into time periods not exceeding 10 days and the mean ratio calculated (unweighted ratio method). The number of larvae examined in each 10-day period ranged from a low value of 43 to over 2,000. From one to thirty stations were included in each period.

Rates of development of the second stage (SII) zoeae were analyzed by examining the ratio of SII:SII + megalops larvae (no SI zoeae were present during this period). The data were grouped into time periods of not more than 13 days. The number of larvae examined in each period ranged from 337 to 1695, while the number of stations ranged from 10 to 23.

For both molting analyses above, weighted ratios were also calculated by pooling data on all larvae from each 10-day period and then determining the ratio of the larval stages in question. This method gave results similar to the unweighted method (in most cases, ± .01), but the results of the unweighted ratio method are reported here because this allows variance of station data to be expressed.

Observations of the stomach contents of yellow fin sole (*Limanda aspera*) collected in early September 1980 (K. Haflinger, Univ. of Alaska, unpubl. data) and plankton samples collected in October 1980 provided some information on the late summer - early autumn presence of megalops larvae of both species and first post-larval (first instar) crabs of *C. opilio*.

Growth Rates

Tanner crab zoeae which are ready to molt to the next larval stage frequently can be identified by the absence of tissue from the distal ends of the carapace lateral spines and rostral and dorsal spines. In some cases, new zoeal or megalopal features can be observed beneath the old carapace in the abdominal region and the ventral portion of the thorax (cf. Drach and Tchernigovtzeff 1967; Van Herp and Bellon-Humbert 1978; Freeman and Costlow 1980a, b; Buccholtz 1982 for similar observations in other decapod larvae). These characteristics can be observed in both freshly caught, molting larvae and in preserved specimens and were used in this study to identify the end of growth in a zoeal stage. The biomass accrued by successive stages of larval development in the two species was determined by comparing the dry weight of: (1) early post-hatch larvae, and (2) very late stage (pre-molt) individuals of each zoeal stage (growth of the megalops stage was not determined in this study). To obtain an adequate number of measurements and to make certain that only early post-hatch larvae were measured, specimens were removed from preserved samples after all the samples had been analyzed; a correction factor for converting preserved dry weight (PDW) to estimated fresh dry weight (FDW) was then applied. This factor was determined by comparing mean PDW and FDW data for both species from two sampling locations where preserved and fresh dried specimens had been removed from the same plankton samples. Estimated fresh dry weights were compared to an assortment of FDW data which we had from field and laboratory samples to make certain that the estimates were in reasonable agreement with the range of values we had observed. The reliability of this method was demonstrated by Omori (1978) for other zooplankters.

With some adjustment (see later discussion) the estimated FDW for early post-hatch, late SI and late SII zoeae were fit to an exponential growth equation to determine specific growth rate (Warren 1971:139). For each zoeal stage:

$$W_2 = W_1 e^{kt}$$

where: W_2 = FDW at time 2 (end of zoeal stage)
W_1 = FDW at time 1 (beginning of zoeal stage)
k = specific growth rate
t = number of days growth

A constant growth rate and a 10% FDW loss at molt (from SI to

SII) were assumed. Boundary conditions on the growth model (such as number of days growth) were determined from other aspects of this study (see Results and Discussion).

RESULTS AND DISCUSSION

Timing of Hatch-out

The results of the hatch-out analysis for *C. bairdi* are listed in Table II, which shows the number of stations involved in the analysis and the mean value and range of larval densities encountered. The analysis is not shown beyond the point in time where maximum mean larval densities were attained. Sampling continued well beyond these dates in 1978 and 1981, and no significant increases in mean larval densities were observed. Thus, the "peak" of the hatch-out curve as determined by larval density estimates had occurred. Figure 2 represents the data from Table II as plots of relative density of larvae over a 40-day period for all three years where a value of 1.0 represents the maximum mean density observed in a particular year. Data for 1980 were infrequent during the period of predicted peak hatch-out (early May), but also show extremely low larval densities ($\leq 1/1000m^3$, n=7) for 18-20 April.

For the three years shown in Fig. 2, the greatest increase in mean larval density occurred between late April and early May and was clearly quite abrupt, inferring a relatively synchronous hatch of larvae throughout the adult populations underlying these stations. In 1978 and 1979, these stations also covered a large part of the outer shelf, and so represent a considerable portion of the outer shelf adult population of this species. The fact that a discernable time-averaged contribution to the larval population did not occur after the peak densities of early May had been attained suggests an appreciable decline in hatching activity. This is corroborated by the fact that most egg-bearing female crabs sampled in late May - early June have immature (recently extruded) egg masses (see D. Somerton's larval paper, this volume). The time period over which SI zoeae molt to SII later in the year indicates that the hatch-out period is about 30-40 days for this species.

The initial hatch-out period of *C. opilio* larvae was not as well documented as that for *C. bairdi*. There appears to be a considerably earlier hatch-out for this species, as shown in Table III with data from 1977 to 1978. Although there is a considerable range in larval densities shown over time (possibly due to a wider range of sample locations than was used for *C. bairdi*), high densities were clearly found by 20 April in both years. Throughout most of the area of the

Table II

Timing of appearance of Stage I zoeae of *Chionoecetes bairdi* in the southeastern Bering Sea by year and date. N1: number of stations sampled during specified period; N2: number of "*C. bairdi* stations" used in the analysis; density of larvae: mean number of zoeae per 1000 m^3 (range in parentheses).

Year	Dates	N1	N2	Density of Larvae
1977	18-19 Apr	13	8	25 (0-19)
	24-25 Apr	19	7	23 (0-100)
	16 May	9	8	1343 (0-4741)
	18 Apr	*	1	58
	24 Apr	*	1	1246
	9 May	*	1	1939
1978	16-21 Apr	31	16	1 (0-19)
	26-28 Apr	26	23	161 (0-704)
	11-14 May	6	6	10,842 (274-24615)
1981	17 Apr	4	4	6 (0-25)
	1 May	1	1	148
	11-14 May	6	3	548 (128-1262)

*observations from a single station outside the area of other stations; data are provided here for comparison.

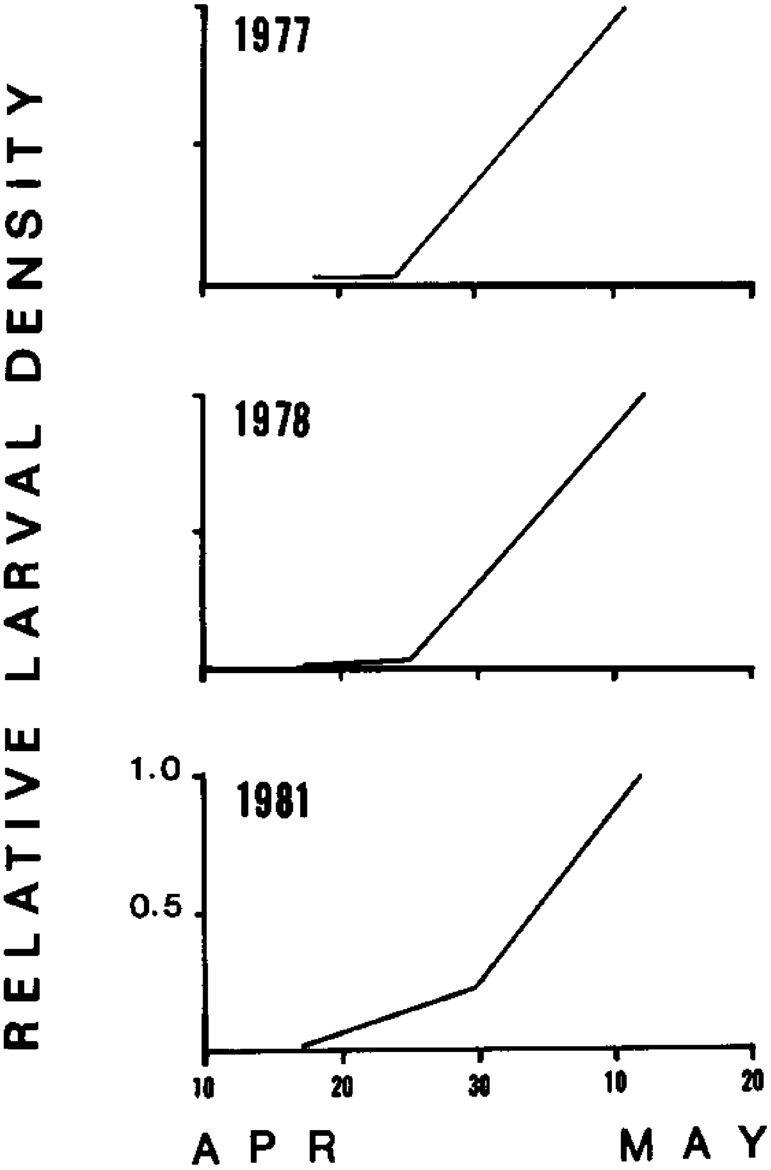

Fig. 2. Appearance of SI zoeae of *C. bairdi* in plankton samples from the southeastern Bering Sea. Data on mean larval concentration (from Table II) are represented as cumulative proportion of the maximum mean density observed at peak hatch-out (see text for details).

Table III

Timing of appearance of Stage I zoeae of *Chionoecetes opilio* in the southeastern Bering Sea by year and date. N1: number of stations where *C. opilio* larvae were found; N2: mean number of zoeae per 1000 m^3 (range in parentheses).

Year	Dates	N1	N2
1977	17-19 Apr	9	1,432 (285-5539)
	24-25 Apr	8	1,671 (242-3,266)
	10 May	9	3,577 (138-22,495)
1978	16-21 Apr	23	17,311 (9-104,448)
	26-28 Apr	23	25,716 (16-253,952)
	11-14 May	14	2,938 (273-13675)

southeastern Bering Sea sampled in this study, 1980 and 1981 were both markedly "poor" years for *C. opilio* larvae (Incze et al., in prep.) and collections were not adequate in either year to describe a hatch-out curve. However, larval densities typical of those two years were found by middle April. Furthermore data on development rates of Stage I zoeae of *C. opilio* and the time of appearance of Stage II zoeae of this species in 1981 (see later sections) also support the suggestion that significant hatch-out of *C. opilio* larvae occurs by middle April, at least two weeks prior to the major hatch of *C. bairdi* larvae. The period of transition of the *C. opilio* larval populations from Stage I to Stage II indicates a 30-40 day hatch-out period for this species as well.

Rates of Development

The larvae of *Chionoecetes* spp. go through a post-embryonic protozoeal stage, two zoeal stages and a megalops stage. The first (protozoea) stage is brief, usually less than an hour (Kon 1967; Kuwatani et al. 1971; Haynes 1973) and probably serves no function other than providing the larvae with relatively smooth external features which reduce the chance of tangling in the dense egg mass; the planktonic role of this stage is probably negligible. Personal observations of hatching *C. bairdi* protozoeae in the laboratory indicate that nearly constant, rigorous flexing of the abdomen (which may also be related to the upcoming molt to SI) is necessary for the animal to remain in the water column. Anaesthetized protozoeae sink, so there appears to be no positive bouyancy which would help to direct this animal toward the upper mixed layer of the ocean. The two zoeal stages and megalops stage, on the other hand, are of long duration. These larval stages of both species are strong swimmers, presumably capable of maintaining their position at desired depths in the water column.

The data on rates of larval development show considerable variability from one station to the next, reflected in a large variance about the mean over 10-day periods (Tables IV and V; Fig. 4). Despite the large variance, these data are useful for pointing out several features of the larval development process in the populations: (1) the point in time where molting to SI begins for each species can be fairly well defined; (2) the length of time required for the population of SI zoeae to molt to SII can be seen as approximately 30-40 days; (3) the difference in timing of the onset of molting in larval populations of the two species can be seen. In particular, data for 1978 and 1979 both show that the molt to SII was well underway in the *C. opilio* population before

Table IV

Proportion of SI to total zoeae of *Chionoecetes bairdi* and *C. opilio* in plankton samples collected in the southeastern Bering Sea: mean of sample observations ± one standard deviation (number of stations sampled in parentheses).

YEAR	SPECIES	DATES				
1978		7-17 May	27-31 May	1-10 June	11-20 June	21-29 June
	C. opilio	1.0 (11)	.92±.17(20)	.81±.22(30)	.34±.25(10)	.25±.29(21)
	C. bairdi	1.0 (7)	1.0 (7)	.99±.01(17)	.99±.01(6)	.85±.23(8)
1979				1-6 June	19 June	21-22 June
	C. opilio			.53±.33(8)	0 (3)	.01±.02(6)
	C. bairdi			.99 (7)	.31±.17(4)	0* (2)
1980		13 May	26-29 May	2-8 June		
	C. opilio	1.0 (1)	1.0 (5)	1.0 (2)		
	C. bairdi	1.0 (1)	1.0 (7)	1.0 (20)		
1981		15-16 May	23-30 May	1-10 June	11-19 June	
	C. opilio	1.0 (4)	.98 (2)	.94±.08(5)	.14±.25(3)	
	C. bairdi	1.0 (19)	1.0 (15)	.98±.04(19)	.54±.36(13)	

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*Four other stations sampled during the period 21-27 June contained SI zoeae of *C. bairdi* but contained too few larvae (<6) to be considered in this analysis; the zero datum is thus artificially low.

Table V

Proportion of SII to total larvae of *Chionoecetes opilio* and *C. bairdi* in plankton samples from the southeastern Bering Sea in 1981: mean of sample observations ± one standard deviation (number of samples in parentheses). No SI zoeae were present for either species during the time period shown.

	27 June-10 July	11-20 July
C. opilio	.78±.34 (23)	.11±.20 (10)
C. bairdi	1.0 (41)	.78±.22 (17)

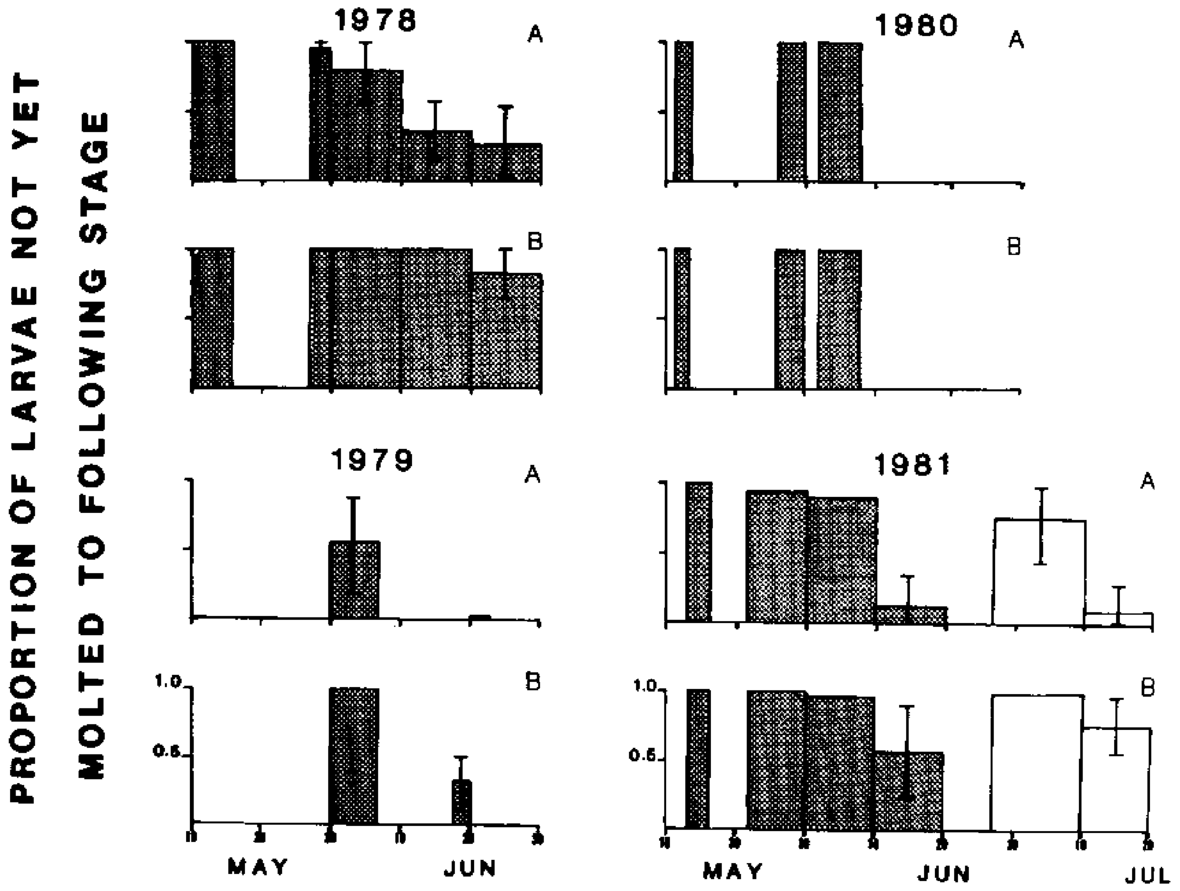

Fig. 3. Rates of molting in larval populations of *C. opilio* (A) and *C. bairdi* (B) during four years of study. Shaded bars show proportion of SI to total zoeae (no megalops present); open bars show proportion of SII to SII + megalops larvae (no SI present). Values shown are mean proportion from sampled stations ± one standard deviation; standard deviations are truncated at 1.0. (See Table IV for data).

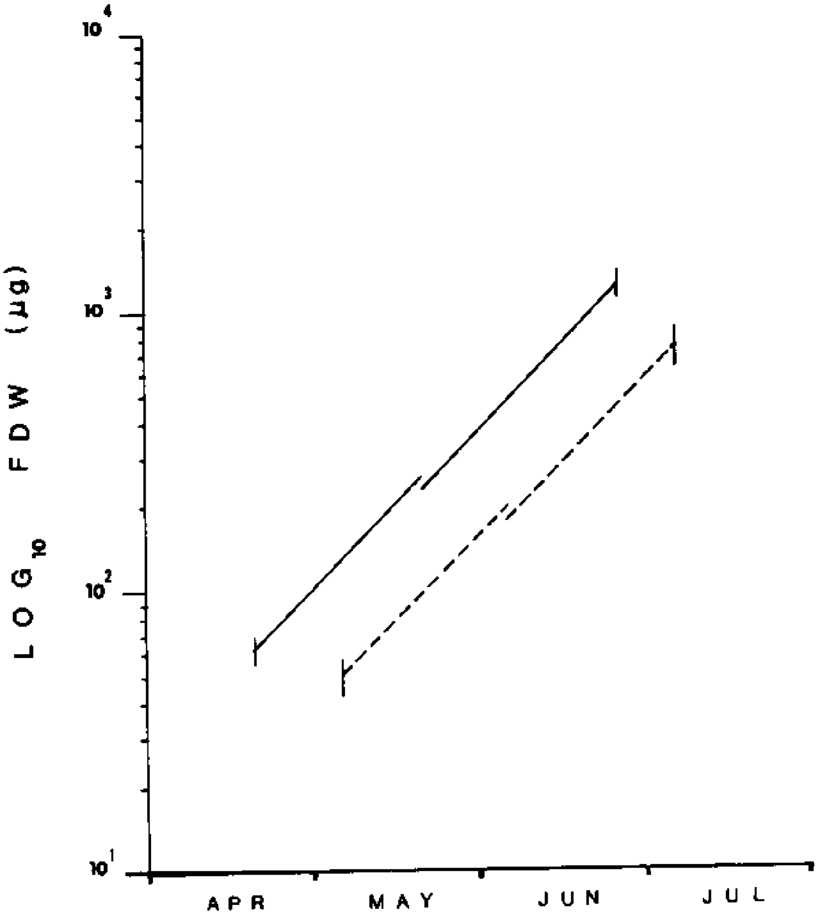

Fig. 4. Growth of *Chionoecetes opilio* (solid line) and *C. bairdi* (dashed line) from hatch-out to late Stage II zoeae for representative hatching dates of 20 April and 5 May, respectively. Discontinuity is molt from Stage I to Stage II; specific growth rate is .047. One standard deviation shown for data at hatch-out and at the end of Stage II.

C. bairdi larvae noticeably began this process. Observations (1) and (3) are consistent with earlier observations on the timing of first appearance of larvae in the plankton. Observation (2) indicates that most of the hatch-out probably occurs over a period of 30-40 days, although other factors (temperature regime, planktic feeding conditions) also may affect duration of the inter-molt period.

Data on the timing of molt from SII to megalops larvae in 1981 show the beginning of this process in *C. bairdi* and the end for *C. opilio* (Table V, Fig. 4). Although the data are not as complete for this molt, the rate of change in the population as a whole during the time period sampled indicates that the period of SII: megalops molting is about as long as the earlier SI:SII transition. The data for *C. bairdi* for this year further show that the molt to megalops larvae began approximately one month after the first SII zoeae appeared.

The data presented above show an approximate 30-day period for each of the two zoeal stages for both species in the southeastern Bering Sea. Furthermore, the approximate 30 to 40-day period of molting in larval populations of each species is an indication that the hatch-out period is of similar duration. The estimates of the duration of the two zoeal stages in the SEBS are in close agreement with most of the observations of *C. opilio* larvae in Japanese waters (Yamahora 1966; Fukataki 1969; Fukui Pref. Mar. Exp. Sta. 1969) although some estimates for the latter environment are for periods as brief as 19-20 days for each stage (Kon 1970). We are unaware of previously published data on the duration of zoeal stages of *C. bairdi* collected from the plankton.

Kon (1970) demonstrated a temperature effect on the duration of the inter-molt periods for zoeal stages of *C. opilio* in laboratory studies: within the range of temperature tolerance of the larvae, increased temperatures resulted in reduced inter-molt periods. This has been experimentally demonstrated for the larvae of other brachyuran crabs as well (e.g. Anger and Nair 1979; Johns 1981). Comparison of the 1978 to 1981 data (Fig. 3) from the southeastern Bering Sea indicates a difference in the timing of molt to SII in *C. opilio*, with 1980 being a relatively "late" year. This difference is not due to differences in the area of sampling and does not appear to be an artifact introduced by grouping the data over the time periods used. The available data on near-surface sea temperatures during the month of May for the years 1978, 1979, 1980 and 1981 show that 1980 was the coolest for this period by approximately 0.5 - 1.0°C in the area of plankton sampling: it is possible that this temperature difference was directly related to the apparent delay in the onset of molting in the larval population, although a closer analysis of this situation is required (Incze, in prep.). It is not possible to rule out the effect of feeding conditions on larval growth rate, and the temperature effect thus may have been indirect (by influencing the developmental status of the plankton community) or may have had combined effects.

Samples collected in early October 1980 indicate that substantial numbers of *C. bairdi* megalops were still in the water column at that time (the estimated densities from October samples ranged from 94-229/1000m^3, number of stations = 4, compared to May samples of SI zoeae ranging from 300-3000/1000m^3 at the same stations). No *C. opilio* larvae were collected in October of 1980, but it must be re-emphasized that this year was one of low larval abundance for this species in most of the area of our plankton studies.

Examination of the stomach contents of yellow fin sole (*Limanda aspera*) collected at 57° 09'N Lat, 166° 39'W Long on 9 September 1980 indicated that settlement of *C. opilio* larvae and metamorphosis to first instar crab had begun by that date, but that substantial numbers of megalops larvae remained, presumably somewhere in the water column [The stomachs of small sole (20-24 cm length) which contained the megalops contained no organisms of benthic origin at the time of sampling. Stomachs of larger sole (24-29 cm length) contained first instar *C. opilio*. Unpublished data are from K. Haflinger, University of Alaska]. These data indicate the beginning of settlement of *C. opilio* larvae to the benthos in the southeastern Bering Sea, but provide no insight into the length of this transition. According to observations in Japanese waters, there may be considerable variation in the length of this stage, with observation in the plankton up to six months after initial appearance of megalops larvae (Fukataki 1969). Prolongation of the megalops stage in Japanese waters was also indicated by examination of the stomach contents of salmonid (Fukataki 1965, 1969) and zoarcid (Ito 1970) fish. A review of previous estimates of the duration of the larval stages of *Chionoecetes* spp. is provided by Adams (1979: 78).

Growth Rates

The growth rates of planktonic animals have traditionally been difficult to measure under natural conditions. Even for meroplankton of species producing only a single brood per season, the hatch-out periods are usually protracted enough that animals collected in the field at any given time represent individuals of a wide range of hatch-out dates and, hence, sizes. For example, in the Tanner crabs the period of hatch-out appears to be about as long as the duration of the first zoeal stage. This makes it difficult to reliably estimate growth from the average weights of individuals collected in the field at various times. However, the ability to identify late stage zoeae (described above) provides a means for measuring larval growth actually experienced in nature.

Using dry weights of preserved specimens and a correction factor of two (PDW X 2 = FDW: see Table VI), the fresh dry weight (FDW) of various larval stages of *C. bairdi* and *C. opilio* caught in the field was estimated (Table VII). Growth curves for larvae of the two species were constructed using these data as follows: (1) the FDW of early post-hatch larvae was set at 50 μg for *C. bairdi* and 63 μg for *C. opilio*[1]; (2) the FDW of late SI and late SII larvae were taken from Table VII; (3) a FDW loss of 10% at molt from SI to SII was assumed (Mootz and Epifanio 1975; Levine and Sulkin 1979, Armstrong and Incze, this volume); and (4) a 30-day period was set for the duration of the first zoeal stage. The growth model was first applied to *C. opilio* data (for which we had identified late SI zoeae). Using a FDW difference of 169 μg (232-69 = 169) and 30 days for the zoeal stage as boundary conditions for growth, the specific growth rate required to meet these conditions was calculated using the equation:

$$W_2 = W_1 \ e^{kt}$$

(see Materials and Methods for details). For *C. opilio* SI zoeae the growth data were fitted when k = .047 and t = 30 days. When the same specific growth rate was applied to the growth projections for SII zoeae of this species, the equation predicted t = 38 days. To keep the zoeal period at 30 days for SII (as indicated by data discussed earlier) would require a specific growth rate equal to .056.

We did not find large numbers of late SI zoeae of *C. bairdi* in our samples, so the *C. bairdi* larval growth rate was derived by setting each zoeal stage equal to 30 days, assuming a 10% FDW loss at t = 30 days (molt), and solving for the FDW difference between fresh-hatch and late SII zoeae. Under these conditions the specific growth rate was .047 for both stages.

The above findings are approximations of specific growth rates experienced by the larvae under natural conditions. Translated to percent biomass increases (e^k-1 = % increase per unit time), the above data indicate growth rates ranging from 4.8% to 5.8% dry body weight per zoeae per day. Assuming constant proportions of carbon to body weight, these values also apply to daily increases in carbon per zoea.[2] Estimates of FDW based on conversion of PDW gave values for <u>late</u> Stage II zoeae which were higher than values found for zoeae collected in the field during the period of time when larvae were molting to megalops stage. This suggests that either (1) the conversion factor (which was based on samples of middle inter-molt

Table VI

Comparison of fresh dry weight (FDW) and preserved dry weight (PDW) of SII zoeae of *Chionoecetes bairdi* and *C. opilio* after nine months of preservation in 3-4% buffered formalin. Samples are from 1981. N: number of samples weighed; Weight: mean ± one standard deviation (one standard deviation expressed as percent in parentheses). Correction factor (CF) is for converting PDW to FDW based on data presented.

SPECIES	CONDITION	N	Weight(ug) $\bar{X}$±s	CF
C. bairdi	FDW	48	490±114 (±23%)	
	PDW	80	221±52 (±24%)	2.2
C. opilio	FDW	15	792±110 (±14%)	
	PDW	50	442±98 (±22%)	1.8

Table VII

Fresh dry weight (FDW) of various stages of development in zoeae of *Chionoecetes opilio* and *C. bairdi* estimated from preserved dry weight using the conversion PDW x 2 = FDW (see Table VI and text for details). All samples are from field collections. Early SI: early post-hatch larvae; Late SI: late Stage I zoeae ready for metamorphosis to SII; Late SII: late Stage II zoeae ready for metamorphosis to megalops larvae. Weights are mean weights (ug) ± one standard deviation (number of measurements in parentheses).

SPECIES	EARLY SI	LATE SI	LATE SII
C. opilio	71±9 (14)	232±49 (10)	1274±160 (12)
C. bairdi	59±9 (11)	--	702±124 (8)

SII zoeae) systematically over-estimates the FDW of late Stage II zoeae, or (2) our field collections for direct FDW determination consistently missed the late stage zoeae. The relative rarity of finding a near-molt individual in plankton samples and the amount of growth attained each day by a large zoea make it easy to see how we could have missed these individuals during normal sampling for fresh dry weight determinations. On the other hand, the possibility of a systematic error introduced by the correction factor also exists. Consequently, the estimated growth rate above must be viewed as an approximation. This approximation nevertheless has considerable value; for while the estimate of final weight may be somewhat high, the projection of mean daily growth requirement is probably quite accurate.[3]

Mootz and Epifanio (1975) and Levine and Sulkin (1979) working with the larvae of two species of crab in laboratory growth studies report that the caloric equivalents of growth range from 0.4 to 2.7 times respiration, and that total energy consumption (ingested ration) ranges from 1.5 to 3.6 x (respiration + growth). These relationships reflect gross growth efficiencies similar to those reported for other small planktonic crustaceans (Mullin and Brooks 1970 a,b; Paffenhoffer 1976) and can be used to approximate ingested energy needs of Tanner crab larvae.

Carbon equivalents of respiration measured in SI and SII zoeae of *C. bairdi* and *C. opilio* range from 3-5.7% body carbon zoea^{-1} day^{-1} (Incze and Paul; Incze, Vidal and Armstrong; Armstrong and Incze in prep.), values similar to the growth rates estimated above. With these data and the above relationships in mind, the adequacy of feeding performance for satisfying growth requirements under various planktonic conditions can be assessed. The above data indicate that ingested ration of growing Tanner crab larvae should be greater than about 14% body carbon zoea^{-1} day^{-1} (this takes into account an assimilation efficiency of 0.80 at a growth rate equal to 5% body weight per zoea per day, but does not consider other sources of energy loss). Compared to values reported for other decapod larvae, our measured rates of growth of Tanner crab larvae are low (Mootz and Epifanio 1974; Anger and Nair 1979; Levine and Sulkin 1979; Dawirs 1980). This may be partly a product of our measuring growth rates actually experienced at sea; but might also be a characteristic of these species in their high-latitude environment: our measured rates of respiration of Tanner crab larvae are also considerably lower than those reported from laboratory studies of other decapod larvae (see Schatzlein and Costlow, 1978).

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TEXT FOOTNOTES

[1] An adjustment was made to data in Table VII for early SI weights. We caught from the plankton *C. bairdi* zoeae on average 11 µg heavier than the initial hatch-out weight measured in the laboratory. We used the laboratory weight of early-hatch *C. bairdi* and assumed a proportional over-estimate of post-hatch weight of *C. opilio* from field collections, thus reducing the estimate for the latter species from 75 to 63 µg.

[2] These estimates are for mean daily growth assuming constant growth rate. The larvae are capable of surviving several days starvation without noticeable effect on subsequent feeding activity (Kon 1979; A.J. Paul, unpubl. data) and presumably may have to do so in nature. Short-term growth rates thus may be higher or lower than the mean rate calculated here.

[3] A small decrease in daily growth rate can produce a fairly large difference in the size of the final weight of zoea after 30 (one stage) or 60 (both stages) days of growth. As a result, the error of the estimate of the daily growth (measured as a percentage of body weight or body carbon) is probably quite small even if the current data provide an over-estimate of final Stage II weight.

Distinguishing Between *Chionoecetes Bairdi* and *C. Opilio* Zoeae Collected in the Southeast Bering Sea

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ABSTRACT

Three morphological characteristics which enable separation of zoea larvae of *Chionoecetes bairdi* and *C. opilio* are discussed; two are described here for the first time. Use of all three characteristics enables species identification of most *Chionoecetes* zoeae found in plankton samples from the southeastern Bering Sea.

INTRODUCTION

Zoeae of *Chionoecetes bairdi* and *C. opilio* are morphologically very similar, being larvae of two very closely related species which apparently still interbreed in nature (Johnson 1976, Pereyra et al. 1976). Several descriptions of zoea larvae of the two species have been published: *C. bairdi* and *C. opilio* Stage I zoeae from the S.E. Bering Sea (Haynes 1973), *C. bairdi* Stage II zoeae from Cook Inlet, Alaska waters (Haynes 1981) and *C. opilio* Stage I and II zoeae from the waters of Japan (Motoh 1973, Kurata 1963[1], Kuwatani et al. 1971). Haynes (1973, 1981) compared zoeae of both species from U.S. and Japanese waters in order to define morphological characteristics which could be used to distinguish between zoeae of the two species in areas where both exist.

Based on examination in our study of several thousand zoeae of both *Chionoecetes* species from the southeastern Bering Sea (*C. opilio and C. bairdi)* and also specimens from the western Beaufort Sea (*C. opilio*) and the Gulf of Alaska (*C. bairdi*), we have found that: (1) the principal criterion employed by Haynes in papers describing the morphological differences between zoeae of *C. opilio* from Japan and *C. bairdi* from U.S. waters (Haynes 1981) is more useful than the criteria he employed earlier to describe differences between Stage I

zoeae of these two species from the southeastern Bering Sea, but (2) additional characteristics are necessary for distinguishing between the species because of variability in the diagnostic length relationships recommended.
In this paper we compare our findings from plankton samples (mostly from the southeastern Bering Sea) with Haynes' findings (Haynes 1973, 1981) and describe two additional characteristics of the zoeae which extend Haynes' (1981) diagnosis of species differences.

Plankton samples from the southeastern Bering Sea are those of Incze et al. (this volume). Samples from Kodiak Is., Alaska were provided to us by A.J. Paul, Institute of Marine Science, University of Alaska, Seward; Lower Cook Inlet, Alaska samples were provided by Dr. T.S. English, School of Oceanography, University of Washington, Seattle; and western Beaufort Sea samples were provided by Dr. R. Horner, Seattle. Specimens were initially preserved in 3-4% buffered formalin and later transferred to 70% ethanol: water with glycerin.

DISTINGUISHING BETWEEN *C. BAIRDI* AND *C. OPILIO*

Observations on Length of Posterior Lateral Spine

Haynes (1973) described morphological features of Stage I zoeae of *C. bairdi* and *C. opilio* hatched from ovigerous females collected in the southeastern Bering Sea. Although the larvae described in his study were very similar, Haynes felt that they could be distinguished on the basis of subtle morphological differences:

> "Stage I zoeae [of the two species] are identical except for a few subtle differences in abdominal morphology. The most obvious difference is in the length of the posterior lateral spines on the third and fourth abdominal segments. In *C. bairdi*, the spines overlap the adjacent segments by about one-third the length of the spines. In *C. opilio*, the spines on the third segment barely extend past the posterior margin of the fourth segment, and those on the fourth segment do not quite reach the posterior margin of the fifth segment."

However, relative length of the posterior lateral spine (PLS) of specimens collected in this study usually did not provide clear evidence of the species according to the criteria outlined above. From examination of several thousand specimens it has become clear that a wide range of PLS lengths exist.

Measurements were made of PLS length relative to the posterior margin of abdominal segments for *C. bairdi* and *C. opilio* from Haynes' (1973) published figures to assist us in comparing Haynes' criteria with the measurements made of zoeae collected in our study. From Haynes' figures the following were calculated: (1) the percent of the third abdominal PLS that extends past the posterior margin of the fourth abdominal segment and (2) the percent of the fourth abdominal segment PLS that extends past, or doesn't quite reach, the posterior margin of the fifth abdominal segment. Our measurements made of Haynes' figures are shown in Fig. 1. Similar measurements were made on a number of Stage I zoeae of *C. bairdi* obtained from two sources: ovigerous females collected off Kodiak Is., Alaska and plankton samples collected in Lower Cook Inlet, Alaska (*C. opilio* has never been reported from these areas). The posterior lateral spines on either side of an abdomen of these zoeae frequently differed in length, as they did in Haynes' (1973) figures. In all cases illustrated in Fig. 1, the measurement of the longer spine was used when the PLS passed the posterior margin of the following segment and the shorter was used when the PLS did not reach this margin. Still, it can be seen (Fig. 1) that the relationships of PLS length to the margin of the following segment in known *C. bairdi* zoeae can vary substantially and can be quite similar to relationships illustrated for *C. opilio* by Haynes (1973). For *Chionoecetes* spp. collected from the plankton of the southeast Bering Sea, where both species exist, the relative lengths of the PLS show a continuum of values which make it virtually impossible to separate zoeae in all but extreme cases.

Further Observations on Abdominal Morphology

Haynes (1973) also observed that Stage I zoeae of *C. opilio* from Japanese waters described by Kurata (1963) primarily differed from his Stage I zoeae in the length of the curved lateral processes on the third abdominal segment. In a subsequent paper, Haynes (1981) compared both stages of *C. opilio*, which he had obtained from Japan, with corresponding stages of *C. bairdi* from Alaska waters, and on the basis of these later observations he concluded:

> "For both stages, zoeae of *C. bairdi* are morphologically identical with zoeae of *C. opilio* from Hokkaido and the Sea of Japan, except for the length of the curved lateral processes on the third abdominal somite. In Stage I and II zoeae of *C. opilio* from Hokkaido and the Sea of Japan,

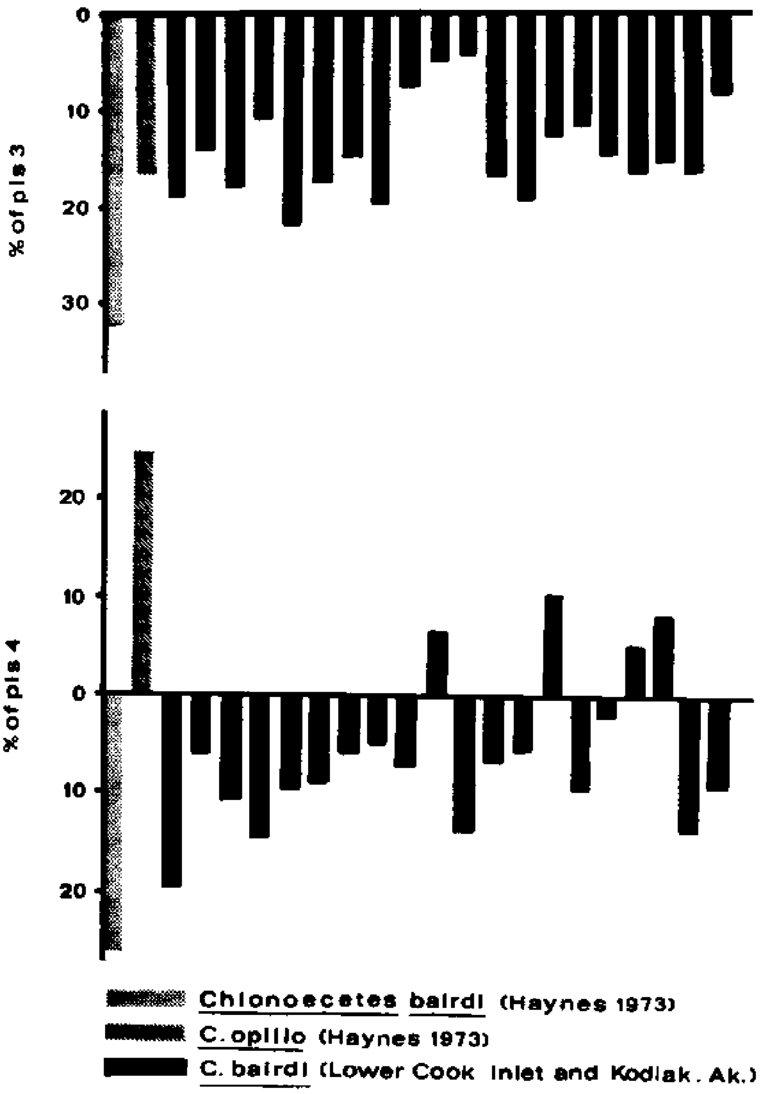

Figure 1. Comparison of PLS length in specimens illustrated by Haynes (1973) and in specimens examined in this study. Figure illustrates: (1) percent of the length of the third abdominal segment PLS that extends past the posterior margin of the fourth abdominal segment (upper chart); (2) percent of the length of the fourth abdominal segment PLS that extends past (downward in this figure) or does not quite reach (upward in this figure) the posterior margin of the fifth abdominal segment (lower graph).

> the curved lateral processes reach the posterior margin of the third abdominal somite, but in Stage I and II zoeae of *C. bairdi*, they are markedly shorter."

Haynes' later paper thus emphasized the use of the curved lateral process on the third abdominal segment [the length of which was previously described for *C. opilio* by Kurata (1963)] as a principal diagnostic feature for distinguishing between both zoeal stages of the two species: one from the eastern Pacific (*C. bairdi*) and one from the western Pacific (*C. opilio*). However, Haynes (1981) acknowledged:

> "Stage II zoea of *C. opilio* from the eastern Pacific Ocean have not been identified, and it is not known if they can be distinguished from Stage II zoeae of *C. bairdi* by the length of their lateral processes."

Therefore, it remained unknown at that time how well these observations would apply to specimens collected in the southeastern Bering Sea.

Using the relationship of the length of lateral process on the third abdominal segment to the posterior margin of that segment (Haynes 1981), we were able to separate numerous *Chionoecetes* zoeae from the southeast Bering Sea into two groups, presumably corresponding to the two species of interest. In many instances, then, the relationship recommended by Haynes (1981) appears applicable when specimens of *C. opilio* are from the eastern Pacific, as well. However, we have found considerable variability in the relative length of the lateral process and it frequently is not possible to distinguish between the two species using this character alone. Specifically, the more slender, longer processes do not always reach the posterior margin of the segment, yet they clearly differ in shape and length from the shorter processes on other zoeae. We searched for additional characteristics in specimens from the clearly separated zoeal groups (using the above lateral process criterion of Haynes) to see if other morphological features could be used to distinguish between the two species when the lateral process length relationship did not clearly indicate one species or the other. Two additional characteristics have proven helpful in this respect: (1) length from the distal end of the rostral spine to the distal end of the dorsal spine and (2) the shape and relative length of the carapace lateral spines. These characteristics are described in the following section.

Additional Morphological Features Useful in Species Identification

Measurements of length from the tip of the rostral spine to the tip of the dorsal spine (rostral-dorsal length = RDL) of Stage I and II zoeae from the southeastern Bering Sea with longer lateral processes [hereafter referred to as knobs, after Kurata (1963)] were always in the range of RDL values given by Motoh (1973, 1976) and Kurata (1963, 1969) for *C. opilio* from Japan (Table 1). That is, specimens diagnosed as *C. opilio* according to Haynes' (1981) lateral process (knob) criterion always had RDL measurements greater than or equal to 4.5 mm. Haynes (1973, 1981) did not specify a difference in RDL measurements between the two species. Those *Chionoecetes* zoeae collected from the southeast Bering Sea which had shorter knobs had RDLs in the range given by Haynes (1973, 1981) for *C. bairdi*, i.e. less than 4.6 mm for Stage I and less than 6.4 mm for Stage II. In addition, we also found that Stage II zoeae with shorter knobs had shorter RDLs than those reported by Haynes (Table 1). Measurements of these RDLs ranged from 5.5 - 5.95 mm. We thus found a consistent relationship of RDL to knob length in specimens for both groups of zoeae: those with obviously short and those with obviously long knobs (lateral processes).

The zoeae from the southeast Bering Sea that constitute these two categories also differed from each other in the shape and length of their carapace lateral spines (CLS). The CLS of zoeae with long knobs appeared straight, while the CLS of zoeae with short knobs appeared to droop downward (ventrally). As a general rule, the straighter CLS were shorter relative to the zoea's RDL, whereas the drooping CLS were longer relative to the RDL. These characteristics in addition to the one proposed by Haynes (1981) were used in our study to distinguish between zoeae of *Chionoecetes* spp. and are summarized in Table 2.

When these characteristics were used, most zoeae of *Chionoecetes* spp. from shelf waters of the southeastern Bering Sea could be tentatively identified as *C. bairdi* and *C. opilio*. This included the numerous specimens in which the knob length relationship did not provide conclusive evidence for species identification. Our identifications were then "tested" against data from plankton studies and information on the distribution and relative abundance of adults of the two species.

Table 1. Rostral-dorsal lengths of *Chionoecetes bairdi* and *C. opilio* Stage I and II zoeae tabulated from the current literature.

	C. opilio Kurata(1963,1969)	*C. opilio* Motoh(1973,1976)	*C. bairdi* Haynes(1973,1981)
Stage I	4.5 - 4.9 mm	4.8 - 5.4 mm	3.96 - 4.55 mm
Stage II	6.0 - 6.9 mm	6.2 - 7.1 mm	5.95 - 6.37 mm

Table 2. Summary of diagnostic features used to identify Stage I and II zoeae of *C. bairdi* and *C. opilio* collected in plankton samples from the southeast Bering Sea: Knob (curved lateral process), RDL (rostral - dorsal length) and CLS (carapace lateral spines) (see text for details).

		C. bairdi	*C. opilio*
Knob		Shorter	Longer
RDL	Stage I	3.96 - 4.55 mm	4.5 - 5.4 mm
	Stage II	5.50 - 6.37 mm	6.0 - 7.1 mm
CLS		Generally long and drooping ventrally	Generally short and straight

APPLICATION OF FINDINGS TO FIELD STUDIES

Certain aspects of the timing of appearance of the larvae in the plankton and spatial patterns of distribution and abundance provided evidence needed to corroborate the species identifications we had made using the above characteristics to extend Haynes' (1981) description. The larvae with the longer RDL and shorter, straighter CLS were found in the plankton earlier in the season than the larvae of opposite characteristics (see Incze et al., this volume). This was consistent with information provided to us by D. Somerton (see D. Somerton's larval paper, this volume), namely, that the state of maturation of egg masses of female Tanner crabs observed during National Marine Fisheries Service surveys in the area indicated that *C. opilio* hatched earlier than *C. bairdi*. The larval species description was further substantiated by specimens collected in areas where the bottom crab fauna was clearly dominated by one species or the other. Finally, areas of the Bering Sea which contained zoeae of only one description during a sampling season eventually gave rise to megalops larvae which were identified to species according to Jewett and Haight (1977); the megalops identifications confirmed our zoea identifications. All the above lines of evidence were in agreement with our zoea species identifications from four years of plankton samples.

Some *Chionoecetes* zoeae from the southeastern Bering Sea could not be categorized by the criteria described above. The RDL of these zoeae, found in water shallower than 200 m, often was in the area of range overlap of RDL for *C. opilio* and *C. bairdi* (Table 1); the knob character was often intermediate; and the CLS character occasionally did not match the knobs even when the latter were distinct. For these specimens, which were not abundant, no species designation could be made. It is possible that these were F_1 progeny of inter-specific matings between *C. opilio* and *C. bairdi*, but it would not be possible to determine this with morphological evidence alone. Since the relationship of genetic phenotype dominance among the various characters is unknown, it is also possible that F_1 progeny were included in one or the other (or both) of the species groups we have established above. Because the degree of inter-specific breeding is unknown, the extent of this error cannot be estimated.

Some plankton samples collected from regions overlying the continental slope contained zoeae which did not conform in appearance to any of the zoeae described above (*C. bairdi*, *C. opilio* or the unidentified *Chionoecetes* zoeae found over the shelf). These may have been the larvae of deeper dwelling species of *Chionoecetes*. As in the case of the shallower unknown zoeae, however, such specimens were not numerous.

We also compared our diagnostic features to zoeae from other areas. *C. bairdi* zoeae from Lower Cook Inlet, Alaska and Kodiak Is., Alaska exhibited all three characteristics listed in Table 2 for *C. bairdi* Stage I zoeae. Stage II *C. bairdi* which we obtained from plankton samples collected from Lower Cook Inlet, Alaska also exhibited all three of the characteristics listed in Table 2 for that stage. *C. opilio* zoeae (only 10 obtained) from the western Beaufort Sea (where *C. bairdi* does not occur) exhibited all the characteristics listed in Table 2 for *C. opilio* Stage I and II zoeae. We thus feel that the additional species characters described in this paper have general applicability to the species descriptions. In our study we found it necessary to use these characters in addition to the diagnostic feature suggested by Haynes (1981) to distinguish between zoeal larvae of *C. bairdi* and *C. opilio*.

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FOOTNOTES

1. Kurata (1963) described Stage I and II zoeae of what he called *C. opilio elongatus* based upon Rathbun's (1924) disignation of the subspecies. According to references cited by Haynes (1981) the sub-specific designation is not warranted, therefore, we have used the species designation *C. opilio* for zoeae described by Kurata.

Reproduction

The Mating Behavior of *Chionoecetes Bairdi*

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INTRODUCTION

The fundamental sequence of events in mating behavior has already been described for *Chionoecetes bairdi* (Takeshita and Matsuura, 1980) and *Chionoecetes opilio* (Watson, 1971 and 1972, and Takeshita and Matsuura, 1980). Similarities and differences between inter-specific and intra-specific matings of these congeneric species have also been noted (Takeshita and Matsuura, 1980). This report confirms the validity of those studies and provides additional details of laboratory mating behavior.

Precocious mating behavior performed by *C. bairdi* males and the extrusion and attachment of infertile eggs by isolated primiparous females are presented as two new concepts to tanner crab biology. Hartnoll (1965) stated that some brachyuran species (such as *Mithrax bicornutus*) may attain sexual maturity prior to the molt stage in which the shape and setation of the chelae undergo a distinct alteration. Mature reproductive tract weights were reported for some *C. bairdi* males which, indeed, had not yet acquired the chela morphology of adults (Brown and Powell, 1972). Hartnoll (1965) further emphasized that the presence of fully formed sperm bounded by spermatophores in the sperm ducts of small, pre-puberty molt stage males was circumstantial evidence of maturity. He reasoned that incontrovertible proof of sexual maturity in the males of some species could only be obtained through mating experiments. During 1981 and 1982, 34 *Chionoecetes bairdi* males with carapace widths less than 70 mm have mated in the laboratory. The mating behavior exhibited by these small males and the reproductive success of a few are described here for the first time.

MATERIALS AND METHODS

Field Collections

This study has utilized only the species *Chionoecetes bairdi*. Large males and all females were captured in otter trawl tows at Womens Bay and Chiniak Bay, Kodiak by biologists William Donaldson (in 1979-1980), William Colgate (1981 and 1982), and David Hicks (1979-1982) of the Alaska Department of Fish and Game. The crabs were shipped from Kodiak either in the hold of the R/V Resolution or by air charter to the University of Alaska's Marine Science Center in Seward. Small males were captured in Resurrection Bay, Seward by beam trawl from a chartered, privately-owned fishing vessel.

Laboratory Provisions and Observations

Holding facilities at the Seward Marine Science Center include four cylindrical 1,895 liter capacity plastic tanks and three cylindrical 1,620 liter capacity plastic tanks (all produced by Frigid Units, Toledo,Ohio). They receive a continuous supply of sea water which is pumped into the laboratory from a depth of 60 meters in Resurrection Bay. Frigid Unit chillers were used to maintain temperatures below six degrees centigrade during periods of elevated external temperature.

Most mating experiments were conducted in a 168 liter aquarium with integral temperature control unit. A 120 liter capacity wooden tank with gravel substrate was used for approximately ten of the matings. Still other experiments were conducted in the 1,895 liter tanks, although their primary use was that of holding. All detailed observations were made at night when external distractions could be limited. At these times, overhead lights were turned off (low level sidelighting did enter the enclosures), observer movements were reduced to a minimum, and notes were recorded by either magnetic tape or hand. The only obvious disturbances were noted when all overhead lights were on and a large object passed close to the aquarium. Some grasping males (before and after copulation) reacted defensively to the shadow by rising onto the tips of their dactyls and turning circularly with one chela opened and raised.

Crabs were usually fed herring twice each week; however, rock sole, sablefish, and pollock were substituted as food whenever possible.

Size and Hardness Measurements

Precision vernier calipers were used to measure the carapace widths of crabs to the nearest millimeter. Determinations of exoskeleton hardness of *Chionoecetes bairdi* females were based upon a subjective system developed by Hiatt (1948). This system designates three degrees of hardness: (1) completely soft; (2) integument partially rigid but easily depressed; and (3) completely rigid (fully sclerotized).

RESULTS

A total of 102 *C. bairdi* matings have been observed in the laboratory over a three year period. Data for the 1982 season are still being tabulated and analyzed; however, portions are included wherever possible.

Every completed intromission consisted of three major episodes: (1) a pre-copulatory period; (2) copulation; and (3) a post-copulatory period. The results of this study are divided accordingly.

The Pre-copulatory Period

This episode commenced when a male *C. bairdi* detected the presence of a molting or recently molted female and it terminated, in completed matings, with the male and female positioned sternum to sternum (both their rostrums pointing in the same direction). In the laboratory, male *C. bairdi* have detected primiparous females as early as 14 days prior to the female's puberty molt. Individual differences are noted in the initial responses of the male to a molting female. Quiescent males suddenly arose from the substrate surface and began walking (locomotion was often preceded by waving movements of the maxillipeds). Actively moving males were observed to stop, wave their maxillipeds, then change their direction toward the female if she was not already in the path of travel. The most energetic and abrupt responses occurred when the male (quiescent or moving) was contacted by a female which had molted within the last 24 hours. In such instances, the males lunged at females and attempted to grasp them with open chelipeds and/or to encircle the female's carapace or pereopods with the distal portion of their own pereopods.

Responsiveness toward molting or recently molted females has been displayed by molting and recently molted males as well as by intermolt males. Two partially soft (post-molt) males, with carapace widths of 113 and 128 mm, grasped soft, newly molted females which escaped within six hours. However, three males which were entering the molt cycle did manage to mate successfully. One of these males (measuring 115 mm carapace width) mated four days before molting; the other two (measuring 115 and 120 mm carapace width) mated only two days before molting.

Evasive and Escape Behavior

Molting and recently molted females often attempted to evade approaching males or, if grasped, attempted to escape. The observed evasion and resistance strategies varied with the carapace hardness of the female and the size of the approaching (or grasping) male (Table 1). Evasion was not commonly demonstrated prior to the molt to maturity but premolt females did offer resistance to being grasped. When the size of the male equalled or exceeded that of the female, such resistance often resulted in the male lifting the female above the plane of his body (with one cheliped) and striking her carapace, abdomen, or pereopods (with the other cheliped). These actions on the part of the male sometimes produced immediate (though usually temporary) quiescence in the female. In other instances, the female continued to push or pinch at the male with one or both chelipeds and to move her pereopods until the male repeated the lifting and beating actions several times.

Small males were outmatched by large females as is evi-

Table 1. Evasive and escape behavior displayed by *Chionoecetes bairdi* primiparous females

Relative size of approaching or grasping male	Description of behavior elicited in female
I. Males of all sizes	A. Pre-grasp evasion
	1. Female moves just above the substrate surface (low profile) in a direction away from the approaching male and at a matching speed
	2. Female runs rapidly in a direction away from the male
	B. Escape attempts once grasped
	1. Female pulls with pereopods of one side of her body while pushing outward with the legs of the opposite side
	2. Female pushes forward with all pereopods in an attempt to move backward
	C. Female resistance once grasped
	1. Female pinches male's pereopod(s) or chela(e) with her own chela
	2. Female presses the tips of her chela(e) against the mate's maxillipeds, rostrum, or cephalo-thorax in straight-arm fashion
	3. Female holds chelipeds directed toward male and with the tips crossed
	4. Female extends first pair of pereopods forward with the dactyls curved inward
	5. Female strikes male with merus, carpus, or propodus of one or more pereopods
	6. Female strikes the male's body with the pointed dactyl tip or with one or both of the first pereopods

Table 1. (cont'd)

Relative size of grasping male	Description of behavior elicited in female
II. Males of size equalling or smaller than female's	Female resistance once grasped
	1. Female quickly flexes all pereopods simultaneously thereby springing straight upward off the substrate
	2. Female elevates the posterior end of her body while lowering the anterior end thereby blocking the male from positioning beneath her sternum
	3. Female quickly pushes the anterior end of her body off the substrate, extends both chelae outward and down, then falls chelae-first on the male
	4. Female elevates the anterior end of her body to shift a small male backward
	5. Female lunges at male with her chelipeds open and extended forward
	6. Female rises to three quarters of her full stance then steps on the male
	7. Female rises onto the tips of her dactyls then sits forcefully downward on the dorsal surface of the male
	8. Female pushes the male against/or drags him over an obstacle (such as a rock)

denced by the fact that none of the 19 separate pre-molt grasps involving small males led to mating (Table 2). Nine of the grasped females escaped through their own efforts. The inability of small males to restrict the movements of molting females and the female's use of her increased bulk and weight in overpowering the male were important factors contributing to the failure of these potential pairings.

For a brief one hour period following the molt to maturity, females were incapable of effective evasion. Initially they emerged from the old exoskeletons by pushing their way upward and backward. Most unattended females continued to move slowly along the surface of the substrate until they were at least one or two body lengths away from the molted exoskeleton. As their outer integument began hardening, females flexed their pereopods and attempted to rise off the substrate

Little or no resistance was offered to grasping at this time, except in instances where the grasping male was inferior in size to the newly molted female. Ten males, ranging in size from 39 to 131 mm, grasped females which had molted less than one hour previously and none of these females escaped through their own efforts. The earliest successful escape by a newly molted female occurred 1.8 hours after her maturity molt and it was out of the grasp of a 51 mm carapace width male.

Sclerotization is a relatively slow process. Fifty-five examined females required 16 to 71 days for complete hardening (53 days was the mean and 57 days was the mode). But females were usually capable of standing and fleeing slowly within two hours after molting. Agility, evasive behavior, and resistance to mating increased as exoskeletons became more firm. Although this did not permit females to escape from large males (larger than themselves), it was very evident in the direct relationship between elapsed time since the molt and percentage of successful escapes from small males (Table 2). Detailed observations are available for 19 females which escaped on 35 separate occasions (Table 3). Twenty-seven of the 35 escapes were from males smaller than 81 mm carapace width. The few escapes from large males all occurred at least 21 days after the female's molt.

Only two of 21 different males successfully regrasped and mated with females which had escaped from them at an earlier time (Table 3). The successful escapers primarily comprised two separate groups: (1) females which forcefully escaped from smaller males; and (2) females which had surpassed the time limit during which they could have produced normal, fertile eggs.

None of the laboratory interactions between males and females have included any form of courtship more sophisticated than straightforward grasping. The females do not have the

Table 2. Summary of outcomes for grasps involving *Chionoecetes bairdi* primiparous females

		Elapsed time (in hrs) between female's puberty molt and grasp								
Type of outcome	Occurrence by male size	-1283 to -25	-24 to -1	0 to 24	25 to 120	121 to 240	241 to 480	481 to 720	721 to 1856	Row totals and % of all grasps[c]
Mating	≤ 80 mm									
	Abs. freq.[a]	0	0	14	4	0	0	0	0	18
	% of col. total[b]	-	0.0	20.9	19.0	-	-	0.0	0.0	15.3
	> 80 mm									
	Abs. freq.	1	3	4	1	1	1	4	4	19
	% of col. total	33.3	60.0	57.1	50.0	33.3	100.0	50.0	9.8	27.1
Simple releases	≤ 80 mm									
	Abs. freq.	0	9	21	4	0	0	0	5	39
	% of col. total	-	47.4	30.0	19.0	-	-	0.0	55.6	33.1
	> 80 mm									
	Abs. freq.	2	2	1	1	1	0	1	29	37
	% of col. total	66.7	40.0	14.3	50.0	33.3	0.0	12.5	70.7	52.9
Female escapes	≤ 80 mm									
	Abs. freq.	0	9	14	8	0	0	2	3	36
	% of col. total	-	47.4	20.9	38.1	-	-	100.0	33.3	30.5
	> 80 mm									
	Abs. freq.	0	0	0	0	0	0	3	5	8
	% of col. total	0.0	0.0	0.0	0.0	0.0	0.0	37.5	12.2	11.4

Table 2. (cont'd)

Type of outcome	Occurrence by male size	Elapsed time (in hrs) between female's puberty molt and grasp								Row totals and % of all grasps
		-1283 to -25	-24 to -1	0 to 24	25 to 120	121 to 240	241 to 480	481 to 720	721 to 1856	
Female released during combat or *after* escape attempts	≤ 80 mm									
	Abs. freq.	0	1	18	5	0	0	0	1	25
	% of col. total	-	5.2	26.9	23.8	-	-	0.0	11.1	21.2
	> 80 mm									
	Abs. freq.	0	0	2	0	1	0	0	3	6
	% of col. total	0.0	0.0	28.6	0.0	33.3	0.0	0.0	7.3	8.6
Total grasps observed	≤ 80 mm Column total	0	19	67	21	0	0	2	9	118
	> 80 mm Column total	3	5	7	2	3	1	8	41	70

[a] Abs. freq. = Absolute frequency of occurrence

[b] % of col. total = Percentage of column total for appropriate male size group

[c] Row total and percentage of all grasps for appropriate male size group

Table 3. Summary of successful escapes by *Chionoecetes bairdi* females from males which had grasped after the molt to maturity

Female number	Range of grasp durations (in hrs)	Range of elapsed times between molt and escape in hours (days)	Number of males from which female escaped	Total number of times female escaped	Male size ranges (in mm)	Do any of the original graspers mate with this female later?
238	0.1 - 0.2	1.8 - 2.0	2	2	51 - 57	No
224	0.0 - 0.2	6.0 - 6.1	1	2	55	No
280	0.1	6.9 - 7.1	2	2	56 - 60	No
219	0.1 - 0.2	8.1 - 10.0	1	3	39	No
247	0.0 - 0.6	8.9	2	2	71	No
231	0.1	10.6 - 11.3	2	2	32 - 48	No
243	0.2 - 0.5	15.0 - 35.9	3	3	55 - 71	No
233	0.3	40.4	1	1	57	No
257	1.5	49.0	1	1	68	No
258	1.1	49.0	1	1	76	No
261	0.0 - 0.4	97.4 - 97.8 (4)	2	3	57 - 59	Yes
23	0.0 - 3.0	510.0 - 513.7 (21)	1	2	170	No
254	0.0 - 1.3	567.2(24) - 1209.4 (50)	2	3	79 - 138	No
24	1.6	641.1 (26)	1	1	119	Yes

Table 3. (cont'd)

Female number	Range of grasp durations (in hrs)	Range of elapsed times between molt and escape in hours (days)	Number of males from which female escaped	Total number of times female escaped	Male size ranges (in mm)	Do any of the original graspers mate with this female later?
246	0.0 - 0.4	682.6 - 683.0 (28)	2	2	79 - 88	No
241	0.0	693.7 (29)	1	1	88	No
227	0.5 - 0.8	883.4(36) - 1058.3 (44)	2	2	79 - 88	No
232	0.0	896.5 (37)	1	1	142	No
234	0.8	1033.9 (43)	1	1	119	No

opportunity to choose a specific mate. However, through resistive and escape behavior they may effectively hinder and frustrate the mating efforts of inferior sized males.

Simple Releases

Seventy-six grasps ended in what are best described as simple releases. Without being disturbed or distracted by an external object or organism and in the absence of escape attempts by the female, grasping males sometimes simply relaxed their chelipeds and permitted a female to depart. This phenomenon was not limited to males of a particular size or carapace condition and the released females included both pre-molt and post-molt individuals which were mature or about to become mature (Tables 4 and 5). Seventy-two of the 75 simple releases can be attributed to: (1) small males which released larger females (39 instances); or (2) large males which released females either far in advance or well after the maturity molt (33 instances). One female was released by a large male which molted less than 48 hours later. Two releases remain unexplained.

Initial detection and grasping of females by males has now been described. Subsequent actions by the male and female were influenced by the female's condition and the relative sizes of the two animals.

Male Assistance During Female Puberty Molts

Large males have been observed assisting females through the final stages of ecdysis. Such assistance included the following activities by males: (1) holding the female off the substrate (and gently bouncing her) with the posterior end of the exoskeleton facing downward thus allowing the female to fall out; (2) holding the legs of the old exoskeleton with one cheliped while poking and pushing the emerging female away from it with the other cheliped; and (3) bracing the old exoskeleton between the meri of both chelae while using the distal ends of both to push the female backward and out. Males that were smaller than the molting female did not assist in any of the observed molts.

The Pre-copulatory Embrace and Mating Preparations

Total duration of the pre-copulatory embrace was primarily determined by its occurrence before or after the female's molt (Tables 6 and 7). When initiated prior to the female's molt, the precopulatory embrace continued for at least 0.4 hours after she emerged. But post-molt initiated pre-copulatory embraces varied from one to 235 minutes and did not reflect a clear relationship to total elapsed time since molt completion.

Assorted actions were exhibited by males during the pre-

Table 4. Simple releases which occurred before the female's puberty molt

Female number	Range of grasp durations (in hrs)	Range of elapsed times between release and molt (in hrs)	Number of different males that grasped then released	Number of times female was grasped then released	Male size range (in mm)	Do any of the original graspers mate with this female later?
24	0.2 - 24.6	1283.0 - 469.5	1	2	122	No
255	0.1	3.9	1	1	76	No
267	0.0 - 0.2	1.5 - 0.7	1	2	92	No
238	0.0 - 1.5	1.1 - 0.7	2	2	48 - 71	No
221	0.0	0.1	1	2	48	No

Table 5. Summary of simple releases which occurred after the female's puberty molt

Female number	Range of grasp durations (in hrs)	Range of elapsed times between molt and release in hours (days)	Number of different males that grasped	Number of times female was grasped then released	Male size range (in mm)	Do any of the original graspers mate with this female later?
238	1.3	1.6	1	1	71	No
266	0.1	1.7	1	1	59	No
273	0.2	2.3	1	1	57	No
236	0.2 - 0.4	4.0 - 808.3 (33)	2	2	48 - 83	No
220	0.0 - 1.3	5.2 - 1570.9 (65)	5	6	57 - 142	No
224	0.0 - 0.1	5.6 - 7.2	5	8	48 - 59	Yes
16	5.5	5.7	1	1	132	No
280	0.0 - 0.4	6.7 - 6.8	2	2	51 - 56	No
231	0.0 - 0.2	10.6 - 12.5	1	6	55	No
232	0.0 - 0.7	11.1 - 1711.3 (71)	7	9	48 - 142	No
243	0.2	14.5	1	1	65	No
258	0.0	50.0	1	1	56	No
257	0.2 - 0.3	50.2 - 51.3	2	2	48 - 56	No
274	0.7	240.7 (10)	1	1	100	No

Table 5. (cont'd)

Female number	Range of grasp durations (in hrs)	Range of elapsed times between molt and release in hours (days)	Number of different males that grasped	Number of times female was grasped then released	Male size range (in mm)	Do any of the original graspers mate with this female later?
241	0.0	668.3 (27)	1	1	83	No
246	0.0 - 0.3	786.2(32)-1620.7(67)	2	2	75 - 127	No
226	0.0	861.0(35)-885.6(36)	3	4	88 - 118	Yes
272	0.0 - 0.6	902.6(37)-1166.6(48)	5	7	79 - 138	Yes
227	0.0 - 0.3	1056.4(44)-1056.9(44)	2	3	75 - 88	No
254	0.0 - 0.5	1165.2(48)-1302.6(54)	5	6	87 - 142	No
249	0.0	1405.0 (58)	1	1	142	No
234	0.0 - 0.1	1677.5(69)-1770.6(73)	3	3	31 - 124	No

Table 6. Duration of pre-copulatory embraces that were initiated before the female's puberty molt

Duration of pre-copulatory embrace (in hrs)	Elapsed time (in hrs) between female's molt and mating	Male carapace width (in mm)
14.5	0.4	92
15.5	0.6	131
24.2	0.2	112
151.6	0.6	112

Table 7. Duration of pre-copulatory embraces initiated after the female's puberty molt

Duration of pre-copulatory embrace (in min)	Elapsed time from molt to intromission (in hrs; days in parentheses)	Male carapace width (in mm)
1	1.0	59
2	2.2	59
2	10.9	127
2	11.3	67
2	205.3 (8)	110
2	1044.0 (43)	110
3	0.2	65
6	541.2 (22)	119
7	2.8	55
7	104.6 (4)	68
9	1.0	57
9	9.0	70
9	1102.4 (45)	110
10	121.7 (5)	59
10	659.3 (27)	119
11	842.8 (35)	142
12	1.0	56
13	58.3	75
13	183.7 (7)	127
13	489.2 (20)	110
16	12.2	116
16	12.7	57
17	31.4	71
19	0.8	122
20	4.3	130
22	56.6	67
23	9.1	69
25	7.0	120
25	8.3	59
25	20.1	69
27	7.0	63
28	1013.5 (42)	119
30	19.2	67
31	5.8	55
33	277.2 (11)	136
34	28.2	147
40	14.3	120
52	11.9	55
55	533.5 (22)	140
57	1856.9 (77)	119
82	3.7	115
100	981.6 (40)	87
103	4.2	83
109	288.0 (12)	88
148	38.7	68
235	1294.1 (53)	119

copulatory embrace. Most males pressed the tips of one cheliped against the surface of the female's carapace, abdomen, or pereopods in a poking or probing motion or in a back and forth stroking motion. Large males typically pressed the smooth, curved, inner surface of the chela against the female's first two abdominal segments in a cradling motion. Lifting and beating behavior, described earlier, was also occasionally exhibited by males as large or larger than the female. If the recipient of such a beating was in a very soft condition then she assumed a totally submissive posture. This was characterized by the ocular peduncles being withdrawn into their orbits, both chelae pressed flatly against the maxillipeds, and the pereopods held limply forward (and typically in a partially flexed position within the horizontal plane of her body). Finally, nine of 57 males and 12 of 57 females flapped their abdomens prior to mating. The male and female jointly participated in four such incidents. No visible secretions or excretions were produced during pre-mating flapping.

Every completed mating was preceded by sternum to sternum positioning of the male with the female. Possession of at least one cheliped was a vital prerequisite for proper positioning prior to mating. This was clearly demonstrated when three males, which had each lost both chelae, were placed on separate occasions in an aquarium with very soft, newly molted, mature females. Each hard, new shell male showed an interest in the nearby female by either standing at an elevated posture and actively moving his mouth parts or by moving toward the female and subsequently encircling her with his pereopods. Two of the males used their pereopods to try to pull the female into a sternum to sternum position but both males lacked the necessary contact for completion of the maneuver.

Successful matings were achieved by assorted sternum to sternum positioning techniques which varied with the size of the male. Shortly before copulating, males held females directly in front and rostrum to rostrum. Each small male, measuring less than 75 mm carapace width, invariably interspersed the distal portions of his pereopods between the female's pereopods. He then palpitated the female's carapace with one or both chelipeds, opened his maxillipeds widely, and positioned between the inner surface of the female's abdomen and her sternum. This positioning was achieved either: (1) by swinging entirely beneath her in a single anterior to posterior motion; or (2) by tilting the female into a plane perpendicular to the substrate while pressing her tightly with his chelipeds held behind her carapace.

Larger males positioned differently. In some instances, a large male would: (1) fold his pereopds thereby sitting on the substrate; (2) encircle the female with his pereopods; (3) place one or both chelae behind the female's abdomen; and (4) pull the female toward himself with the use of his chela(e) and longer pereopods while pushing upward (lifting) with his shorter pereopods. The latter action placed the coupled animals perpendicular to the substrate. During this procedure, it was common to see the male palpitate the female's carapace with his chelipeds. In other instances, especially those involving males larger than 130 mm carapace width, positioning was less complicated. First, the male would rise to about two-thirds or three-quarters of his full stance and spread his pereopods very widely. Then, grasping the female with one chela, he would simply turn her upside down (but facing in the same direction) and place her beneath himself sternum to sternum. Finally, the male would press his free chela behind the female's carapace thus assuring close contact.

In every mating, the female participated behaviorally by lowering her abdomen prior to or while being positioned sternum to sternum. During some unsuccessful mating attempts, the female did not lower her abdomen. Even in those instances, the male made no effort to force the female's abdominal flap open. Very soft females were particularly compliant during pre-copulatory positioning and some fully lowered their abdomens as early as one minute before the males commenced the prerequisite maneuvers. With the male in a sternum to sternum position above or below the female, the pre-copulatory period came to a close and the crabs were ready to enter the next reproductive phase.

The Copulatory Period

This episode encompasses the physical processes of intromission. It commences as the male inserts his intromittant organs into the female's reproductive tract and ends as he withdraws them. In each observed mating, exposure of the male's intromittant organs occurred concurrently with sternum to sternum positioning. Insertion was usually performed within seconds after positioning; however, small males sometimes required several attempts for proper insertion. Repeated insertion attempts were also made by some of the males which copulated with females more than 15 days after the puberty molt.

The three smallest males, which actually copulated with primiparous females, measured 55 mm carapace width. Even smaller males grasped females (Tables 3 and 5); but, although their first pleopods had the adult shape and sufficient spread to span the lateral distance between the female's gonopores, the smallest grasping males failed to copulate.

For several seconds before, during, and after pleopod insertion, males usually held their first maxillipeds extended open and downward while the exopodites of their second and third maxillipeds beat rapidly. Additional male movements during copulation were somewhat dependent upon the male's size. Males which were smaller than their female partners predominantly remained beneath the females throughout copulation (Table 8). These males held their chelae firmly against the protogastric or rostral regions of the females' carapaces and their pereopods were bent upward and inward with the dactyls angled over or near the coxae of the females' pereopods. Males which exceeded the size of the females were capable of standing and walking with the females in mating position beneath. Such movements happened when other crabs (particularly other males) approached. Chela to chela blows and grasps were sometimes exchanged between mating males and challengers. But none of these conflicts resulted in the challenger separating the copulating couple. The largest males (exceeding 125 mm carapace width) stood high off the substrate during intromission and usually kept only one chela in contact with their mates.

Females remained submissive throughout copulation and their movements were primarily confined to brief snterior-posterior swivelling motions accompanied by simultaneous flexures of all pereopods. Males responded to such movements by pressing one cheliped against the females' maxillipeds and thereby quieting them. A few hard, new shell females pushed their chelae against the males' maxillipeds, ocular peduncles, and/or chelae and received identical treatment in response.

Primiparous matings occurred in the laboratory as late as 77 days after the female's molt to maturity (Table 9). Duration of intromission tended to increase with amount of elapsed time between molting and mating and ranged from 3.0 to 54.5 minutes. The simple arithmetic mean for 101 timed primiparous intromissions was 13.7 minutes. Observed multiparous copulations were considerably more lengthy, lasting between 15 and 35 minutes (Table 10) with a mean value of 24.5 minutes. No males smaller than 120 mm carapace width participated in the multiparous matings. Although smaller males grasped multiparous females, they were unable to overpower the females' resistive efforts.

Various methods were employed by males in extracting their pleopods from the females' gonopores. If standing, a male accomplished this act in the following manner: (1) he folded his pereopods inward and tilted the anterior end of his body upward while lowering the posterior end of his body toward the substrate; (2) he grasped the female's pereopods with one or both chelae or, alternatively, placed his chelae behind the female's carapace or abdomen; and (3) he either lifted the female away and upward so that she now faced him rostrum to rostrum or he pivoted on the proximal cheliped segments (in contact with the anterior margin of the female's carapace) while using his last two pairs of pereopods to push backward and away from the female and upward into a horizontal position. On the other hand, if a male was positioned beneath a female during copulation then dismounting required a different approach. By the more direct but less common version, a male would press his chelae against the an-

Table 8. Mating positions assumed by *Chionoecetes bairdi* males

Male carapace widths (in mm)	Number of males that positioned above female	Number of males that positioned beneath female
50 - 59	2	12
60 - 69	3	17
70 - 79	1	3
80 - 89	12	5
90 - 99	13	0
100 - 109	6	2
110 - 119	19	1
120 - 129	8	0
130 - 139	5	0
140 - 149	3	0

Table 9. Duration of copulation and the post-copulatory embrace in *Chionoecetes bairdi* matings

Elapsed time from molt to intromission (in days)	Number of observations	Copulation duration (in minutes) (1) Range (2) Mean (3) Standard deviation	Post-copulatory embrace duration (in hours) (1) Range (2) Mean (3) Standard deviation	Male carapace widths (in mm) (1) Range (2) Mean
0 - 5	51	3.0 - 22.2 7.7 3.2	1.2 - 6.5 2.7 1.1	55 - 147 80
6 - 10	4	6.4 - 17.1 12.5 4.5	1.5 - 2.0 1.8 0.8	110 - 128 119
11 - 20	15	5.1 - 44.2 18.4 11.5	1.3 - 4.4 2.4 0.8	81 - 136 100
21 - 30	19	7.6 - 35.2 17.5 9.6	1.5 - 3.4 2.2 0.5	84 - 140 103
31 - 40	4	6.2 - 28.3 17.3 9.4	2.4 - 3.6 3.0 0.8	88 - 143 107
41 - 55	5	14.6 - 52.5 30.3 13.8	4.0 4.0 0.0	95 - 119 111

Table 9. (cont'd)

Elapsed time from molt to intromission (in days)	Number of observations	Copulation duration (in minutes) (1) Range (2) Mean (3) Standard deviation	Post-copulatory embrace duration (in hours) (1) Range (2) Mean (3) Standard deviation	Male carapace widths (in mm) (1) Range (2) Mean
61 - 77	3	28.2 - 54.5 37.4 14.8	3.1 - -	95 - 119 103
Totals	101	3.0 - 54.5 13.7 10.6	1.2 - 6.5 2.5 1.0	55 - 147 87

Table 10. Intromission duration for multiparous *Chionoecetes bairdi* females

Intromission duration (in min)	Male carapace width (in mm)	Female number
15	127	417
18	138	402
20	124	402
21	124	401
21	136	406
23	152	414
24	124	409
25	138	415
25	138	402
26	152	412
27	138	413
28	138	407
29	127	410
30	138	408
35	142	403

Total number of observations = 15
Mean value for intromission duration = 24.5 min

terior dorsal portion of the female's carapace or grasp her pereopods, bend at least two pairs of his pereopods beneath the ventral surface of the female, then push upward with the pereopods. Immediately thereafter, he would quickly reposition his pereopods in order to regain a horizontal stance. Most small males initially used their pereopods to orient vertically to the substrate then proceeded to dismount in the same manner as large males (described above).

The behavior of mating females did not provide any forewarnings that intromission was about to end. However, sudden, brief changes in male behavior often immediately preceded this event. These signals were very abruptly manifested as wide extension of the maxillipeds and/or palpitating movements of the male's chelipeds upon the female's carapace. Concurrently, the male sometimes encircled the female's pereopods with his own pereopods.

The Post-copulatory Period

Post-copulatory Grasps

Having completed intromission, 72 out of 104 pairs of *C. bairdi* remained together until the female extruded eggs. Thirty-two matings ended with the following unusual results: (1) eggs were not extruded after the female had mated with a very small (less than 61 mm carapace width) male (five instances); (2) eggs were not extruded by the female when copulation occurred 22 to 77 days after her maturity molt (eight instances); (3) a small grasping male (less than 70 mm carapace width) released the female prior to extrusion (eleven instances); and (4) a large grasping male mated with the female more than nine days after her maturity molt and released her prior to extrusion (eight instances). Normal post-copulatory grasps ranged between 1.2 and 6.5 hours in length with a mean value of 2.5 hours (Table 9). However, grasps lasting up to 123 hours were noted for some males which mated with females 22 or more days after the maturity molt and without subsequent egg extrusion (Table 11).

Throughout the post-copulatory period, the male and female faced each other. The male did not hold the female above the horizontal plane of his body except in a few instances where post-copulatory beatings were administered. Within minutes after the termination of intromission, the male would flex his abdomen, swing the first pair of pleopods dorsoventrally, and/or move each member of the pair in a slight scissoring motion. Several males emitted a small volume of opaque material and spermatophores from the distal tips of the first pleopods soon after mating. Females, which later became ovigerous, responded to these activities by fully lowering and then flapping their abdomens. Males smaller than 80 mm carapace width had difficulty holding the large

Table 11. Matings of primiparous *Chionoecetes bairdi* females which did not result in egg extrusion

Elapsed time between the puberty molt and mating (in days)	Duration of copulation (in min)	Duration of post-copulatory embrace (in hrs)	Male carapace width (in mm)
27	52	4.6	119
35	14	50.9	143
40	6	45.7	88
43	31	123.2	110
44	27	14.8	95
60	28	42.5	95
68	29	115.0	95
77	54	3.1	119

females high enough above the substrate to provide clearance for flapping. In some of these cases, the females elevated themselves on dactyl tips and flapped their abdomens anyway. Large males stood well above the substrate and the graspees had sufficient clearance for flapping without need of additional elevation.

Concerted efforts were often displayed by the female as she prepared her pleopods for the impending extrusion of eggs. Pleopods were waved in a dorsoventral direction, pushed toward the perimeter of the abdominal flap with the tips of one cheliped, grasped and pulled lengthwise in a combing motion between the propodus and dactyl of the cheliped, and flexed inward forming a loosely layered hemisphere then flexed outward toward the perimeter of the abdomen. Soft, newly molted females pressed their chelae against the inner surfaces of their abdomens, producing greater concavity there. Brood chamber preparations ceased at least 20 minutes prior to the actual extrusion of eggs.

Some females were lightly bounced up and down by grasping males during the post-copulatory period. Additional interactions included: (1) the use of one chela (by the male) to poke, stroke, or beat the female's carapace, abdomen, and/or pereopods; and (2) male pereopod kicks aimed at the female's pereopods. Hitting or striking motions, such as those noted above, were most frequent in the post-copulatory episodes involving females that failed to extrude eggs and in multiparous matings.

A gradual reduction was observed in the stances of all paired crabs near the middle of the post-copulatory period. However, as this episode dtew to a close, a more striking change occurred. Minutes before extrusion commenced, the male and female both increased movements of their first, second, and third maxillipeds (particularly the exopodites of the second and third pairs).

It is noteworthy that the post-copulatory embrace was greatly extended in instances where mating occurred weeks after the female's maturity molt and eggs had not been extruded (Table 11). Very variable post-copulatory grasp durations were noted in association with multiparous matings (Table 12). Some of these matings happened before the females had even completely removed empty egg cases from their pleopods. Such females were released hours or days before they were ready to extrude new eggs. The ensuing lag time between release and extrusion enabled more than one male to mate with some multiparous females.

Egg Extrusion

Ejection of eggs into the brood chamber was accomplished in less than 10 minutes by two primiparous females. Unfortunately, the small number of observations precludes estimation of probable

Table 12. Duration of the post-copulatory embrace in *Chionoecetes bairdi* multiparous matings

Duration of post-copulatory embrace (in min)	Male carapace width (in mm)	Female number
1	136	406
1	152	412
3	138	404
39	142	402
307	142	407
781	138	408

upper and lower time limits. During the process of extrusion, very small numbers of eggs have been seen leaking toward the female's mouth from beneath the anteriormost apex of her abdomen. This phenomenon has been observed twice and on both occasions the female and male simultaneously further increased the movements of their mouth parts. Within seconds the male raised onto the dactyls of his pereopods and released the female.

Every completed primiparous mating resulted in one of three outcomes: (1) extrusion of fertile eggs; (2) extrusion of eggs which failed to undergo normal cleavage and were eventually sloughed off; or (3) no extrusion of eggs. The first outcome transpired through matings between mature males and females. Thusfar, the smallest male that successfully mated and contributed to the production of viable offspring, measured 68 mm in carapace width. The development of eggs spawned in 1982 is being monitored in an attempt to further assess the reproductive potential of small males. Data from the two previous seasons is insufficient for a proper determination of the size at which 50% of the males are mature. Viability of eggs is temporally limited and this places an additional constraint on mating success. One female produced viable zygotes after mating with a male eight days past her puberty molt.

The second outcome noted above resulted when either: (1) a small immature male mated with the female; or (2), regardless of the male's size and maturity, an extended period (exceeding eight days) had expired between the female's puberty molt and intromission. Five different males measuring between 55 and 59 mm carapace width mated with primiparous females on 12 separate occasions. Their attempts at reproduction are considered to be precocious because not one of the matings yielded viable zygotes. Eleven of the twelve females extruded eggs within a normal time period after mating but cleavage did not proceed normally and the zygotes eventually died and deteriorated.

The third outcome occurred when: (1) a small (and apparently immature) male mated with the female; (2) a dying female expired shortly after mating; or (3) an extended period of time (exceeding 21 days) had elapsed between the female's puberty molt and intromission.

Behavior After the Post-Copulatory Release

Thirty-three out of fifty-six males lowered and then flexed their abdomens after releasing extruding females. The males did not eject any visible material while waving their pleopods. But 17 different males grasped at their first pleopods and then drew their chelae over the surface of their maxillipeds in wiping motions. Few males showed any interest in the female once she extruded eggs and no male attempted to mate with an ovigerous, primiparous female. However, some males demonstrated a capacity for multiple matings with the female prior to the extrusion of eggs.

Upon being released, a newly molted female was entirely capable of evading other crabs. This was possible because, at the time of normal release, her exoskeleton was sufficiently firm for agile and rapid locomotion.

Primiparous females which had mated while in a soft condition were free of grasping marks (on the meri of their pereopods). Conversely, two females which underwent primiparous mating more than 60 days after the puberty molt bore fresh white grooves and scrapings on the surfaces of their pereopods. Fourteen out of 15 females involved in the observed multiparous matings bore fresh grasping marks when released by the males.

Extrusion of Eggs By Isolated, Unmated, Primiparous Females

Sixty-one newly molted, mature females were isolated from males before, during , and for at least nine days after molting. Twenty-eight of the females extruded eggs while in isolation. Although the eggs attached normally, none underwent cleavage. However, as viewed with the unaided eye, the eggs maintained normal size, shape, and color for more than five weeks after being extruded. By the eighth week after extrusion, the non-fertilized eggs were dectably pale and the innermost ones had started turning tan in color. Microscopic inspection revealed that, by the eighth week: (1) the vitelline membranes of most eggs were shredding; (2) opaque white spots were developing on and within the eggs; and (3) some eggs were filled with transparent tea colored fluid.

Brief Interactions Involving Recognition Errors

Males sometimes made apparent recognition errors by grasping immature females, ovigerous, primiparous females, other males, and even crab shaped rocks (Table 13). Molting or recently molted, mature females were present when a few of these errors were made and in each instance the male seemed to have already become adjusted to his surroundings. Only small males (less than 80 mm carapace width) grasped immature females. Small males have also grasped other small males, larger males, and ovigerous,primiparous females. Larger males have grasped ovigerous, primiparous females, other males, and rocks. When one male was grasped by another the graspee usually responded by using his chelae to push the grasper or to grasp back. This behavior elicited release. Immature females and ovigerous, primiparous females were either simply released by males or managed to escape (Table 13). The grasping male typically poked or stroked the graspee but never progressed to the point of sternum to sternum positioning.

Table 13. Interactions between *C. bairdi* males and immature or ovigerous, primiparous females

I. Female escapes out of the male's grasp

A. Female escapes before molting

Female condition	Hours before molt at time of escape	Male carapace width (in mm)	Grasp duration (in hrs)	Female number
Immature	4.5	48	0.0	222
Immature	4.4	48	0.0	222
Immature	4.2	48	0.0	222
Immature	3.5	56	0.0	222
Immature	3.4	56	0.1	222
Immature	1.6	49	0.1	222
Immature	0.1	59	0.0	279

B. Female escapes after molting

Female condition	Elapsed time from molt to escape (in hrs)	Male carapace width (in mm)	Grasp duration (in hrs)	Female number
Ovigerous primiparous	6.5	48	0.1	273
Immature	11.2	65	0.0	217
Immature	1107.3	57	0.6	222
Immature	1303.6	75	0.0	222

Table 13. (cont'd)

II. Male simply releases female

Female condition	Elapsed time since molt at release (in hrs)	Male carapace width (in mm)	Grasp duration (in hrs)	Female number
Ovigerous, primiparous	16.1	127	1.8	16
Ovigerous, primiparous	17.1	127	0.5	16
Ovigerous, primiparous	24.6	122	0.3	11
Ovigerous, primiparous	83.2	132	0.1	12

DISCUSSION

All results reported in this study are based upon laboratory observations of mating behavior. The conditions that are provided for the crabs in the laboratory can not and do not exactly recreate the conditions which constitute their natural ecological niche. For this reason, care must be exercised when attempting to apply the results of a laboratory study in explanation of natural phenomena. It is possible that *Chionoecetes bairdi* may display more complex behavior in its natural habitat than it does in the laboratory. However, individuals which had been in captivity for as short a period as one day displayed behavior which was indistinguishable from that of individuals held for months. This fact offers hope that at least the sequence and types of behavioral elements displayed are not greatly altered as a result of laboratory confinement.

The duration of some events (such as pre-molt grasping and the pre-copulatory embraces intitiated after the female's molt) may be greatly affected by extrinsic factors not reproducible in the laboratory. Therefore, some events have not been examined in great detail although they have been included in the description of the mating behavior repertoire.

Sudden responses of males to molting females (juvenile and mature) in the absence of any visible, physical, behavioral cues by the female strongly suggest that at least one pheromone must be involved in the attraction. Chemical attractants have been demonstrated or implicated in the mating behaviors of several brachyurans (including *Portunus sanguinolentus* (Ryan, 1966), *Carcinus maenas* (Eales, 1974), and *Libinia emarginata* (Hinsch, 1968)). Since *C. bairdi* males are attracted to juvenile and pubescent molting females, the molting hormone crustecdysone may be the initial attractant. Males are capable of distinguishing mateable females from newly molted juveniles and ovigerous, primiparous females. Males also show strong behavioral responses (releases) in the presence of extruding females and are attracted to multiparous females at the time the females' eggs hatch. The latter phenomenon has also been observed in *Libinia emarginata* by Hinsch (1968). Therefore, it is tempting to speculate that additional chemicals may have roles in: (1) identification of receptive, primiparous females; (2) negative feedback to grasping when eggs are extruded and the female is no longer receptive; and (3) attraction of males by receptive but non-molting, old shell multiparous females.

In the absence of impending molt, it is significant that multiparous *C. bairdi* females: (1) do attract males; (2) mate in the hard, old shell condition; (3) sometimes mate before all of the zoeae have been released from their brood chambers; and (4) sometimes undergo multiple matings during the time that they remove empty egg cases (left by the previous brood of offspring) from their pleopods. Perhaps, as suggested by Hinsch (1968) for

Libinia emarginata, the attraction of males to multiparous females is mediated: (1) chemically by the ripening ovary or by substances released by the emerging zoeae; (2) by submissive or receptive female behavior; or (3) by a combination of all three. Further study is needed to confirm and measure hormonal and pheromonal regulation of reproductive behavior.

Pre-molt grasps have been observed both in the natural environment (Brown and Powell, 1972) and in the laboratory (Watson, 1972 and this study). Brown and Powell (1972) reported a carapace width range of 93 to 116 mm for *C. bairdi* males that were grasping non-ovigerous, old shell females at the time of capture. Twenty-seven males grasped grasped pre-molt pubescent females, in the present study, but only four males exceeding 91 mm carapace width prolonged the grasp through molting to mating. Pre-molt grasps by small males ended in simple releases or female escapes.

After the female has molted she is exceptionally vulnerable to: (1) predation by other species (or even other *C. bairdi* females); or (2) grasping by *C. bairdi* males. Males as small as 55 mm mated with newly molted, mature females but the smallest reproductively successful male (whose copulation resulted in the production of viable offspring) measured 68 mm carapace width. Histological preparations of the posterior vas deferens of these small males contained fully formed sperm in spermatophores and the reproductive tracts were open and complete. The failure of sperm from very small males remains unexplained. Eggs that have been inseminated (through copulation) by sperm from very small males commenced cleaving but failed to continue beyond approximately 128 cells. Hinsch (1969) reported the presence of spermatophores filled with sperm in the vasa derentia of quite small males of *Libinia emarginata* (1.9 cm in length) "... before the crab has attained its full size and presumably, the ability to mate".

There is no apparent advantage to precocious mating by males and, quite possibly, very small males may be prevented from mating under natural conditions by agonistic interactions with larger males. In the laboratory, *C. bairdi* males reacted submissively when grasped by males of superior size and strength. When two or more males of distinctly unequal size and strength grasped a mateable female, the largest male invariably forced his opponents away.

Females exhibited evasive and resistive behavior after molting as soon as they could support their weight and walk. Their evasive and resistive behavior increased with elapsed time since the completion of ecdysis. Thus, within three hours of molting, mature females regained sufficient strength and agility to overpower some small males.

Mating females all exhibited submissiveness and compliance toward their mates at the time of sternum to sternum positioning. But in instances where the male's size advantage was slight, the mating position was achieved only after he controlled and suppressed resistance and escape attempts by the female. The ability of female brachyurans to resist mating efforts has also been observed by Chidester (1911) in the Portunidae. Old shell, multiparous *Chionoecetes bairdi* females showed the greatest adeptness at discouraging mating attempts by small grasping males. No male smaller than 120 mm carapace width mated with a multiparous female during the laboratory observations.

According to Hartnoll (1969), for the Cancridae, " All accounts emphasize that the male treats the female gently throughout (mating), and that the female is cooperative, sometimes in response to stroking by the male". *C. bairdi* males were similarly very gentle with soft or partially rigid females. But as the intervening time between the puberty molt and mating increased so also did the frequency of beating actions and the force exerted in grasping. Two hard, new shell females and almost all multiparous females bore fresh white scars on the meri of their pereopods subsequent to mating.

Earlier observations of mating behavior in *Chionoecetes opilio* (Watson, 1971 and 1972, and Takeshita and Matsuura, 1980) and *C. bairdi* (Takeshita and Matsuura, 1980) agree well with the general sequence of events noted in this study. In fact, Takeshita and Matsuura (1980) have effectively shown that interspecific behavioral differences are slight and not a block to interspecific matings in the laboratory. The existence of *C. bairdi X C. opilio* hybrids (Karinen and Hoopes, 1971) in the Bering Sea confirms that interbreeding also occurs in the natural habitat.

The duration of observed copulations (Takeshita and Matsuura, 1980, and this study) falls within the lower time range noted by Hartnoll (1969) for the Brachyura. *C. bairdi* males are usually positioned uppermost during copulation, although individuals smaller than 80 mm carapace width tend to position beneath the female. As noted in *Machrocheira kaempferi* matings (Hartnoll, 1969), it is common to see a male *C. bairdi* palpitate the female's carapace with his chelae immediately before copulation.

The post-copulatory embrace terminates as eggs are extruded by the female approximately 2.5 hours after mating. The reason for extrusion (rather than absorption) of unfertilized eggs by only about 50% of the isolated, newly molted, mature females is unknown. These females flex their abdomens periodically (as do normally mated females) and comb their egg masses with their chelae. Perhaps some of the deteriorating eggs are consumed thereby contributing to the female's nutritional intake.

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ABSTRACT

A distinct sequence of behavioral events has been observed during the mating of the brachyuran crab *C. bairdi*. Every successful mating (resulting in the production of fertilized eggs) observed in the laboratory could invariably be subdivided into three successive temporal periods which were marked by the completion of specific actions. The first (or pre-copulatory) period included the following primary enevts: (1) initial grasping of the female by the male; (2) stroking, poking, or even pounding actions performed on the female by the male; and (3) sternum to sternum positioning of the reproductive partners with simultaneous relaxation of their abdomens. The second (or copulatory) period encompassed activities which initialized, continued, and completed the physical process of intromission. In the third (or post-copulatory) period, the primary events were: (1) continued grasping of the female by the male; (2) extrusion of the egg mass into the brood chamber; and (3) cessation of grasping. The diversity of secondary events which occurred during specific matings varied greatly and the manner in which they were manifested was influenced by factors such as the relative sizes of the reproductive partners and the carapace condition of the female at the onset of the pre-copulatory period.

Two notable peculiarities were observed in the reproductive behavior of *C. bairdi*. First, very small males grasped newly molted females and mated precociously without subsequent production of viable zygotes. Second, 28 primiparous females, which had been isolated from males before, during, and after the molt to maturity, extruded unfertilized, inviable eggs. In each instance, the eggs attached to the pleopods and were a normal orange color but failed to cleave and gradually faded before being sloughed off. More frequently (in 33 cases), the eggs produced by unmated primiparous females were resorbed rather than extruded.

Mating Frequency and Sperm Storage as Factors Affecting Egg Production in Multiparous *Chionoecetes Bairdi*

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INTRODUCTION

Evidence exists which suggests that multiparous *Chionoecetes bairdi* (Rathbun) may either breed to obtain fresh sperm or utilize sperm stored from a previous mating season to fertilize eggs. The female of this species, called snow or Tanner crab, reaches a terminal size with the molt to maturity. The female must breed within one week after this final molt in order to produce eggs (unpublished). Spermatophores not utilized to fertilize an egg clutch remain stored in the spermatheca. It has been demonstrated that *C. opilio* can utilize this stored sperm to fertilize a subsequent egg clutch (Watson, 1972). Based on laboratory observations, Watson (1972) reported that multiparous female *C. opilio* seemed incapable of mating.

The evidence which suggests that multiparous individuals are commonly rebred is the presence of grasping marks on the females' legs, which are caused by the mating embrace of the male. These grasping marks are absent in soft-shell primiparous females mated in the laboratory (unpublished). Therefore, it is reasonable to assume that the grasping marks on multiparous individuals are the result of repeated breeding. Over 90 percent of the multiparous crab captured near Kodiak for this study had these grasping marks on their walking legs. However, prior to this report, no matings of multiparous females of the genus *Chionoecetes* had been observed.

In the fishery only males are harvested. The effect of removing males on the reproductive habits and fecundity of the species has not been examined. It is necessary to describe the importance of mating and spermatophore storage as fertilization strategies for the species before the impact of male removal on population fecundity can be determined. The objective of this study was to examine the percentage of multiparous female *C. bairdi* that mate and determine the effect of utilizing stored sperm versus fresh sperm on fecundity.

METHODS

Specimens of *Chionoecetes bairdi* were captured by trawl in the Kodiak area and transported to the University of Alaska's marine laboratory in Seward. Some of the crab were held in 2,000 liter refrigerated indoor tanks at 4° to 6°C. They were fed a variety of fish and shellfish twice per week. Males over 110 mm carapace width were placed in one tank with females and when matings were observed, both male and female crab were marked with leg tags. Additional crab were placed in two outdoor 10^6 liter, $6^{\circ}C$ saltwater ponds. One pond contained males and females, while only females were placed in the other pond. The walking legs of the females placed in the pond containing male crab were wrapped with electricians tape to ensure that new grasping marks would be identifiable. In addition, 20 females, with tape wrapped legs, were held isolated from males during the mating and egg extrusion period. This group served as a control to determine if grasping like marks would be left on the tape by the females themselves. The tape on all females isolated from males remained unmarked.

Approximately one month after extrusion of new eggs the females were killed, examined for grasping marks, and the egg mass and spermatheca removed. Eggs were stripped from the pleopods of the first 70 egg clutches and an aliquot of at least 200 counted eggs separated and dried to a constant weight at $80^{\circ}C$. The average dry weight, to 0.0000 g, of one egg was calculated from these subsamples. The number of eggs in all egg clutches was determined by dividing the average weight of one dry egg into the dry weight of the total egg mass.

The spermatheca of each female was examined visually for the presence of fresh ejaculate. Fresh ejaculate is deposited in a liquid matrix, white in color, while ejaculate that has been stored from previous matings forms into a distinctive amalgated mass slightly yellow or brown in color.

RESULTS

The frequency of mating of old shell female *Chionoecetes bairdi* averaged 98 percent in two groups of female crab totalling 140 females. One group, consisting of 28 females, was held in a laboratory tank with 16 males. Fifteen of these females were observed in the mating act and had fresh sperm in their spermatheca. Eleven of the remaining females had fresh sperm in their spermatheca indicating that they had mated unobserved. One female was bred but remained barren (Table 1). One female produced eggs utilizing stored sperm. The size of the males mating with the females ranged from 124 to 142 mm and averaged 137 mm. The second group of 112 females were held in an outdoor 10^6 liter saltwater pond with 134 males. There were 108 females that had punctures in the tape wrapping their walking legs indicating that they had been grasped. These females and the remaining four females in the group all had fresh sperm in their spermatheca (Table 1).

Table 1. Frequency of mating for multiparous *Chionoecetes bairdi* based on the presence of fresh sperm in the spermatheca.

Number Females	Number Males	Sex Ratio Male/Female	Number Females Bred	% Females Bred	Number Having Grasping Marks	% Barren Females	Holding Conditions
28	16	1/1.8	27*	96	27	3.5%	$2x10^3$ liter laboratory tank
112	134	1/1.2	112	100	108	0%	$1x10^6$ liter outdoor pond

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*Actually observed 15 of the matings.

To determine if utilizing stored sperm had any effect on the number of eggs extruded by multiparous females, 112 individuals, carrying eggs that would soon hatch, were placed in a 10^6 liter saltwater pond containing no males. New eggs were extruded by 109 (97 percent) of these females. A preliminary comparison of the number of eggs produced by these females and females utilizing fresh sperm to produce eggs occurs in Figure 1. There appears to be no marked difference in the number of eggs produced by females utilizing fresh and stored sperm. There were three (3 percent) barren females in the group forced to use stored sperm. Two barren females were killed and their gonads were found to be full of orange ovarian material and both had empty spermathecas. To test the hypothesis that limited sperm availability precluded the production of eggs by these three females the remaining barren female, after a week of isolation, was placed in a tank with males where she was observed to breed and extruded fertile eggs.

One multiparous female has been kept isolated from males for two breeding seasons. She produced a normal size egg clutch the first year but was barren the second year.

DISCUSSION

The results of this preliminary study indicate that, if males are present in sufficient numbers, over 90 percent of the multiparous *C. bairdi* will mate to obtain fresh sperm before extruding eggs. These results are in direct contrast to Watson's (1972) theory that mating of the multiparous *C. opilio* is a rare or nonexistent occurrence. If isolated from males, the majority of the *C. bairdi* females can rely on sperm stored in their spermatheca to fertilize at least one egg clutch of normal size. Approximately 3 percent of the multiparous *C. bairdi* must rebreed to obtain sperm to fertilize new eggs or remain barren.

Before the existing information on the breeding behavior of multiparous *C. bairdi* can be utilized in producing a management strategy, the effect of sex ratio on breeding frequency and the number of egg clutches that can be fertilized by females relying solely on stored sperm needs to be described.

ACKNOWLEDGMENTS

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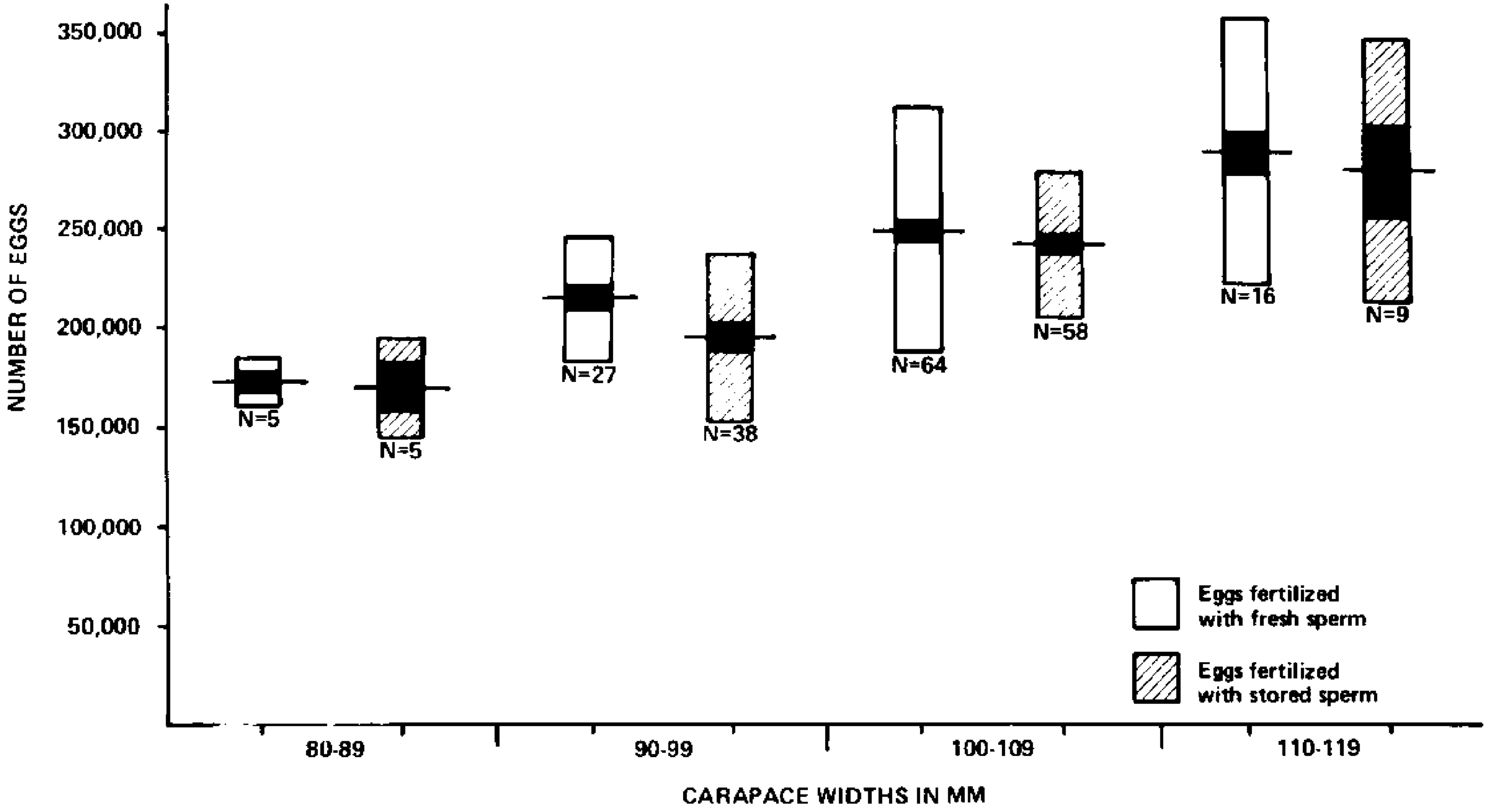

Figure 1. A preliminary comparison of the number of eggs produced by multiparous females using stored sperm and those using fresh sperm.

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ABSTRACT

The frequency of mating of 140 multiparous *Chionoecetes bairdi* was 98 percent. These freshly bred females, and a group of females forced to utilize sperm stored from a previous mating season, extruded egg clutches of similar sizes.

The results indicate that if males are present in sufficient numbers, over 90 percent of the multiparous females will breed before egg extrusion. Stored sperm has been demonstrated to be viable for at least one year. It remains to be determined how many egg clutches *C. bairdi* can produce using stored sperm.

Bipartite Breeding: A Hypothesis of the Reproductive Pattern in Tanner Crabs

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The typical reproductive pattern of many crab species is one in which breeding is monopolized by large dominant males (Powell et. al. 1973; Edwards 1966). In this paper I examine evidence suggesting that species in the genus *Chionoecetes* may have a different pattern of reproduction, one in which small males are not necessarily excluded from mating. This reproductive pattern is bipartite, that is, mating occurs among members of two distinct life history groups, one composed of primiparous females and recently matured males and the other composed of multiparous females and large males.

Bipartite breeding is suggested by studies of the ontogenetic migration patterns of both *C. opilio elongatus* and *C. tanneri* and by underwater observations of mating *C. bairdi*.

ONTOGENETIC MIGRATIONS

Two species, *C. opilio elongatus* and *C. tanneri*, have well defined ontogenetic depth migrations (Pereyra 1966, 1968; Kon 1969) which result in a spatial separation of primiparous and multiparous females.

In the region of the Sea of Japan surveyed by Kon (1969), *C. opilio elongatus* are primarily restricted to the continental slope in a depth zone extending from 200 m to 400 m. During spring, surface currents carry the planktonic larvae of this species seaward and result in the young crabs settling to the bottom at depths greater than those occupied by the adult population. As the crabs develop, they migrate shoreward, reaching a depth of approximately 225 m by the time they have grown to the instar preceeding maturity. Both sexes mature and mate in this zone, then migrate back into deeper water. Mature females disperse between the depths of 240 m and 260 m and remain there for the rest of their lives. Mature males disperse between 275 m and 375 m. Although mature males may migrate seasonally into shallower water, they apparently never return to a depth as shallow as 225 m.

Two important aspects of the reproductive biology of *C. opilio elongatus* are evident. First, the spatial segregation of recently matured males from large males insures that primiparous females are primarily mated by the former. Second, the seasonal migration of large males may be for breeding purposes, and, if so, then multiparous females must be their partners because these are the only potentially receptive females found in the region into which males migrate.

Off the Oregon coast, *C. tanneri* are restricted to the continental slope between depths of 450 m and 2,000 m (Pereyra 1966, 1968). Similar to *C. opilio elongatus*, *C. tanneri* have an offshore transport of planktonic larvae and a return migration into shallower water by young crabs. Large immature crabs of both sexes congregate between 900m and 1,200 m. Adult females congregate between 600 m and 730 m. Adult males seasonally migrate from 500-550 m in summer to the region occupied by adult females in winter. Since the distributions of adult males and females merge when larval hatching and egg extrusion occur, Pereyra (1966) concluded that the migration was for breeding purposes. Unfortunately, sampling was not conducted at depths greater than 900 m during winter, when *C. tanneri* probably mature, therefore it is not known whether large juvenile females migrate into the shallower region occupied by adult females before or after they undergo their puberty molt. If juvenile females mature at depth, then their breeding partners are almost certainly the small males they are associated with because *Chionoecetes* females mate almost immediately after their puberty molt (Watson 1970). Considering that in three succesive years of sampling, some adult females were found below 900 m in spring but none were found in summer, it is quite likely that females mature at depth, then migrate into shallower water. If this is true, then *C. tanneri* also appears to have a bipartite breeding pattern comprised of two spatially segregated groups, one consisting of recently mature crabs and one consisting of older crabs.

UNDERWATER OBSERVATIONS

Bipartite breeding is also suggested by underwater observations of mating *C. bairdi*. Two different studies conducted in a relatively shallow bay near Kodiak, Alaska, reported finding primiparous females which were being grasped in precopulatory embraces by small males. In one study, Donaldson (1975), the mean carapace width of the males was 109 mm (N=33); in the other study, Brown and Powell (1972), the mean carapace width was 116 mm (N=48). Both sizes are quite similar to the 110-113 mm size of 50% maturity (Brown and Powell 1972), but are smaller than the average size of mature male *C. bairdi* (approximately 130-140 mm). Donaldson (1975) also reported finding, in an area several miles away from and closer to deep water than his primary sampling site, two multiparous females being grasped by males (122 mm and 130 mm) which were significantly larger (Mann-Whitney test, $p < .02$) than the grasping males at the primary site.

Although these observations covered only a small portion of the depth range inhabited by *C. bairdi*, they indicate that, at least in some locations, small males are not excluded from breeding and that their partners are primiparous females.

DISCUSSION

Although the above evidence is not conclusive, it does suggest that several species in the genus *Chionoecetes* have bipartite breeding. From an evolutionary perspective, such a reproductive pattern is difficult to explain because intraspecific competition should exclude small males from mating. There are two possible explanations, both of which require a spatial segregation of puberty molting females from multiparous females. First, bipartite breeding could be due to proximity of large adult males to multiparous females. For species such as *C. opilio elongatus* and *C. tanneri*, which have a clear depth stratification by size, seasonally migrating males are more likely to encounter multiparous females than primiparous females. Without the interference of larger males, small males would be able to mate with primiparous females. This proximity effect is more difficult to apply to stocks such as *C. bairdi* and *C. opilio* in the eastern Bering Sea which do not have a distinct depth stratification by size (Somerton 1981). Second, bipartite breeding could be the result of large males choosing multiparous females in preference to primiparous females. Multiparous females may be more valuable because they produce more eggs than equal size primiparous females (54% more for *C. bairdi* in the eastern Bering Sea, Somerton and Meyers, in prep.). I do not believe, however, that such a choice would be made on an individual level (a large male should not distinguish between a multiparous and a primiparous female if all three were placed in an aquarium), rather, large males should search for groups of multiparous females similar to the way optimal foragers search for the richest food patches in a coarse grain environment (MacArthur and Pianka 1966).

Further speculation on the mechanisms of bipartite breeding is premature until this hypothesis can be rigorously tested, but such a test will require additional data on the sizes of males found mating primiparous and multiparous females under natural conditions.

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ABSTRACT

Spatial distributions of *Chionoecetes opilio elongatus* and *C. tanneri* and underwater observations of breeding *C. bairdi* suggest that mating in these species occurs among members of two life history groups, one composed of primiparous females and recently matured males and the other composed of multiparous females and large males.

Feeding, Growth and Distribution

Food of the Tanner Crab *Chionoecetes Bairdi* Near Kodiak Island, Alaska

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INTRODUCTION

The Tanner crab, *Chionoecetes bairdi* Rathbun, is a dominant epibenthic member of the continental shelf of the Gulf of Alaska and southeastern Bering Sea (Ronholt et al. 1978; Jewett and Feder 1981). This species has been harvested commercially in the northern Gulf of Alaska since 1961, and the Kodiak Island area has historically yielded the highest domestic production (Donaldson 1980). The Kodiak fishery harvested 108.9 x 10^3 metric tons (mt) between 1967 and 1981. During the 1981 season, 5.3 x 10^3 mt of this crab yielded 7.9 million dollars to domestic fishermen (Guy C. Powell, Alaska Department of Fish and Game, pers. comm.).

In order to effectively manage a fishery, knowledge of the distribution, abundance, biology, and behavior of the species is essential. Data on the distribution and abundance of adult *C. bairdi* on the Kodiak Shelf are compiled annually by the Alaska Department of Fish and Game (e.g., see Donaldson 1980). The early life history, size and growth, and reproductive biology of this crab have been described (Brown and Powell 1972; Haynes 1973; Hilsinger et al. 1975; Hilsinger 1976a; Jewett and Haight 1977; Donaldson et al. 1981; also see Hilsinger 1976b for a bibliography of the genus *Chionoecetes*). The feeding habits of *Chionoecetes* spp. have been examined from many areas: *C. opilio elongatus* from Japanese waters (Yasuda 1967), *C. opilio* from the Gulf of St. Lawrence (Powles 1968) and the Bering Sea (Tarverdieva 1976; Cunningham 1969; Feder and Jewett 1978, 1980, 1981), and *C. bairdi* from the Bering Sea (Tarverdieva 1976), Cook Inlet (Paul et al. 1979), Prince William Sound (Feder and Paul 1977; Feder and Matheke 1980; Feder and Hoberg 1981) and Kodiak Island (Feder and Jewett 1977). Previous feeding studies on the genus, with the exception of the work by Cunningham (1969), have been semi-quantitative, i.e., tabulated as frequency of occurrence of various prey taxa. The present paper examines semi-quantitative and quantitative feeding data of *C. bairdi* from inshore and offshore locations near Kodiak Island, Alaska (also see Jewett and Feder in press). These data are compared with those for *Chionoecetes* spp. elsewhere. Additionally, food comparisons are made with the red king crab, *Paralithodes camtschatica*, a species whose range often overlaps that of *C. bairdi* in Kodiak Island waters.

MATERIALS AND METHODS

Chionoecetes bairdi was collected in 1978-1979 near Kodiak Island by trawling and SCUBA. The NOAA ship *Miller Freeman* was used for offshore sampling, and the M/V *Yankee Clipper* and the R/V *Commando* were used for nearshore work. Nearshore areas most extensively sampled by trawl included Izhut Bay, located on the southeast side of Afognak Island, and Kiliuda Bay, located on the east side of Kodiak Island (Fig. 1). Additional nearshore sampling was conducted by SCUBA in Near Island Basin. Offshore stations (18) sampled by trawl were primarily outside of various bays and on the shelf along the eastern and southern side of Kodiak and Afognak islands.

Sampling from the *Miller Freeman* was conducted 21-24 March and 19 June-9 July 1978 and 14-24 February 1979, using a 400-mesh Eastern otter trawl (12.2 m horizontal opening). The *Yankee Clipper* sampled 10-22 April, 7-15 May, 7-22 June, 9-21 July, and 8-23 August 1978. The *Commando* also sampled from 7 to 15 May, 7-22 June, 9-21 July, 8-23 August and 4-17 November 1978, and 1-20 March 1979. A try net (6.1 m horizontal opening) was deployed from the *Yankee Clipper*, and a try net and Eastern otter trawl were used from the *Commando*.

A small number of juvenile Tanner crabs ⩽ 40 mm carapace width (CW) was collected with a SCUBA-operated, qualitative sediment sweep in October 1979. The sweeps were obtained with a fine-mesh nylon net supported on a 30 x 90 cm steel frame. The net was swept across the sediment surface, penetrating approximately 7 cm.

Tanner crabs used for stomach analysis were examined by one of two methods: (1) those with carapace widths greater than 40 mm were examined semi-quantitatively (frequency-of-occurrence method) and quantitatively (wet weight), and (2) those with carapace widths 40 mm or less were examined by the frequency-of-occurrence method only. The percent frequency of occurrence is the percent of the total number of stomachs examined that contain various prey taxa. Carapace width (CW) is defined as the straight-line distance across the widest part of the carapace, excluding spines, at right angles to a line drawn from the rostrum to the medial posterior margin of the carapace. Stomachs (including the posterior portion of the esophagus) of crabs > 40 mm CW were removed on the ship and fixed in 10% buffered formalin for final identification at the Institute of Marine Science, University of Alaska, Fairbanks. Crabs ⩽ 40 mm CW were preserved whole in 10% buffered formalin, and stomachs were later removed and examined in the laboratory in Fairbanks. Crabs were categorized as belonging to one of two exoskeletal classes, following Donaldson (1980): (1) new-shell – exoskeleton hard with the dorsal side of the carapace brownish-red, scratching in ventral side limited or lacking, epiphytic growth limited or lacking, pterygostomial and branchial spines sharp, and dactyls sharp; (2) old-shell – skip-molt(s) with carapace hard and brownish, sternum and ventral side of the legs with numerous scratches and abrasions, epiphytic growth possibly present, pterygostomial and branchial spines worn and dactyls worn.

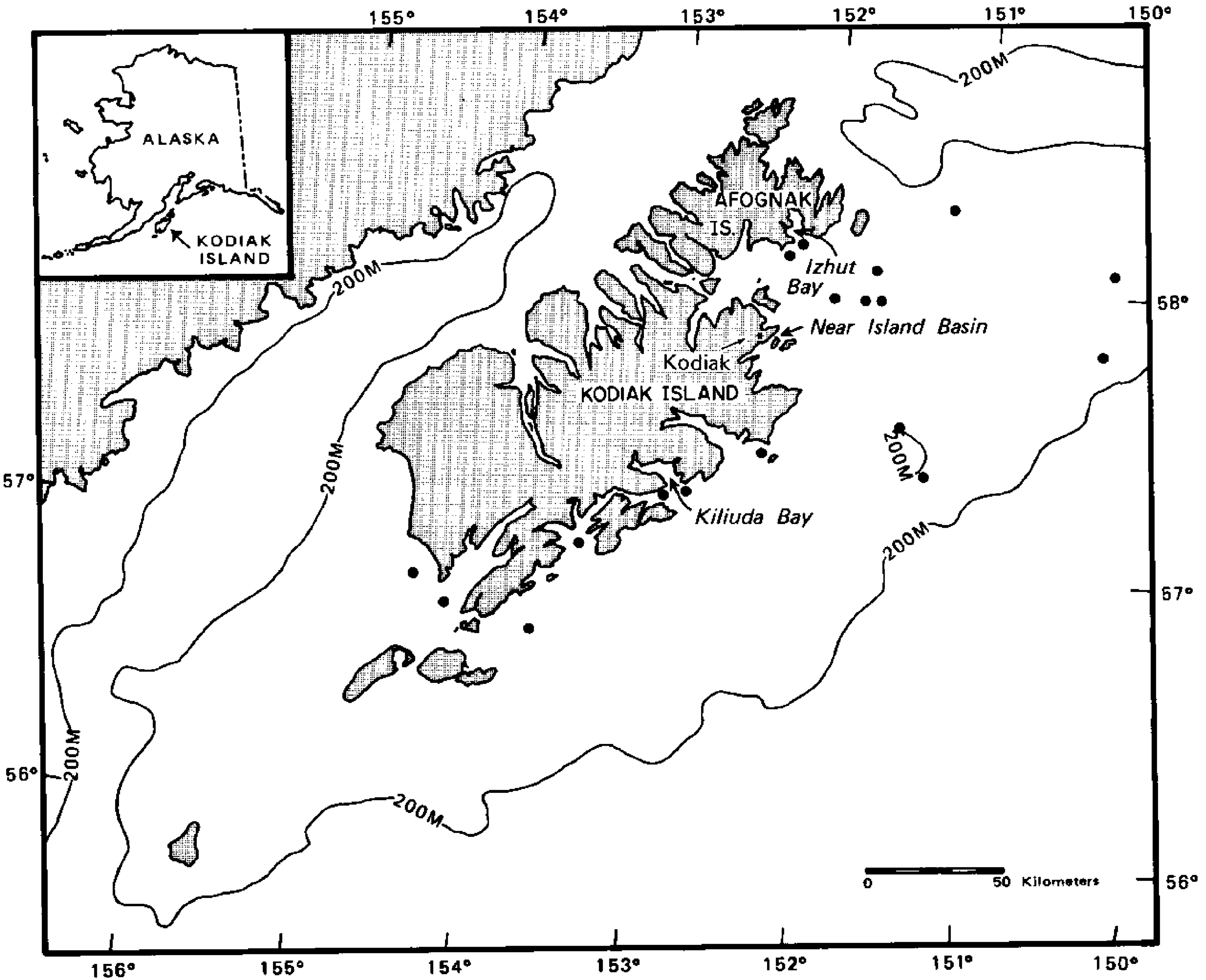

Figure 1. Locations where Tanner crabs (*Chionoecetes bairdi*) were collected for stomach analysis, 1978-1979.

Large crabs were divided into eight size groups between 41 and 192 mm CW; the crabs were obtained from eight depth strata between 11 m and 197 m.

In the laboratory, stomach contents were removed and sorted by taxon. For crabs > 40 mm CW, each taxon was weighed to the nearest 0.001 g. Each taxon weight was obtained by weighing a vial with a known quantity of water and then weighing the vial and water plus the taxon; the difference between the two weights was recorded as the taxon weight. All items in stomachs, including skeletal material and sediment, were tabulated as food. Bivalve mollusk prey items consisted of approximately 50% shell material and 50% soft parts.

Since the weights of crab stomach contents were not normally distributed, the median rather than the mean weight value was used as the measure of central tendency in all statistical analyses. The Wilcoxon Signed Ranks Test (Zar 1974) was used to test differences in feeding between sexes. The Kruskal-Wallis Test (Zar 1974) was used to determine differences in feeding between sampling areas, periods, depths, and crab sizes and classes, using rank sum values of food weights. Food weight values used in the analysis of the quantity of food by crab sizes were first converted to relative values in order to relate the weight of the food to the weight of the crab from which the food was taken. Converted values were obtained by dividing the weight of the stomach contents by the wet weight of the crab. A probability value was calculated in each Kruskal-Wallis Test, and, if it was found to be less than 0.05, a procedure was employed to make multiple comparisons using rank sums (Dunn, 1964) to decide which populations differed. The Mann-Whitney Test (Zar 1974) was used to test feeding differences between crab exoskeleton classes.

RESULTS

Food of Crabs > 40 mm CW

Stomach contents of 1,025 Tanner crabs > 40 mm CW from three areas and nine sampling periods were examined quantitatively; 857 (84%) contained food. There was no significant difference in the quantity of food consumed between males and females (Wilcoxon Rank Sum Test: $P = 0.220$; Zar 1974); thus, food data for both sexes were combined.

Prey items belonged to seven groups: Annelida (Polychaeta), Mollusca, Arthropoda (Crustacea), Echiura, Echinodermata, Chordata (Osteichthyes), and plant material (Table 1). Arthropods dominated by food weight; Osteichthyes (fishes) and mollusks were the second- and third-most important food groups,

Table 1. Important food items in the stomachs of 857 *Chionoecetes bairdi* (> 40 mm CW) collected from the Kodiak Island area, 1978-79.

Food Items	Percent Food Wet Weight	Percent Frequency of Occurrence
Annelida (total)	3.0	21.7
Capitellidae	0.4	1.4
Nephtyidae	1.1	1.8
Other annelids	1.5	--[a]
Mollusca (total)	12.2	56.0
Bivalvia (total)	11.8	54.7
Nuculana spp.	0.7	4.1
Yoldia spp.	2.1	6.2
Nucula tenuis	0.4	7.9
Axinopsida serricata	0.9	11.6
Macoma spp.	5.6	15.2
Other bivalves	2.1	--
Gastropoda	0.4	4.7
Other mollusks	< 0.1	--
Arthropoda (total)	37.2	56.1
Isopoda	0.7	0.9
Crangonidae	0.3	0.8
Pandalidae	4.2	2.9
Other shrimps	3.9	13.3
Paguridae	2.2	2.6
Pinnixa spp.	3.8	5.1
Chionoecetes bairdi	11.5	15.8
Other crabs	6.7	8.6
Other arthropods	3.9	--
Echiura		
Echiura echiurus	0.4	8.5
Echinodermata (total)	< 0.1	7.1
Ophiuroidea	< 0.1	3.4
Other echinoderms	< 0.1	--
Osteichthyes	13.8	25.6
Unidentified animal material	32.7	71.4
Plant material	0.3	5.7
Unidentified material	< 0.1	14.4
Sediment	1.3	56.4

[a] Dashes indicate that the percent frequency of occurrence is unavailable.

respectively. Annelids, echiurids, echinoderms, and plant material contributed little (3.8%) to the overall food weight. Sediment occurred in 56.4% of all crabs examined, but only accounted for 1.3% of the weight (Table 1). Crustaceans and mollusks dominated in terms of frequency of occurrence; fishes and annelids followed in importance.

The crustacean food group was dominated by juvenile *Chionoecetes bairdi* (11.5% by weight and 15.8% by frequency of occurrence). Crustaceans of lesser importance were isopods, crangonid and pandalid shrimps, and pagurid and pinnotherid crabs. Fishes accounted for 13.8% of the total food wet weight and occurred in 25.6% of the crabs containing food.

Molluskan prey was dominated (by weight) by the bivalves *Macoma* spp. and *Yoldia* spp. Mollusks of lesser importance were the bivalves *Nuculana* spp., *Nucula tenuis*, and *Axinopsida serricata*, and unidentified gastropods.

The mean amount of prey in stomachs of feeding individuals was 0.81 g/crab.

Sampling Period, Area, and Depth

The effect of the sampling period on the weight of food consumed by Tanner crabs was tested. A significant difference ($P < 0.05$) in the amount of food consumed among months was found (Table 2). The six pairs that were different revealed that crabs from March, May, June, and July 1978 contained less food than did crabs from November 1978 and February 1979.

The weight of food in crabs was significantly different ($P < 0.05$) among the three sampling areas (Table 3). Crabs from Izhut Bay contained less food than did crabs from the Kodiak Shelf stations.

The amount of food consumed by crabs at different depths between 11 m and 197 m was significantly different ($P < 0.05$); crabs at 26-50 m contained less food than did crabs from 126-150 m (Table 4).

Size and Class of Crabs

Most of the eight crab size groups each contained from 9% to 21% of all crabs examined; however, the largest size group (180-192 mm CW) contained only 1% of all crabs. The converted weight of food consumed was significantly different ($P < 0.05$) among crab size groups. Eight pairs of groups were different, and all of these pairs were crabs < 100 mm CW versus crabs > 100 mm CW (Table 5). The smaller crabs contained significantly more ($P < 0.05$) food than did large crabs.

Table 2. Kruskal-Wallis one-way ANOVA for *Chionoecetes bairdi* food weight and sampling period.

Sampling Period	Stomachs w/Food No.	%	Rank Sum[a] of Contents	Average Rank Sum of Contents
Mar 1978	66	75	21826.5	330.7
Apr 1978	25	89	9453.0	378.1
May 1978	35	78	12324.0	352.1
Jun 1978	101	75	34636.5	342.9
Jul 1978	236	83	99637.5	422.2
Aug 1978	40	87	18206.5	455.2
Nov 1978	73	90	34956.5	478.8
Feb 1979	191	91	97302.0	509.4
Mar 1979	90	84	39310.5	436.8

Pairs Significantly[b] Different ($P<0.05$) Stomachs w/Food
Mar 1978 < Nov 1978
Mar 1978 < Feb 1979
May 1978 < Feb 1979
Jun 1978 < Nov 1978
Jun 1978 < Feb 1979
Jul 1978 < Feb 1979

[a] Calculated test statistic = 50.96. Calculated P-value ∿ 0 assuming a χ^2 distribution with 8 d.f.

[b] Multiple comparison test (Dunn 1964).

Table 3. Kruskal-Wallis one-way ANOVA for *Chionoecetes bairdi* food weight and sampling area.

Sampling Area	Stomachs w/Food No.	%	Rank Sum[a] of Contents	Average Rank Sum of Contents
Izhut Bay	347	83	138629.5	399.5
Kiliuda Bay	117	82	49171.0	420.3
Kodiak Shelf	393	84	179852.5	457.6

Pairs Significantly[b] Different ($P<0.05$)

Stomachs w/Food

Izhut Bay < Kodiak Shelf

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[a] Calculated test statistic = 10.34. Calculated P-value = 0.005 assuming a χ^2 distribution with 2 d.f.

[b] Multiple comparison test (Dunn 1964).

Table 4. Kruskal-Wallis one-way ANOVA for *Chionoecetes bairdi* food weight and depth.

Depth (m)	Stomachs w/Food No.	%	Rank Sum[a] of Contents	Average Rank Sum of Contents
11- 25	31	89	11602.5	374.3
26- 50	107	88	39181.0	366.2
51- 75	159	77	71473.5	449.5
76-100	199	82	85983.5	432.1
101-125	65	83	28949.5	445.4
126-150	98	92	47089.5	480.5
151-175	91	89	37838.5	415.8
176-197	107	80	45535.0	425.6

Pairs Significantly[b] Different ($P<0.05$)

Stomachs w/Food

26-50 < 126-150

[a] Calculated test statistic = 14.35. Calculated P-value = 0.04 assuming a χ^2 distribution with 7 d.f.

[b] Multiple comparison test (Dunn 1964).

Table 5. Kruskal-Wallis one-way ANOVA for *Chionoecetes bairdi* converted food weight and crab size groups.

Carapace Width (mm)	Stomachs w/Food No.	Stomachs w/Food %	Rank Sum[a] of Contents	Average Rank Sum of Contents
41- 59	112	90	60580.8	540.9
60- 79	79	90	40977.3	518.7
80- 99	103	91	49131.0	477.0
100-119	102	78	45196.2	443.1
120-139	180	83	65322.0	362.9
140-159	174	79	65911.2	378.8
160-179	101	81	39056.7	386.7
180-192	6	75	1450.2	241.7

Pairs Significantly[b] Different ($P<0.05$)

Stomachs w/Food

41-59 > 120-139

41-59 > 140-159

41-59 > 160-179

60-79 > 120-139

60-79 > 140-159

60-79 > 160-179

80-99 > 120-139

80-99 > 140-159

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[a] Calculated test statistic = 63.83. Calculated P-value $\sim$ 0 assuming a χ^2 distribution with 7 d.f.

[b] Multiple comparison test (Dunn 1964).

New-shell crabs consumed a significantly greater ($P < 0.05$) amount of food than did old-shell crabs (Mann-Whitney Test: Zar 1974; Table 6).

Food of Crabs ≤ 40 mm CW

Stomach contents of 475 Tanner crabs ≤ 40 mm CW from three areas and eight sampling periods were examined by the frequency-of-occurrence method of analysis; 449 (95%) contained food. Mollusks were important food items among these small crabs (Table 7). Unidentified bivalves and the small clams *Axinopsida serricata* and *Nucula tenuis* were most frequently found in crabs from Izhut and Kiliuda Bay. Other important foods in these two bays were fishes, decapod crustaceans, and polychaetes, in decreasing order of importance. Unidentified bivalves, *A. serricata*, the small snail *Lacuna variegata*, amphipods, and fishes frequently occurred in Near Island Basin crabs. Sediment was common in stomachs from all three areas.

DISCUSSION

Virtually all previous food data on *Chionoecetes* spp. are based on the frequency-of-occurrence method, a technique that assesses feeding trends but often fails to give an accurate interpretation of food dependencies. Food items with a high (or low) percent frequency of occurrence do not necessarily equate with a high (or low) percent food weight. For example, in the present study, annelids occurred in 21.7% of crabs > 40 mm CW, but only accounted for 3.0% of the food wet weight. Similarly, sediment occurred in 56.4% of the large crabs, but only accounted for 1.3% of the food wet weight (Table 1).

Although data derived from different methods of food analysis are not typically comparable, some similarities in the two types of analyses in the present study were apparent. When the dominant food items were ranked from highest to lowest percent by weight and frequency of occurrence, the highest ranked items in both analyses were generally similar. For example, five of the six main food items grouped by percent frequency of occurrence were the same items as the five main prey grouped by percent food wet weight (see Table 1). This similarity between the dominant prey by percent food wet weight and percent frequency of occurrence was also apparent for king crabs examined from Kodiak Island waters (Jewett and Feder 1982).

The major food groups (based on weight data) in the present study for *C. bairdi* are similar to those of *C. opilio*

Table 6. Mann-Whitney one-way ANOVA for *Chionoecetes bairdi* food weight and crab exoskeleton class.

Exoskeleton Class	Stomachs w/Food		Rank Sum[a] of Contents	Average Rank Sum of Contents
	No.	%		
New-shell	555	86	246652.5	444.4
Old-shell	302	79	121000.5	400.6

[a] Calculated test statistic = 92362. Calculated P-value = 0.006 assuming normal distribution (one-tail). Thus, new-shell crabs contain significantly more food than old-shell crabs.

Table 7. Important food items in the stomachs of 449 *Chionoecetes bairdi* (≤ 40 mm CW) collected from the Kodiak Island area, 1978-79. Food items are at the most practical level of identification. Items are listed in order of decreasing percent frequency of occurrence from all areas combined.

	Percent Frequency of Occurrence			
Food Items	All Areas N = 449	Izhut Bay N = 190	Kiliuda Bay N = 210	Near Is. Basin N = 49
Sediment	60.4	63.7	53.3	77.6
Unid. animal remains	52.3	58.4	36.2	98.0
Axinopsida serricata	35.6	36.8	29.5	57.1
Bivalvia	34.3	38.9	24.3	59.2
Osteichthyes	21.4	32.6	12.4	16.3
Foraminifera	16.9	17.9	18.1	8.2
Nucula tenuis	15.8	15.3	20.0	-[a]
Polychaeta	14.5	19.5	12.4	4.1
Decapoda	12.7	21.6	7.6	-
Crustacea	8.7	11.6	8.1	-
Echinodermata	7.1	8.4	6.7	4.1
Amphipoda	7.1	7.4	1.4	30.6
Lacuna variegata	6.7	-	-	61.2
Unid. crab	6.5	2.6	11.4	-
Ophiuroidea	5.3	7.9	3.8	2.0
Chionoecetes bairdi	4.5	5.3	3.8	4.1
Plant	4.5	3.7	6.2	-
Gastropoda	4.2	5.3	4.3	-
Nuculanidae	4.0	7.4	1.9	-
Oenopota spp.	2.0	-	-	18.4

[a] Dashes indicate that particular food was not present in crabs at that location.

from the southeastern Bering Sea reported on by Cunningham (1969). Foods of the two species of Tanner crabs were dominated by mollusks (mainly bivalves) and crustaceans (mainly brachyuran crabs).

Food studies using the frequency-of-occurrence method of analysis on *C. bairdi*, as well as other *Chionoecetes* spp., reveal similarly dominant foods or food groups (Table 8). Most studies show that bivalve mollusks, as well as crustaceans (primarily shrimps and crabs), are frequently taken by this crab genus. Other food groups that commonly occur are polychaetes, ophiuroids, and fishes. Barnacles, an important food resource for Tanner crabs in Cook Inlet (Paul et al. 1979), are rarely taken by these crabs elsewhere. The barnacles that were taken in Cook Inlet had been recently recruited on volcanic bombs following an eruption on Augustine Island in 1975 (Feder et al. 1978).

Tanner crabs, like the often co-occurring red king crab (*Paralithodes camtschatica*), migrate to shallow water to spawn in late winter and spring; however, the reproductive activity of Tanner crabs does not occur in waters as shallow as that of king crabs (Jewett and Feder 1982). The data in the present study suggests that Tanner crabs feed more to capacity during non-spawning periods (i.e., November to February) (Table 2), while outside of bays and in localized areas (Kodiak Shelf stations at 126-150 m) (Tables 3 and 4). This is in contrast to king crabs, whose tendency to feed to capacity is greater immediately after spawning, during spring and summer months (Jewett and Feder 1982). Localized areas on the Kodiak Shelf (126-150 m) are also important to king crabs for food consumption. Therefore, Tanner and king crabs partition the same feeding grounds by exploiting these grounds at different periods.

When *C. bairdi* was examined by size groups in the present study, it was apparent that small crabs (41-99 mm CW) generally fed more to capacity than did larger crabs (120-179 mm CW) (Table 5). Similarly, in the southeastern Bering Sea, small *C. bairdi* (24-60 mm CW) and *C. opilio* (23-44 mm CW) fed more intensively than did large *C. bairdi* (⩾ 61 mm CW) and *C. opilio* (⩾ 45 mm CW), respectively (Tarverdieva 1976). One might expect to find that small crabs feed more intensively than do large crabs, since the molting frequency among small crabs is greater, requiring a greater energy demand. Small king crabs also feed more to capacity than do large crabs (Logvinovich 1945; Cunningham 1969; Jewett and Feder 1982).

Food consumption among new-shell crabs is greater than among old-shell individuals, presumably because the major period of tissue growth occurs immediately after molting and

Table 8. Foods, listed in order of relative importance, found in the stomachs of *Chionoecetes* spp. from various regions. All data in references cited are based on frequency of occurrence of food items.

	Chionoecetes bairdi				
Relative Importance	Present[a] Study	Ugak Bay[b] Alitak Bay	Prince[c] William Sound	Cook[d] Inlet	S.E. Bering[e] Sea
1	Fishes	Bivalves	Polychaetes	*Macoma* spp.	Polychaetes
2	Polychaetes	Shrimps	Ophiuroids	Pagurids	Bivalves
3	*Axinopsida sericata*	Polychaetes	Fishes	*Balanus* spp.	Ophiuroids
4	*Chionoecetes bairdi*	Nuculanids	*Nucula tenuis*	Bivalves	Amphipods
5	Shrimps	Brachyurans	-	Crangonids	Gastropods
6	*Nucula tenuis*	Fishes	-	Polychaetes	Decapods

	Chionoecetes opilio				
Relative Importance	S.E. Bering[e] Sea	S.E. Bering[f] Sea	S.E. Bering[g] Sea	Norton Sound[h] Chukchi Sea	Gulf of[i] St. Lawrence
1	Polychaetes	Polychaetes	Brachyurans	*Nucula tenuis*	*Yoldia* sp.
2	Bivalves	Ophiuroids	Bivalves	Crustaceans	Polychaetes
3	Ophiuroids	Bivalves	Ophiuroids	Polychaetes	Ophiuroids
4	Amphipods	Fishes	Polychaetes	Amphipods	Amphipods
5	Decapods	Amphipods	Algae	Fishes	Fishes
6	Gastropods	Decapods	-	Ophiuroids	Unid. eggs

Table 8. Continued

Chionoecetes opilio elongatus Relative Importance	 Sea of[j] Japan
1	Ophiuroides
2	*C. o. elongatus*
3	*Portlandia pygmaea*
4	Bivalves
5	Gastropods
6	Shrimps

[a] Includes all crabs.
[b] Feder and Jewett 1977.
[c] Feder and Hoberg 1981.
[d] Paul et al. 1979.
[e] Tarverdieva 1976.
[f] Feder and Jewett 1980.
[g] Cunningham 1969.
[h] Feder and Jewett 1978.
[i] Powles 1968.
[j] Yasuda 1967.

because metabolic reserves are accumulating in preparation for the subsequent molt (Lockwood 1967). Some ecdysis classes of new-shell king crabs also consume significantly more food than do old-shell crabs (Jewett and Feder 1982).

The crustaceans that dominated the prey of Tanner crabs in the present study as well as some other studies were mainly pandalid and crangonid shrimps (Yasuda 1967; Feder and Jewett 1977, 1978; Paul et al. 1979) and young Tanner crabs. Tanner crabs, unlike king crabs, are cannibalistic (Yasuda 1967; Powles 1968; Feder and Jewett 1977; Paul et al. 1979).

Bivalves, and protobranchs in particular, are important prey for *Chionoecetes* in most areas where this crab genus occurs (Table 8). In Alaskan waters, many of the small, relatively soft-shell genera (e.g., *Nucula*, *Nuculana*, *Yoldia*, *Macoma*, and *Axinopsida*) taken by Tanner crabs are also prey of king crabs, although king crabs also consume small to large specimens of hard-shell bivalve genera (e.g., *Clinocardium* and *Serripes*) (Feder and Jewett 1981; Jewett and Feder 1982) as well.

The importance of fishes as a prey for Tanner crabs in the present study is greater than that reported by other investigators (Table 8). Fishes presumably represent a prey of opportunity. It is probable that schooling fishes, fed upon by marine birds and mammals near the surface occasionally fall to the bottom after injury or regurgitation by these predators; the damaged or dead fishes, in turn, are utilized by the crabs (see Jewett and Feder 1982 for similar observations on king crabs).

Sediment, frequently found among Tanner crab stomach contents, is presumably ingested incidentally while taking target prey items (Tarverdieva 1976; Feder and Jewett 1977, 1978, 1980; Paul et al. 1979), but may represent a resource of importance. Yasuda (1967) found that benthic diatoms and foraminiferans were abundant in *C. opilio elongatus* in the Sea of Japan, and postulated that these items were taken incidentally, along with food and sediment. However, Moriarty (1977) reported on the occurrence of sediment in the stomach contents of five species of penaeid shrimps, and theorized that nutritional benefit of sediment to these shrimps may be derived from a film of organic carbon, including bacteria, on sediment particles. Rice (1980) suggested that, in nutritionally-impoverished situations, accidental or deliberate ingestion of sediment by crangonid shrimps and the apparent ability of these shrimps to utilize carbon resources associated with sediment, enhances their nutritive uptake at this time. Tanner crabs, especially young ones, may benefit from ingesting sediment as is suggested for penaeid and crangonid shrimps, in addition to utilizing the diatoms and foraminiferans within the sediment.

Food groups taken by Tanner crabs ≤ 40 mm CW were similar to those taken by larger crabs (> 40 mm CW). Bivalve mollusks and decapod crustaceans predominated in both sizes of crabs, but the tiny bivalves *Axinopsida serricata* and *Nucula tenuis* were most frequently utilized by small crabs. Pagurid crabs, barnacles (*Balanus* spp.), and the clam *Spisula polynyma* were the most common prey of Tanner crabs ≤ 50 mm CW in Cook Inlet, Alaska (Paul et al. 1979).

The present study identified the dominant prey taken by *C. bairdi* near Kodiak Island. Also delineated were the sampling periods, areas, depths, size classes, and crab exoskeleton classes that were most important in terms of quantity of stomach contents. However, additional data are needed to clarify the feeding biology of this dominant crab in Alaskan waters. Some parameters that need to be addressed include: (1) the feeding frequency of the crab; (2) the time required for passage of food through the digestive tract; (3) the caloric content of prey items; (4) the importance of calcareous foods before and after ecdysis; and (5) the interaction of the Tanner crab with its competitors. Furthermore, it is important to quantify the availability and productivity of the food resources utilized by Tanner crabs in regions that traditionally produce large commercial quantities of crabs. The above information will contribute to a better understanding of the feeding dynamics of Tanner crabs in Alaskan waters.

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ABSTRACT

Stomach contents of 1,025 Tanner crabs (*Chionoecetes bairdi*) > 40 mm carapace width (CW) from three areas and nine sampling periods were examined quantitatively near Kodiak Island, Alaska; 857 (84%) of the crabs contained food. Arthropods (mainly juvenile *C. bairdi*) dominated the food weight. Fishes and mollusks (mainly the bivalves *Macoma* spp. and *Yoldia* spp.) were the second- and third-most important food groups, by weight. No significant difference in quantity of food between sexes was observed; however, significant differences were apparent in quantity of food consumed from sampling periods, areas, depths, size groups, and crab exoskeleton classes. Consumption was greater during November and February, when the crabs were outside of the bays in localized deep-water (126-150 m) areas on the Kodiak Shelf. Small Tanner crabs (40-99 mm CW) generally contained more food than did large crabs (100-179 mm CW), and new-shell crabs consumed a greater amount of food than did old-shell crabs.

Stomach contents of an additional 475 Tanner crabs ≤ 40 mm CW were examined near Kodiak Island by the frequency-of-occurrence method of analysis; 449 (95%) contained food. Mollusks (mainly the bivalves *Axinopsida serricata* and *Nucula tenuis*), fishes, decapod crustaceans, and polychaetes were found, in decreasing frequency of occurrence. Sediment was also frequently found.

Food of the Snow Crab (*Chionoecetes Opilio*) From the Southwestern Part of the Gulf of St. Lawrence (Chaleur Bay Area)

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INTRODUCTION

The feeding habits of *Chionoecetes opilio* have been the subject of a few studies: Yasuda (1967), in Japan, Tarverdieva (1976), in Bering Sea, Powles (1968) and Miller and O'Keefe (1981) in the Gulf of St.Lawrence. None gives informations either on the daily rythm of feeding or on the relationship between diet and benthic fauna. The purpose of the present work is to give more informations on those last points and to look at the predation of this crab on the benthic invertebrates in the entrance of the Chaleur Bay (Fig. 1).

METHODS

Observations were made on 480 crabs of both sexes caught with a small beam-trawl in May 1980 at depths increasing from 75 m on muddy gravels, to 120 m, on mud.

Shell-widths were found to range between 45 to 65 mm for the females and 35 to 110 mm for the males (Fig. 2). The stomachs were removed immediatly after each haul and preserved separatly in buffered formalin solution. Prey organisms were identified to the lowest possible taxon. Stomach content was expressed in terms of fresh weight. An index of fullness was calculated following Tarverdieva's method (1978) in referring the overall mass of group

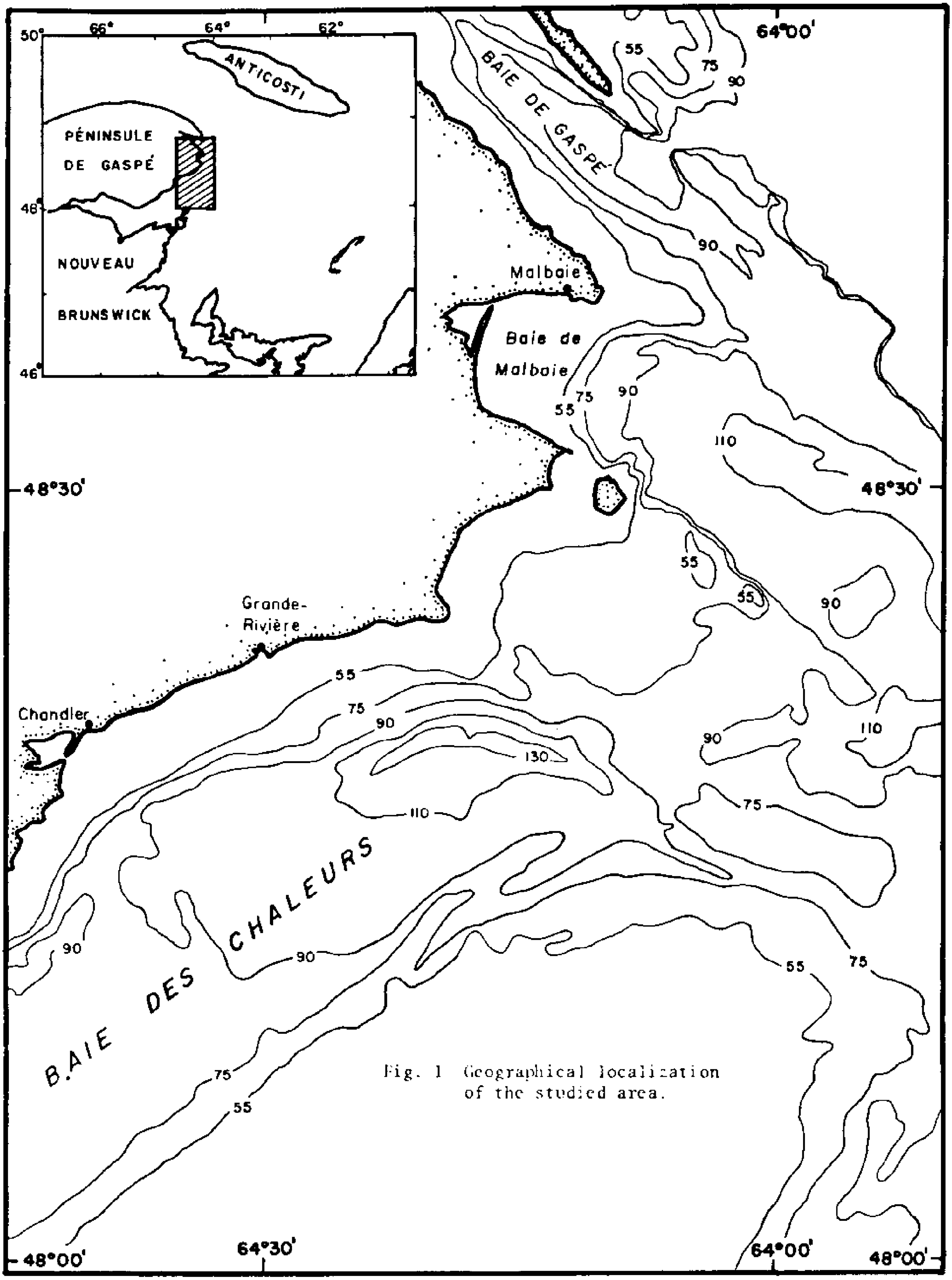

Fig. 1 Geographical localization of the studied area.

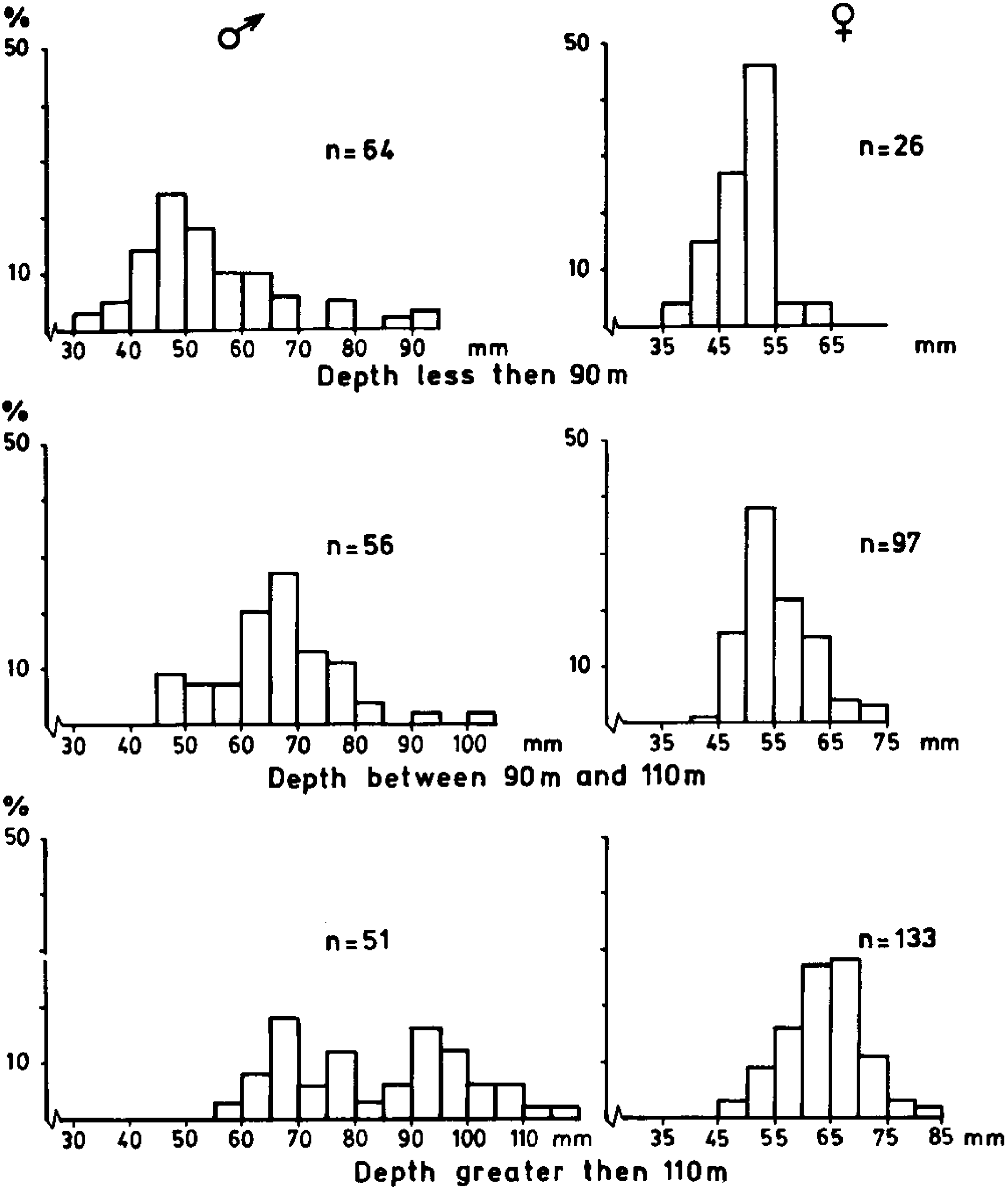

Fig. 2 Size frequency distributions of sampled crabs.

stomach contents to the overall mass of the crabs themselves and multiplied by 10,000. Correlation between hour of collection and index of fullness gives an indication of the daily rythm of feeding, which permitted to calculate the daily ration. We determined the speed of digestion from the decrease in index of fullness between sampling time (Tarverdieva 1978) and calculated an average quantity of food digested per hour. Daily ration is then equal to this value multiplied by 24 hours assuming a constant evacuation rate (Nieland 1980).

Percentage of total food and frequency of occurrence of each prey were calculated for the overall results and for three depth intervals of collection. In this latter case, frequencies of occurrence were standardized as they add to 100 to make comparisons easier.

Even if occurrence gives already a good estimate of predation behaviour, a food type preference was calculated using the electivity index of Ivlev (1961):

$$E = r_i/P_i$$

Where r_i is the proportion of the prey i in the diet and P_i the proportion of the same prey in the environment, deducted from benthic fauna study (Desrosiers et al. same symposium).

RESULTS

In the studied area, the crabs appeared to feed throughout the day but the main activity was nocturnal (Table 1). At midnight 100% of the crabs have eated and the index of fullness was the highest with 19.1^{o}/ooo. A second peak was noticed just before sunset (1700 hrs) with 91% of stomachs containing at least a prey and a fullness index equal to 3.4^{o}/ooo. At sunrise (500 hrs) observations are conflictive as 100% of crabs contained a prey while fullness index was only 0.5^{o}/ooo. This can be explained either by an advanced digestion or by a beginning of feeding behaviour: in both cases it means a feeding activity near that hour. A diurnal activity remains possible: at 1100 hrs 80% of observed crabs have eaten and fullness index was 1.3^{o}/ooo.

The evacuation rate varied from 0.8^{o}/ooo per hour, between 1700 hrs and 1900 hrs, to 8.7^{o}/ooo per hour between 2400 hrs and 200 hrs when index of feeding was the highest. The average is then equal to 2.8^{o}/ooo per hour wich means a daily ration equal to 0.7% of the wet weight.

The diet is heterogeneous, but dominated by Crustacea which represent 34% of the preys and occur in 64% of the stomachs (Table 2). They belong mainly to Decapoda, Amphipoda and Cumacea. Some shell fragments may indicate that cannibalism is possible but not certain. Mollusca represent 21% of the stomach contents and

Table 1 Daily feeding rythm of *C. opilio* in the entrance of the Chaleur Bay.

Hour	Total number	Number of empty stomachs	Index of fullness $^{o}/ooo$
16	32	6	0.7
17	108	10	3.4
18	132	8	2.6
19	37	5	1.8
20	21	15	0
21	13	2	2.4
23	7	0	6.8
24	22	0	19.1
2	28	1	1.7
4	22	7	2.4
5	28	0	0.5
10	15	5	0.2
11	15	3	1.3
	480	62	

Table 2 General results on the food of *C. opilio* in the entrance of the Chaleur Bay

Stomach content	P%	F%
Crustacea		
unidentified, shell fragments	28.0	54.8
Decapoda: Hippolitidae, Mysidacea, Crangonidae	3.1	5.5
Amphipoda: Melitidae, Ampeliscidae *Protomedia sp., Pontoporea femorata, Aceroïdes latipes*	1.1	1.9
Cumacea: Diastylidae, Leuconidae (*Leucon sp., Eudorella* sp.)	1.8	3.3
Total crustacea	34.0	63.8
Polychaeta		
unidentified	7.4	14.4
Tubes fragments	2.3	4.5
Ampharetidae, Eunicidae, Chloremidae *Lumbrinereis fragilis, Maldane sarsi, Melinna sp., Nicomache lumbricalis, Pectinaria granulata, Pherusa plumosa*	2.0	3.7
Total polychaeta	11.7	22.6
Mollusca		
unidentified, calcareous shell fragments	8.5	16.5
Pelecypoda: *Macoma calcarea, Yoldia sp., Nucula sp.*	3.5	7.1
Gastropoda: *Solariella sp., Lora sp.,* operculae	8.7	15.5
Total mollusca	20.7	31.1
Echinodermata		
Ophiura sp., mainly	16.5	32.2
Fish	2.9	5.7
Vegetal fragments	5.6	10.8
Eggs	2.4	4.7
Unidentified organic fragments	6.3	12.2

are found in 31% of the crabs; Gastropoda are the most important prey in this group. Echinodermata form 17% of the food and occur in 32% of the observed stomachs; they are represented mainly by *Ophiura sp.* (*O. sarsi*, probably), pieces from Echinoïdea are also found. Polychaeta is the fourth prey in importance with 12% of the total food and 23% as frequency of occurrence.

This general pattern is modified by depth of sampling (Table 3). In percentage of total number of preys, Crustacea dominate at every depth intervals. Mollusca represent the second part of the food to the depth of 110 m but on deeper bottom they are supplanted by Echinodermata. The largest index of occurrence is represented by Crustacea and Mollusca down to the depth of 110 m. Below that depth they are replaced by Echinodermata. Polychaeta are always the less represented prey. Ivlev's electivity index gives a different pattern. At every depth, Echinodermata are the preferential prey with very high values of this index. Mollusca represent the second prefered food, especially on deeper bottoms. Crustacea show an index equal to unity, or close. Electivity index for Polychaeta is very close to zero at every depth.

DISCUSSION

The daily rythm of feeding of *C. opilio* is very similar to the rythm observed for *Paralithodes camtschatica* by Tarverdieva

Table 3 Repartition of the preys following depth of sampling.

D = average density (m^{-2}) of the taxon in the environment
P = percentage of total food
F = frequency of occurrence (%)
I = Ivlev's index of electivity

	< 90 m				90 - 110 m				≥ 110 m			
	D	P	F	I	D	P	F	I	D	P	F	I
Crustacea	444	45	46	1	170	36	38	2	171	43	31	1
Polychaeta	650	10	10	0	606	16	18	0	251	12	15	0
Mollusca	193	28	27	2	55	31	26	5	9	18	20	20
Echinodermata	18	17	17	12	13	17	18	11	3	27	34	34
No. of stomachs	83				152				183			

(1978). The main feeding activity is observed at midnight which confirms general observations on the species (Brunel 1960). The calculated daily ration (0.7% of the body weight) is higher than the one recorded for Kamchatka crab, 0.3% (Tarverdieva 1978). Since the calculation is based on few measurements and since seasonnal and life cycle variations were not taken in account, the ration of *C. opilio* must be considered as an approximation.

The observed diet confirms the omnivorous character of snow-crab as noticed by several workers (Adams 1979). The predominance of Ophiuroïdea in the diet of crabs caught on deep bottoms corresponds to the observations of Yasuda (1967) in Japan. In Newfoundland, at 200 m depth, polychaetes, sea-stars and clams represented the most frequent preys (Miller and O'Keefe 1981). In the Gulf of St.Lawrence, Powles (1968) found the highest index of occurrence for bivalves. Tarverdieva (1976), in Bering sea, observed that the diet was dominated by polychaetes, followed by Crustacea, Mollusca and Echinodermata.

Changes of food with depth follow the modifications of benthic fauna and structure of crab population (Desrosiers et al. same symposium). Upper levels correspond to the richest area which supports the maximum of abundance of young crabs. Adult crabs are found in deeper depth caracterized by poorer benthic communities where the lowest abundance of available preys is compensated by the greater mobility of the predators. Similar changes of food following crab size was observed by Tarverdieva (1976). It is also possible that cannibalism, noticed by Powles (1968), limits the abundance of young crabs on the deep muddy bottoms.

All calculated indices show that it is not the most abundant prey which is consumed in priority. It appears that *C. opilio* is an opportunistic feeder mainly on species living on or at small depth in the sediment and presenting reduced mobility. This strategy is well demonstrated by the frequencies of occurrence of Echinodermata and Crustacea. Both taxa are present at every depth, but, on shallow bottoms, Crustacea are represented by numerous epibenthic species which are available at lower cost, especially for small crabs, and therefore the most represented prey. On deeper bottoms of the studied area, Crustacea are mainly represented by tubicoles Amphipoda (Ampeliscidae ...) less catchable and Ophiuroïdea become the most important prey. Even if polychaetes are very abundant in the environment, they are represented by species either burried in sediment (Maldanidae, Ampharetidae) or very mobile (Eunicidae, Chloremidae) and therefore less available for crabs.

Ivlev's index of electivity compares the food composition and the structure of the community which supports the predator. It indicates, in fact, a level of predation on species of this community. Than the effect of feeding of *C. opilio* on polychaetes is negligible while very important on echinoderms, which appear to be the prefered prey. On the other hand, Crustacea are eaten mostly by random and support a moderate predation by crabs. Molluscs remain a choisen prey, especially on deep bottoms, which may explain the dominance of this taxon in the diet observed by Powles (1968).

CONCLUSION

The results of the present work may have a limited scope as the study is restricted both in space and time. However, we can retain a certain generalization from the changes in the diet composition with increasing depth. These changes may suggest that the feeding habits of *C. opilio* may be modified during its growth, modification which could also correspond to changes in its environment as large crabs move to deeper bottoms. A second important point is the high level of predation exerced by adult crabs on preys presenting a rather low density: in this case predator-prey relationships may have a non negligible effect on exploited stock of *Chionoecetes opilio*.

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ABSTRACT

The stomachs of 480 *C. opilio* from the entrance of the Chaleur Bay were collected in May 1980. 418 contained the remains of at least one prey. Snow-crabs feed mostly in the middle of the night but feeding activity seems possible throughout the day and particularly at sunset and sunrise. Crustacea occupied on the average 34% of the stomach content, Mollusca 21%, Echinoderma 17% and Polychaeta 12%. The frequency with which these preys occurred was 64% for Crustacea, 32% for Echinoderma, 31% for Mollusca and 23% for Polychaeta. This overall pattern depended on the depth of sampling. Above 90 m Crustacea occurred most frequently, followed by Mollusca and Echinoderma. Below 110 m, the order was changed to Echinoderma, Crustacea and Mollusca. Ivlev's electivity index was highest for Echinoderma at every depth but increased from shallow to deeper bottoms. Those observations indicate an opportunistic feeding behaviour on epifauna. A depth segregation observed between mature and immature males also suggests some change of diet during the life history of the snow-crab.

Estimating the Frequency of Molting in Adult Male *C. Bairdi* in the Eastern Bering Sea

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Crabs have a steplike pattern of growth characterized by periodic molting and rapid increases in size alternating with relatively long intermolt periods without dimensional growth. Such a pattern of growth can be considered as a product of two size dependent functions. One describing the growth increment gained at each molt and the other describing the frequency of molting. For species in the genus *Chionoecetes*, molting frequency has proved to be more difficult to estimate, especially for adult males, than growth per molt. Techniques used for estimating molting frequency of juvenile *C. bairdi* (Donaldson et al 1981) and *C. opilio elongatus* (Ito 1970), which are based on the progression of modes through sequences of size frequency histograms, will rarely be effective for adult males both because modes become indistinguishable in the larger sizes and because large males may periodically defer molting, or skipmolt, for one or more years in succession.

The most promising technique for estimating molting frequency of adult males is one which utilizes permanent tags, or tags that are retained through a molt. Such tags have been used to estimate molting frequency for *Cancer pagurus* (Hancock and Edwards 1967) and *Paralithodes camtschatica* (Balsiger 1974; McCaughran and Powell 1977), both of which have a skipmolting phase similar to *Chionoecetes*. National Marine Fisheries Service (NMFS) is currently tagging both *C. bairdi* and *C. opilio* in the eastern Bering Sea, using techniques described in Fijita and Takeshita (1979), but the number of tag returns is presently insufficient to estimate molting frequency for either species.

Tagging studies can be expensive and when tagging is not feasible, alternative methods for estimating molting frequency should be considered. One possible alternative method, which I examine in this paper, utilizes an index of postmolt age known as shell condition and independent estimates of growth per molt. This method is used to estimate molting frequency for male *C. bairdi* in the eastern Bering Sea.

DATA AND METHODS OF COLLECTION

Samples of *C. bairdi* were collected annually, from 1969 to 1975, using bottom trawls on NMFS crab stock assessment surveys to the eastern Bering Sea. Sampling usually occured between May and August, but in 1969 and 1970, sampling occured between March and April. Carapace width was measured with calipers to the nearest 1 mm. Shell condition, a subjective estimate of postmolt age based on deterioration of the exoskeleton and accumulation of epifauna, was classified according to the following four point scale.

Shell condition	Assumed time since last molt	Characteristics
1	< 2 weeks	Carapace pliable, sternum light yellow or white
2	> 2 weeks < 1 year	Carapace hard, sternum light yellow or white, little wear on carapace spines or dactyla tips, little epifauna
3	> 1 year < 2 years	Carapace hard, sternum dark yellow with many brown scratches, dactyla worn and blunt, barnacles usually present
4	> 2 years	Same as shell condition 3 except that wear on spines and dactyla is more pronounced and attached barnacles are larger

Growth per molt was estimated from size frequency data using techniques discussed in Somerton (1981).

SHELL CONDITION: ASSUMPTIONS AND VALIDATION

Shell condition is a valid index of relative postmolt age only to the extent that two assumptions are met. First, the features upon which shell condition is based, that is, scratches, discoloration and amount of epifauna, must increase with time uniformly for all crabs and must be judged and scored by all personnel in a similar manner. Second, since skipmolt crabs cannot be distinguished from premolt crabs on the basis of shell condition alone, sampling must occur after the molting season is completed. Even if these two assumptions are met, however, shell condition only indicates relative, not absolute, postmolt age. For Bering Sea tanner crab, the shell conditions of adult females were used to verify the postmolt age of the various shell condition categories.

Since females cease molting at maturity, their shell condition should continue to increase with time from the puberty molt onwards. Therefore, if an identifiable cohort of females could be sampled in successive years after they mature, their observed shell conditions could be compared to their known postmolt age. The problem with this approach is that normally a cohort of females matures each year, thus it is impossible to distinguish one age cohort from the next except by using the observed shell conditions. The validation thus becomes circular and therefore invalid. In the southern part of the Bering Sea, however, *C. opilio* have infrequent recruitment and over a span of several years the adult female population may consist of a single age class.

Such a situation occured starting in 1969. In spring, 1969, 82% of the adult female *C. opilio* examined were scored as shell condition 1, indicating that nearly the entire population of adult females in the survey area consisted of a single year class which had recently matured. In fall, 1969, 90% of the adult females were correctly scored as shell condition 2. In spring, 1970, 94% of adult females were again scored as shell condition 2. Since these females had not molted for one year, shell condition 2 was an incorrect score, but if they had been sampled in summer, like all succeeding years, then it is quite likely that more females would have been scored correctly as shell condition 3. In summer, 1971, 86% of the females were correctly scored as shell condition 4. Finally, in summer, 1972, 94% of the females were again scored correctly as shell condition 4. Thus, except for the apparent misclassification of crabs in 1970 due to the early date of the cruise, shell condition was almost always scored correctly according to definition.

Although for adult females shell condition accurately reflects the postmolt age, this may not be true for males because in early summer, when most sampling in the Bering Sea has occured, essentially all female puberty molting has been completed, but male molting may still be in progress. To determine approximately when male molting occurs, the percent of large (>100 mm) male *C. bairdi* recorded as shell condition 1 was calculated by 10 day intervals over the duration of each summer cruise. Although there was considerable variability between years, the percentage of freshly molted crabs generally peaked near the end of June and the beginning of July, essentially the midpoint of the surveys. Incomplete molting confuses the interpretation of shell condition data because skipmolting crabs were not distinguished from those which would molt later in the year. Consequently, estimates of the proportion of males skipmolting based on the NMFS shell condition data overestimate the true proportions skipmolting.

DESCRIPTION OF THREE MOLTING PROBABILITY MODELS

Molting frequency, expressed as the annual probability of molting, was estimated for large (>50 mm) male tanner crab by fitting molting probability models to shell condition data. Three types of molting probability models were examined, all consider molting probability to be a function of size.

The first model considers molting to be a Bernoulli trial, where all crabs of a given size are equally likely to molt, regardless of whether they molted or skipmolted in the previous molting season. Model 1 may be expressed as:

$$M^{w+\delta w}_{t+1} = P^{w}N^{w}_{t}$$

$$S^{w}_{t+1} = (1 - P^{w})N^{w}_{t}$$

where N^{w}_{t} is the number of crabs at size w before molting, $M^{w+\delta w}_{t+1}$ is the number of newly molted crabs one growth increment larger than w, S^{w}_{t+1} is the number of skipmolt crabs at size w and P^{w} is the probability of molting at size w. This model is essentially the same as the one used by Hancock and Edwards (1967) for *C. pagurus* and by Weber and Miyahara (1962) for *P. camtschatica*.

The second model extends the first to include molting probabilities that are conditioned on past molting history (crabs which molt in one season may be more or less likely to molt in the next season than crabs which did not molt), thus the probability of molting depends upon the present shell condition as well as size. Model 2 may be expressed as:

$$M^{w+\delta w}_{t+1} = P(M^{w+\delta w}_{t+1}|M^{w}_{t})M^{w}_{t} + P(M^{w+\delta w}_{t+1}|S^{w}_{t})S^{w}_{t} + P(M^{w+\delta w}_{t+1}|SS^{w}_{t})SS^{w}_{t}$$

$$S^{w}_{t+1} = [1 - P(M^{w+\delta w}_{t+1}|M^{w}_{t})]M^{w}_{t}$$

$$SS^{w}_{t+1} = [1 - P(M^{w+\delta w}_{t+1}|S^{w}_{t})]S^{w}_{t}$$

where SS^{w}_{t} is the number of double skipmolting crabs, and all other variables are identical to Model 1. Molting probabilities are conditioned on the present shell condition, thus $P(M^{w+\delta w}_{t+1}|M^{w}_{t})$, $P(M^{w+\delta w}_{t+1}|S^{w}_{t})$, $P(M^{w+\delta w}_{t+1}|SS^{w}_{t})$ are the molting probabilities conditioned on whether a crab molted, skipmolted or double skipmolted at the last molting opportunity. To reduce the number of undetermined parameters, it was assumed that crabs do not skipmolt more than twice, thus $P(M^{w+\delta w}_{t+1}|SS^{w}_{t}) = 1$. Model 2 is similar to the models developed by Balsiger (1974) and McCaughran and Powell (1977) for *P. camtschatica*, except that the probabilities are conditioned on the molting history of one rather than two previous years.

The third model extends the second by including a parameter which accounts for differential mortality between molting and skipmolting crabs. Models 1 and 2 implicitly assume that natural mortality is the same for molting and skipmolting crabs, but, if molting crabs are exposed to an additional risk, either due to the physiological stress of molting or due to increased vulnerability to predation, or if natural mortality is size dependent (molted crabs are larger than those that did not molt), these models would underestimate the true probability of molting. Model 3 thus includes an additional, size dependent, parameter representing the probability of surviving a molt. This model may be expressed as:

$$M_{t+1}^{w+\delta w} = s^w P(M_{t+1}^{w+\delta w}|M_t^w)M_t^w + s^w P(M_{t+1}^{w+\delta w}|S_t^w)S_t^w + s^w SS_t^w$$

$$S_{t+1}^w = [1 - P(M_{t+1}^{w+\delta w}|M_t^w)]M_t^w$$

$$SS_{t+1}^w = [1 - P(M_{t+1}^{w+\delta w}|S_t^w)]S_t^w$$

where s^w is the probability of surviving a molt at a premolt size of w and all other variables and parameters are the same as Model 2.

FITTING THE MODELS TO SHELL CONDITION DATA

For all three models, the estimation of molting probabilities requires estimates of the number of crabs in each 1 mm size interval which either molted (shell condition 1 and 2), skipmolted (shell condition 3), or double skipmolted (shell condition 4) in each year. To simplify computations, the number of premolt crabs was also calculated for each 1 mm size interval in each year. Premolt crabs are molted crabs shifted backward to the size they were before molting. Since this shift requires estimates of premolt size given postmolt size, a "reverse" Hiatt plot (Somerton 1980) was developed by regressing premolt size on postmolt size. Thus, for each of five years of data (1971-1975), four size frequency arrays were constructed: 1) the number of molting crabs (M_t^w); 2) the number of skipmolting crabs (S_t^w); 3) the number of double skipmolting crabs (SS_t^w); and 4) the number of premolt crabs ($M_{t+1}^{w+\delta w}$).

For Model 1, the probability of molting in each 1 mm size interval was estimated by the proportion molting in each year, that is:

$$P_t^w = \frac{M_{t+1}^{w+\delta w}}{N_{t+1}^w} = \frac{M_{t+1}^{w+\delta w}}{M_{t+1}^{w+\delta w} + S_t^w + SS_t^w}$$

Since Model 1 probabilities are not conditioned on previous molt history, the number of crabs molting at a given size is simply equal to the number of premolt crabs in that year. Thus, an independent estimate of molting probability can be calculated for each year of data. This is not true for Models 2 and 3 where molting probabilities are conditioned on past molting history because the past molting history of molted crabs is unknown. For these models, the data for one year is used to represent the molt states (i.e. molted, skipmolted, double skipmolted) before the molting season and the data for the next succeeding year is used to represent the molt states after molting. Thus, the number of independent estimates of molting probabilities is one less than the number of years of data.

Molting probability estimates for each of the five years of data were combined by calculating the weighted average, with weights equal to the inverse of the binomial variance. Thus:

$$P^w = \frac{\sum_t W_t^w P_t^w}{\sum_t W_t^w} \qquad \text{where } W_t^w = \frac{N_t^w}{P_t^w(1 - P_t^w)}$$

where P_t^w, W_t^w and N_t^w refer to the estimated molting probability, binomial weight and number of crabs in year t and size class w. The weighted average skipmolt probabilities (1-P) are shown in Fig. 1.

For Model 2, the conditional probabilities of molting in each size class were estimated using multiple regression. The equations were first rewritten as:

$$\begin{array}{lcll}
M_2^{w+\delta w} - SS_1^w & = & P(M_{t+1}^{w+\delta w}|M_t^w)M_1^w & + \; P(M_{t+1}^{w+\delta w}|S_t^w)S_1^w \\
\vdots & & \vdots & \quad \vdots \\
M_5^{w+\delta w} - SS_4^w & = & P(M_{t+1}^{w+\delta w}|M_t^w)M_4^w & + \; P(M_{t+1}^{w+\delta w}|S_t^w)S_4^w \\
M_1^w - S_2^w & = & P(M_{t+1}^{w+\delta w}|M_t^w)M_1^w & \\
\vdots & & \vdots & \\
M_4^w - S_5^w & = & P(M_{t+1}^{w+\delta w}|M_t^w)M_4^w & \\
S_1^w - SS_2^w & = & & \quad P(M_{t+1}^{w+\delta w}|S_t^w)S_1^w \\
\vdots & & & \quad \vdots \\
S_4^w - SS_5^w & = & & \quad P(M_{t+1}^{w+\delta w}|S_t^w)S_4^w
\end{array}$$

where the subscript 1 denotes 1971, 2 denotes 1972 etc. Thus, for each 1 mm size interval there are 4 x 3 = 12 equations with two unknown parameters. In matrix form the equations may be expressed as:

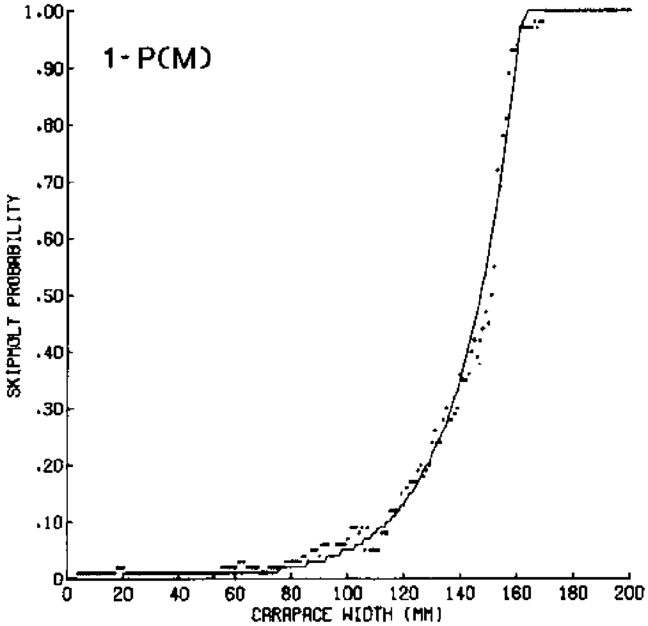

FIGURE 1

Estimated annual skipmolt probabilities for Model 1, by 1 mm increments of carapace width, and the fitted generalized logistic equation.

$$\begin{array}{ccccc} \begin{bmatrix} M_2^{w+\delta w} - SS_1^w \\ \vdots \\ S_4^w - SS_5^w \end{bmatrix} & = & \begin{bmatrix} M_1^w & S_1^w \\ & \vdots & \\ 0 & S_4^w \end{bmatrix} & & \begin{bmatrix} P(M_{t+1}^{w+\delta w} | M_t^w) \\ P(M_{t+1}^{w+\delta w} | S_t^w) \end{bmatrix} \\ Y & = & X & & B \end{array}$$

The least squares estimates for the molting probabilities within each 1 mm size interval are then (Draper and Smith 1981):

$$\hat{B} = (X'X)^{-1}X'Y$$

The estimated conditional skipmolting probabilities are shown in Fig. 2.

For Model 3, because it contains products of parameters and is therefore nonlinear, the parameters were estimated using nonlinear least squares. The survival probability, and the two conditional molting probabilities for each 1 mm size interval were thus estimated by minimizing:

$$\begin{aligned} F = \sum_t \Big\{ & (M_{t+1}^{w+\delta w} - s^w P(M_{t+1}^{w+\delta w} | M_t^w) M_t^w - s^w P(M_{t+1}^{w+\delta w} | S_t^w) S_t^w - s^w SS_t^w)^2 \\ & + (S_{t+1}^w - (1 - P(M_{t+1}^{w+\delta w} | M_t^w)) M_t^w)^2 \\ & + (SS_{t+1}^w - (1 - P(M_{t+1}^{w+\delta w} | S_t^w)) S_t^w)^2 \Big\} \end{aligned}$$

The estimated conditional skipmolting probabilities and molting mortalities are shown in Fig. 3.

A generalized logistic function (Fletcher 1975) was fit, using nonlinear regression, to the skipmolting probabilities of each model. This function can be expressed as:

$$Y = \left[1 + (n-1) e^{-m(X-x_0) n^{\frac{n}{n-1}}} \right]^{\frac{n}{1-n}}$$

where Y is skipmolt probability, or molting mortality, X is carapace size and n, m and x_0 are parameters. The estimated parameters of the logistic functions are shown for each model in Table 1.

RESULTS

For all three models, the estimated skipmolt probabilities increased with size, at an accelerating rate, from near zero

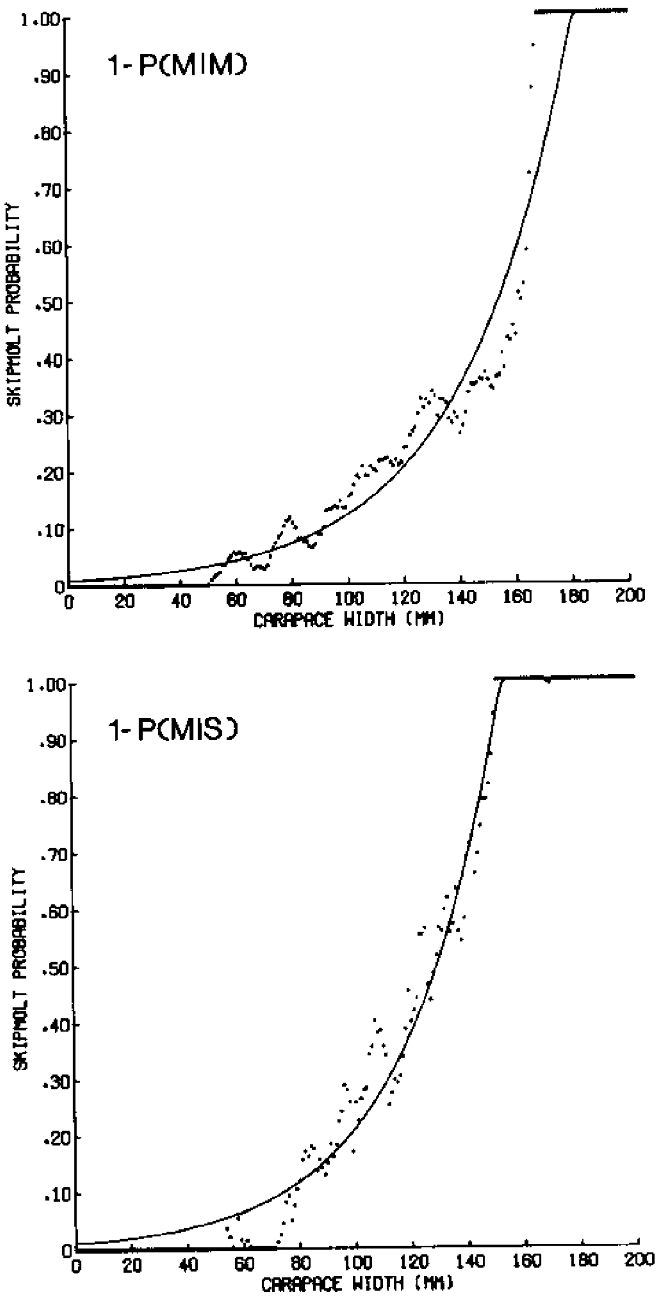

FIGURE 2

Estimated annual skipmolt probabilities for Model 2, by 1 mm increments of carapace width, and the fitted generalized logistic equations. The two figures show the skipmolt probabilities conditioned on whether a crab molted (1 - P(M|M)) or skipmolted (1 - P(M|S)) in the previous molting season.

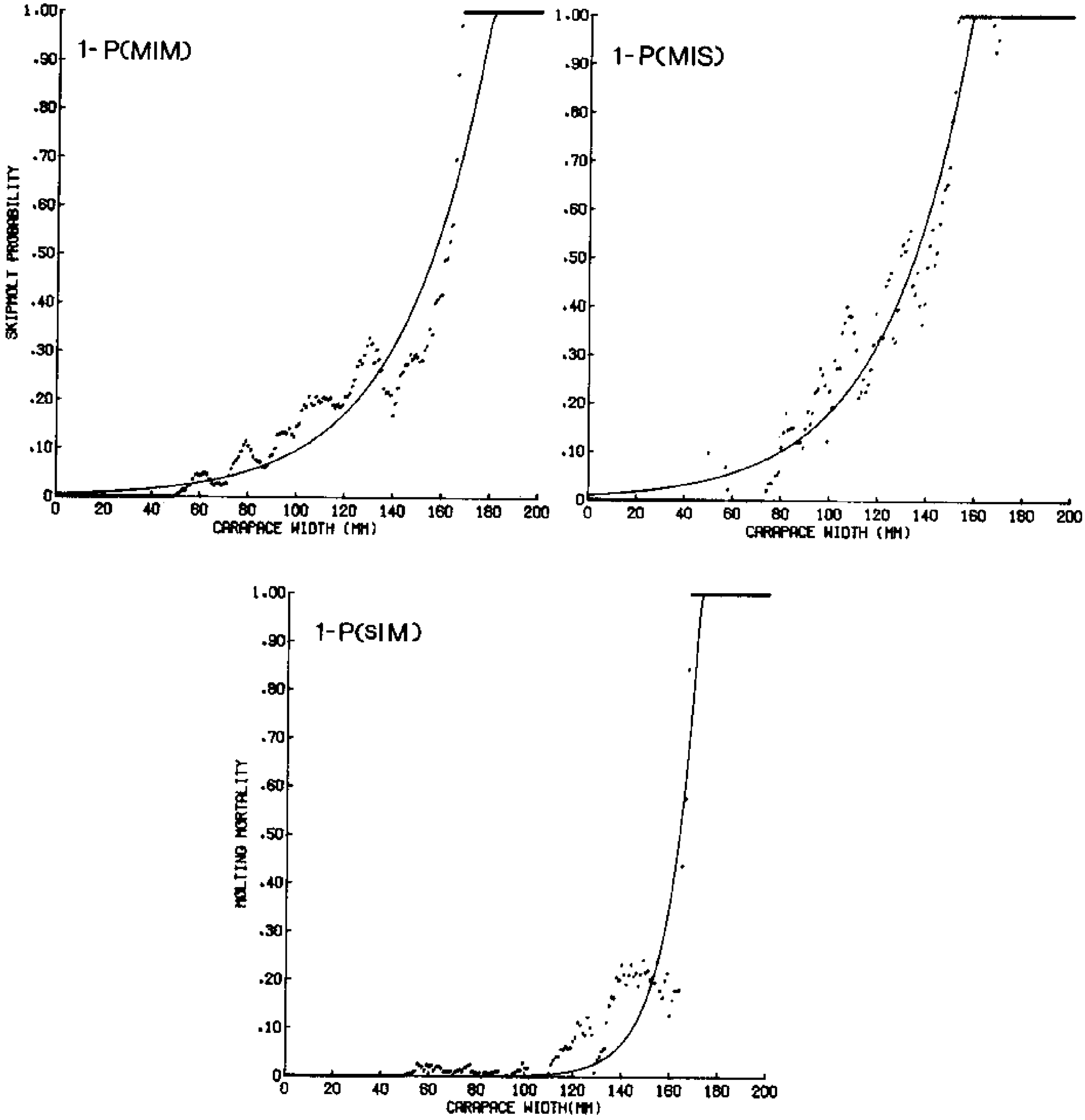

FIGURE 3

Estimated annual skipmolt and molting mortality probabilities for Model 3, by 1 mm increments of carapace width, and the fitted generalized logistic equations. The two upper figures show the skipmolt probabilities conditioned on whether a crab molted (1 - P(M|M)) or skipmolted (1 - P(M|S)) in the previous molting season. The lower figure shows the probability of dying at a molt (1 - P(s|M)).

TABLE 1

Estimated parameter values of generalized logistic equations fit to the skipmolting probabilities of each of the three proposed molting probability models.

Model	Probability	m	n	x_0
1	1 - P	.0405	23.02	158.60
2	1 - P(M|M)	.0243	79.03	178.45
	1 - P(M|S)	.0272	69.16	150.79
3	1 - P(M|M)	.0266	52.36	177.39
	1 - P(M|S)	.0279	129.48	157.12
	1 - s	.0740	35.01	170.70

at 50 mm to one at 150-160 mm. This indicates that male *C. bairdi* essentially cease molting after reaching a size of 160 mm. The primary difference between models was that skipmolt probabilities estimated by Model 2 and Model 3 were slightly higher in the small and intermediate size range (<120 mm) than those estimated by Model 1.

If tanner crab periodically skipmolt, then a crab which had skipmolted in one year should be less likely to skipmolt in the following year than a crab which had molted. For both Model 2 and Model 3, however, the probability of skipmolting was slightly greater for skipmolt crabs than for molted crabs. Although some tanner crabs may be more prone to skipmolt than others, I believe this result could be due to inadequacies in either the models or the data. Permanent tagging data, which would show the molting patterns of individual crabs, is needed to clarify this apparent inconsistency.

DISCUSSION

Although, in this study, molting probabilities were estimated from shell condition data, the three proposed molting-probability models are equally suited for estimating molting probabilities from tagging data. Tagging data provide better estimates of molting frequency than shell condition data because they are free of the subjectivity that is inherent with shell condition data. But when tagging is not feasible, a shell condition study should be considered. To be successful, however, such a study must insure that the shell condition data is collected after the molting season is completed and must include some method of calibrating shell condition scores with crabs of known postmolt age.

Regardless of the methods used to estimate the annual molting probabilities of adult males, the ultimate purpose of these estimates is almost always the prediction of age and growth. A growth simulation program (GROW) can be used for this purpose (program GROW, written in FORTRAN IV, is discussed in Somerton (1981) and is available from the author). Starting from an initial size distribution of a cohort, GROW predicts the size distribution in subsequent years based on input values of molting probabilities and growth per molt functions. The mean sizes in successive years define a growth curve relative to the age of the initial cohort. One useful feature of GROW is that the output size distributions are an approximate age-size key, which, if the methods discussed in Clark (1981) are utilized, can then be used to decompose size frequency histograms into age frequency histograms.

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ABSTRACT

The frequency of molting, expressed as the annual probability of skipmolting, was estimated for adult male *Chionoecetes bairdi* using indices of postmolt age known as shell condition. Three different molting probability models were proposed. The first model assumed that the probability of molting was independent of past molting history. The second model assumed that the probability of molting was dependent upon whether or not molting occured in the previous year. The third model extended the second by allowing differential mortality between molting and nonmolting crabs. The estimated skipmolt probabilities of all three models increase with crab size from near zero at 50 mm to one at 150-160 mm. This result indicates that male *C. bairdi* in the eastern Bering Sea rarely molt after attaining a size of 160 mm.

Edaphic Segregation Within a Population of *C. Opilio* in the Southwestern Part of the Gulf of St. Lawrence (Chaleur Bay Area)

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INTRODUCTION

In the Gulf of St.Lawrence, the distribution of *Chionoecetes opilio* is known to be related to the deep muddy bottoms (Brunel 1962, Powles 1968) even if the species may also be found on harder bottoms (Deveau et Aucoin 1966). On those sandy and gravelly sediments, Ledoyer (1975) and Miller (1975) observed concentrations of small crabs and that first author suggested a stratification within the population: the juveniles would congregate at the upper levels on gravel mixed bottoms while the adults would stay mainly at lower levels on mud. As Powles (1966) observed young crabs also on muddy bottoms, the hypothesis of segregation within the population in relation to different bottoms was not really confirmed.

The purpose of the present work is to study the repartition of the young stages of *Chionoecetes opilio* in relation with environmental factors such as deph, substratum and benthic fauna.

METHODS

The sampling was pursued during the summer of 1980 in the entrance of the Chaleur Bay (Quebec) between 64° and $64^{\circ}30'$W and $48^{\circ}10'$ and $48^{\circ}38'$N at depths varying from 70 m to 120 m (Fig. 1 and 2). The nature of the bottom were known to vary from pelitic

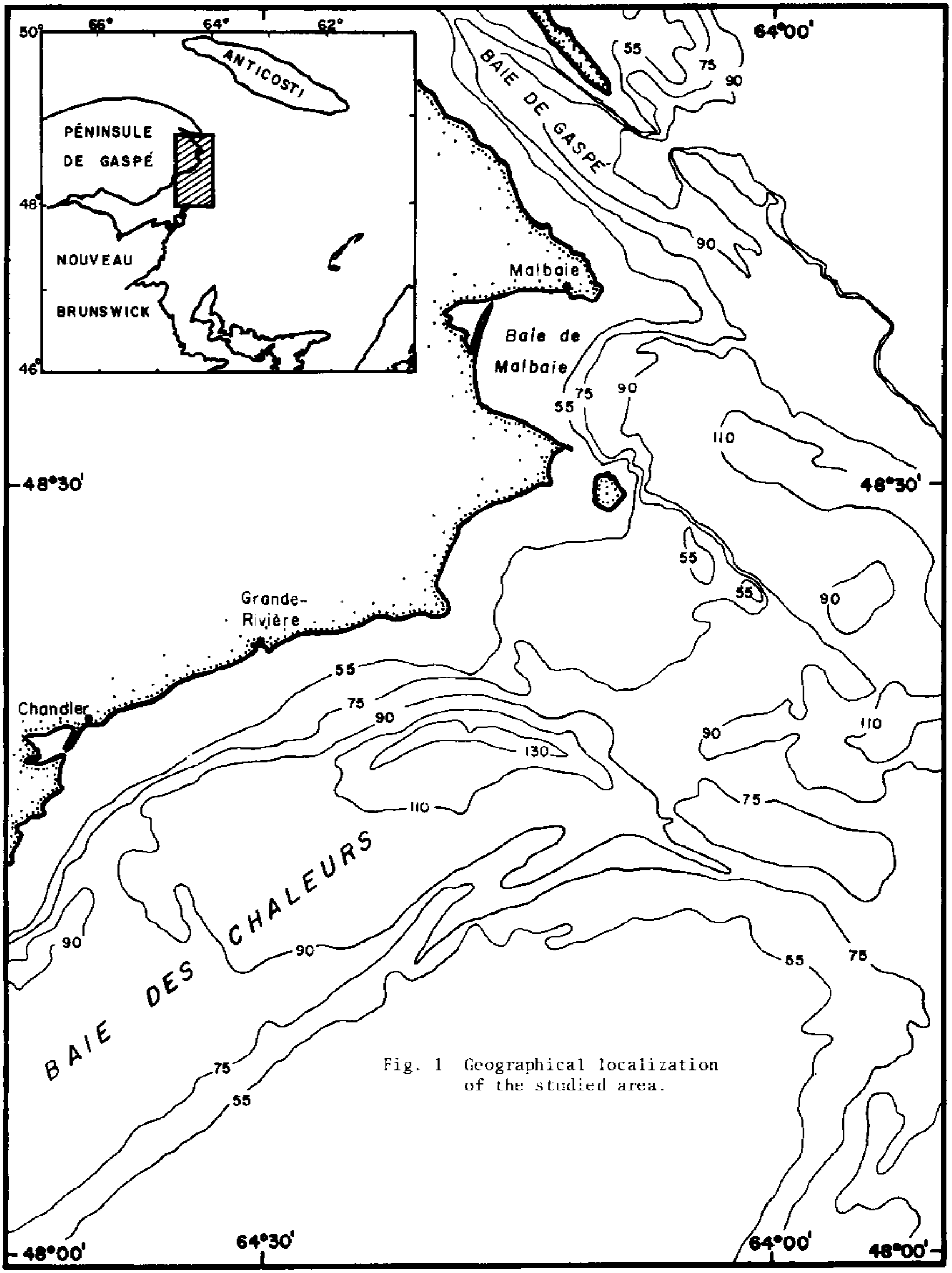

Fig. 1 Geographical localization of the studied area.

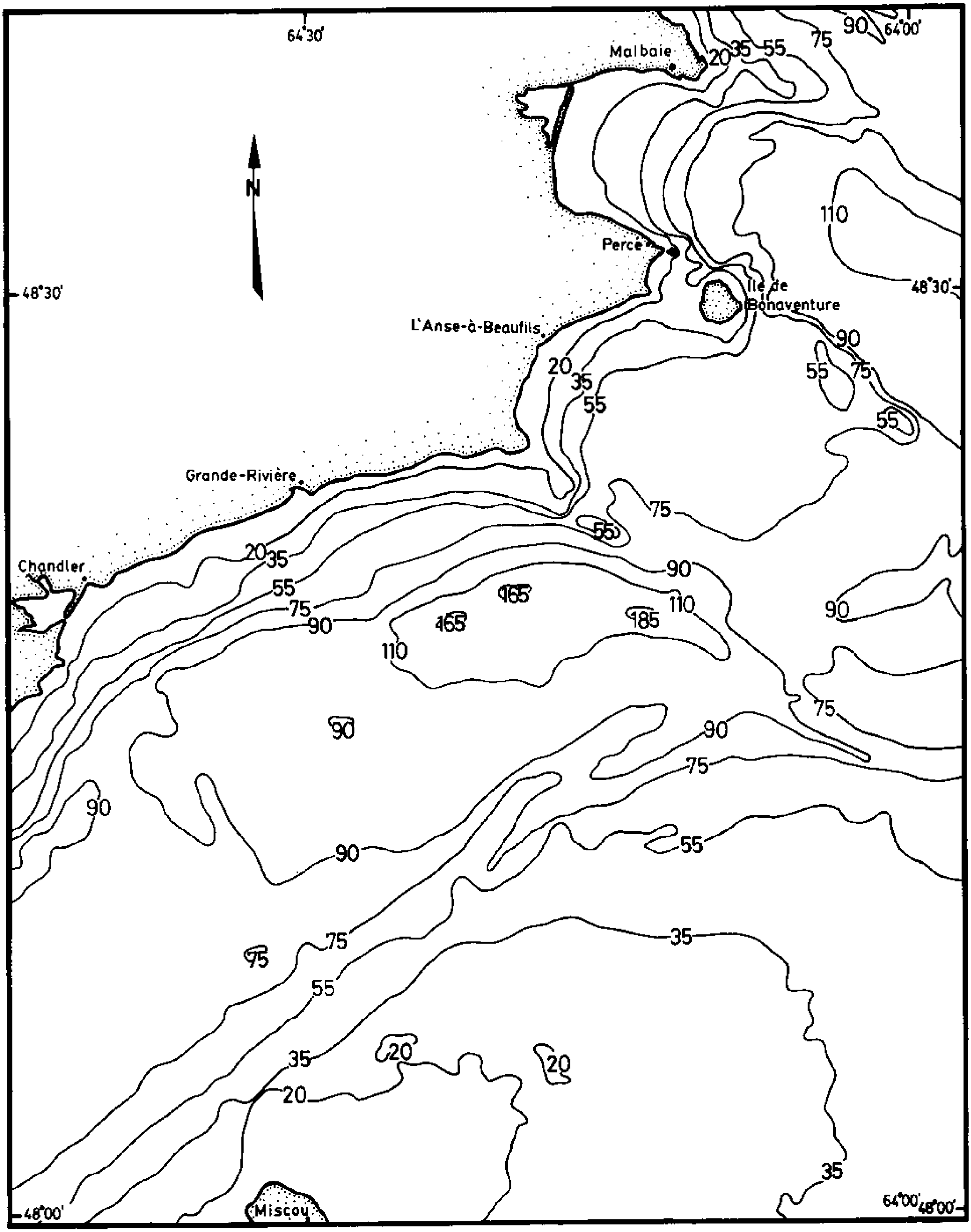

Fig. 2 Detailed bathymetric map of the studied area (depth in meters).

gravels to mud (Loring and Nota 1973). A complementary sedimentological study was undertaken in this area to define more precisely the relation between the benthic fauna and the substratum. Benthic fauna and sediments samples were collected with a Van Veen grab (0.1 m^2) at 63 stations localized following a bathymetric gradiant (Figure 3). Grain size analysis of the sediments were conducted with Rivière's method (1977).

The macrobenthic animals were identified to the species and the following biocenotic coefficients were calculated: abundance, dominance, average dominance, occurrence (Picard 1965), index of occurrence and biological index (Guille 1970). The cartography of benthic communities was realized by similarity coefficient of Sanders (1960).

The crab samples were collected by two different methods. In may 1980, 51 hauls were effected using a small beam-trawl with a stretched mesh size of 25 mm (Fig. 4). In September the same year, conical traps with 50 mm size mesh were used; eight trap were placed at depths between 80 and 90 m, 8 under 90 m, in the Malbaie Bay, and 4 under 110 m in the Chaleur Bay trench.

Shell width was measured for each crab and a maturity index was determined by measuring, the claw width for the males and the width of the 5th abdominal segment for the females. We considered as immature males with a ratio claw width/shell width less than 0,19 and females with a ratio abdomen width/shell width less than 0,55 (Watson 1970).

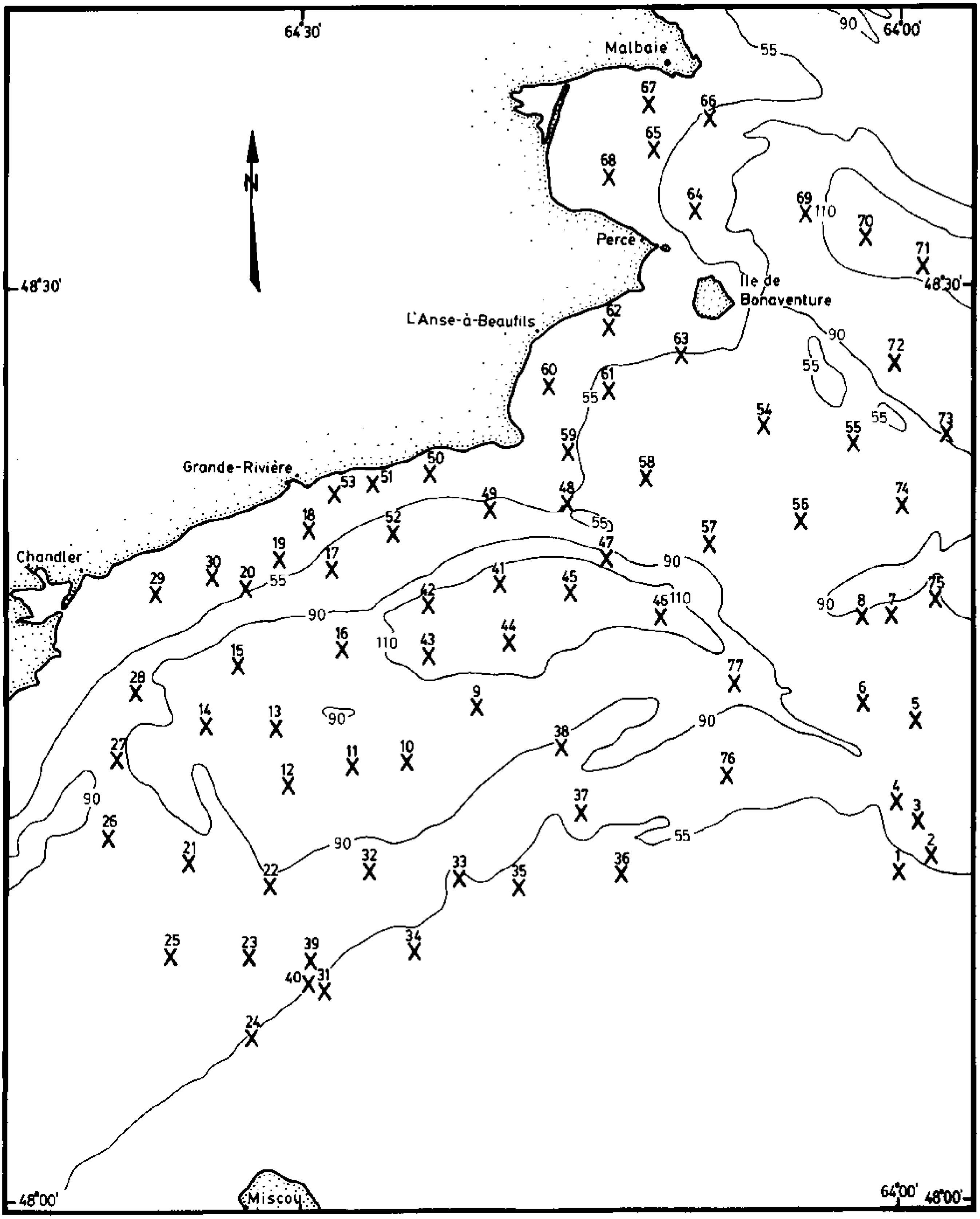

Fig. 3 Localization of the macrobenthic fauna samples.

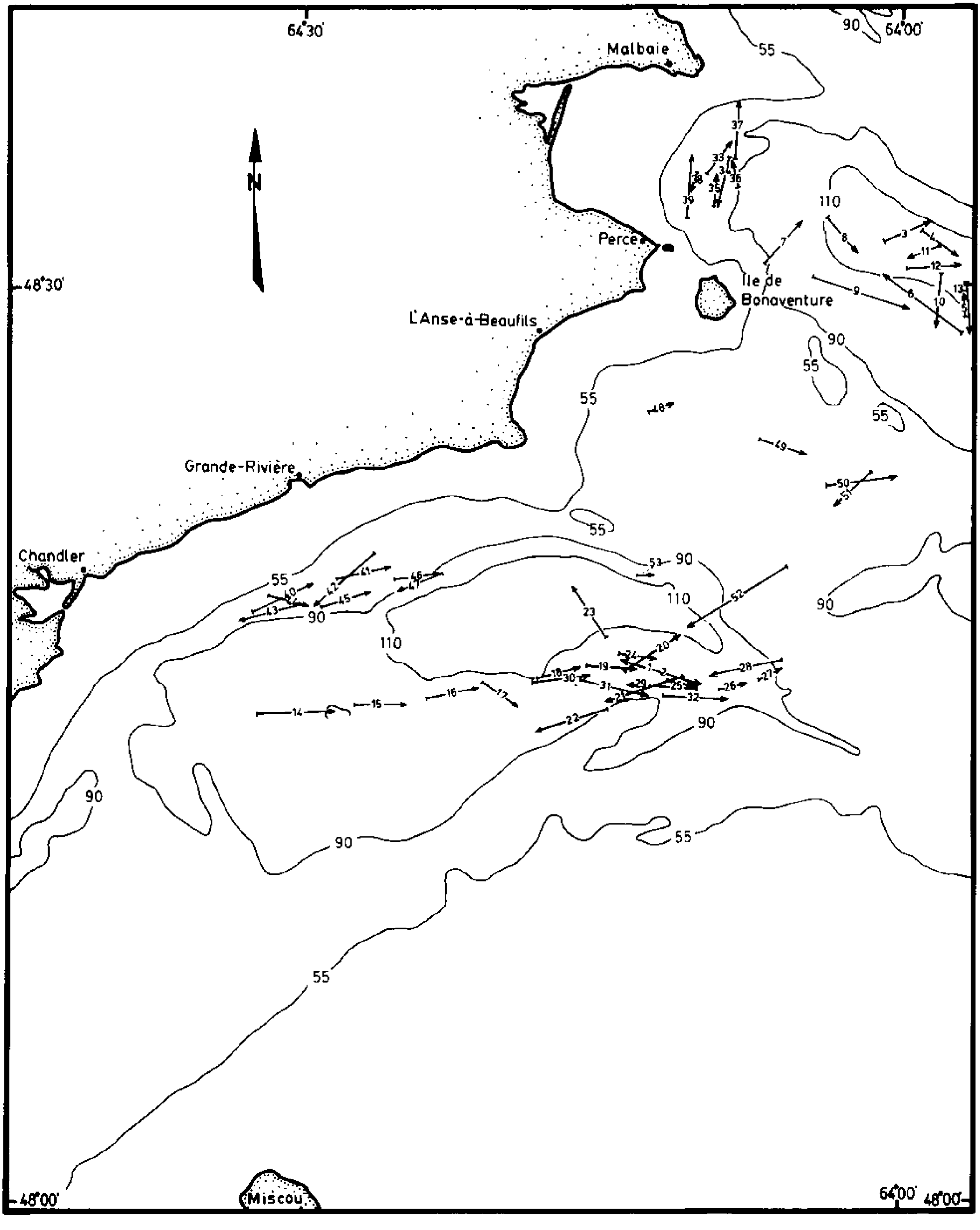

Fig. 4 Localization of the beam-hauls.

RESULTS

Sedimentological analysis

The sedimentological study showed 4 types of substratum: pelitic gravels, muddy sand, sandy mud and mud. Those types of sediments are distribued in parallel with the north coast, following an increasing bathymetric gradiant (Fig. 5). Similarly to the findings of Loring and Nota (1973) and Ledoyer (1975) we observed a large muddy area in the Chaleur Bay isolated from the Gulf by an important gravelly shoal created by the bottom currents.

Benthic communities analysis

Benthic communities could be grouped in 2 principal biota (Fig. 6). The first one, associated with the heterogeneous sediments (pelitic gravel and muddy sand) was characterized by a *Macoma calcarea* community, dominated mainly by the *Crustacea* and Polychaeta representing respectively 35% and 32% of the 156 inventoried species. The taxa Mollusca and Echinodermata with respectively 22% and 8%, were also well represented. However, if we consider the total number of individuals, there is a marked preponderance of the Polychaeta (Table 1). The biological index shows that this type of population is very diversified and dominated by 10 species (Table 1).

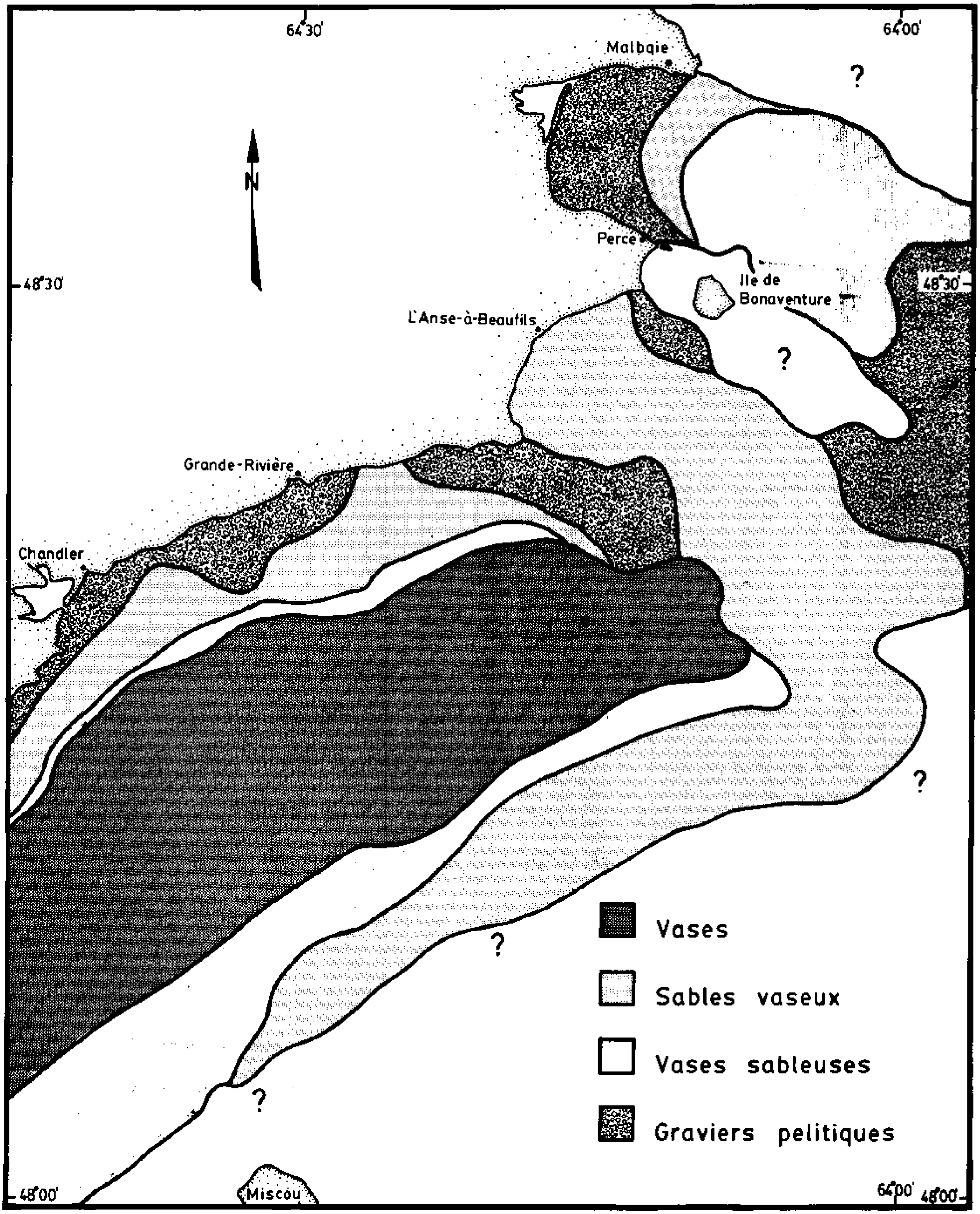

Fig. 5 Distribution of the different types of sediment. (vase = mud, sables vaseux = muddy sand, vases sableuses = sandy mud, graviers pelitiques = pelitic gravels.

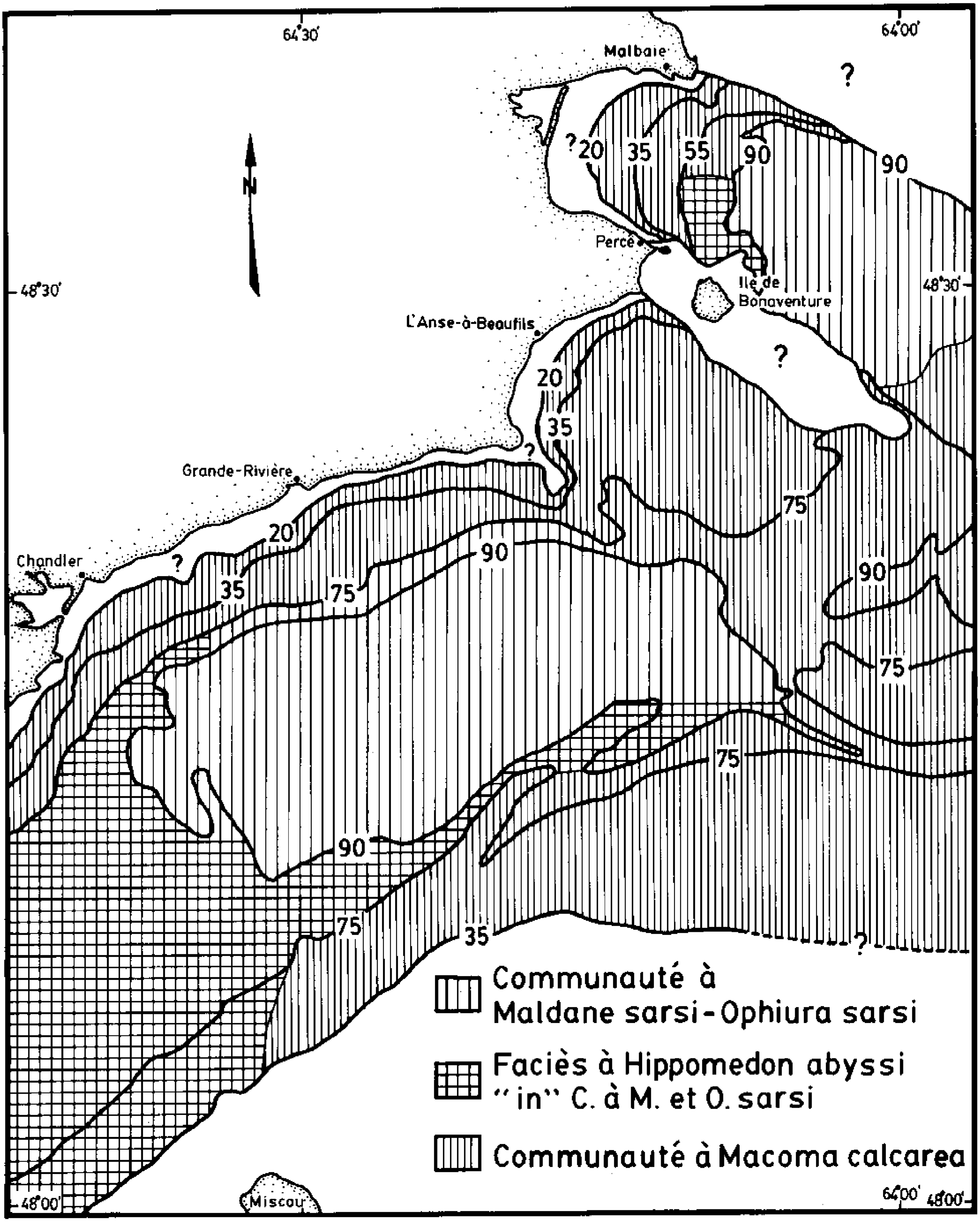

Fig. 6 Distribution of the major benthic communities.

TABLE 1

Qualitative and quantitative analysis for the *Macoma calcarea* community.

Taxa	Number of species	% of number of species	Number of individuals	% of number of individuals
Sipunculidea	1	0.6	36	0.6
Polychaeta	50	32.1	3448	53.1
Crustacea	55	35.2	2041	31.4
Mollusca	35	22.4	858	13.2
Echinodermata	12	7.7	105	1.6
Ascidiacea	3	1.9	7	0.1
	156	100.0	6495	100.0

Result of the biological index for the 10 principal species of this community.

Species	Rank										F	Ib.	D.M.	D.C.
	1	2	3	4	5	6	7	8	9	10				
Prionospio cirrifera	6	6	4	7	2	1	2		1	2	97	219	9.89	9.89
Protomedeia sp.	4	4		3	2	2	3		2		76	135	6.47	16.36
Macoma calcarea	2	5	3	3		1	1	2	3	1	91	132	4.27	20.63
Prionospio steenstrupi	2	2	4	1	3	2	3	4		2	91	131	4.98	25.61
Lysippe labiata		3	3	1	4	3	2	1	2		85	112	3.69	29.30
Euchone sp.	5	1	2		5				1		64	107	5.31	34.61
Scoloplos acutus	1	4	1	1	1		3	2	4	2	91	95	3.86	38.47
Philomedes globosus	3		3		3	2	2			2	70	92	4.94	43.41
Eudorellopsis sp.	1	2	2	3	1	1		1	1		76	81	3.71	47.12
Leucon nasiocoïdes	5	2	1								67	76	4.71	51.83

F = Occurrence Ib. = Biological Index D.M. = Average dominance D.C. = Cumulated dominance

The second biota, associated with greater depth and finer sediments (sandy mud and mud), is characterized by a *Maldane sarsi* and *Ophiura sarsi* community with, in the upper levels on *Hyppomedon abyssi* facies. Here again the community is dominated by the Polychaeta and the Crustacea, with respectively 43% and 36% of the inventoried species, followed by Mollusca (15%) and Echinodermata (4%). However in this community the crustacea dominates in number of individuals (49%) (Table 2). The biological index shows a good homogenity in this community, dominated by 10 species (Table 2).

Crab population study

The shell-width distribution of males in Malbaie Bay (Fig. 7 et 8) shows a significant increase of size with depth. Above 75 m, sizes are concentrated around a mode at 48 mm; between 75 m and 90 m, this mode remains but the principal peak appears at 64-68 mm; below 90 m depth, two modes are noticed, at 68 mm and 96 mm. This pattern observed in May remains almost the same in September. In Chaleur Bay, size distribution is quite similar with almost the same position of the modes (Fig. 9).

Such an increase of size is also observed for females. In Malbaie Bay, samples collected in May above 90 m show a strong peak at 52 mm and below this depth two modes at 52 mm and 64 mm (Fig. 10). In September (fig. 11), in the same area, size distri-

TABLE 2

Qualitative and quantitative analysis for the *Maldane sarsi* and *Ophiura sarsi* community.

Taxa	Number of species	% of number of species	Number of individuals	% of number of individuals
Sipunculidea	1	1.1	10	0.6
Polychaeta	38	43.2	703	45.4
Crustacea	32	36.3	760	49.2
Mollusca	13	14.8	62	4.0
Echinodermata	4	4.5	14	0.9
	88	100.0	1549	100.0

Result of the biological index for the 10 principal species of this community.

Species	Rank										F	Ib.	D.M.	D.C.
	1	2	3	4	5	6	7	8	9	10				
Maldane sarsi	9	7	4	1	1	1	1				93	214	20.94	20.94
Lumbrinereis fragilis	1	2	9	5	2	2	1	1			85	164	7.07	28.01
Prionospio cirrifera	3	5	2	3	2	1	1	1			70	131	10.06	38.07
Hippomedon abyssi	7	3	1			1	1	1			48	112	13.74	51.81
Pontoporeia femorata	3	4	2	2			2		3		67	110	6.90	58.70
Byblys gaimardi		1	1	4	2	4		3	1		67	88	3.63	62.33
Melita formosa	1		3	1	4	1		1	2		52	77	3.71	66.04
Protomedeia sp.	1			1	2	3	3	1	1	1	56	62	2.00	68.04
Leucon nasicus		2	2	2		2				1	48	59	2.88	70.92
Prionospio steenstrupi		2			3		2				48	44	2.11	73.03

F = Occurrence Ib. = Biological Index D.M. = Average dominance D.C. = Cumulated dominance

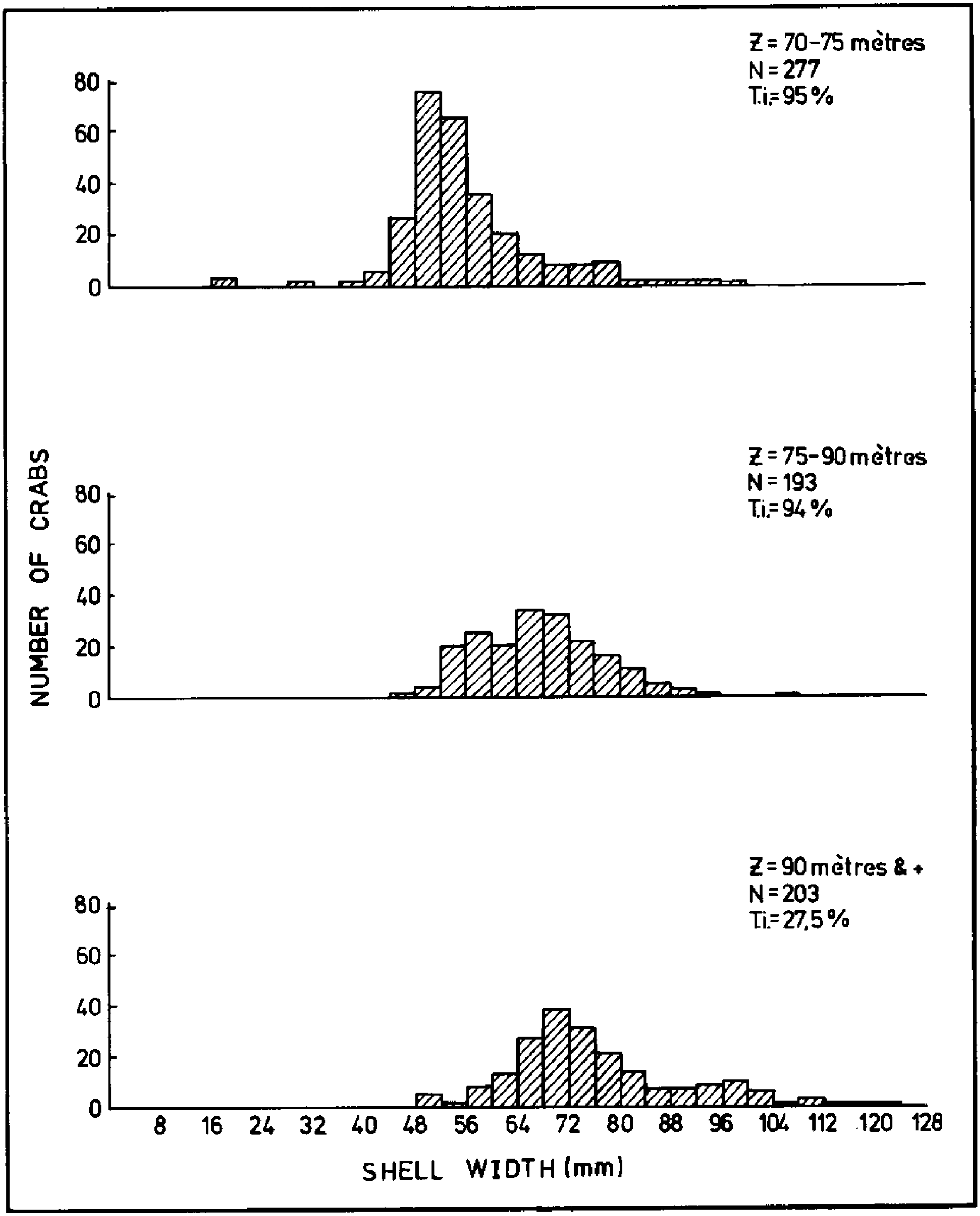

Fig. 7 Size frequency distributions of male crabs in Malbaie Bay (May 1980). Z = depth in meters, N = total number, T.i. = percentage of immatures.

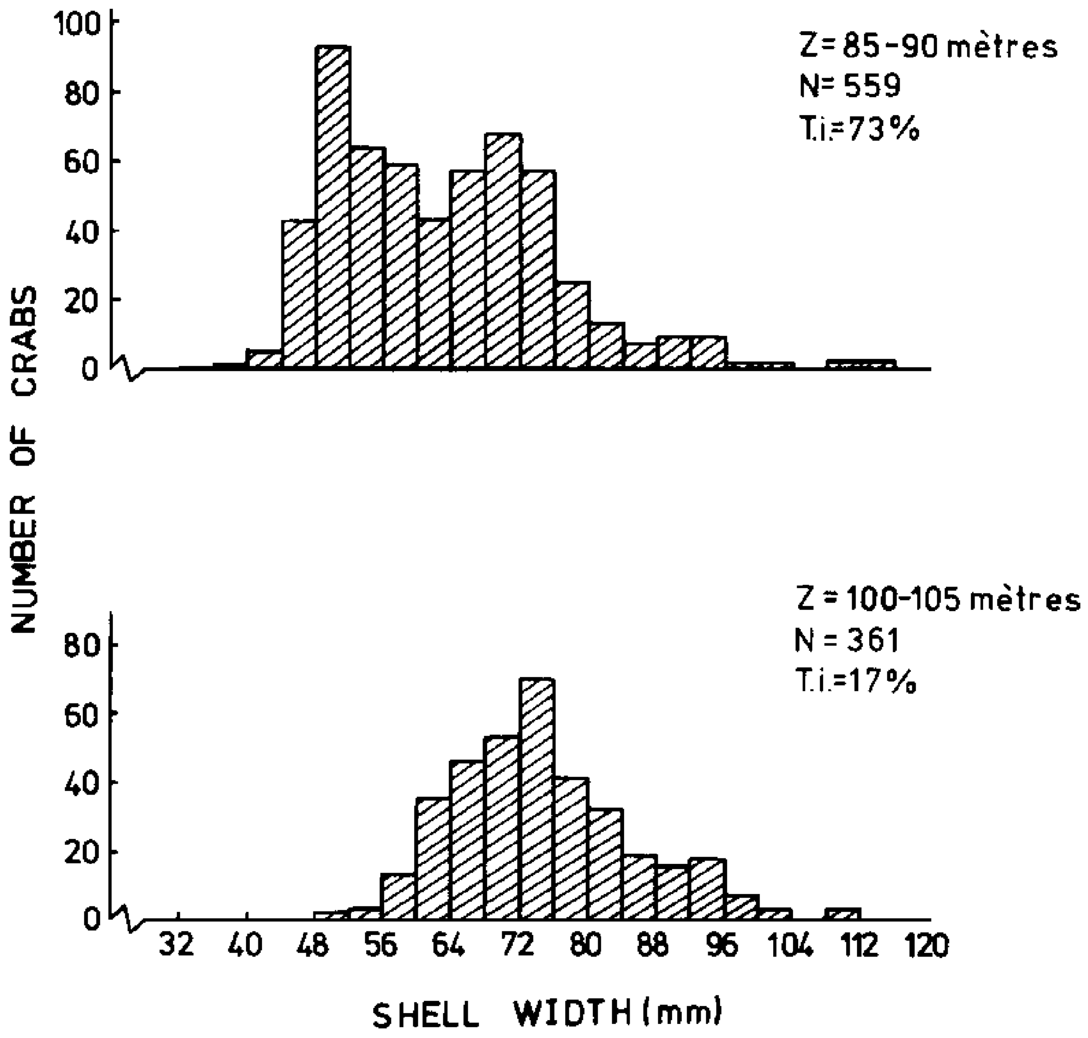

Fig. 8 Size frequency distributions of male crabs in Malbaie Bay (September 1980).
Z = depth in meters, N = Total number, T.i. = percentage of immatures.

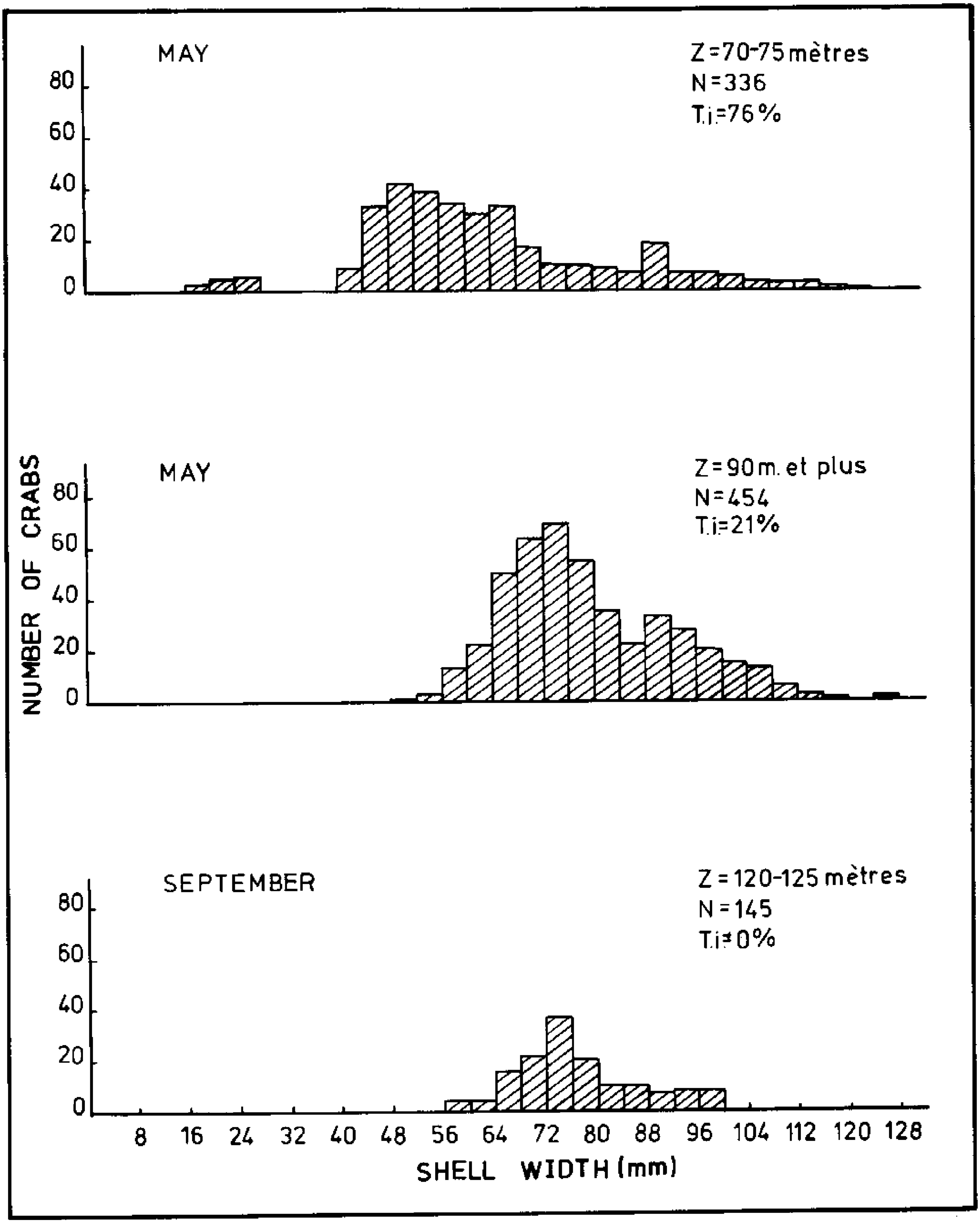

Fig. 9 Size frequency distributions of male crabs in Chaleur Bay.
Z = depth in meters, N = total number, T.i. = percentage of immatures.

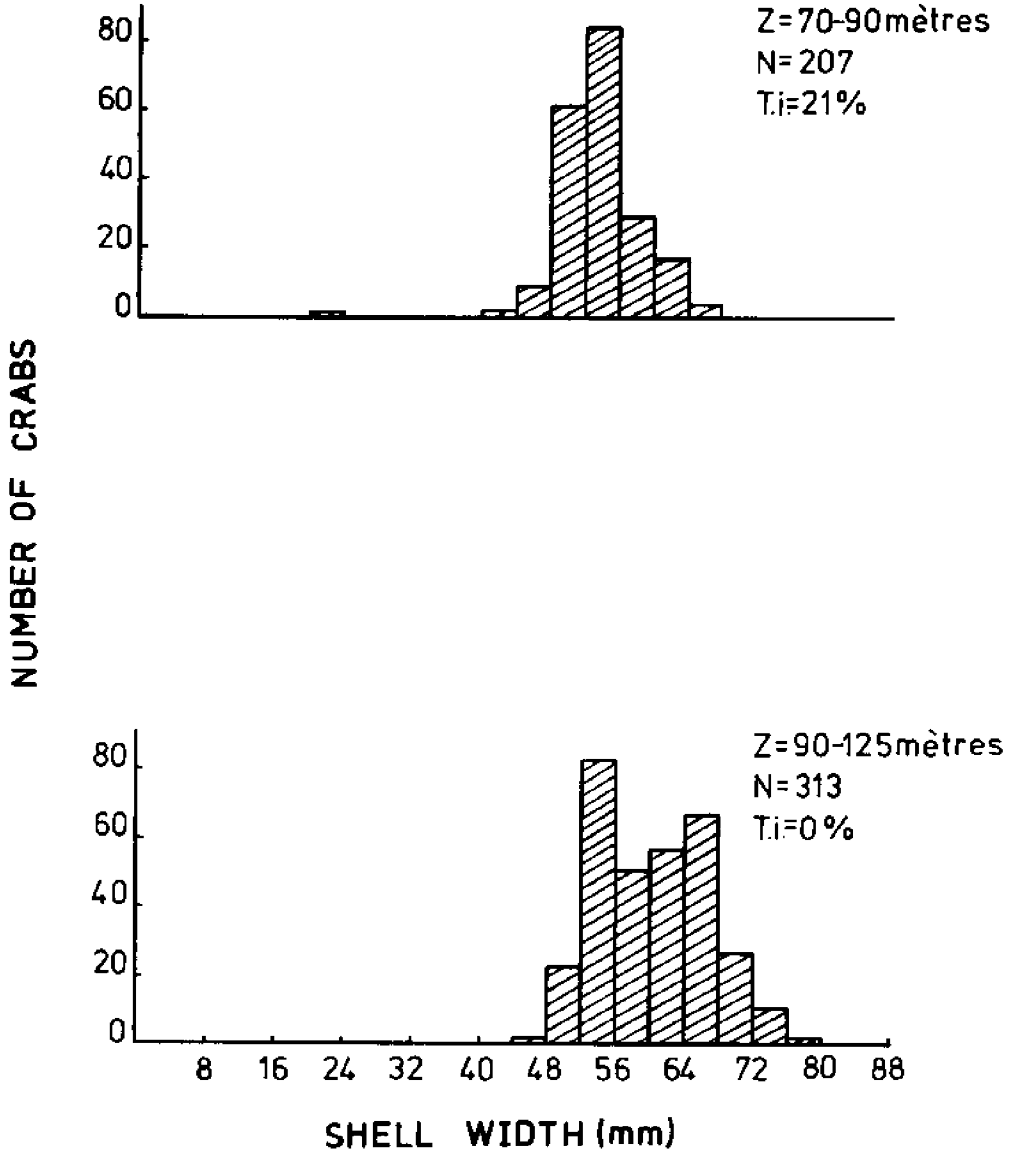

Fig. 10 Size frequency distributions of female crabs in Malbaie Bay (May 1980).
Z = depth in meters, N = total number, T.i. = Percentage of immatures.

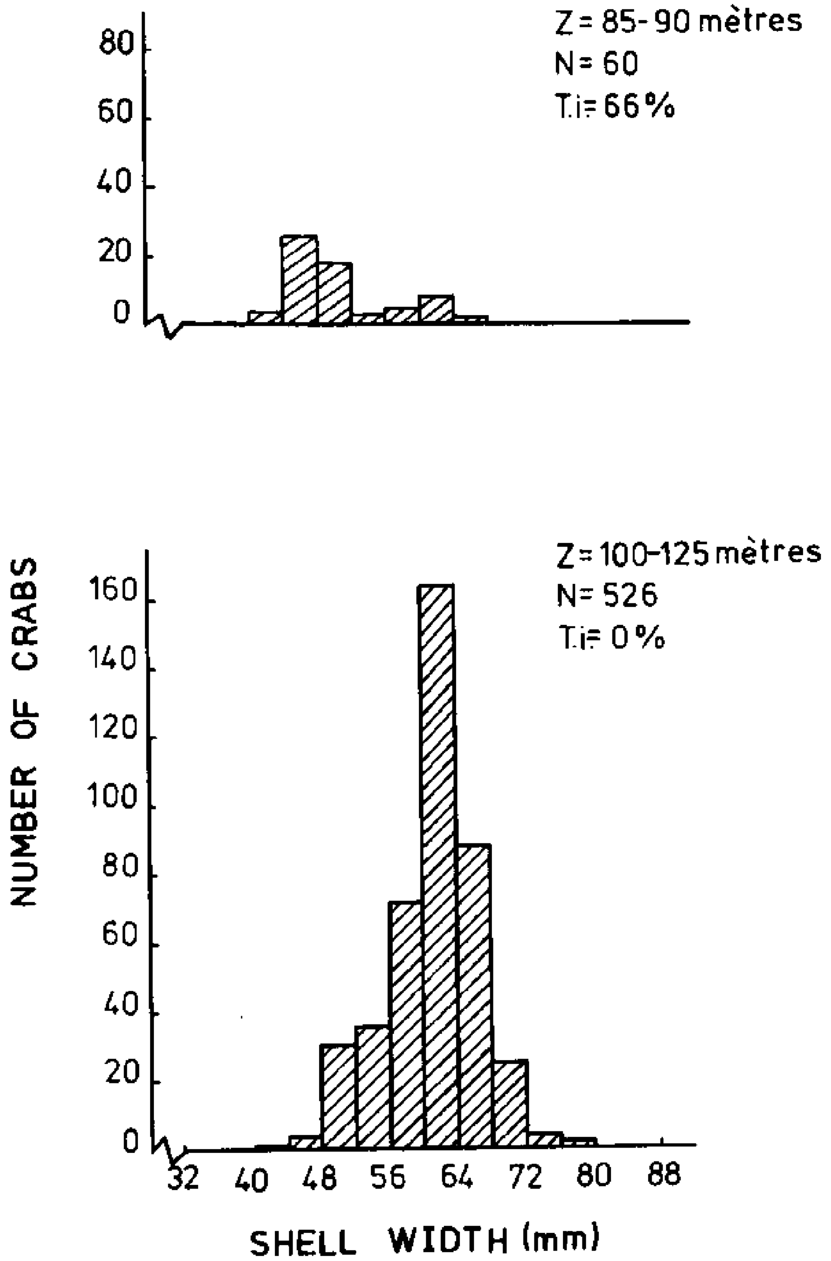

Fig. 11 Size frequency distributions of female crabs in Malbaie Bay (September 1980). Z = depth in meters, N = total number, T.i. = percentage of immatures.

bution above 90 m, shows two modes (44 mm and 60 mm), but on deeper bottoms a mode at 60 mm remains unique. Those observations are also valuable for Chaleur Bay (Fig. 12).

The distribution of immatures crabs shows changes between depths, seasons and sexes. In May, immature males from Malbaie area were mostly present above 90 m where they represented 94% of the individuals, while below this percentage decreased to 27.5%. In September, samples collected above 90 m showed only 73% of immatures. In Chaleur Bay in May, 76% of crabs were immatures above 80 m and 21% below 90 m depth; in September, only data from depth below 120 m were collected and 100% of males were mature.

For the females of the Malbaie area, 21% were immature in May, above 90 m and 100% were mature below this depth. In September 66% of the females were immature at the upper level. In Chaleur Bay, 60% of the females were immature above 90 m depth in May, and 100% were mature on deep bottoms at the both periods.

DISCUSSION

Sedimentological results correspond to the observations of Loring and Nota (1973) for the studied area. The four types of sediments support two benthic populations partially described by Ledoyer (1975) and Bellan (1978) and which correspond, according to our data, to the *Macoma calcarea* community, on pelitic gravels and muddy sand, and to *Maldane sarsi* and *Ophiura sarsi* community

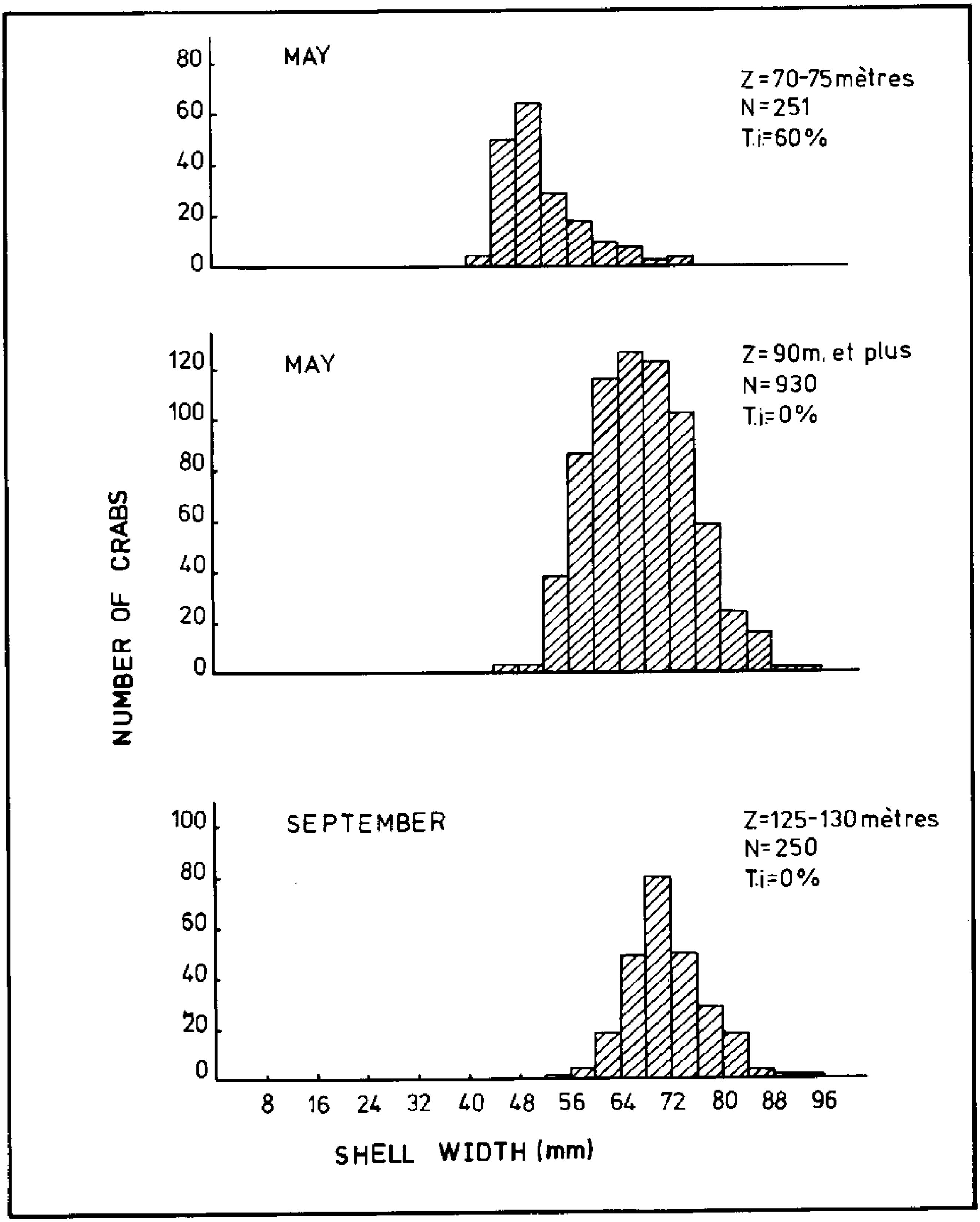

Fig. 12 Size frequency distributions of female crabs in Chaleur Bay.
Z = depth in meters, N = total number, T.i. = percentage of immatures.

on sandy mud and mud. The limit between the two benthic assemblages seems to lie around the 75 m depth.

Crabe size increases with depth. This observation was made, in Newfoundland area, by Miller and O'Keefe (1981), using a commercial mesh size which did not give information on young stages. The methodology used for the present study allowed us to collect immature crabs and females and completes more accuratly the anterior works. The presence of young *C. opilio* on heterogeneous bottoms at upper levels confirms the observations of Ledoyer (1975) and Miller (1975). The fact that the immature and mature crabs exhibit a distinctive distribution allows us to advance the hypothesis of a certain segregation within the population. Immature stages appear to be distributed preferentially on bottoms where *M. calcarea* community is implanted. This environment may favour young *C. opilio* in presenting a better protection against predators while the benthic community, with its dominant species (mobile Crustacea, Bivalves ...), offers a better selection of food for small individuals (Brêthes et al. same symposium). Mature stages are distributed mainly on sandy mud and mud where *Maldane sarsi* and *Ophiura sarsi* community is found.

Seasonnal changes in proportion of immatures in the population are most important between 75 m and 90 m depth where a *Hyppomedon abyssi* facies was noticed. From spring to autumn, the percentage of immature males decreases from 94% to 73% suggesting that a maturity molting appears in summer and may be followed by a move down to deeper bottoms in winter. An inverse pattern is observed for females with an increasing of immature fraction from May to September: the maturity molting would happen than in winter, certainly just before copulation, in spring (Watson 1970).

It is possible to assume that after the metamorphosis of the planctotrophic stages of *C. opilio*, early benthic stages are uniformly distributed on the different types of sediments, but the individuals located on heterogeneous bottoms are favoured and may account for the largest part of the recruitment. Following their growth they move down to greater depth and the drastic change of benthic environment occurs concurrently with the maturation process. Watson (1970) observed that copulation takes place between freshly molted females and hard shelled males: this fact may suppose a certain seasonnal migration of males from deep muddy bottoms to the upper ones. But, in fact, the distribution of early benthic stages is not known and the seasonnal migration of males is just an assumption. Those aspects have to be studied further for a better comprehension of *C. opilio* ecology.

ACKNOWLEDGEMENTS

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ABSTRACT

In May and September 1980, samples of *C. opilio* were taken in the entrance of the Chaleur Bay (Quebec) at depths varyings between 70 and 120 m, using beam-hauls and conical traps. Size-frequency distributions of male snow-crabs were related to the depth of sampling. Above 90 m depth, the size of male crabs ranged mainly from 40 mm to 65 mm, while below this depth the crabs were larger than 65 mm. The maturity index (claw width vs shell width) indicates that immature and mature males were located on shallow and deeper bottoms respectively. The limit between the mature and immature stocks was about 90 m depth. Sixty three grab samples were collected concurrently for sedimentological and benthic infauna characterizations. Immature males were principally associated with the muddy sand and pelitic gravel substrates, occupied by the *Macoma calcarea* community. Mature males were associated with mud and sandy mud substrates inhabited by *Maldane sarsi* and *Ophiura sarsi*. The distribution of female crabs seemed to indicate a similar segregation. Sexual maturity appears to be the factor which determines the transition from hard substrates to the softer substrates where the snow-crabs are exploited.

Tagging

Tanner Crab Tag Development and Tagging Experiments 1978-1982

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INTRODUCTION

Management of tanner crab (*Chionoecetes bairdi*, *C. opilio*) resources requires investigation of their *life histories*. Important aspects of their life histories include age and growth, mortalitiy rates, and migrations. Because crustaceans lose all of their hard parts during ecdysis, there are no structures for age determination and tagging becomes an essential study tool. An external tag that 1) identifies an individual, 2) is retained through successive molts, 3) is highly visible, and 4) is minimally harmful to the animal is required.

Considerable effort has been directed towards the development of permanent tags for crabs and lobsters. Use of the "spaghetti" loop tags on king crabs (*Paralithodes* spp.) (Anonymous, 1954; Stevens, 1955; Hayes, 1963; Gray, 1965) has been one successful approach. Butler (1957) used a stainless steel wire with a Petersen disk for tagging dungeness crab (*Cancer magister*). A curved needle was used to thread the wire through holes in the carapace and into underlying tissues. A similar tag has been used on *C. pagurus* in Europe (Edwards 1978). Smith (1940 developed a celluloid dart tag for lobsters (*Homarus americanus*) that was inserted in the second or third abdominal segments. Gunderson (1964, 1967) devised a lobster tag consisting of two plastic strips joined by a nylon thread that was inserted dorsally through the membrane between carapace and abdomen. The sphyron lobster tag (Scarratt and Elson, 1965) consisting of an anchor of stainless steel wire, a double strand of polyethylene monofilament, and a numbered disk was also inserted dorsally through the membrane between the carapace and abdomen. Scarratt (1970) modified the sphyron tag by replacing the flat vinyl label with extruded vinyl tubing. All of these tags were retained through molting in at least some instances.

Tanner crabs present a special problem in that the carapace covers the membrane between carapace and abdomen, as well as the suture line. For this reason, tags must either be inserted through the carapace, or under the margin of the carapace. Thorenson (1967) and Dell (1968) described an anchor (or T-bar) tag and a rapid applicator developed by Floy Tag and Manufacturing, Inc. 1/ Karinen's successful use of this system on tanner crab was reported in 1970 (anonymous). Nine male *C. bairdi* were tagged in the body musculature proximal to the third *walking leg* and 33% molted successfully. Japanese investigators successfully tagged both *C. bairdi* and *C. opilio* using the T-bar system (Fujita and Takeshita, 1979). Eight of the 15 crabs tagged under the shell margin and through the posterior suture molted with no difficulty as did seven of the 21 crabs tagged through the carapace. While both of these experiments were carried out over a short period of time, they suggested that the T-bar design showed promise.

1/ Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

The basic T-bar tag (Fig. 1) was used to mark red king crab (P. camtschatica) during NMFS tagging experiments in 1973 and 1976. Application was rapid and the T-bar toggle proved to be a firm anchor. Later examination of the tag and tag wound on recaptured crab, however, indicated the T-bar tag interfered with ecdysis. The carapace around the tag wound tended to catch on the "shoulder" formed by the joining of the large diameter tubing bearing the tag legend, and the smaller diameter nylon shaft. A similar problem was anticipated if this tag was used to mark tanner crabs.

Successful use of anchor tags on lobsters and encouraging results with the T-bar system strongly suggested that T-bar tags could be modified for use. Placement of the tags on tanner crabs, however, remained an open question. In 1978, the NMFS (in cooperation with the Alaska Department of Fish and Game, ADF&G) began tagging experiments with modified tags. These experiments were designed to investigate short-term tagging mortality, tag retention, and the effects of tag placement as well as to elucidate aspects of life history.

METHODS AND MATERIALS

Three modifications of the basic T-bar tag were developed and used as primary marks during the experiments (Fig. 1). The basic T-bar and a modified Petersen disk tag were used as secondary marks in double tagging experiments. Primary and secondary tags and tag placement are described below.

Tapered T-bar Tag

A first modification of the basic T-bar was developed early in 1978. The nylon shaft between the T-bar toggle and tubing was tapered from 2.0 mm diameter at the junction of the tubing to 0.9 mm at the toggle. Tapering was intended to allow the carapace to work up the shaft during ecdysis and allow completion of molting. Tapered tags required a larger diameter needle (2.7 mm vs 1.9 mm) in the tagging gun to allow passage of the shaft. Tags were inserted through the carapace middorsally about 25.0 mm forward of the posterior margin of the carapace.

Cooperative evaluation studies of the tapered T-bar tag were carried out by the NMFS and ADF&G in April 1978 (Alaska Department of Fish and Game unpublished). These studies were designed to evaluate tagging mortality, tag placement, structural failure, and tag clipping problems. Tagged crab, held in submerged pens, were periodically examined by scuba divers for tagging mortality and tag retention. Structural failure and tag clipping studies were conducted utilizing the fish hold of a commercial vessel. Tagged crab were placed in the vessel's hold and allowed to mix with the catch of a subsequent fishing trip. At the time of delivery, the fish hold was examined for lost and damaged tags, while crab were checked for tag damage or loss. No

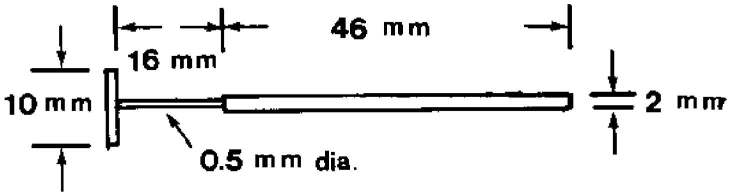
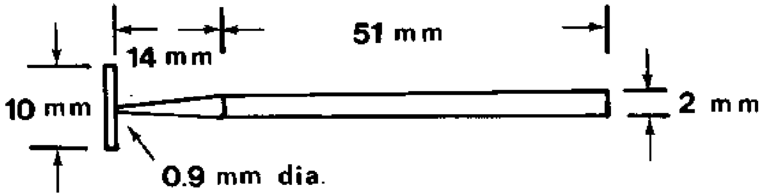
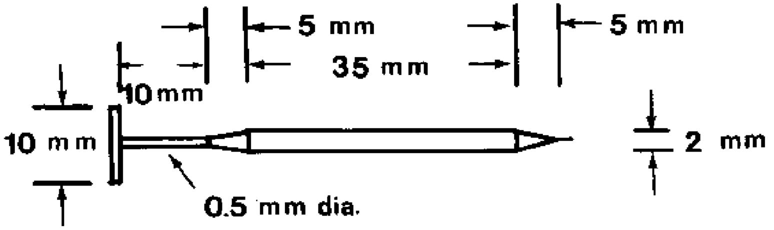
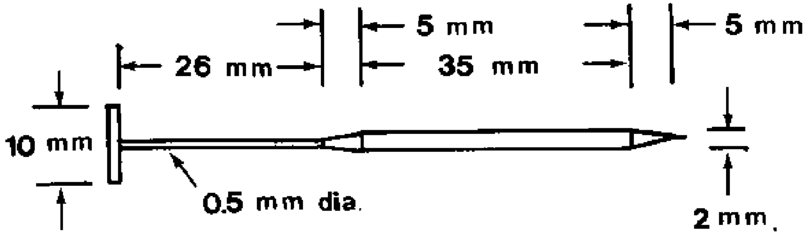
NAME	DESIGN	MATERIAL
Basic T-Bar		Unstressed nylon shaft #20 yellow polyurethane tubing bearing legend
Tapered T-Bar (1978)		Tapered nylon shaft stressed, #20 orange tubing bearing legend
Experimental Short Shaft (1979, 1980)		Stressed nylon shaft extended through both cones and #20 orange tubing bearing legend
Experimental Long Shaft (1979, 1980)		Stressed nylon shaft extended through both cones and #20 orange tubing bearing legend

Figure 1 -- Basic T-bar tag and modifications used to tag tanner crab (*Chionoecetes spp.*) during NMFS tagging experiments 1978-80.

significant tag-induced mortality was observed in either study. Of the crab held in the vessel hold, 63% of the suture line tags were retained, while only 39% of the carapace tags were retained. Tag loss was due to structural failure and clipping by other crabs. These preliminary studies also showed other faults in the tagging system. The tapered shaft would not readily feed through the needle of the tagging gun. The diameter of the hole punched in the carapace by the needle was too small for ready entrance of both needle and tag. T-bar toggles were sometimes clipped off by the tagging gun at the junction of the T-bar toggle and tapered shaft. Subsequent field trials in 1978 confirmed the results of the previous cooperative evaluation and the need for further modification.

Experimental Short Shank Tag

Early in 1979, consideration was given to designing more durable tapered tags, and identifying additional points of insertion in the crab. Stressed nylon monofilament shafts were used for this tag. To eliminate the shoulder problem, a cone with a base diameter equal to the legend bearing tubing was glued onto the shaft 15.0 mm from the T-bar toggle. The monofilament shaft was extended through the legend bearing tubing and a second cone was glued on the shaft at the distal end to hold the legend bearing tubing in place. Extending the shaft through the tubing was intended to stop tags from being severed by other crabs in densely packed vessel live tanks.

Experimental short shank tags were used as a primary mark on *C. bairdi* in 1979 and *C. opilio* in 1980. Tags were inserted at two *locations*:

1) through the carapace, middorsally, about 25.0 mm from the posterior margin; and,

2) under the carapace and through the suture line at the base of the fourth right walking leg.

Experimental Long Shank Tag

This tag is identical to the experimental short shank except that a longer (31.0 mm) shaft was between the T-bar toggle and proximal cone. Longer shafts were intended either to reduce the possibility of tags being drawn inside the carapace, or to allow deeper tag insertion in muscle tissue at the base of the fourth walking leg.

Modified Petersen Disk Tag

This tag was the secondary mark used during the 1978 tagging experiment. A barbed nylon shaft (20.0 mm long x 3.3 mm wide) was used to attach this tag. The shaft was inserted into a prepunched hole in the center of the right branchial area. Holes were punched with a 6.4 mm diameter pointed rod. It was used to mark approximately 50% of the double-marked crab during the 1979 tagging experiment.

Basic T-bar Tag

This tag was used as a secondary mark during the 1979 and 1980 tagging experiments. The T-bar was inserted through the center of the right branchial portion of the carapace.

Returns from a 1980 fishery (February-April) were briefly examined prior to the 1980 tagging effort. This examination indicated that the loss rate of basic T-bar tags was not noticeably greater than that of disk tags. Consequently, only the basic T-bar tag was used as the secondary mark in later experiments.

Vessel and Fishing Gear

Tagging was conducted aboard chartered commercial crab fishing vessels. These vessels were 33-38 m in length (Fig. 2) and diesel powered with engines ranging from 550 to 1,125 horsepower. All deck machinery was driven by hydraulics.

Standard 2.0 to 2.1 m double-frame king crab pots (Fig. 3) covered with 152 mm stretched mesh nylon web were used to capture crab. Panels of 76 mm stretched mesh web were attached to two sides of the pots to prevent escape of the smaller tanner crabs. Two tunnels were located on opposite sides of the pot and had openings of 0.20 m x 0.91 m recessed about 0.6 m from the sides of the pot. The size of the tunnel openings was restricted by 25 mm x 0.10 m x 1.07 m wooden boards secured across the entrances to prevent entrance of king crabs. Pots were fished singly, and each was equipped with its own buoy line attached to two inflatable buoys. Chopped frozen herring (*Clupea harengus*), packed in perforated, 1.9 liter, plastic containers, was used as bait. Bait containers were suspended between the tunnel openings in the pot.

Following initial capture, vigorous and uninjured crab with all appendages were placed in a holding tank until they were tagged and released.

RESULTS AND DISCUSSION

During 1978-80 a total of 10,405 *C. bairdi* and 10,835 *C. opilio* were tagged and released on tanner crab fishing grounds in the eastern Bering Sea (Fig. 4). Male *C. bairdi* $\geq$ 140 mm carapace width were tagged in 1978; and, males $\geq$ 110 mm carapace width were tagged in 1979. Male *C. opilio* $\geq$ 80 mm were tagged in 1980 (Table 1).

Tapered T-bar tags were used to mark 2,258 *C. bairdi* during 1978. Two individuals were recovered during the fishery (4-7 months after tagging) and neither had retained the modified tapered T-bar tag (Table 2). During fishing seasons of 1979-82 an additional 98 crab from the 1978 tagging were recovered. Of these, only 33 individuals or 34% had retained the tapered T-bar tag.

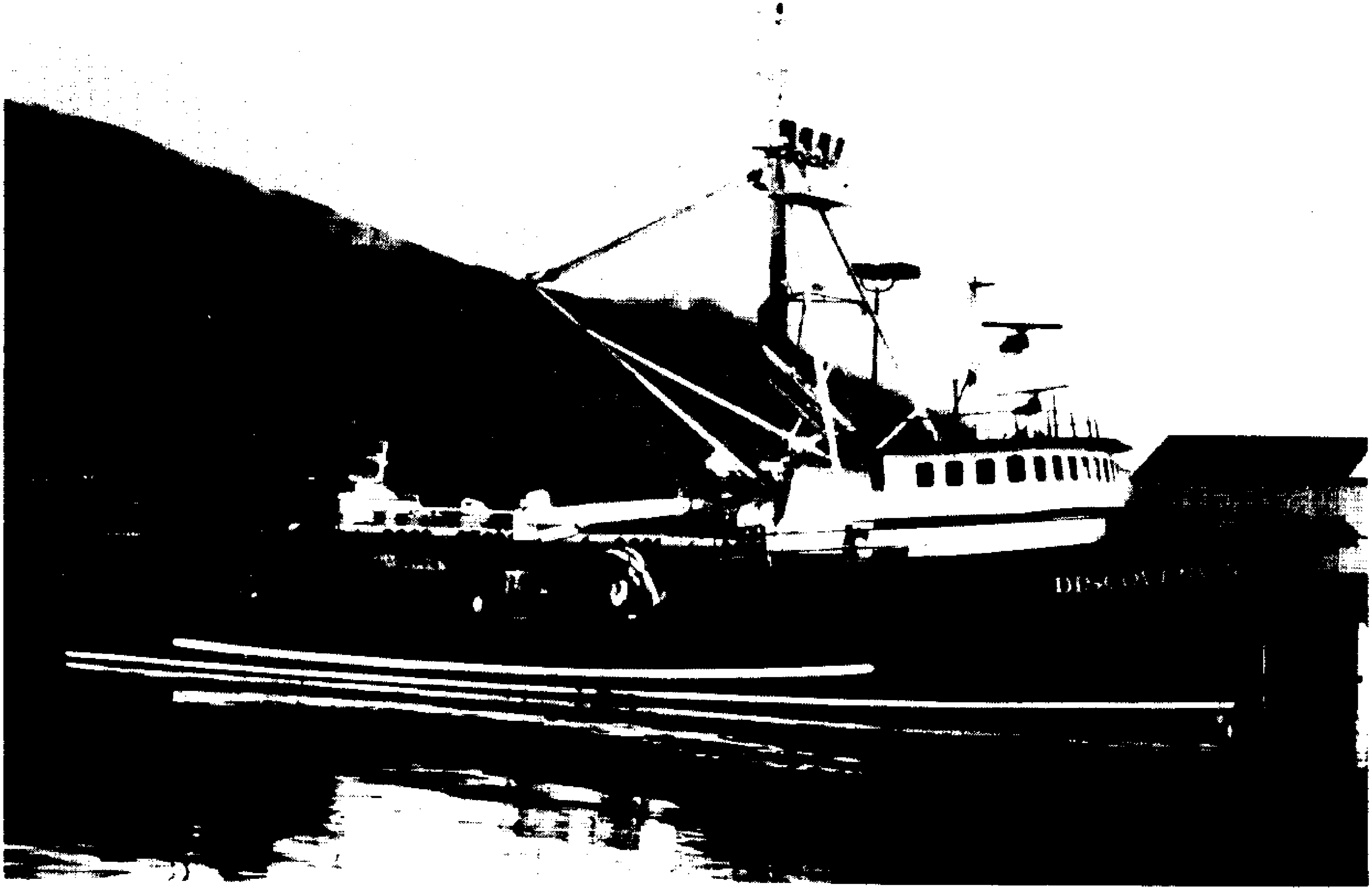


Figure 2. Bering Sea crab vessel chartered for 1979 tagging cruise. Overall length 33 meters.

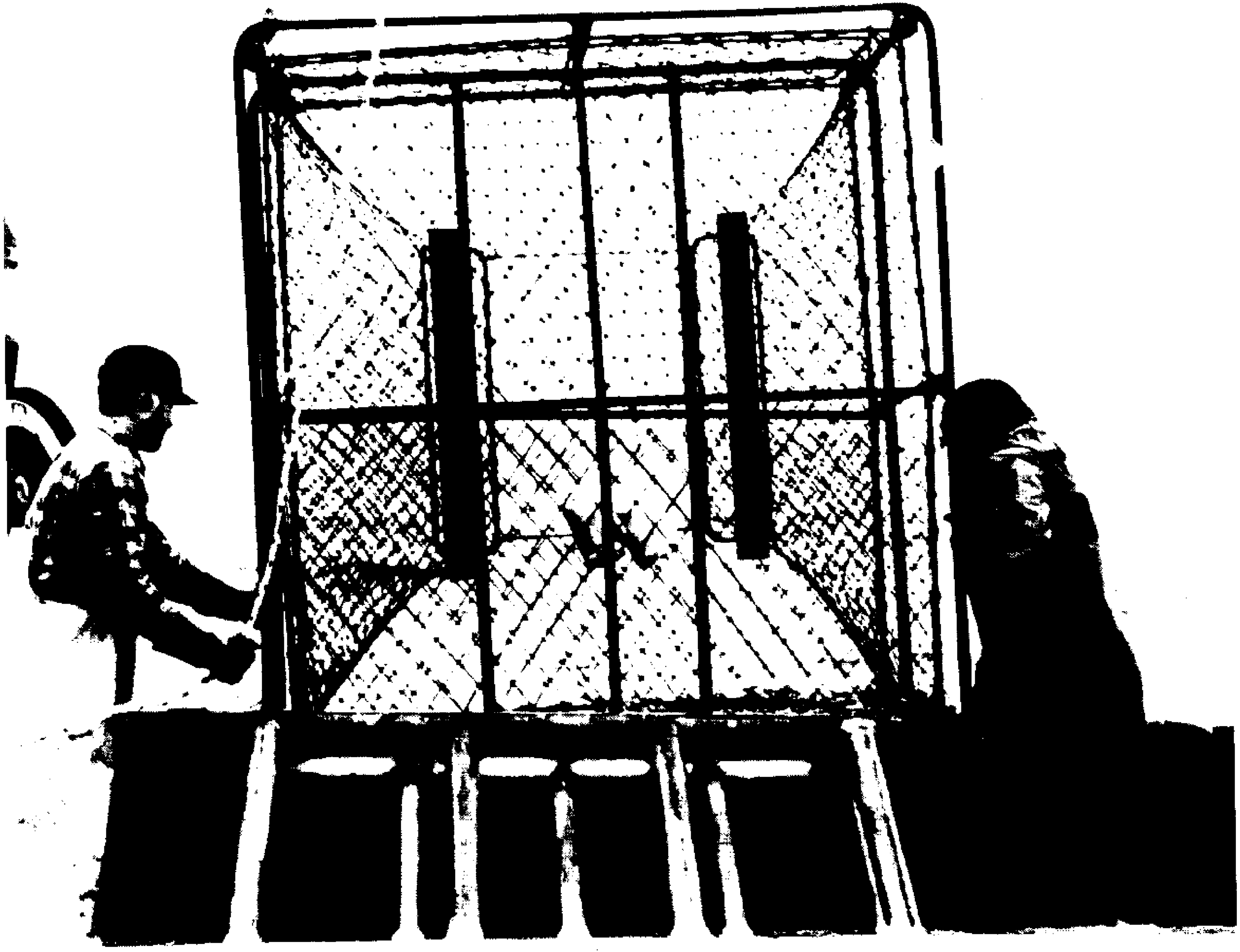


Figure 3. Standard 2.4 x 2.4 meter crab pot with tunnel boards and side panels.

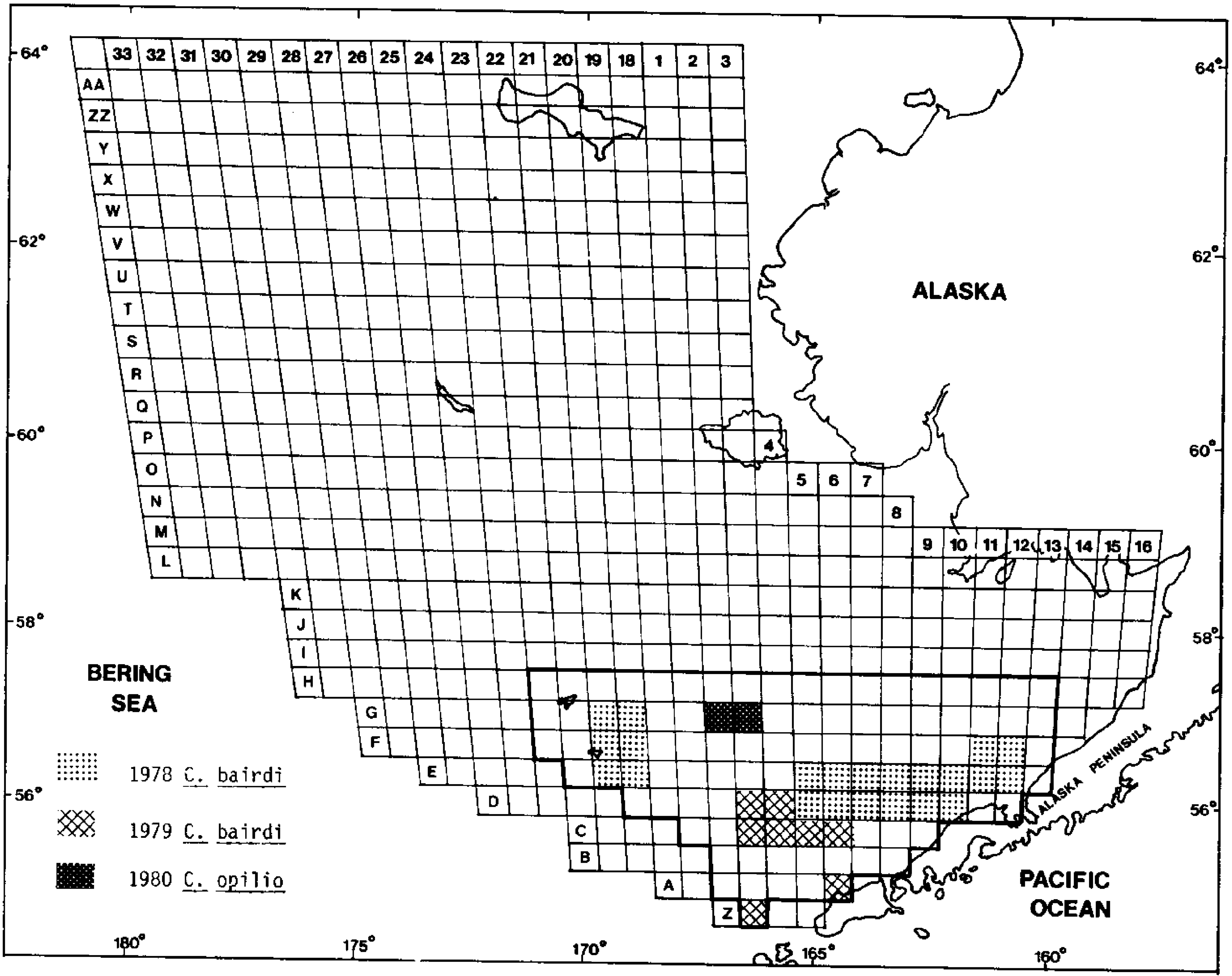


Figure Tanner crab fishing grounds(☐) and location of tagging experiments 1978-80.

Table 1 -- Number and type of tags released.

Year	Species	Carapace Width	Primary Tag	Location	Number	Secondary Tag	Location	Number
1978	*C. bairdi*	≤140.0 mm	Taperd T Bar	Carapace	1,122	----	----	----
					1,136	Disc	Rt. Branchial	1,136
1979	*C. bairdi*	≥110.0 mm	Experimental Short Shank	Carapace	1,627	----	----	----
					845	Stnd. T Bar	Rt. Branchial	845
					845	Disc	Rt. Branchial	845
			Experimental Short Shank	Right Posterior	1,660	----	----	----
					605	Stnd. T Bar	Rt. Branchial	605
					542	Disc	Rt. Branchial	542
			Experimental Long Shank	Left Posterior	1,001	----	----	----
					497	Stnd. T Bar	Rt. Branchial	497
					525	Disc	Rt. Branchial	525
1980	*C. opilio*	≥ 80.0 mm	Experimental Short Shank	Carapace	1,925	----	----	----
					1,747	Stnd. T Bar	Rt. Branchial	1,747
			Experimental Short Shank	Right Posterior	1,710	----	----	----
					1,737	Stnd. T Bar	Rt. Branchial	1,737
			Experimental Long Shank	Left Posterior	1,749	----	----	----
					1,967	Stnd. T Bar	Rt. Branchial	1,967

and secondary (T-bar) tags through a molt or molts. The experimental long shaft T-bar tag (inserted in muscle tissue at the base of the fourth walking leg) appeared to be retained through the molt more often than the other T-bar models tested. About half of the crabs showing growth were marked with this tag, while the number tagged with experimental long shaft tags was less than 29% total releases.

Eastern Bering Sea *C. bairdi*, recaptured within 12 months of release, increased an average of 21.0 mm or 15.1% in carapace width. Carapace widths at time of release ranged from 122 to 163 mm. In Ugak Bay (Kodiak Island) *C. bairdi* ranging from 110 to 148 mm carapace width when tagged, showed an average growth of 24.6 mm or 18.6% (NMFS, unpublished data). In Chiniak Bay (Kodiak Island), growth per molt for male *C. bairdi* between 120 and 129 mm averaged 26 mm or 20.9% (Donaldson, 1980). Average growth per molt of *C. bairdi* in Kodiak Island waters is slightly larger than it is in the Bering Sea, and may reflect the generally warmer conditions found in Kodiak.

Only six *C. opilio* recaptured within 12 months of release exhibited growth. These crab ranged in size between 108 and 124 mm when released and displayed an average increase of 15.6 mm or 13.7%. Of these, three crab were tagged with experimental long shaft tags and three with the experimental short shaft tags (Table 5). Proportional increase in size at molting appears to be smaller for *C. opilio* than *C. bairdi*.

Movements of Tagged Crabs

Information on movements of *C. bairdi* was obtained from 1979 tag releases. Detailed information on the location of recapture is available for 32 crab recovered in 1980 and for 60 crab recovered in 1981. *C. bairdi* recaptured within 1 year of release displayed an average net distance moved of 73.3 km with a range of 7.2 to 87 km. Crab at large for 1 to 2 years moved greater distances, averaging 80 km and ranging from 10 km up to 359 km. Most frequently, movement for both groups was to the south or southwest.

Distances travelled by *C. bairdi* in the eastern Bering Sea appear to be substantially greater than those in the Gulf of Alaska. Donaldson (1980) found the average movement of individuals in the Kodiak Island area to be about 24 km and in a general inshore-offshore direction. Bathymetry of the Kodiak Island region is highly irregular and includes numerous bays, banks, and gulleys which probably influence both direction and distance travelled by tanner crabs. An absence of bays and a relatively uniform bathymetry in the eastern Bering Sea could have contributed to the greater distances travelled by *C. bairdi* in this region.

Forty-nine *C. opilio* tagged during 1980, were recaptured during the 1981 fishing season with sufficient information to be examined for distance and direction of movement. Net distances from release sites ranged from 10.6 to 170.7 km, and averaged about 79 km. A majority of individuals moved in a south to southwest direction.

Table 2 -- Number and type of tags recovered and number and type of tags not retained - *C. bairdi*.

Release Year	Recovery Year	Primary Tag	No. Recovered	No. Not Retained	Secondary Tag	No. Recovered	No. Not Retained	Average Time At Large Days
1978	1978	Tapered T-Bar	0	2	Disc	2	0	126
	1979		29	0	----	--	--	225
			44	48	Disc	90	2	
	1980		7	0	----	--	--	588
			8	9	Disc	15	2	
	1981		1	0	----	--	--	930
			2	3	Disc	5	0	
	1982		0	1	Disc	1	0	1,330
1979	1979	-----	--	--	----	--	--	
1979	1980	Exp Short Shank/ Carapace	106	--	----	--	--	314
			55	3	Standard T-Bar	52	6	
			50	1	Disc	40	11	
		Exp Short Shank/Right Posterior	48	--	----	--	--	
			38	3	Standard T-Bar	36	5	
			16	7	Disc	15	8	
		Exp Long Shank/Left Posterior	67	--	----	--	--	
			30	7	Standard T-Bar	36	1	
			56	6	Disc	51	11	
1979	1981	Exp Short Shank/ Carapace	37	--	----	--	--	281
			12	--	Standard T-Bar	9	3	
			4	--	Disc	4	--	
		Exp Short Shank/Right Posterior	48	--	----	--	--	
			11	--	Standard T-Bar	11	--	
			13	1	Disc	11	3	
		Exp Long Shank/Left Posterior	20	--	----	--	--	
			10	--	Standard T-Bar	8	2	
			27	2	Disc	20	9	
1979	1982	Exp Short Shank/ Carapace	3	--	----	--	--	1,004
			--	--	Standard T-Bar	--	--	
			--	--	Disc	--	--	
		Exp Short Shank/Right Posterior	9	--	----	--	--	
			--	--	Standard T-Bar	--	--	
			1	--	Disc	1	--	
		Exp Long Shank/Left Posterior	1	--	----	--	--	
			1	--	Standard T-Bar	1	--	
			1	1	Disc	1	1	

Table 3 -- Number and type of tags recovered and number and type of tags not retained - *C. opilio*.

Release Year	Recovery Year	Primary Tag	No. Recovered	No. Not Retained	Secondary Tag	No. Recovered	No. Not Retained	Average Time At Large Days
1980	1980	Exp Short Shank/ Carapace	9	--	----	--	--	15
			8	--	Standard T-Bar	7	1	
		Exp Short Shank/ Posterior	11	--	----	--	--	
			7	2	Standard T-Bar	9	1	
		Exp Long Shank	8	--	----	--	--	
			16	2	Standard T-Bar	14	4	
1980	1981	Exp Short Shank/ Carapace	23	--	----	--	--	315
			26	1	Standard T-Bar	26	1	
		Exp Short Shank/Right Posterior	57	--	----	--	--	
			46	3	Standard T-Bar	44	5	
		Exp Long Shank/Left Posterior	38	--	----	--	--	
			26	--	Standard T-Bar	22	4	
1980	1982	Exp Short Shank/ Carapace	2	--	----	--	--	698
			1	--	Standard T-Bar	1	--	
		Exp Short Shank/Right Posterior	--	--	----	--	--	
			--	--	Standard T-Bar	--	--	
		Exp Long Shank/Left Posterior	--	--	----	--	--	
			--	--	Standard T-Bar	--	--	

Table 4. Calculation of tag loss rates for *C. bairdi* tagged in 1979 and returned in 1980.

Primary Tag (A)	Secondary Tag (B)	Number Returned			Loss Rates			
		A	B	AB	A	SE	B	SE
Exp Short Shank Carapace	Standard T-Bar	6	3	49	0.06	0.03	0.11	0.06
Exp Short Shank	Disc	11	1	39	0.02	0.02	0.22	0.04
			Pooled Data*		0.04	0.03	0.14	0.05
Exp Short Shank Right Posterior	Standard T-Bar	5	3	33	0.08	0.05	0.13	0.05
Exp Short Shank Right Posterior	Disc	8	7	8	0.50	0.13	0.50	0.12
			Pooled Data		0.13	0.08	0.19	0.08
Exp Long Shank Left Posterior	Standard T-Bar	1	7	29	0.19	0.07	0.03	0.03
Exp Long Shank Left Posterior	Disc	11	6	45	0.12	0.05	0.20	0.05
			Pooled Data		0.14	0.05	0.08	0.05

*Pooled data weighted by reciprocal variances (w). Pooled loss rates = Σ W (loss rate) / Σ W.

Table 5 -- Growth data from 1978-1982 tag recoveries.

Primary Tag	Location	Secondary Tag	Location	Release Date	Width mm	Recovery Date	Width mm	Growth mm	% Increase	Average Time At Large	
										Month	Days
		Chionoecetes bairdi:		Recovered within 12 months of release.							
Exp S S	Carapace	T-Bar	R Branchial	5/22/79	122	5/13/80	153	31	25.4	11	21
Exp L S	L Posterior	None	---	6/08/79	129	4/10/80	161	32	24.8	10	6
Exp S S	Lost	T-Bar	R Branchial	5/27/79	139	4/23/80	159	20	14.4	11	26
Exp L S	L Posterior	T-Bar	R Branchial	5/25/79	139	4/05/80	153	14	10.1	10	2
Exp L S	L Posterior	None	---	5/25/79	139	4/23/80	165	26	18.7	11	0
Exp S S	Carapace	T-Bar	R Branchial	5/22/79	139	4/29/80	161	22	15.8	11	7
Exp L S	L Posterior	None	---	6/08/79	142	5/14/80	171	29	20.4	11	6
Exp L S	L Posterior	T-Bar	R Branchial	6/08/79	143	5/09/80	154	11	7.7	11	1
Exp L S	L Posterior	T-Bar	Lost	6/08/79	144	4/10/80	161	17	11.8	10	2
Exp L S	L Posterior	None	---	6/08/79	145	3/31/80	158	13	9.0	9	23
Exp S S	Carapace	None	---	6/09/79	149	4/27/80	175	26	17.4	10	18
Exp L S	L Posterior	None	---	6/08/79	154	4/28/80	173	19	12.3	10	20
Tapered T-Bar	Carapace	None	---	8/20/78	163	4/05/79	177	14	8.5	7	17
		Chionoecetes bairdi:		Recoverd more than 12 months after release.							
Exp S S	R Posterior	T-Bar	R Branchial	6/06/79	140	3/15/81	161	21	15.0	21	9
Tapered T-Bar	Carapace	None	---	8/17/78	142	3/17/80	154	12	8.5	24	0
Exp S S	Carapace	None	---	6/09/79	149	3/04/81	169	20	13.5	21	25
		Chionoecetes opilio:		Recovered within 12 months of release.							
Exp S S	Lost	T-Bar	R Branchial	5/31/80	108	6/15/80	123	15	13.9	0	15
Exp L S	L Posterior	None	---	5/28/80	110	5/04/81	117	7	6.4	11	26
Exp L S	L Posterior	T-Bar	Lost	5/28/80	112	4/13/81	129	17	15.2	9	15
Exp S S	R Posterior	None	---	5/22/80	114	5/08/81	137	23	20.2	11	16
Exp S S	R Posterior	T-Bar	R Branchial	5/31/80	115	3/14/81	125	10	8.6	9	14
Exp L S	L Posterior	None	---	5/28/80	124	4/20/81	140	16	12.9	9	23
		Chionoecetes opilio:		Recovered more than 12 months after release.							
Exp S S	Carapace	None	---	5/20/80	97	5/09/82	107	10	10.3	23	19

During the 1979 experiment, 8,147 *C. bairdi* were tagged with the experimental short shank and experimental long shank tags at various locations (Table 1). Both types of experimental tags appeared to be improvements over the tapered T-bar tag design. Six hundred and sixty one marked crab were recaptured during the 1980-82 fishing seasons (Table 2). Of the 323 double-marked crab that were recaptured, only 31 did not retain an experimental tag.

Experimental short and long shaft T-bar tags were used in 1980 for tagging *C. opilio*. Locations of tag insertion were the same as those used in 1979. Of the 10,835 individuals tagged and released in 1980, a total of 277 *C. opilio* were recovered during the 1980, 1981, and 1982 fishing seasons (Table 3). Tag retention again appeared relatively high. Only 8 of the 131 recaptured double-marked crab failed to retain an experimental tag.

In summary, experimental long and short shaft T-bar tags appeared to have much better tag retention than the tapered T-bar.

Tag Retention

Double tagging of tanner crabs was carried out in 1978, 1979, and 1980 for the purpose of estimating tag loss rates. Methods described by Seber (1973) were used to calculate the probability of tag loss. Calculated tag loss rates for tags released in 1979 and recovered in 1980 indicate a similar retention rate for the experimental short shank and experimental long shank tags (Table 4). In addition to the considerable improvement of the experimental models over the tapered T-bar design, loss rates of the experimental models compared to the basic T-bar design were nearly identical. Rates of T-bar tag loss were also about the same as those of disk tags. Use of the experimental tags also appeared to improve tag retentions through ecdysis.

The tag retention data indicated that tag loss was not an insurmountable problem, at least during the first year after release, but gave little guidance as to the overall problem of low return rates. The rates of returns for all marked tanner crabs were much lower than anticipated on the basis of estimated exploitation rates in excess of 40% annually. For example, the expected number of returns for legal size ($\geq$ 140 mm carapace width) *C. bairdi* tagged in 1979 and recovered in 1980, exclusive of tag loss but incorporating rates of natural mortality ($M = 0.233$, Somerton, 1981) and fishing exploitation (61%), was estimated to be 1,360 individuals. Actual returns totalled only 476 crab or 35% of the expected amount. Possible reasons for low return rates include 1) tagging mortality, 2) tag loss, and, 3) the nonreporting of tagged crab.

Growth

Little information on growth per molt has been obtained from the tagging effort. Only 16 *C. bairdi* and seven *C. opilio* have been returned that showed an increase of carapace width (Table 5). Of the 10 crabs that were double tagged, eight retained both primary

Although only 1 year's recovery data are available, movements of C. opilio appear to be similar to those of C. bairdi. It is worth noting, however, that the geographic distribution of fishing effort may have influenced results for both species.

SUMMARY

Three years of tagging experiments on tanner crabs in the eastern Bering Sea have generated valuable, although limited, information. Findings from these experiments are as follows.

1) Experimental T-bar tags were developed which appear to have high rates of retention for long time periods but provide only limited growth information because they are not consistently retained through a molt.

2) Returns of tagged crabs were substantially lower than anticipated. The expected number of returns for legal size ($\geq$ 140 mm carapace width) C. bairdi tagged in 1979 and recovered during the following year was estimated to be about 1,360 individuals, but actual returns totalled only 476 crab or 35% of the expected amount. Tagging mortality, tag loss, and nonreporting of tagged crab were possible reasons for the low number of returns.

3) Only 23 growth records were obtained from the 3 years of field experiments out of the 21,240 crab tagged with various T-bar tags.

4) Thirteen C. bairdi, ranging in size from 112 to 163 mm carapace width grew an average of 21.0 mm (15.1% growth) during the 12 month period between release and recapture. Six C. opilio (ranging in size from 108 to 124 mm carapace width) at large for the same length of time exhibited an average size increase of 14.7 mm or 12.9% growth.

5) Net yearly movement of C. bairdi averaged about 43.3 km for individuals at large for up to 1 year and 80 km for those recaptured between 1 and 2 years after release. The greatest net distance travelled in 1 year was 85 km. Most movement appeared to be in a south to southwest direction; however, recoveries of tagged crabs were probably influenced by the distribution of commercial fishing effort.

6) C. opilio appeared to move greater net distances in a year than C. bairdi. The average distance travelled between release and recapture was about 78 km and most movements were in a south to southwest direction.

7) The very low number of growth records obtained from these tagging experiments indicates a need for additional modification of these experimental T-bar tags before they can be considered an effective mark for tanner crabs.

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Abstract

The National Marine Fisheries Service (NMFS), Kodiak Laboratory, has been experimenting with the development of a permanent tag for two commercially important species of tanner crabs since 1978. Prototype tags for use in the eastern Bering Sea were placed on *Chionoecetes bairdi* in 1978 and 1979, and on *C. opilio* in 1980. Tag development, tagging methods, types and numbers of tags released, tag retention, and tag recovery through March 1982 are presented. Growth and migration for each species by year and the continuing need for a permanent tag are discussed.

A Recent Development in Tagging Studies on Snow Crab, *Chionoecetes Opilio* in Newfoundland-Retention of Tags Through Ecdysis

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Introduction

Efforts to gain information on snow crab *Chionoecetes opilio* (O. Fabricius) growth parameters have been ongoing for a number of years. Ito (1970), Kon et al. (1968), and Kanno (1975) studied growth and frequency of molting in snow crab by examining the size-frequency distribution of animals. Miller and Watson (1976) reported on molting in the laboratory of snow crab from the Gulf of St. Lawrence. Although these investigations provided valuable insights into snow crab growth, data on actual growth per molt under natural conditions are currently lacking.

In Newfoundland, *C. opilio* inhabits very deep water (174-412 m) making observations of molting activity by means of SCUBA impossible. The only option available therefore is the use of a tag which will be retained by a molting animal. This has been done successfully by many workers on various crustacean species (Scarratt 1970; Ennis 1972; Bennett 1974; Gundersen 1961; and Edwards 1965). Hilsinger et al. (1975) were successful in recovering *C. bairdi* which had successfully molted in their natural habitat and retained

Floy "T-bar" tags. Fujita and Takeshita (1979) reported that both C. opilio and C. bairdi molted and retained Floy "T-bar" tags while held in salt water tanks on board a Japanese research vessel. This report describes the successful retention of a Floy "T-bar" tag through ecdysis by C. opilio in their natural environment.

Materials and Methods

During the spring of 1979, tagging of C. opilio began in Conception Bay, Newfoundland (Fig. 1, management area 16). Animals were captured by means of Japanese-style conical traps baited with squid (Illex illecebrosus) and set approximately 36 m apart in long-line fleets of 8-12 traps. Traps were hauled at approximately 24 h intervals. Snow crab were removed from the traps and measured across the widest part of the carapace by means of vernier calipers. Hard-shelled animals ($\leq$ 100 mm carapace width) were then tagged in the following manner. Using slight pressure, the carapace was lifted upwards, the needle of the tagging gun was then inserted through the suture line just over the juncture of the fourth walking leg, the needle was angled downward obliquely into the muscle of the shoulder and the tag was then inserted (Fig. 2). The "set" of the tag was tested by a gentle tug. If the tag was secure the animal was immediately released. If the tag was not secure the animal was retagged or discarded depending on whether or not the animal had been injured during the initial tagging. During this at-sea tagging program a sample of approximately 60 animals in 1979 were transported to the Marine Sciences Research Laboratory, Logy Bay, Newfoundland. Animals were tagged in a manner identical to that used at sea in order to test for tag loss under crowded conditions. Tagged

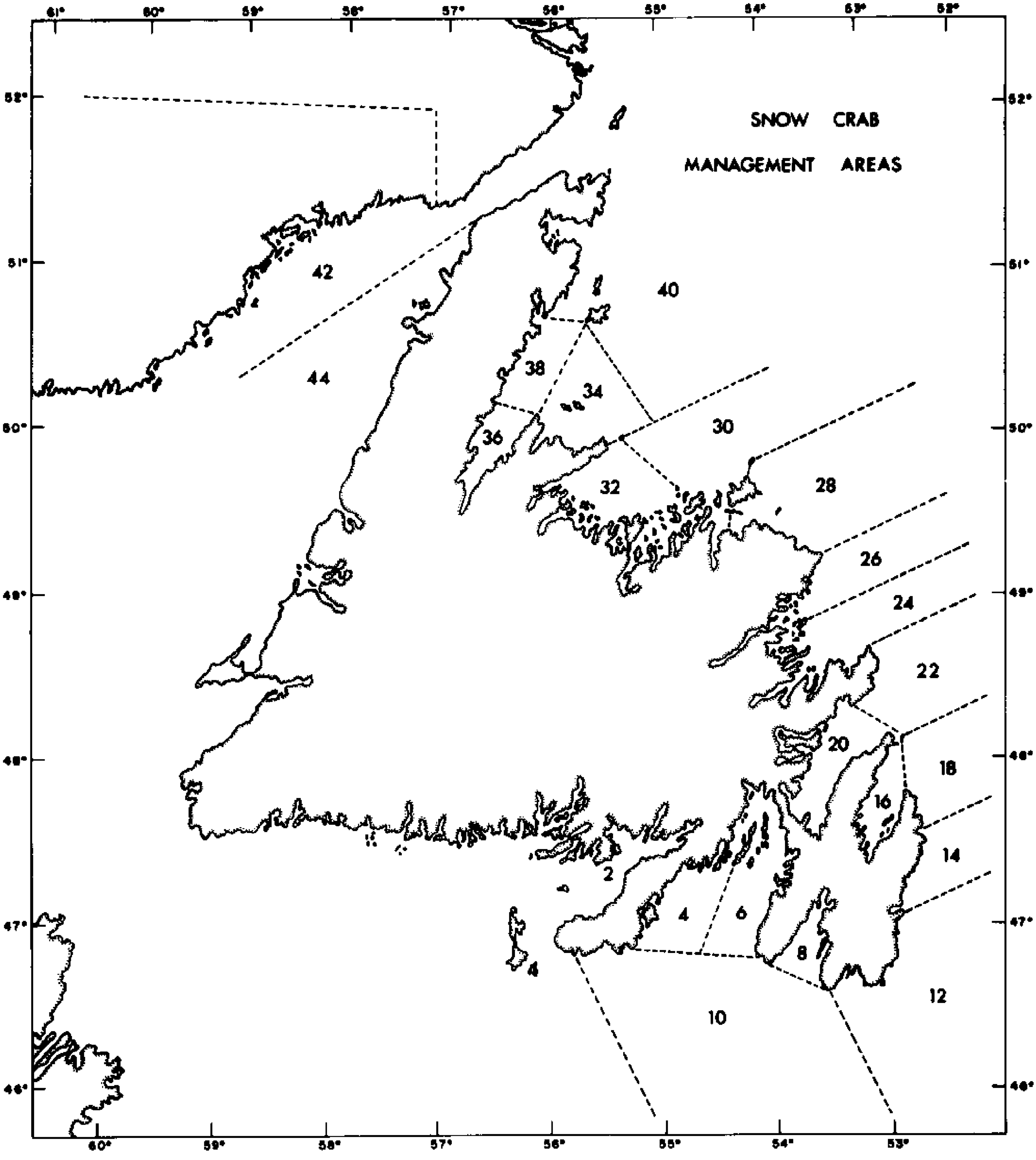


Fig. 1. Newfoundland snow crab management areas (after R.J. Miller, unpublished). For this study, tagging was conducted in Areas 16, 18, 24, and 26.

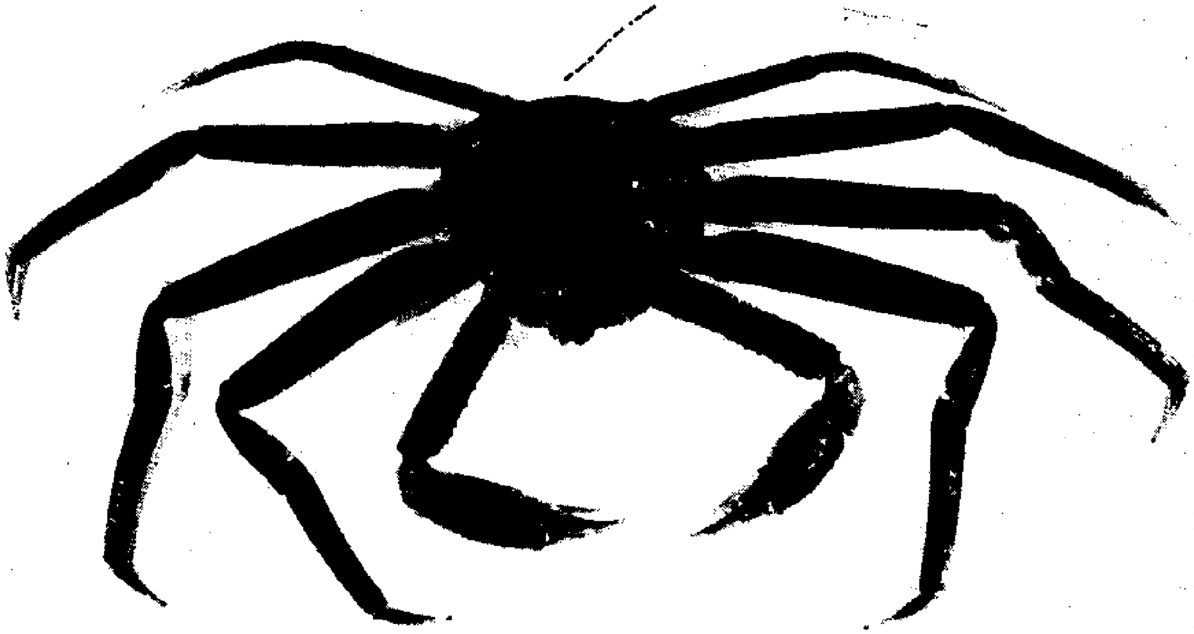


Fig. 2. Male snow crab tagged with Floy "T-bar" tag.

animals were held under high density conditions in tanks adjacent to untagged animals that were also held under crowded conditions. Animals were examined weekly in order to determine tag retention and general vigor.

Throughout the course of these laboratory experiments over three months in duration, no animal lost its tag. Unfortunately, it was not possible to determine whether or not animals retained tags through a molt as a sudden temperature increase resulted in over 90% mortality over a two-day period.

A total of 5481 snow crab with maximum carapace widths ranging from 65 to 100 mm were tagged in four areas: Bonavista, Trinity and Conception bays and in the large commercial fishery area northeast of St. John's (Fig. 1).

Results and Discussion

To date, 7 animals that have successfully molted and retained their "T-bar" tags have been recovered. Growth increments have varied ranging from 13 to 35% (Table 1). The shell condition of all animals that had molted were shell of the year; 6 animals had hard shells while one animal, #2, was soft shelled.

Animal #5 is interesting in that in only 6 months it not only increased in size by 35% but also recovered to the hard-shelled condition. Preliminary data based on tagging and recovery of soft-shelled animals in Bonavista Bay indicate that recently-molted animals require at least 1½ months to recover to a hard-shelled condition (Taylor, unpub. data). Therefore, it is conceivable that this particular animal molted twice during its time at large.

Table 1. "T-bar" tag returns - molted snow crab.

No.	Date tagged	Date recovered	Days at large	Carapace width pre-molt (mm)	Carapace width post-molt (mm)	Growth	
						mm	%
1	May 7/79	June 17/81	772	94	118	24	25.5
2	Aug. 16/79	May 5/81	628	100	122	22	22.0
3	Mar. 29/80	May 25/81	423	100	114	14	14.0
4	Apr. 28/80	Nov. 1/80	188	92	104	12	13.0
5	Nov. 12/80	July 14/81	245	97	131	34	35.1
6	Mar. 23/80	Sept. 18/81	545	86	107	21	24.4
7	Apr. 28/80	Apr. 5/82	708	88	106	18	20.5

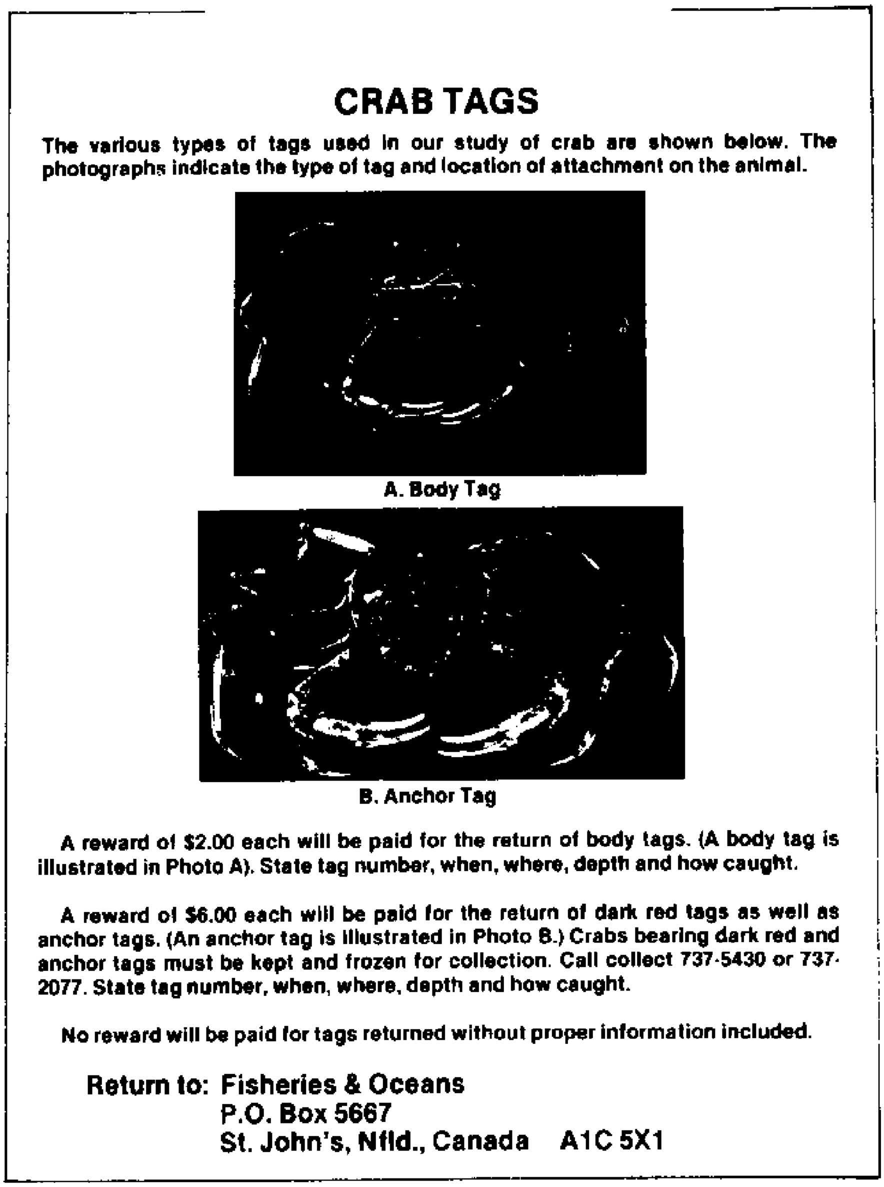
Table 2. Summary of "T-bar" tag returns, May 1979-October 1981.

Year	No. Tagged	Area	No. Returned (%)		No. Returned (%) with crab		No. Returned (%) without crab	
1979	1060	16, 18	72	(6.8)	16	(1.5)	56	(5.3)
1980	1768	16, 18	79	(4.5)	35	(2.0)	44	(2.5)
1981	2519	16, 24, 26	46	(1.8)	27	(1.1)	19	(0.8)

Excluding snow crab #5 which had increased in carapace width by 35%, the mean percentage growth increment of animals examined in this study was 20.0%. Miller and Watson (1976) reported a mean growth increment of 18.4% for mature male snow crab from the Gulf of St. Lawrence, while Hilsinger et al. (1975) had a mean growth increment of 18.6% for C. bairdi that had been tagged, released and recaptured. Results of t-tests performed showed that there was no significant statistical difference in percentage growth increments for the three studies (P values of 0.4-0.5).

Many animals that were tagged and held at the laboratory developed shell necrosis around the area of tag insertion. However, none of the animals examined upon recapture from the commercial fishing grounds exhibited any sign of shell deterioration. This is possibly due to the fact that bottom temperatures are extremely low in the snow crab's natural habitat -1.0 to 1.0°C.

Many tags were returned without the required information. The fact that most of these were returned by processing plant employees indicates that fishermen have difficulty in readily identifying and retrieving these tags even though each fisherman is given a reward poster (Fig. 3) which clearly illustrates the type and location of the various tags used in our tagging studies. Also, the tags are brightly colored (yellow, pink and orange) in order to attract attention. It is noteworthy that the incidence of tags returned without the animals has decreased somewhat since tag rewards were raised in July 1981 from four dollars to six dollars while, at the same time, rewards for tags without the crab were maintained at two dollars.



CRAB TAGS

The various types of tags used in our study of crab are shown below. The photographs indicate the type of tag and location of attachment on the animal.

A. Body Tag

B. Anchor Tag

A reward of $2.00 each will be paid for the return of body tags. (A body tag is illustrated in Photo A). State tag number, when, where, depth and how caught.

A reward of $6.00 each will be paid for the return of dark red tags as well as anchor tags. (An anchor tag is illustrated in Photo B.) Crabs bearing dark red and anchor tags must be kept and frozen for collection. Call collect 737-5430 or 737-2077. State tag number, when, where, depth and how caught.

No reward will be paid for tags returned without proper information included.

Return to: Fisheries & Oceans
P.O. Box 5667
St. John's, Nfld., Canada A1C 5X1

Fig. 3. "Reward" poster illustrating various tags used in Newfoundland tagging studies.

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Effects of Harvesting

Some Effects of Long-Term Exploitation of *C. Opilio* Stocks in the Southwest Japan Sea

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INTRODUCTION

In the southwest Japan Sea, Zuwai crabs (*Chionoecetes opilio*) are harvested by the Danish seine fishery during the five winter months. This crab constitutes the greater part of the catches taken by seiners from depths between 200 and 350 m in the sea off Hyogo Prefecture (Figure 1). For example, during November 1966 to March 1967 about 23.7 tons of male crabs and 2.6 tons of female crabs were caught by one fishing boat of 25 gross tons in the area.

The landing in 1964 marked the peak of the crab fisheries in the southwest Japan Sea and resulted mainly from increasing intensity of exploitation by modernized seiners and increasing market demand. The catch of Zuwai crab shows a sharp downward trend in its main fishing grounds since 1964. The fishermen and the fishery scientists involved with this species have been working on development of a method for profitable management of the resource. Unfortunately, no effective actions have been taken by the fisheries management authority to date.

The primary objective of this report is to examine the apparent effect of exploitation on crab populations in the region of Hyogo Prefecture, and to demonstrate adequate measures for conservation of the crab resource. To accomplish this, it is necessary to summarize results of previous investigations and note the many biological problems to be solved.

LONG-TERM CHANGES IN CATCHES OF ZUWAI CRAB

This information was extracted from the annual catch records compiled by the Japanese Bottom Trawl Association. Landings from 1953 to 1980 were recorded as weight in metric tons by sex of crab. Statistics used here for the Danish seiners (average gross tonnage, average horsepower) are available in Annual Reports of the Hyogo Bottom Trawl Association.

The sum of the catches of male and female crabs landed at Hyogo Prefecture from 1953 to 1980 is shown in Figure 2. There was an upward trend from 1953 to 1964, but landings from 1965 to 1980 have sharply declined except during 1969 to 1972. The weight of crabs landed at the ports in Hyogo Prefecture during the last reported fishing season was 1,352 tons, a 73-percent reduction over the 16-year period.

The striking features of changes in catch (Figure 2) include the increase of landings during 1969 to 1972 and the increased horsepower of seiners (Figure 3) followed by catches typically less than 1,500 tons. Concurrently, there

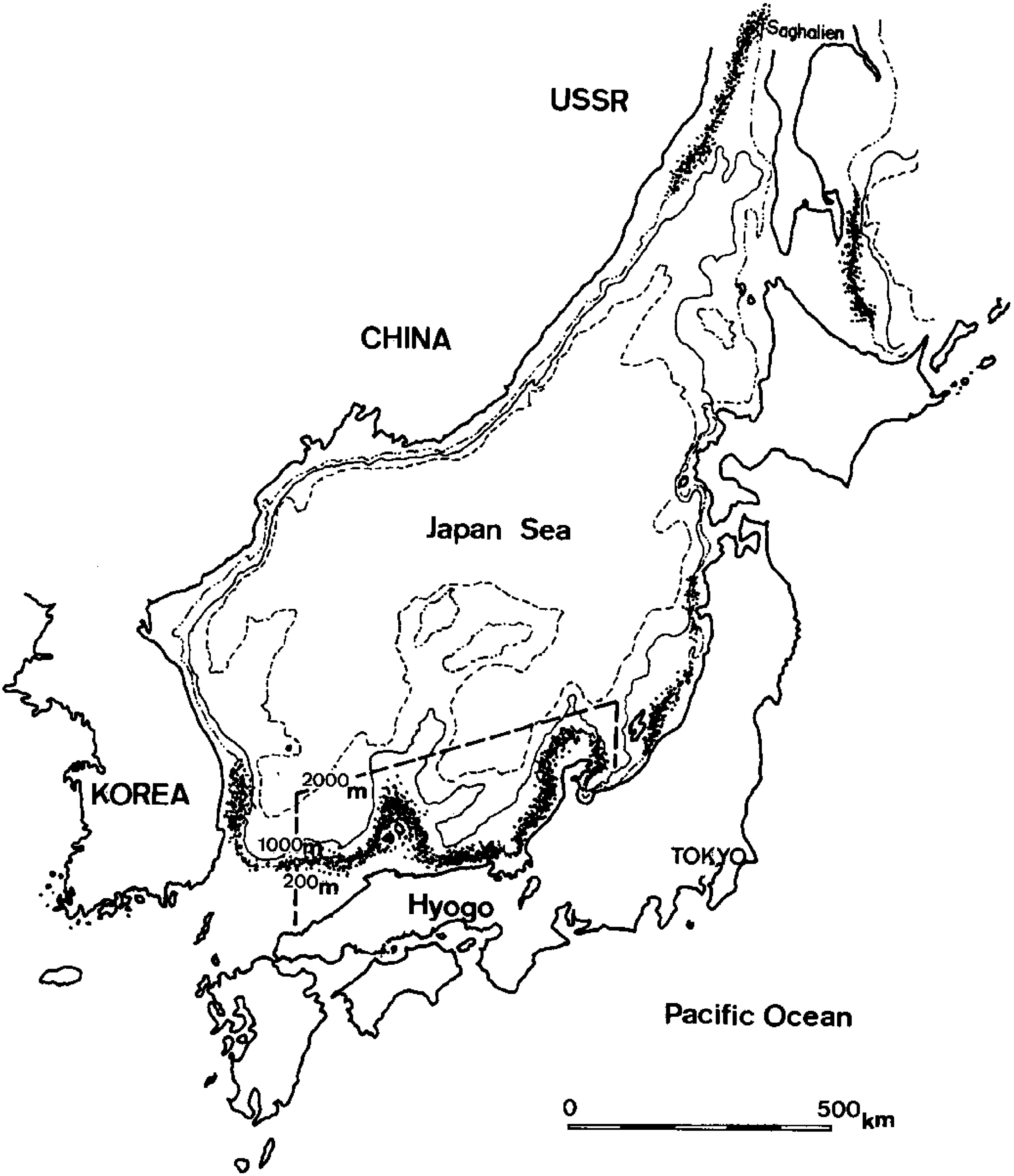

Figure 1. Main areas fished commercially by Danish seiner in the Japan Sea, and distribution of *C. opilio*.

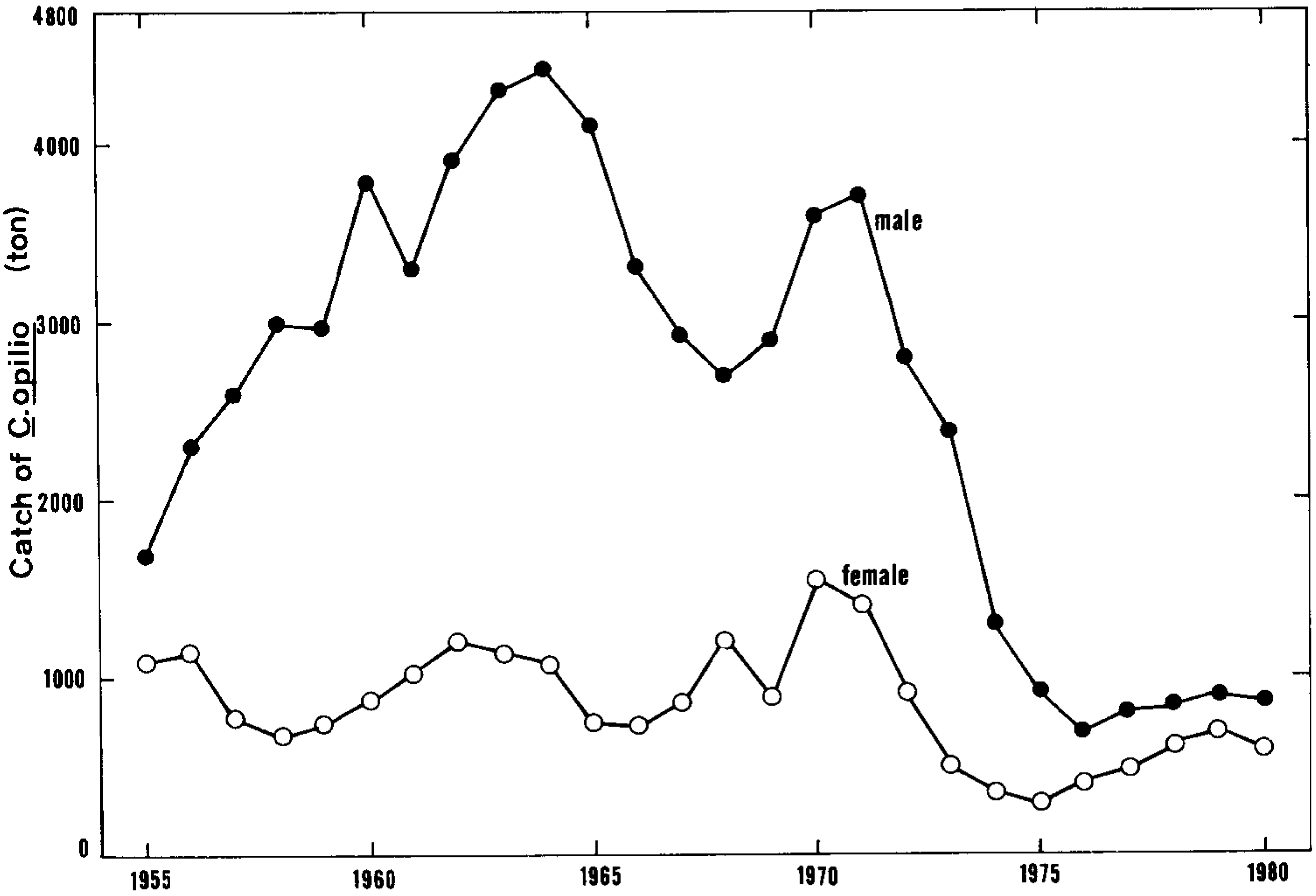

Figure 2. Catches of male and female crabs landed at Hyogo Prefecture.

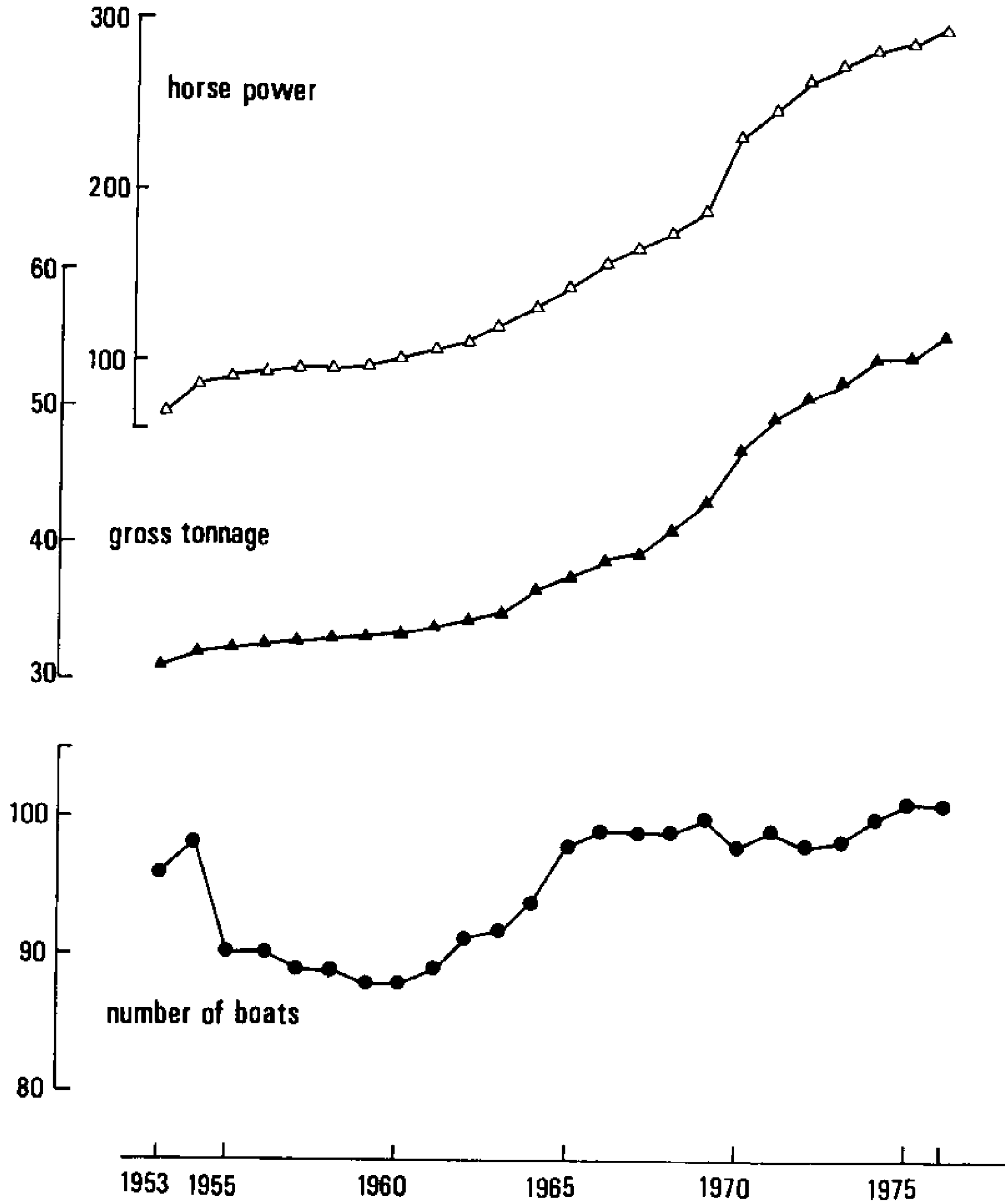

Figure 3. Increases of horsepower, gross tonnage and number of offshore Danish seiners belonging to Hyogo Prefecture.

was a progressive replacement of male crab by female crab in the catch. It appears that increased landings from 1969 to 1972 were due mainly to the changeover to 60 horsepower vessels, an increase of 32 percent in horsepower. The reasons for the fluctuations in catch over the 25-year period would be better understood if the horsepower of seiners had been intensified with three steps, less than 100 horsepower (1953-1960), 100 to 200 horsepower (1961-1969), and more than 200 horsepower (1970-1980) as shown in Figure 3. With the more powerful vessels it is likely that the increase of the area swept by the net resulted in greater exploitation efficiency and increased exploitation of juvenile and young crabs living together with commercially important adult crabs.

DIFFERENCES IN BATHYMETRIC DISTRIBUTION BETWEEN THE 1964 AND 1975 FISHING SEASONS

During September 1963 and August 1964 the Hyogo Prefectural Fisheries Experimental Station carried out an ecological study on the Zuwai crab in the sea off Kasumi in cooperation with the Japan Sea Regional Fisheries Research Laboratory (Kobayashi, 1977). Experimental fishing was carried out by the station for 10 years using the same gear and sampling sites in order to see the effect of long-term exploitation on the bathymetric distribution of the Zuwai crab (Kobayashi, 1977). The data published in these surveys were used in the present study.

The stations in the study were in a straight line at 25 m depth intervals from 175 to 350 m and were sampled over all experiments. The eight stations from 175 to 350 m were sampled once a month with a Danish seine having a cod end with 3.6 cm mesh (stretched) and the fishing time of 50 to 60 minutes. The duration of tow included the final stage of casting off the sweep line, chains, and warps and ended when hauling in the gear was initiated. The difference in depth between the beginning and the end of the tow was on the order of 7 m.

From December 1974 to April 1975 a total of 32 sampling periods occurred at the same sampling stations at 25 m depth intervals from 200 to 350 m as in 1964 to 1965. Crabs were grouped into the same categories as in 1964 to 1965 to compare abundance with the previous bathymetric distributions. The crabs were grouped into three size classes of carapace width regardless of the degree of maturity; juvenile crabs (30 mm and below), young crabs (31 to 70 mm), and adult crabs (71 mm and above).

Distribution of Juvenile Crabs

Juvenile crabs, 2,005 females and 1,881 males, were taken from 200 to 350 m in depth with the greatest abundance appearing to be from 275 to 250 m. The bathymetric distributions for the juvenile crabs by sex and season are shown in Figure 4. The distribution patterns of male and female crabs are similar to each other throughout a year. Juvenile crabs were concentrated at greater depths from 275 to 350 m during March and April and July and August (Figure 4). The disappearance and appearance of juvenile crabs suggest that either smaller crabs are lost to predation or disease or they grow. It is reasonable to suppose the increased abundance in the juvenile class results from recruitment as growth proceeds. A Danish seine does not take crabs smaller than 10 mm, and growth of these small crabs might contribute to increases in the juvenile group. It seems that the juveniles of about 13.5 mm carapace width appear in summer, having been hatched in spring (February through April) (Sinoda, 1970). After the period of recruitment into the catchable size range, the juvenile crabs gradually move into shallower water.

Distribution of Young Crabs

The carapace width of mature female crabs seems to be above 60 mm, and the data on young females used here are from immature individuals only. The 50-percent maturity point of male crabs appears to occur between 50 and 60 mm carapace width, thus young males classified (31 to 70 mm) here might consist of both immature and mature crabs.

The copulation of the primary spawning group is in September and October (Ito, 1967), and that of the adult spawning group is in January and February as shown in Table 1. In order to spawn, crabs migrate into shallow water and, after copulation, migrate back to deeper water (Ito, 1967). In Figure 5, the observed bathymetric data for September and October are grouped into two depth categories. We can suggest that the group G_2 (Figure 5) represents the primary spawning population and G_1 represents younger population. During September and October the G_1 was more abundant at 300 to 350 m, and G_2 at 200 to 250 m. After primary spawning, both populations, G_1 and G_2, may intermix at depths of between 200 and 275 m in early winter. The two groups may be concentrated around 275 m depth in midwinter; the upward movement of group G_1 may continue, and group G_2 may migrate to deeper water during about March and April with the segregation of the two sexes. In spring or early summer the primary spawning crabs with very small and undeveloped eggs seem to recruit into the more advanced spawning groups.

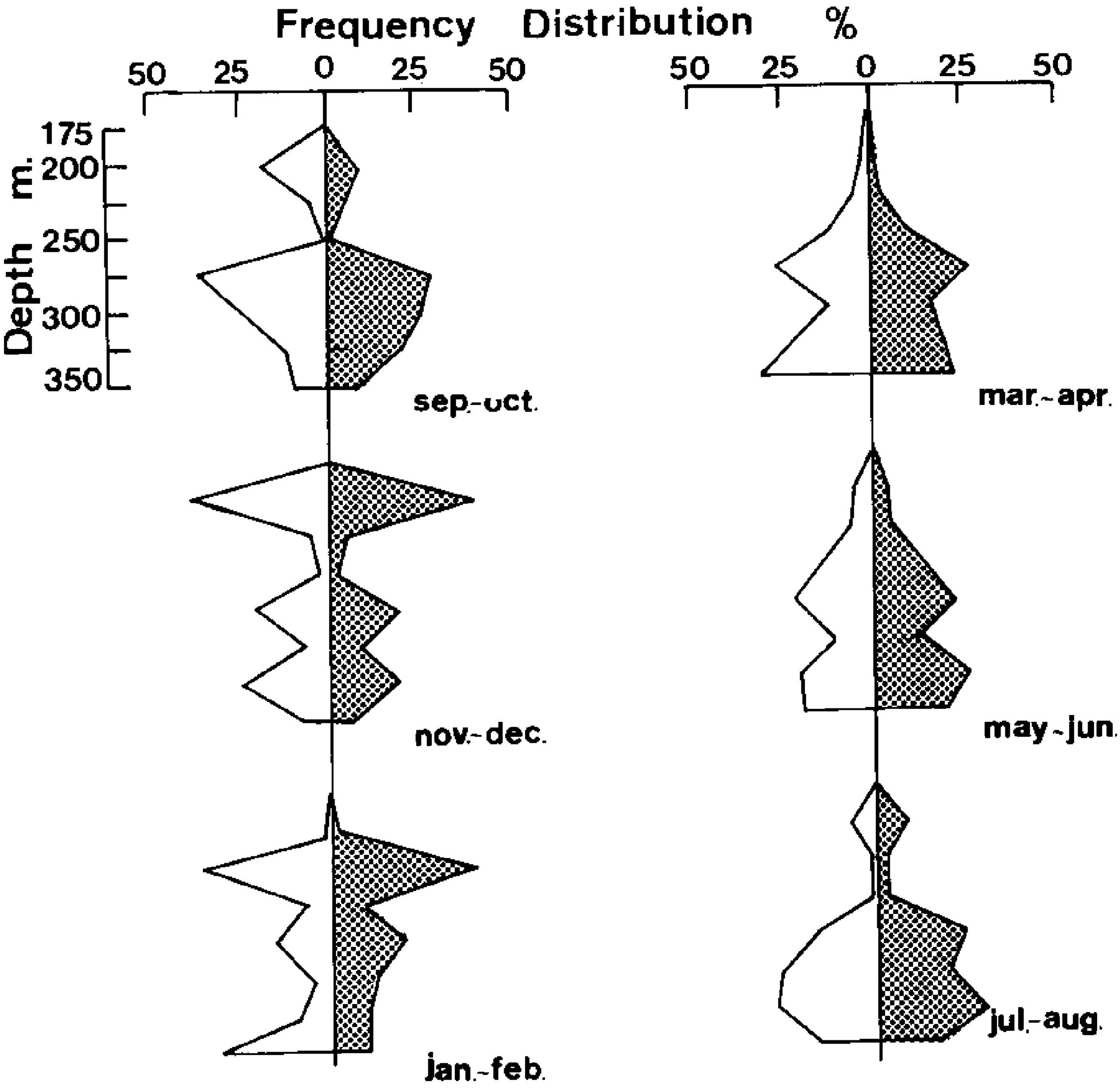

Figure 4. Bathymetric distribution and its seasonal variation of juvenile crabs, open area: females, closed area: males.

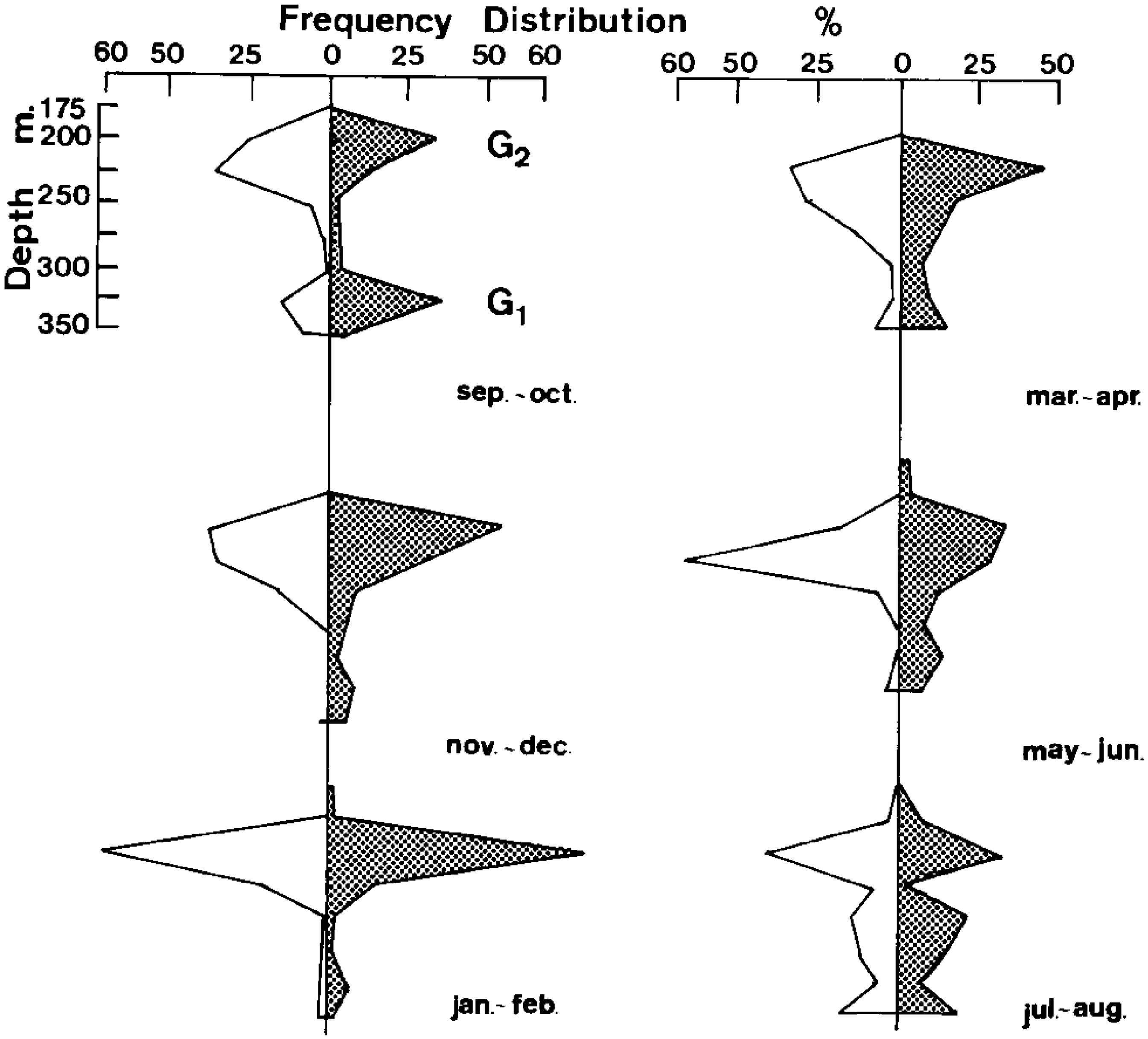

Figure 5. Bathymetric distribution and its seasonal variation of young crabs. Keys as in Figure 4. G_1: adult spawning group, G_2: primary spawning group.

Distribution of Adult Crabs

The seasonal pattern of bathymetric movements of the two sexes was complicated, as shown in Figure 6. Males were encountered at depths from 175 to 350 m, but females were concentrated at depths of from approximately 225 to 275 m. The male population exhibited seasonal bathymetric movements, and the females were stationary. During summer and autumn the two sexes were separated, with the males most abundant between 250 and 350 m, and the females between 225 and 250 m. After the period of separation, the male population may move gradually into the shallower water where the female is abundant. Two distinct groups in depths of from 225 to 275 m and from 300 to 350 m are observed in January and February (Figure 6). No difference between the size distributions of these two groups was recognized, but the shallow group had many soft crabs (Yoshida, 1941). Perhaps the two sexes were concentrated at two depths for spawning and the appearance of two groups resulted from the complexity of the bathymetric and horizontal movement. The spawning season of this species has been reported as January through March in the Japan Sea (Table 1).

As summarized in Figure 7, juvenile crabs that had been captured abundantly from 275 to 350 m and the primary spawning group that had been more abundant in shallow water (200 to 250 m) have disappeared. This finding implies that the recruitment into the catchable stock of Zuwai crab has been seriously damaged. It is suggested that intensive exploitations of the stock, not only adults but immature crabs, by Danish seiners is an important factor in this population decline. As mentioned earlier, catches have reached the lowest level since 1974, and there has not been an upward trend although Danish seiners have installed the more powerful engines. Therefore, it is suggested that because of possible damages to the young crab population, catches below 1974 levels may occur in the southwest Japan Sea in the future.

DECREASE IN AVERAGE CARAPACE SIZE OF MALE CRABS

A gradual decrease in average carapace size of male crabs in the landings is described as one effect of exploitation of the stock. Since 1964 the carapace measurements of male crabs landed at Kasumi port have been made, and the average carapace size of male crabs has also been obtained from experimental fishing. As small crabs of less than 9 cm carapace width cannot be legally landed, the asymptotic carapace width of male crabs as successive exploitation may be around 9 cm after a sufficiently long period. Conversely, the average carapace width of crabs caught by experimental fishing may be dissimilar because measurements of carapace size were made for all crabs appearing in the net.

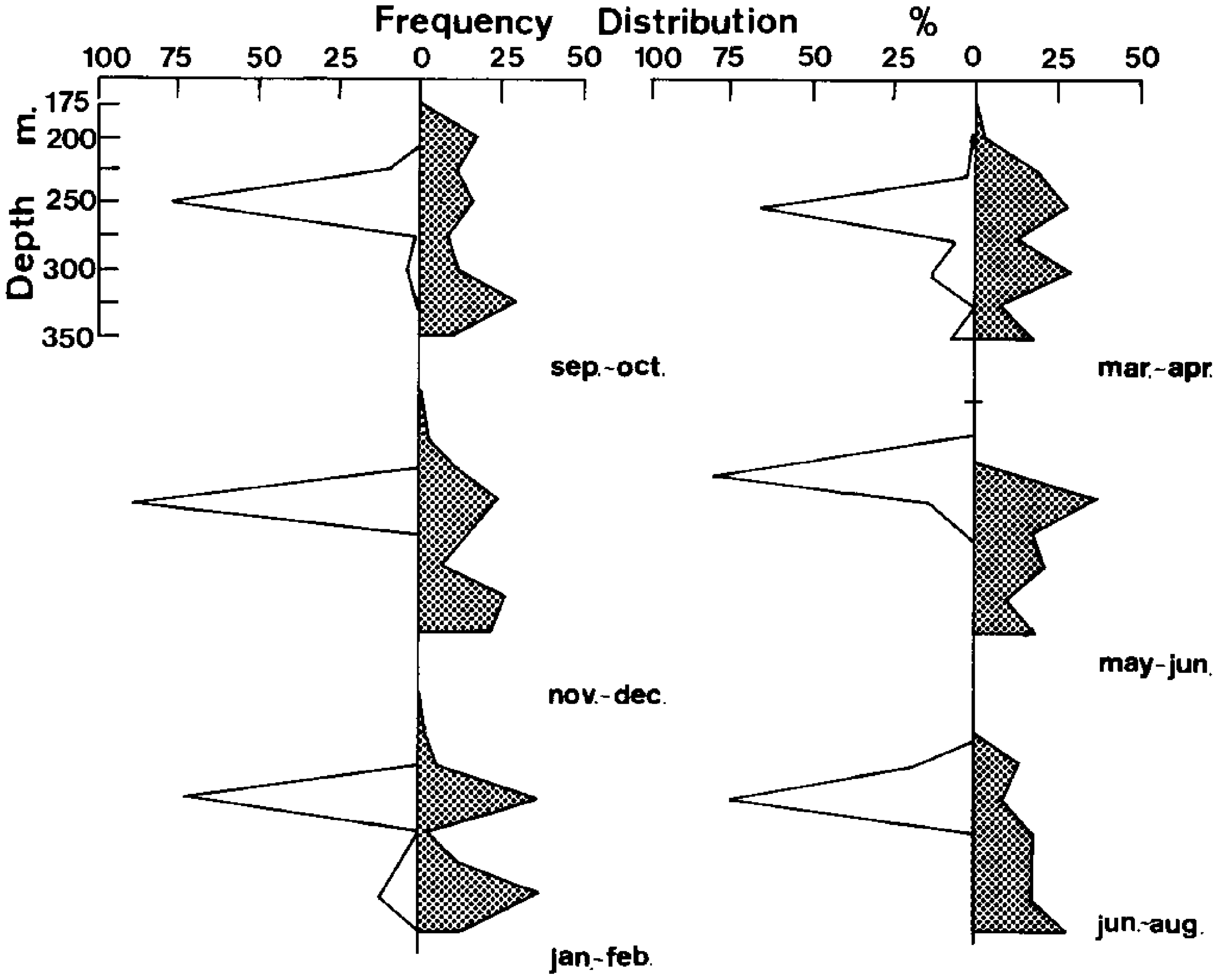

Figure 6. Bathymetric distribution and its seasonal variation of adult crabs. Key as in Figure 4.

TABLE 1

SPAWNING SEASON OF ZUWAI CRAB, *CHIONOECETES OPILIO*, ESTIMATED BY FOUR RESEARCHERS

	K. Ito (1967)	T. Kobayashi (1966)	T. Kon (1970)	H. Yoshida (1941)
Primary Spawning Group	Sep.-Oct.	Aug.-Oct.	Jun.-Sep.	-
Adult Spawning Group	Feb.-Apr.	Feb.-Mar.	(Dec.-Apr.)	Feb.-May

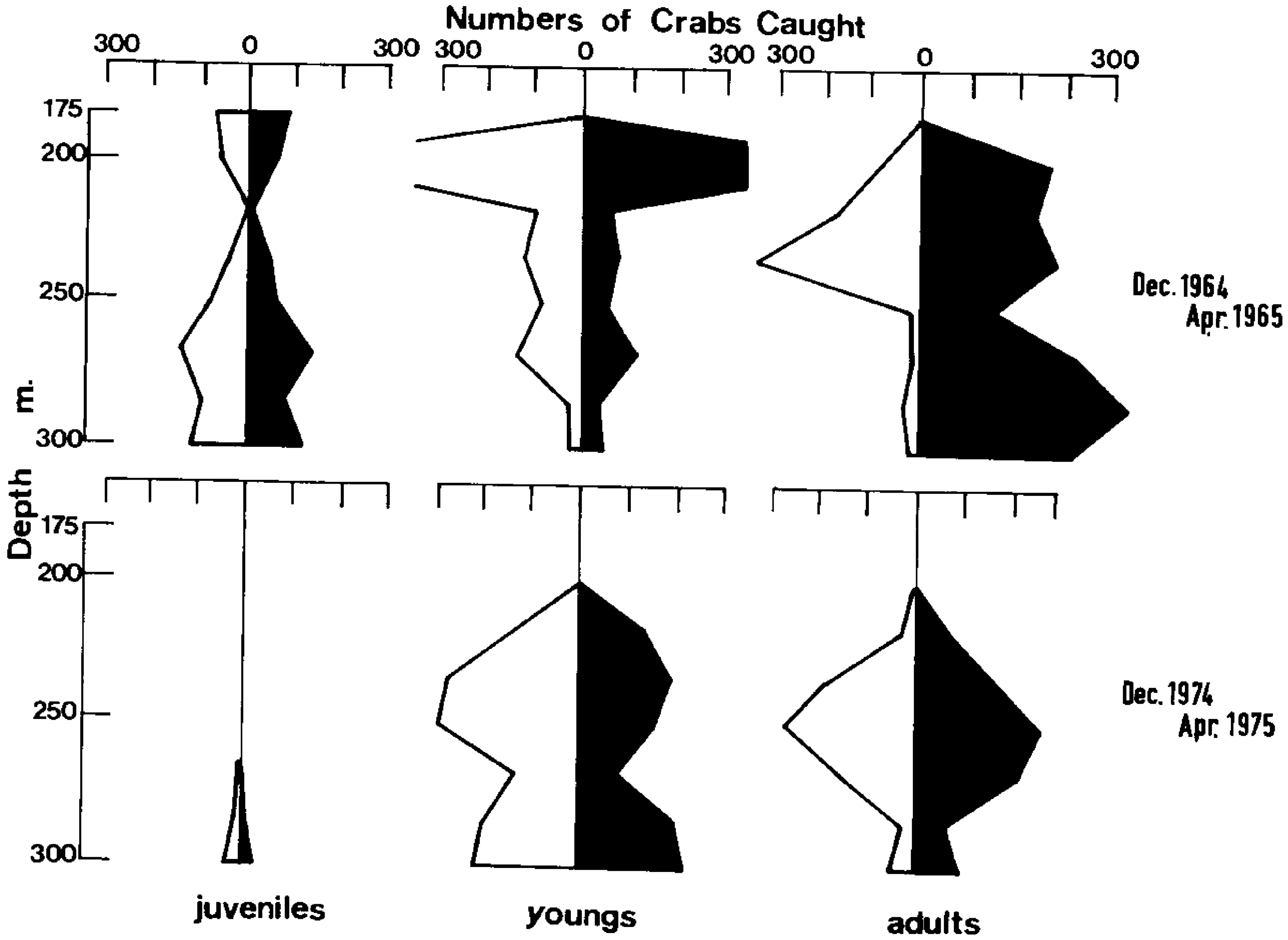

Figure 7. Comparison of bathymetric distributions between two fishing seasons, open area: females, closed area: males.

It appears that about 24 percent contradiction in the carapace width has resulted from long-term fishing from 1964 to 1980 (Figure 8). Asymptotic carapace widths in both catches, estimated by Kawakami and Kitahara's equation (Kawakami and Kitahara, 1964), are 91.5 mm (commercial catch) and 57.5 mm (experimental catch), respectively.

For the crab fishery by Danish seine, the selectivity curve of cod-end is not precise, and there is chance for capturing a variety of sizes. In practice, crabs of 10 to 30 mm carapace widths caught in a net are returned to the sea after sorting the legal-sized crabs. It is likely that juvenile stocks are heavily exploited, thus leading to a decrease in the average size of crab. Since early mortality rates are important in determining future abundance of a stock, this gradual decrease in crab size from about 120 to 90 mm is an advance sign indicating poor landings in coming years.

HIGH MORTALITY OF FEMALE CRABS

Catches of female crabs are restricted to the egg-carrying group and immature ones are not landed. The bathymetric distribution of females is rather shallow and aggregative, thus they can be more easily fished than males. In carapace size compositions, four distinguishable groups are seen (Sinoda, 1968). Each group may be recognized as a molt class. According to existing knowledge concerning the molting cycle of this crab, they molt once a year. The oldest group as shown in Figure 9 presents some difficulty because this group is considered to contain more than one age class since mature females do not molt. In tagging experiments, crabs marked at the berried stage have been recaptured one to three years later with same size carapaces as when they were released. Although it is not known how long the female crab has lived from terminal molt to the time of marking and how long the crab would live if not recaptured, if a three-year life span is assumed, the number of the oldest group can be given by:

$$N = N_{t_c} \frac{1 - S(\Delta t + 1)}{1 - S}, \qquad (1)$$

and

$$\frac{N}{N_{t_c}} = \frac{S(1 - S(\Delta t + 1)}{1 - S}, \qquad (2)$$

where:

N : Total number of the oldest group (Group II in Figure 9)

N_{t_c} : Number of the youngest class in N

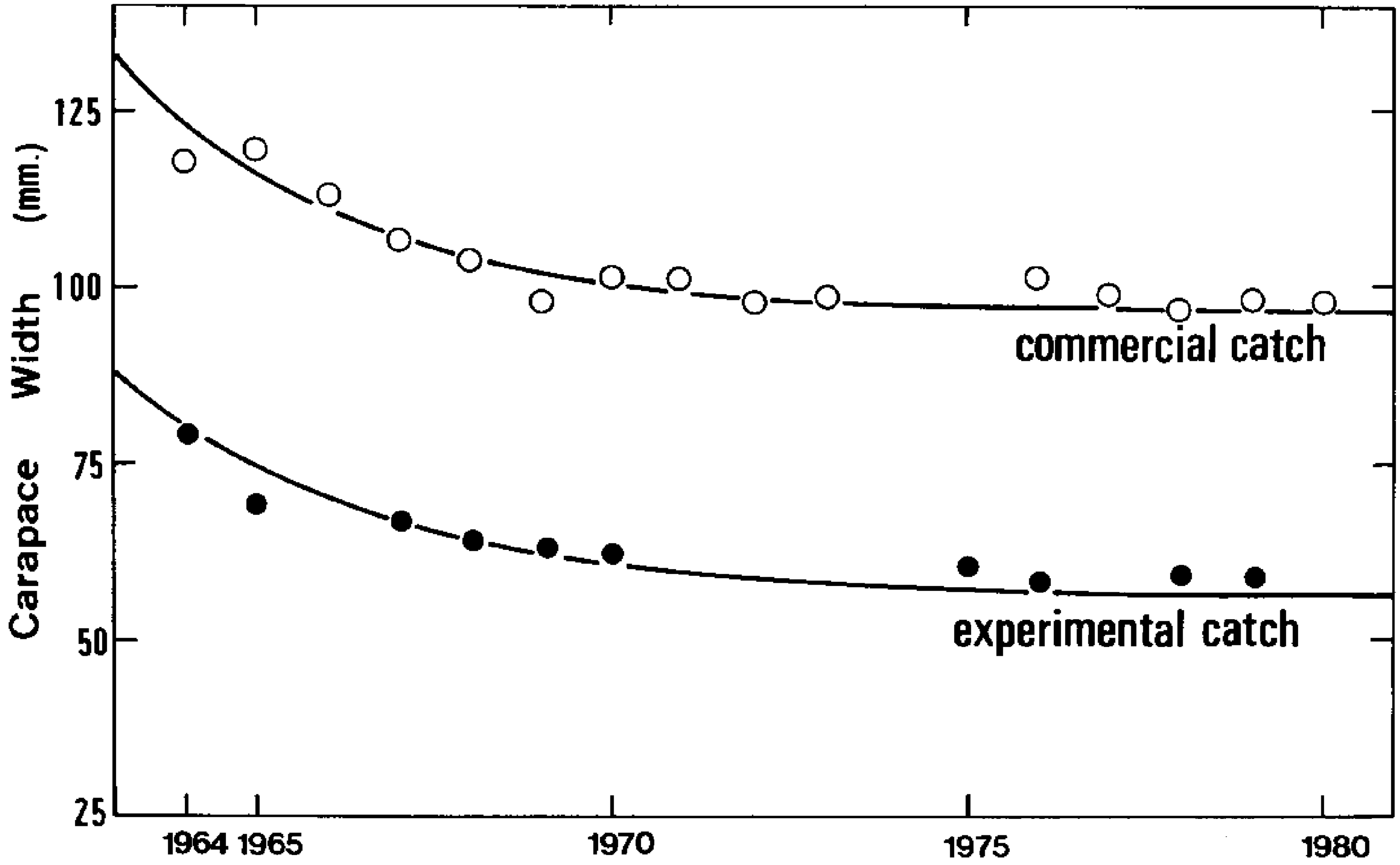

Figure 8. Calculated and observed carapace widths.

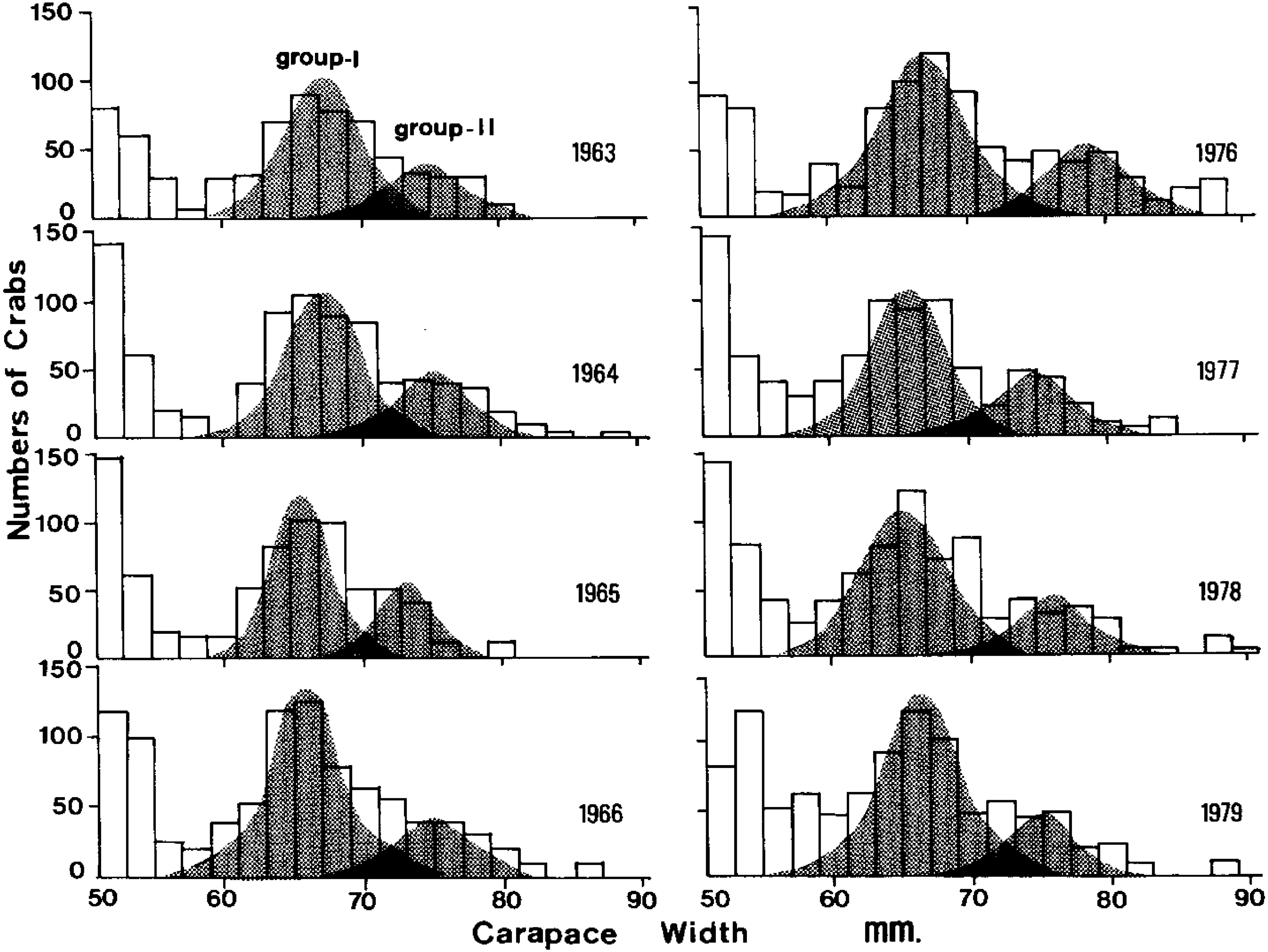

Figure 9. Carapace width compositions of female crab caught by experimental seinings.

N_{t_c-1} : Number of one year younger group than N_{t_c} (Group I)

S : Survival rate of mature crab

Δt : Life span after terminal molt

From equation (2) we can easily obtain the value S for various Δt as shown in Figure 10, in which S is converted into total mortality coefficient Z, assuming that the life span Δt is three years (Sinoda, 1968). During the early period (1963 to 1966), the values of Z reached around 1.5 year^{-1}, and consistently high figures are evaluated over five years, 1977 to 1979, when landings of female crab showed a slight upward trend.

A consistent increase in the total fecundity of crab stocks which incorporates protection of berried females is urgently required. Because it is extremely difficult to assess mortality in natural stocks, as a temporary measure, the nonselective exploitation of female crabs should be legally prohibited.

DISCUSSION

It should be emphasized that the marked decline of landings is further demonstrated by a decreased mean carapace size and by the high mortality rate for females. This situation suggests that fishing mortality with nonselective trawls has outweighted recruitment by the prerecruit age group. Danish seiners harvest significant numbers of the incoming recruit group, thus an upward trend for landings probably will not appear.

The decrease in prerecruit crab exploitation suggests that we must take drastic measures; for example, a full prohibition of fishing the Zuwai crab during the 5 to 10 year period in a given ground, open and closed areas. Immediately following the closure of a fishing area, the numbers of crabs caught would be down. The immediate loss of landings is unavoidable; however, the crab stock would increase again with protective management.

In the present situation, the mesh size of net commercially used may lead to an increase in the demand for small-sized crabs, therefore the mesh size must be enlarged. The important problem associated with the mesh size control is the catch of other commercially important fish and shrimp together with Zuwai crab. To minimize immediate losses it may be better to increase the mesh size in small stages rather than to have a large increase.

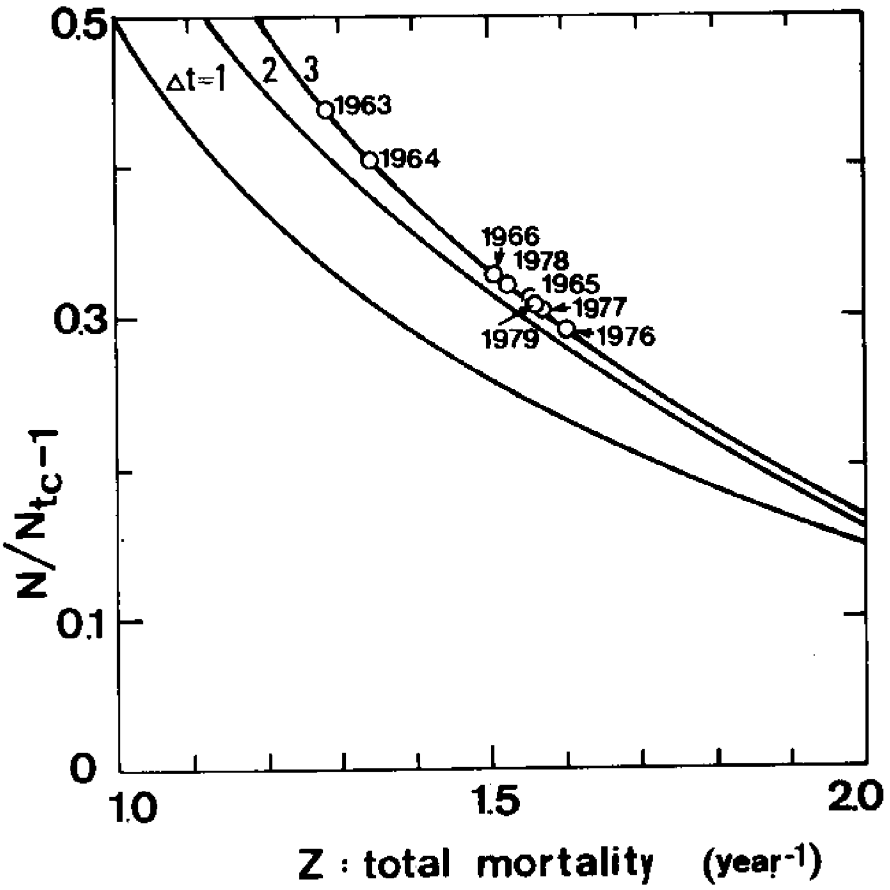

Figure 10. Relationship between N/N_{tc-1} and Z, into which S in equation (2) is converted, Δt: lifespan after terminal molt.

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ABSTRACT

The most productive area for *C. opilio* is the sea off Hyogo Prefecture, from which a total of 6,500 tons (1964) were captured by Danish seiners. After intensive exploitation over the following 10 years, the catch was approximately 1,900 tons in 1974. Experimental fishing data indicated a considerably different catch composition between two statuses of the stock.

To assess factors contributing to the decline of landings, bathymetric distributions for the juveniles (less than 3 cm carapace width), youngs (3.1 to 7.0 cm) and adults (more than 7.1 cm) are described on the basis of published information. Juveniles of both sexes congregate through a year, and the adult males are found deeper than the females. The seasonal congregation and dispertion of the mature males with the females depends upon spawning behavior.

Due to the difference of spatial distribution of males, and/or the aggregative distribution of females, we might bring upon the intensive exploitation of females as demanded at the fish market and current poor landings as a consequence.

The Effects of Exploitation on Snow Crab Populations of the Southwestern Gulf of St. Lawrence Between 1975 and 1981

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INTRODUCTION

Development of the fishery

Snow crab exploitation in eastern Canada started in 1968 in the Gulf of St.Lawrence. Fishing grounds visited at the onset of the fishery were situated in eastern Baie des Chaleurs and in the Bay of Gaspé, as well as in western Cape Breton Island and on the north shore of the St.Lawrence Estuary. Then the fishing fleet extended progressively its activities towards Magdalen Islands, in the vicinity of Orphelin and Bradelle Banks. Newfoundland snow crab fishery only started in the early 70's. Finally, Nova Scotia began exploiting the resource in 1977, on fishing grounds near Cape Breton (fig. 1).

In 1978, restricted inshore areas were defined around most of Cape Breton; these areas were to be fished only by inshore Nova Scotia vessels (areas B and B'). In 1980, similar restricted inshore areas for snow crab exploitation were defined along the north shore of the Estuary and Gulf of St.Lawrence, in the province of Quebec (areas C and C'). Thus, in 1982, from a management point of view, there are 3 distinct areas for snow crab exploitation in the Gulf of St.Lawrence.

First, the southwestern Gulf of St.Lawrence area (area A), where 118 vessels from 12 to 28 m in length are exploiting the resource, 62 of which are more than 15,2 m (50 feet) long. Each license allows the use of 150 traps, and all fishing grounds outside the restricted inshore areas can be fished by the licenses holders. If we exclude 5 or 6 vessels which use japanese conical traps in region 1a, all units of the fleet are fishing with rectangular traps (1,5 x 1,5 x 0,6 or 1,8 x 0,6 m). Southwestern Gulf of St.Lawrence snow crab fishery

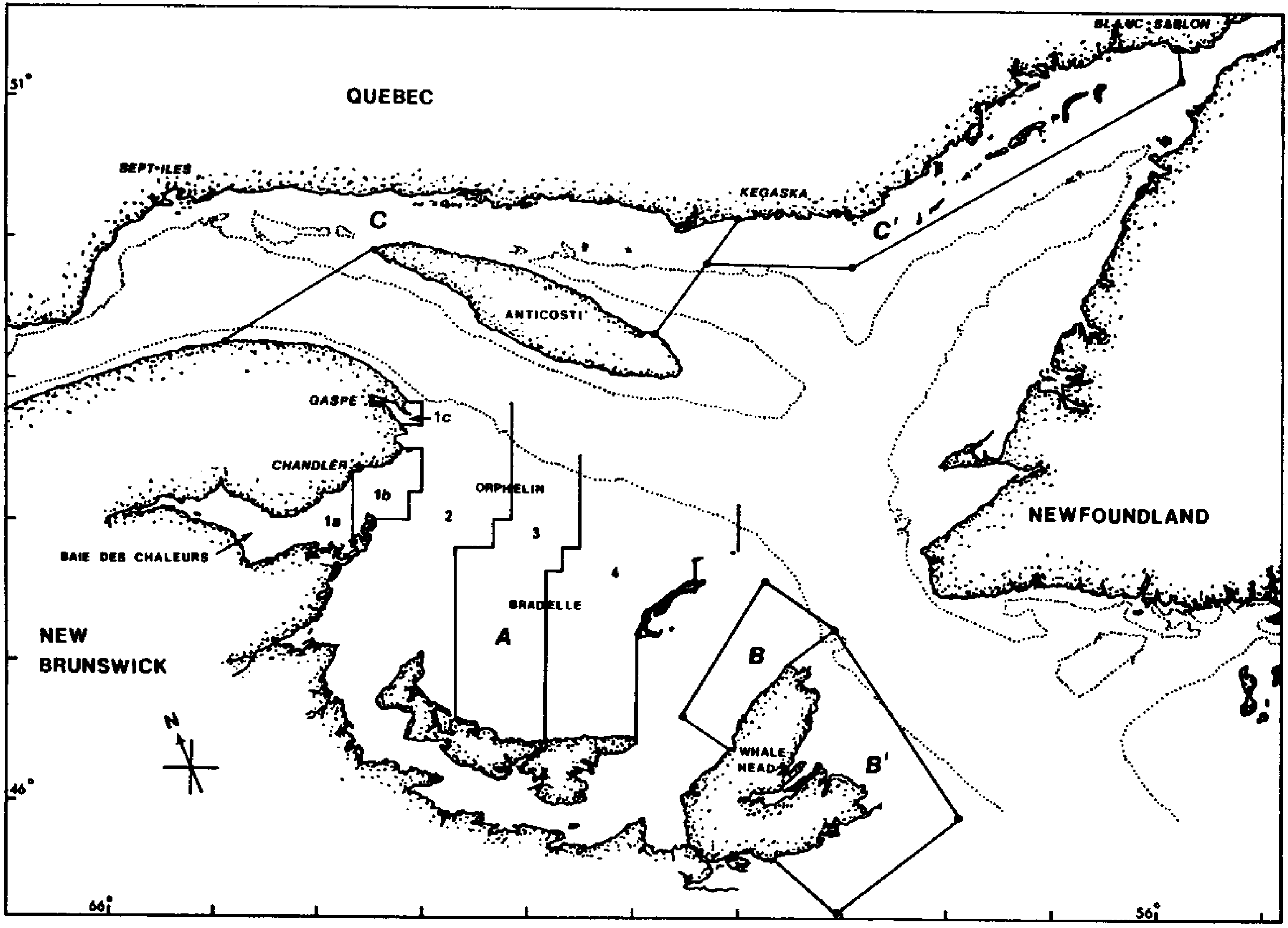

Fig. 1. Snow crab study regions (1 to 4) shown within area A in the southwestern Gulf of St. Lawrence, Canada. Restricted fishing areas B, B', C and C' also shown.

accounts for the largest part of snow crab landings. In 1981, this fishery landed 19768 tons out of a total catch of 22000 tons for the entire Gulf (Table 1).

In Cape Breton restricted inshore area (area B) there are about 50 vessels between 7 and 13 m in length. These vessels are polyvalent, exploiting other species during part of the season.

Finally, in the restricted inshore area (areas C and C') along the north shore of the Estuary and Gulf, there are approximately 60 vessels measuring between 10 and 14 m. These vessels use both conical and rectangular traps. Most vessels exploit other species in addition to crab. In 1981, they landed 1804 tons of snow crab.

This paper deals only with southwestern Gulf of St.Lawrence snow crab stocks which have been mainly exploited since 1968 by both provinces of Quebec and New-Brunswick.

Studies on southwestern Gulf of St.Lawrence stocks

Since the beginning of the fishery and up to 1971, most biological work on snow crab in the Gulf was performed by St-Andrews (New-Brunswick) research laboratory. Since 1975, studies on southwestern Gulf stocks was started by Quebec's Department of Industry and Commerce and since 1977, research on snow crab stocks in the whole Gulf is performed also by Canada's Department of Fisheries and Oceans, both in St-Andrews and Quebec City laboratories.

Table 1. Atlantic Canada annual Snow crabs landings (m.t.) from 1966 to 1981.

Year	Nova Scotia	New Brunswick	Quebec	Prince Edward Island	Newfoundland	Southwestern Gulf of St.Lawrence [7]	Atlantic Canada Total
1966[1]	-	16	14	-	-	30	30
1967[1]	241	221	6	29	-	227	497
1968[2]	651	3 470	461	337	93	3 931	5 012
1969	107	6 364	1 890	66	390	7 617	8 817
1970	174	5 012	1 728	56	892	5 675	7 862
1971	136	4 633	825	-	1 378	5 418	6 972
1972	60	4 744	774	20	1 485	5 416	7 083
1973	128	5 995	1 145	198	2 652	7 054	10 118
1974	232	5 756	1 117	68	3 426	6 764	10 599
1975	392	4 098	601	49	2 011	4 679	7 151
1976	488	6 086	1 496	5	2 668	7 565	10 743
1977[3]	869	7 331	2 082	-	3 937	9 330	14 219
1978[4]	3 096	7 935	2 410	-	7 582	10 098	21 023
1979[4]	2 768	10 950	4 774	452	11 195	15 079	30 139
1980[5]	2 568	9 991	6 416	297	8 915	14 852	28 187
1981[6]	1 463	13 941	7 631	-	10 708	19 768	33 743

[1] Statistique Canada

[2] Revue statistique annuelle de pêche canadienne, 1955-1976, Vol. 9

[3] Revue statistique annuelle de pêche canadienne, 1977, Vol. 10

[4] Revue statistique annuelle de pêche canadienne, 1979, Vol. 12

[5] Les pêches canadiennes - Débarquements, Dir. de la politique économique, Dir. gén. de l'expansion économique

[6] Les pêches canadiennes - Débarquements, Dir. de la politique économique, Dir. gén. de l'expansion économique (données préliminaires)

[7] Landings from Quebec and New-Brunswick only. Quebec landings from the North Shore were substracted

MATERIAL AND METHODS

Since 1980, the research on snow crab populations by the province of Quebec is performed by Department of Agriculture, Fisheries and Food. Before 1980, fisheries jurisdiction was under the authority of Department of Industry and Commerce. Since 1975, port and at-sea sampling has been carried out on snow crab populations and since 1978, catch report and logbook data have been collected from Quebec fishermen.

Port and at-sea sampling

Port sampling of southwestern Gulf snow crab populations was carried out between 1975 and 1980. Its major goal was to assess the impact of exploitation on the stocks. Sampling was realised in ports of Gaspé peninsula and Magdalen Islands, in order to cover all fishing grounds visited by the Quebec fleet. The whole area was divided into 6 regions (1a, 1b, 1c, 2, 3, 4) as shown in Fig. 1, on the basis of both geomorphological and management criteria.

Since crabs below the 95 mm (minimum legal size) carapace width cannot be landed, port sampling would then give a biased estimate of population size structure. In addition, whenever recruitment prediction becomes one of our main objectives, port sampling should be replaced by at-sea sampling. In 1980, both port and at-sea sampling were performed and, in 1981, port sampling was abandonned.

Sampling was realized at sea in 1976, 1980 and 1981. In 1976, sampling was carried out with 70 mm mesh size traps in the southwestern Gulf area in June and July. Since 1980, at-sea sampling is made on fishing vessels. In 1980, observations were made only on catch taken from fishermen's gear (mesh size

130 mm). In 1981, traps with mesh size 50 mm were put on board commercial vessels, and observations were made from both commercial and modified gear.

Since 1975, data obtained from both port and at-sea sampling dealt only with shell size and hardness of male snow crabs. Females, whose landing is prohibited, were only enumerated. Snow crab size is determined by the maximum width of the carapace. Measurements were made with a special gauge to the nearest millimeter. This gauge is described in Watson (1971). Shell hardness was determined according to a 3-stage subjective scale: soft, intermediate and hard shell. These stages are described in Appendix 1. More information on snow crab sampling techniques can be found in Lussiaa-Berdou *et al* (in preparation).

Logbooks

Catch per unit effort (CPUE) data from 1975 to 1977 were not obtained directly on a day-to-day basis, but were given afterwards by fishermen and processors. Since 1978, logbooks are given to fishermen, therefore improving considerably the quality of information collected. Details on snow crab fishery logbooks system of Quebec are given in Lamoureux (1981). Most of fishing vessels fill the logbooks correctly as far as fishing effort and catches are concerned. Thus, in 1980, more than 67% of catch landed by Quebec's fishing vessels in the southwestern Gulf of St.Lawrence was reported on logbooks, and was used to estimate CPUE levels.

RESULTS

Characteristics of the fishery

Landings from Quebec and New-Brunswick

Table 1 gives the landings for each province on the atlantic coast of Canada, since 1966. The values for the southwestern Gulf of St.Lawrence were obtained from those of Quebec and New-Brunswick only. We assumed that the negligible catch from Prince-Edward Island were taken on the fishing grounds of west coast of Cape Breton (area B, Fig. 1). It is also possible that a negligible fraction of Quebec and New-Brunswick catches originated from the west coast of Cape Breton during certain years. Traditionnally the crab fishery in the Gulf has been seasonnal; it extends usually from early May to the end of October.

From 1968 to 1974, landings fluctuated between 3931 and 7054 tons. Following a reduction of landings in 1975, they steadily increased until 1979 when they reached 15079 tons. The state of the international markets in 1980, brought an early closure (August) to the fishery, thus reducing landings to 14852 tons. In 1981, landings reached their highest level for the whole atlantic coast of Canada also reached a peak in 1981, with catches of 33743 tons (Table 1).

Until 1977, the southwestern Gulf always contributed for at least 66% of the landings on the atlantic coast of Canada. Posterior to 1978, Newfoundland and Nova-Scotia greatly increased their participation in the fishery.

Fishing effort

Table 2 gives an estimate of the fishing effort, in terms of total traps used by the vessels active in the fishery, since 1968. Data from Bailey (1978) were mostly used for the period prior to 1975.

At the beginning of the fishery in 1968, the average number of traps per vessel approximated 30. A rapid increase in the number of traps per vessel was observed in New-Brunswick until 1974, when it reached 121. At this time vessels from Quebec had an average of only 63 traps. From 1975 to 1981, the average number of traps went from 63 to 109 in Quebec, while it increased from 120 to 145 in New-Brunswick. The increase in the size of vessels in Quebec after 1974, by allowing the use of a greater number of traps per unit, seems to have been responsible for a greater fishing effort (Fig. 2). The number of vessels fishing actively also rose considerably in Quebec, after 1974.

In Quebec, in 1975, only 2 vessels out of 12 measured more than 15,1 m and in 1978, 9 out of 27. Finally, in 1981, 22 vessels out of 45 in Quebec measured more than 15,1 m. Larger vessels can carry more traps and reach fishing grounds with higher yields further offshore.

Since 1974, the major displacement of large New-Brunswick vessels from the ground fishery to the crab fishery, always kept the proportion of crabbers of more than 15,1 m above 50% in this province (Table 2). Some of the vessels from New-Brunswick fishing for crabs also participate every year in the ground fishery. Quebec boats remain in the crab fishery during all the season.

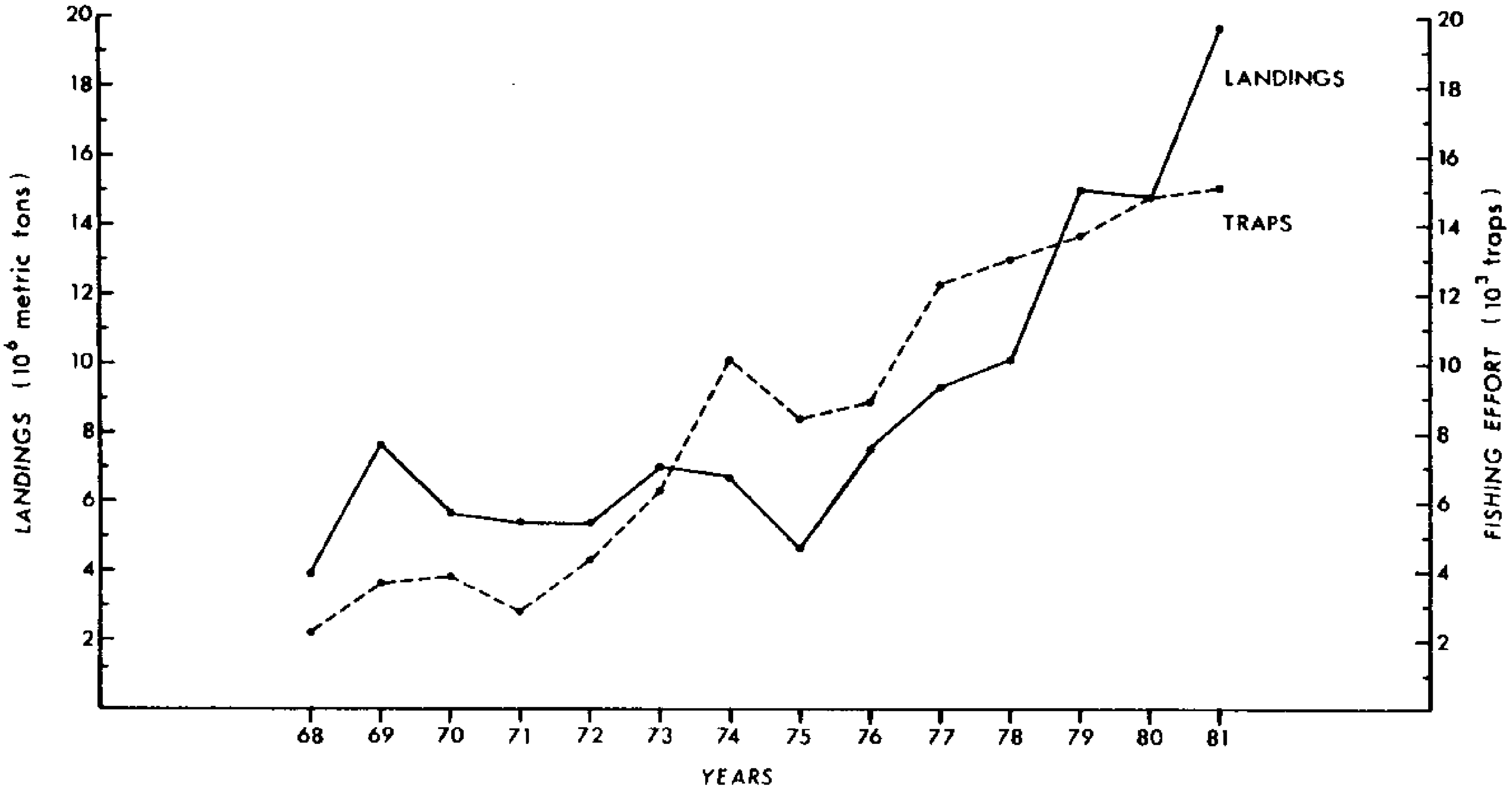

Fig. 2. Landings and fishing effort in the southwestern Gulf of St.Lawrence, between 1968 and 1981.

Table 2. Fishing effort estimate and C.P.U.E. for crab boats from Quebec and New-Brunswick, in the southwestern Gulf of St.Lawrence, between 1968 and 1981.

Year	Quebec			New Brunswick			Total estimate	C.P.U.E.^{5}
	Number of boats^1	Average number of traps per boat	Total of traps	Number of boats^1	Average number of traps per boat	Total of traps	of traps	(Kg/trap haul)
1968^3	9	(30)^2	270	56	35,0	1960	2230	30,3
1969^3	17	34,5	586	68	45,4	3087	3673	38,3
1970^3	15	48,8	725	55	56,2	3091	3816	52,2
1971^3	6	46,7	280	38	67,1	2550	2830	47,5
1972^3	9	57,3	516	42	90,2	3790	4306	42,2
1973^3	9	62,2	560	53	109,1	5782	6342	19,7
1974^3	13	(63)	819	85	120,5	10245	11064	15,9
1975	12	63,1^3	756	64^3	120,0^3	7680	8436	13,7
1976	18	82,6^3	1494	62^3	120,0^3	7440	8934	16,5
1977	22	(90)	1980	72^3	143,9^3	10361	12341	18,1
1978	27	95,2	2571	(72)	(145)	10440	13011	18,0
1979	33	100,2	3305	(72)	(145)	10440	13745	23,8
1980	42	104,2	4377	(72)	(145)	10440	14817	34,9
1981	45	108,5	4883	71^4	(145)	10295	15178	

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[1] Boats effectively active at fishing

[2] Values in brackets are personal estimates; real values were not available

[3] Obtained from Bailey (1978)

[4] According to Richard Bailey, personnal communication, 1982

[5] Data from 1968 to 1974 are from Bailey (1978); data from 1975 to 1980 are from Lamoureux (1981)

Catch per unit of effort

Before 1972, high CPUE values were rather usual, since new fishing grounds were still being discovered. CPUE variations between 1974 and 1980 were analysed in a previous document (Lamoureux, 1981). From 1972 to 1975, CPUE values dropped from 42,2 to 13,7 kilograms per trap haul (Table 2). However, from 1975 to 1980, although there was a major increase of the fishing effort, CPUE values went from 13,7 to 34,9 kilograms per trap haul.

The effects of exploitation

Populations size structure

Port sampling between 1975 and 1980

Between 1975 and 1980, a total of 59257 male crabs were sampled in various ports of the Gaspé peninsula and on Magdalen Islands. As far as possible, the sampling covered all the crab fishing grounds visited by boats from Quebec on the west side of the Magdalen Islands (in the southwestern Gulf of St.Lawrence). But, it was only after 1978 that vessels from Quebec started visiting more regularly grounds near Bradelle Bank, thus allowing us to sample the regions 3 and 4. Three sampling periods we defined during the fishing season, the first being May-June, the second, July-August and the third, September-October.

Size frequency distributions are given in figure 3 for the whole southwestern Gulf. As we are dealing here with port sampling only, we don't expect to find modes below the minimum legal size of 95 mm. Because of this, most of the time we will be in the presence of unimodal size distribution. From 1975 to 1978 the modal class size oscillate between 97 and 102 mm. The size classes between 92 and 122 mm are heavily represented. From 1979 and on, there is a progressive reduction of size classes above 102 mm. The strict enforcement of the 95 mm legal size regulation in 1980, managed to eliminate most of the smaller crabs from the landings (Fig. 3).

Size frequency distributions for each of the 6 specific regions sampled in the southwestern Gulf are shown in figures 4 to 8. Remarks made above on the southwestern Gulf as a whole holds true for most of the 6 specified regions: we observe the same gradual reduction of higher size classes after 1978 and the disappearence of sublegal size crabs from the landings in 1980.

At-sea sampling

In 1976 and 1981, at-sea sampling was done using respectively 70 and 50 mm mesh size traps.

The Baie des Chaleurs (regions 1a and 1b) size frequency distributions given for 1981 in Fig. 9, show major pre-recruitment peaks at 72 mm (region 1a) and at 92 mm (region 1b). The data from 1976 are not abundant enough to allow for such observations.

On Orphelin Bank (region 2), pre-recruitment was relatively scarce in 1976 compared with 1981. In fact, more than 54% of the 838 males sampled during the May-June period of 1981, were below 95 mm. A mode appears at 72 mm (Fig. 10). Harvesting of legal size crabs would be responsible for the increased abundance of pre-recruits (74,6%) during the July-August sampling period of 1981.

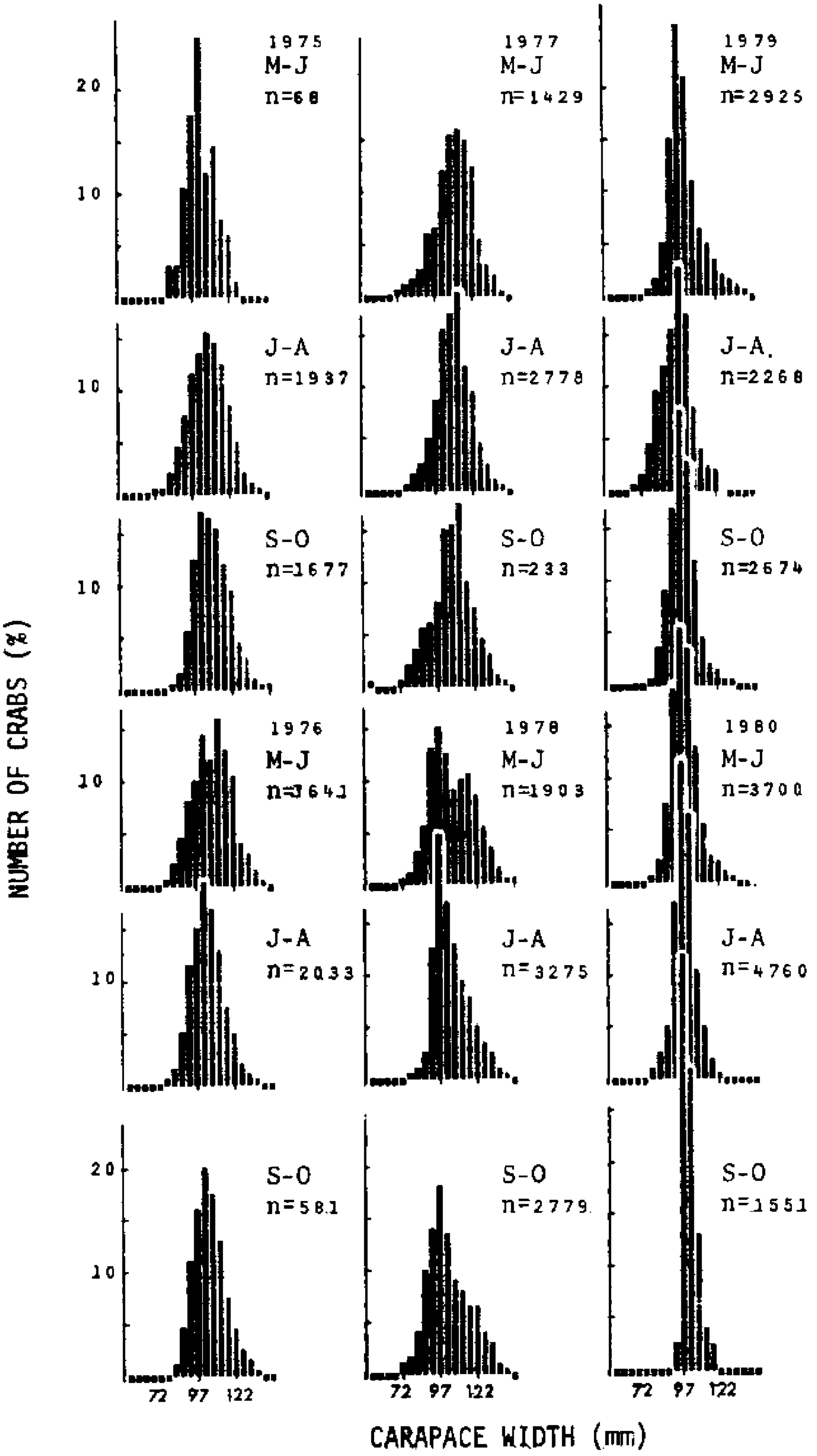

Fig. 3. Size frequency distribution of male snow crabs in Quebec's landings from the southwestern Gulf of St.Lawrence, from 1975 to 1980.

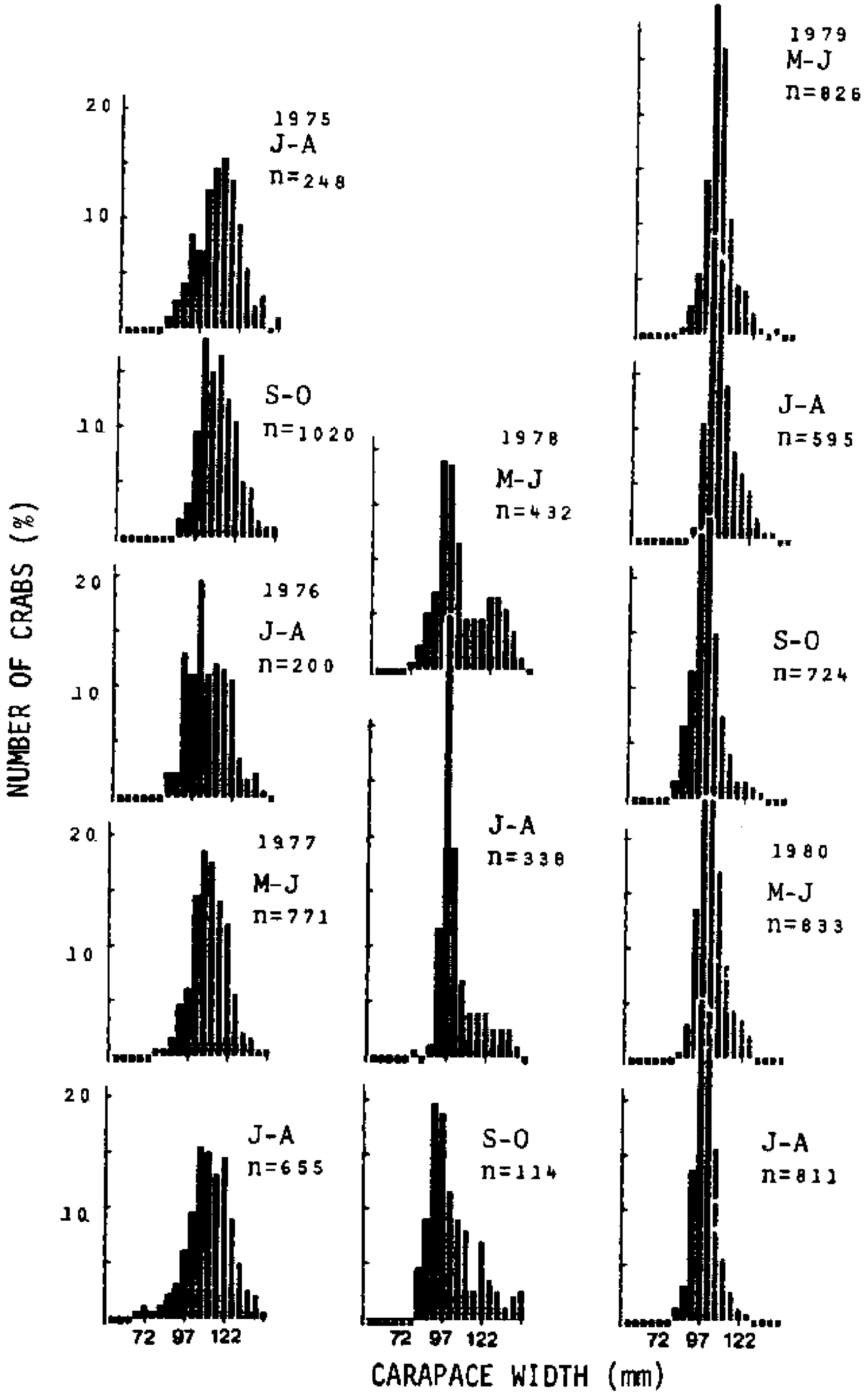

Fig. 4. Size frequency distribution of male snow crabs in Quebec's landings from region 1a, in the southwestern Gulf of St.Lawrence, from 1975 to 1980.

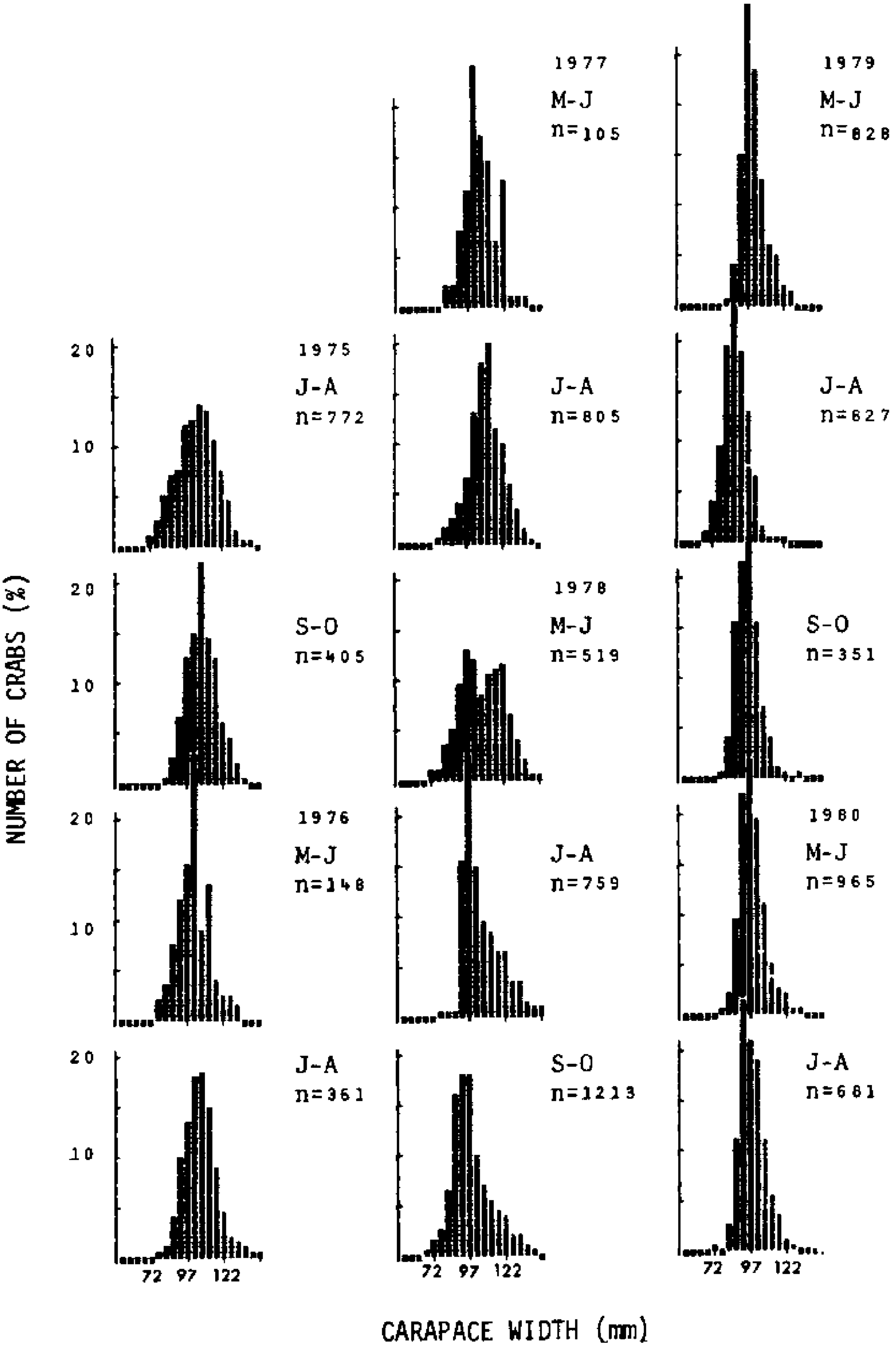

Fig. 5. Size frequency distribution of male snow crabs in Quebec's landings from region 1b, in the southwestern Gulf of St.Lawrence. from 1975 to 1980.

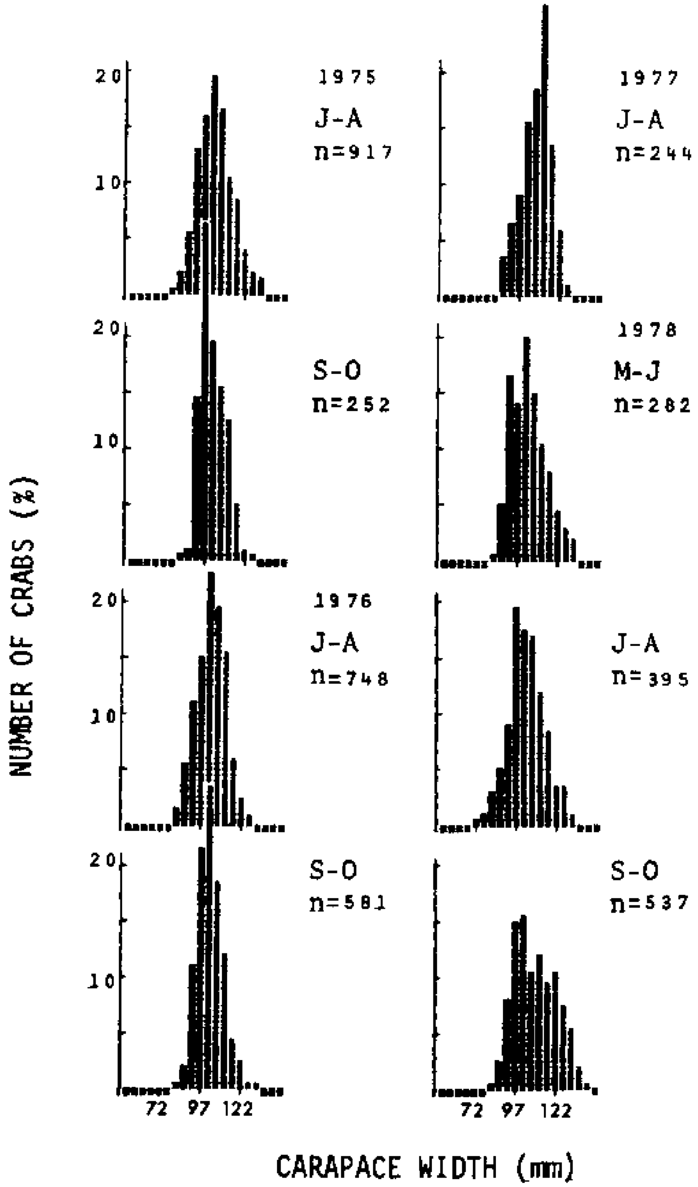

Fig. 6. Size frequency distribution of male snow crabs in Quebec's landings from region 1c, in the southwestern Gulf of St.Lawrence, from 1975 to 1978.

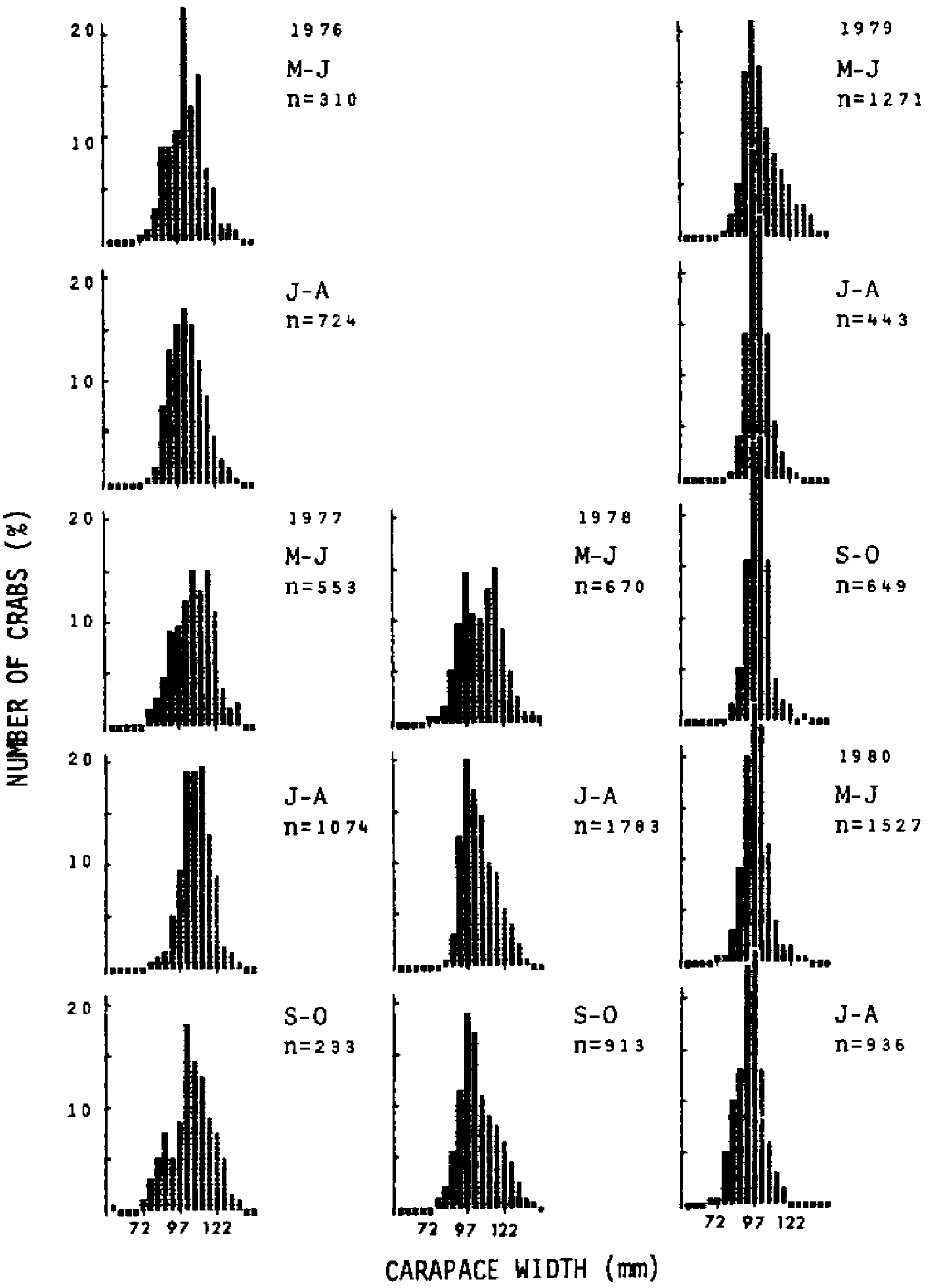

Fig. 7. Size frequency distribution of male snow crabs in Quebec's landings from region 2, in the southwestern Gulf of St.Lawrence from 1976 to 1980.

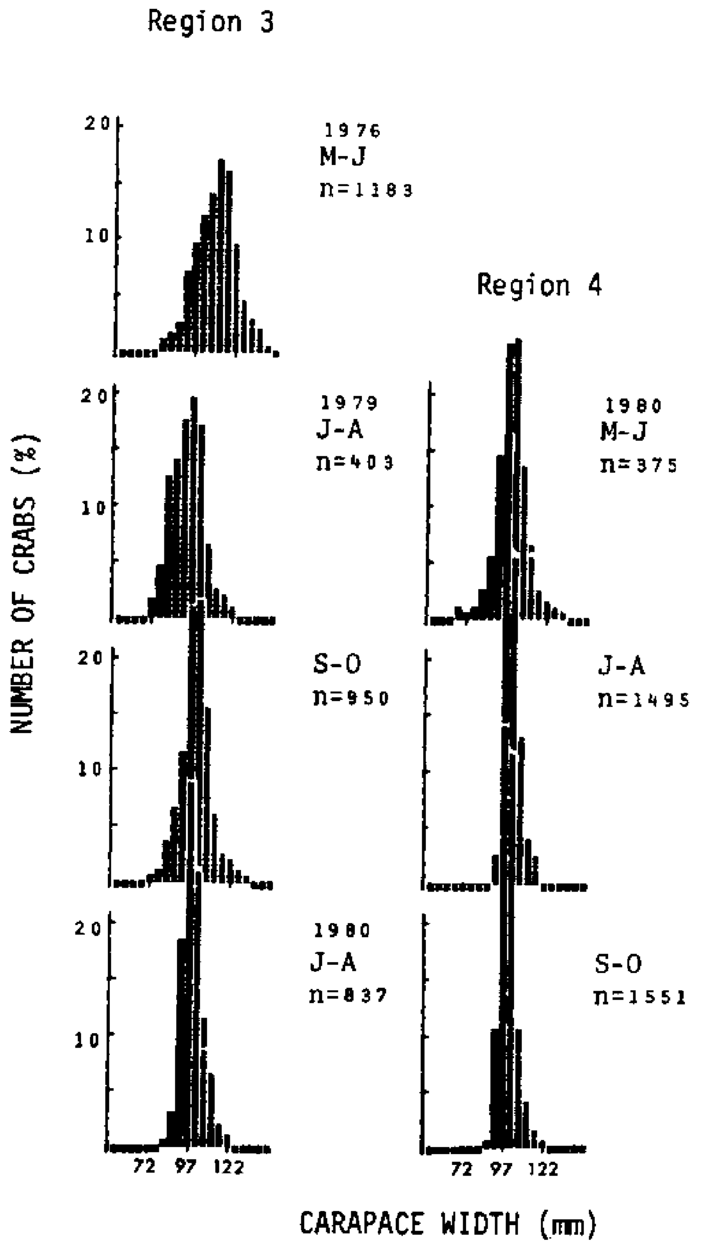

Fig. 8. Size frequency distribution of male snow crabs in Quebec's landings from regions 3 and 4, in the southwestern Gulf of St.Lawrence, for 1976, 1979 and 1980.

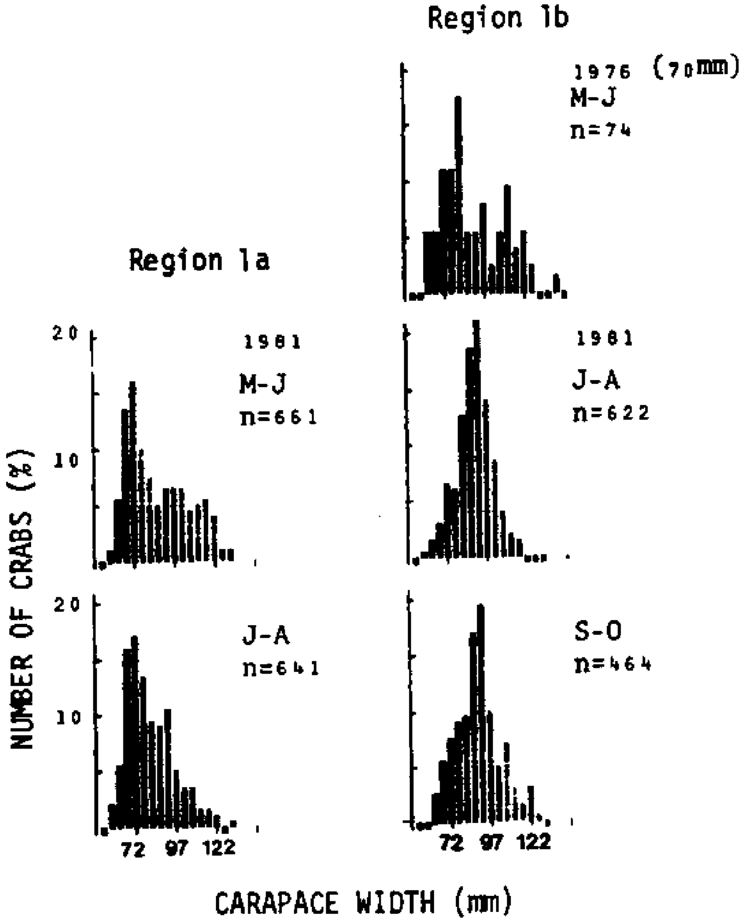

Fig. 9. Size frequency distribution of male snow crabs sampled at-sea in regions 1a and 1b, in the Gulf of St.Lawrence, in 1976 and 1981.

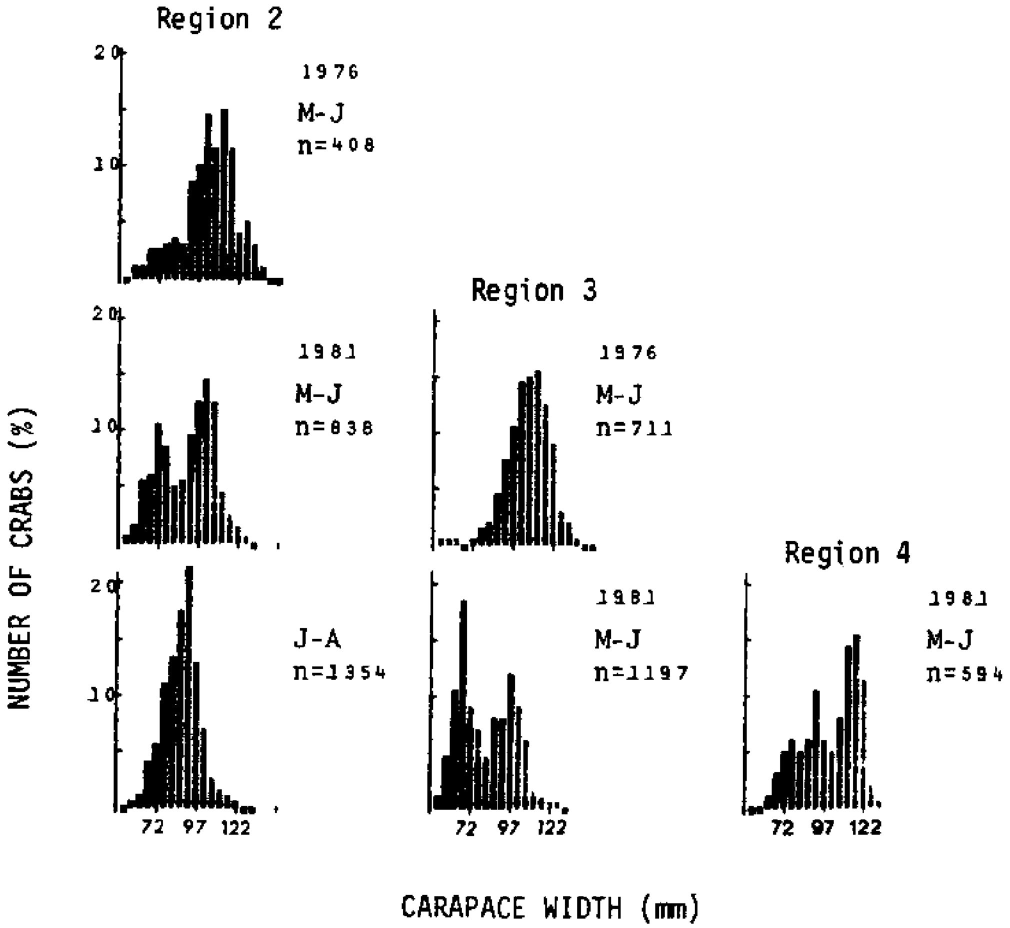

Fig. 10. Size frequency distribution of male snow crabs sampled at-sea in regions 2, 3 and 4, in the Gulf of St.Lawrence, in 1976 and 1981.

The crab population on West Bradelle Bank (region 3) shows a similar trend as the one on Orphelin Bank (region 2): few pre-recruits in 1976, and their major increase in 1981, with 70,5% of the crabs being concentrated around a first mode at 67 mm (Fig. 10). There is a second mode at 97 mm.

On East Bradelle Bank (region 4), we also observe a similar mode for pre-recruits in 1981, although only 36,5% of the crabs were below 95 mm (Fig. 10).

Size of crabs and CPUE

From 1975 to 1976, the mean size of crabs sampled in ports fluctuate around 105 mm (Table 3). It then increase to 109,8 mm in 1977. It drops from 105,8 to 96,6 mm from 1978 to 1979. Following the strict enforcement of the legal size limit in 1980, the mean size of landed crabs remains close to 100 mm. In the future, with the strict enforcement of the legal size limit and the disappearance of larger crabs, we can expect that the mean size remains close to 100 mm.

Each of the specific regions show the same trend as the whole southwestern Gulf: a mean size increase in 1977, followed by a gradual decrease until 1980 (Table 3).

Figure 11 shows annual CPUE values in parallel with mean size of crabs from port sampling, for the southwestern Gulf, between 1974 and 1980. Figures 12a and 12b give a similar comparison between CPUE and mean size for pooled data of regions 1a and 1b, and for region 2 respectively. In all cases we observe the same trend: an important CPUE increase accompanied by a major reduction of the mean size of male crabs.

Table 3. Mean size (mm) of snow crab from port sampling in the southwestern Gulf of St. Lawrence, between 1975 and 1980.

Year	Period	Regions 1a	1b	1a & 1b	1c	2	3	4	All regions[1]
1975	M-J	104,0	-	104,0	-	-	-	-	104,0
	J-A	108,9	104,8	106,9	103,5	-	-	-	105,7
	S-O	111,0	107,8	109,4	101,9	-	-	-	106,9
1976	M-J	-	101,7	101,7	-	103,5	109,5	-	104,9
	J-A	107,1	105,9	106,5	103,3	103,9	-	-	105,0
	S-O	-	-	-	101,9	-	-	-	101,9
1977	M-J	111,2	106,4	108,8	-	107,8	-	-	108,5
	J-A	113,5	110,3	111,9	107,3	107,9	-	-	109,8
	S-O	-	-	-	-	104,8	-	-	104,8
1978	M-J	104,5	107,5	106,0	103,9	107,6	-	-	105,8
	J-A	103,6	105,7	104,7	103,6	105,2	-	-	104,5
	S-O	103,7	98,5	101,1	109,3	104,5	-	-	104,0
1979	M-J	99,8	100,9	104,4	-	104,1	-	-	100,3
	J-A	103,6	88,5	96,1	-	100,1	94,2	-	96,6
	S-O	96,4	96,1	96,3	-	99,9	100,1	-	98,1
1980	M-J	102,4	99,6	101,0	-	98,3	-	99,9	100,1
	J-A	100,6	97,9	99,3	-	93,9	99,8	100,1	98,5
	S-O	-	-	-	-	-	-	100,8	100,8

[1] In 1975, 1976 and 1977, some of the crabs measured could not be assigned to a specific region.

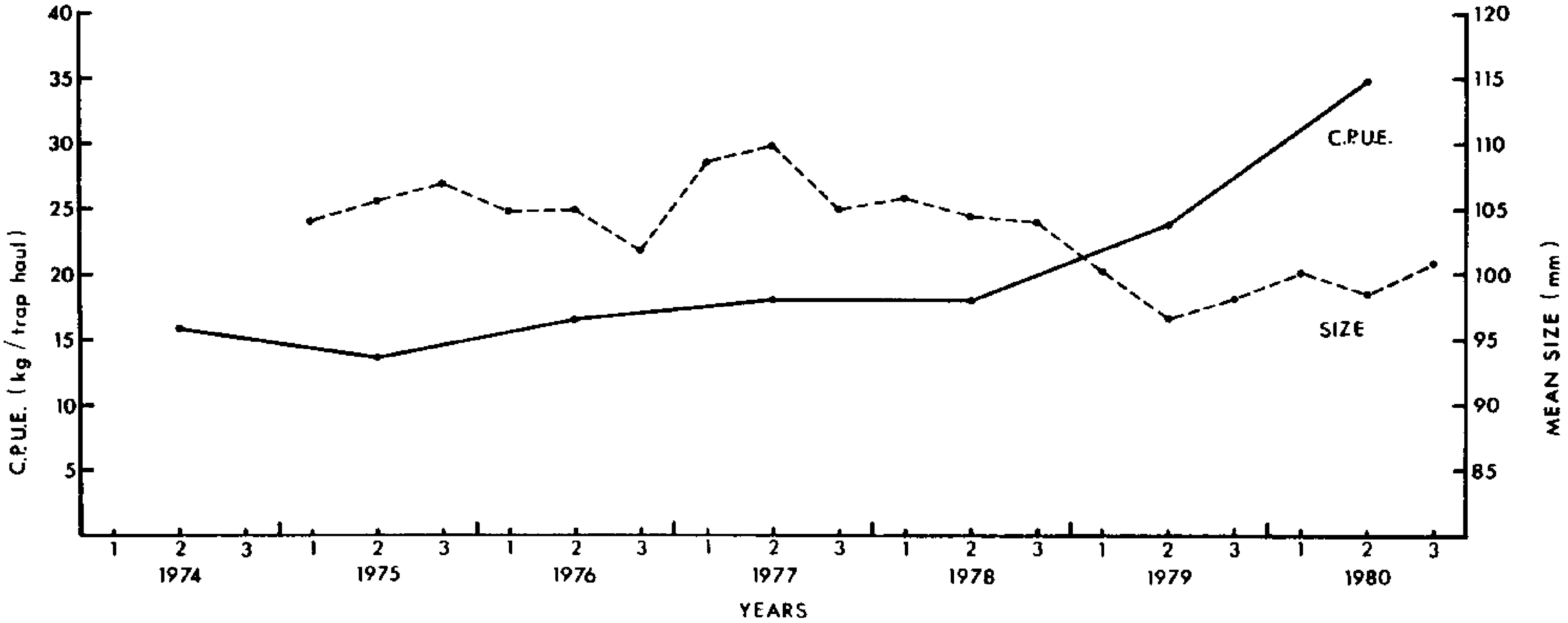

Fig. 11. Annual C.P.U.E. values from 1974 to 1980, and mean size of male crabs from port-sampling at three periods during the fishing seasons of 1975 to 1980, in the southwestern Gulf of St.Lawrence. Period 1: May-June; Period 2: July-August; Period 3: September-October.

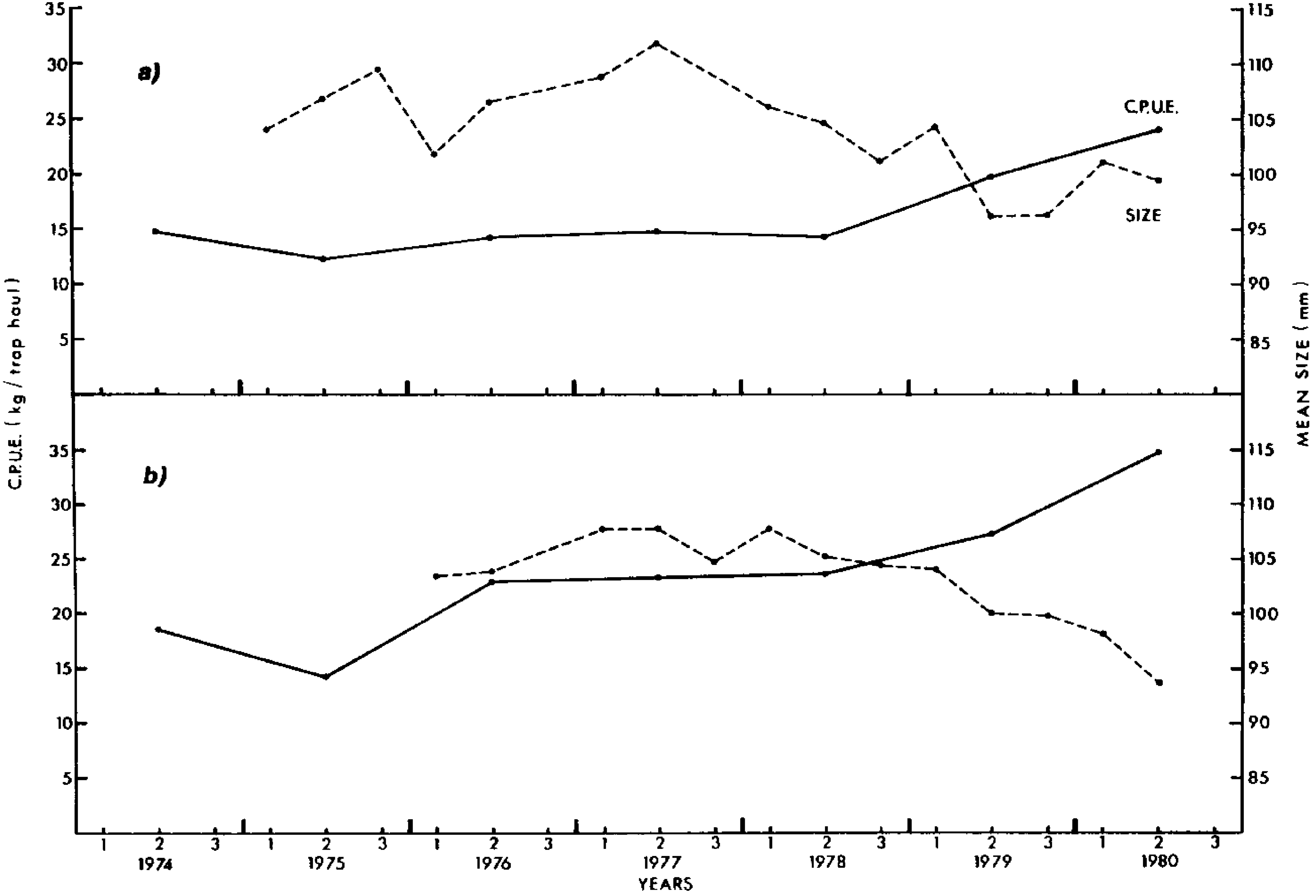

Fig. 12. Annual C.P.U.E. values from 1974 to 1980 and mean size of male crabs from port-sampling at three periods during the fishing seasons of 1975 to 1980, in regions 1 a and 1 b (fig. 12a) and of 1976 to 1980 in region 2 (fig. 12b), in the southwestern Gulf of St.Lawrence.

Relative abundance of soft and intermediate-shelled crab

Soft and intermediate-shelled crab and fishing effort

Molting cycle is important when studying the snow crab populations in the southwestern Gulf, because of its impact on the fishery. For Baie des Chaleurs (regions 1a and 1b) and Orphelin Bank (region 2), we observe that the abundance of crabs with soft and intermediate shell fluctuates and shows a net reduction from 1979 on. During the same period, the fishing effort increases steadily, at least until 1980. The real fishing effort being unavailable for these regions (1a, 1b and 2), we can only evaluated it indirectly by using the number of vessels of size less than 15,2 m (table 4). We know that these vessels can not fish further east than region 2 and larger vessels don't contribute to a significant proportion of the landings from these regions. From 1975 to 1981, there were no changes in the New-Brunswick fleet while there were some in the Quebec fleet. In fact the number of Quebec vessels of size less than 15,2 metres increases from 7 in 1975 to 27 in 1980. In 1981, it goes down to 24. So, the hypotheses that a greater fishing effort causes an increase in the abundance of soft shell crabs in landings does not seem to hold, at least not for Baie des Chaleurs and Orphelin Bank.

Molting cycle and CPUE

Figure 13 shows fluctuations of crabs with soft and intermediate shell and CPUE values at the beginning, in the middle and at the end of the fishing seasons of 1975 to 1981. Those two parameters fluctuate, either in or out of phase, in such a way that there is no statistically significant relationship between the two variables ($p >$,05, Kendall rank correlation).

Table 4. Number of vessels of size less than 15,2 m (50') engaged in the snow crab fishery, areas 1 and 2.

Year	< 50' (50,2 m)
1975	10
1976	14
1977	18
1978	18
1979	21
1980	27
1981	24

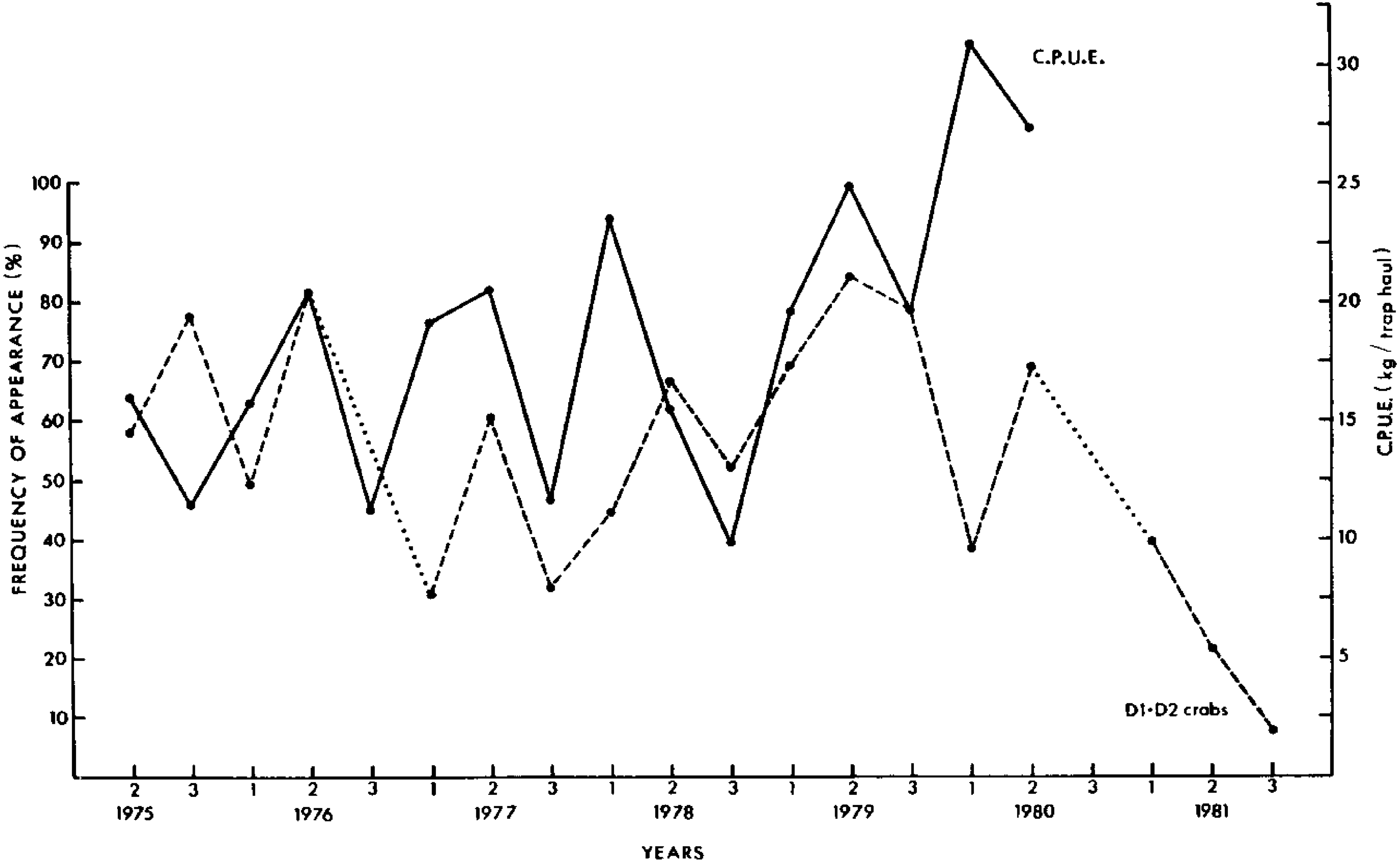

Fig. 13. C.P.U.E. values and frequency of appearance of soft (D1) and intermediate-shelled (D2) crabs in regions 1 a , 1 b and 2, at three periods during the 1975 to 1981 fishing seasons.

CPUE variations study between 1975 and 1980 allowed us to demonstrate the occurrence of winter molting for snow crab in the southwestern Gulf of St.Lawrence (Lamoureux, 1981). Figure 13 sums up those results for the Baie des Chaleurs and Orphelin Bank regions together. We notice that CPUE values at the beginning of a fishing season are always higher than values at the closure of the previous one. Thus, since 1975, winter molting always contributed to recruitment.

Figure 13 shows also that in 1976, 1977 and 1979, CPUE increases from the first to the second sampling period. This suggests that recruitment may have resulted from molting during the fishing season. In fact, during these three years, we observe a major increase in the percentage of crabs with soft and intermediate shell from the first to the second period. In 1980, although there was an important increase of the proportion of crabs with soft and intermediate shell, we note a CPUE decrease between those two periods of sampling (Fig. 13). This can be explained by the important slow down of the fishery followed by an early closure in August 1980. In 1978, the increase in percentage of crabs with soft and intermediate shell from the first to the second sampling period seemed to have had no significant impact on CPUE levels (Fig. 13).

Thus, from 1976 to 1981, it seems that summer molting did not occur with the same intensity and regularity.

DISCUSSION

The exploitation of southwestern Gulf of St.Lawrence snow crab stocks by Quebec's fleet could be divided into two periods: a period of exploration and a period of expansion. During the exploratory phase, catch levels showed important fluctuations, which could be related to the learning of the fishing techniques, as well as to the extension of the fishing area. In addition, recruitment levels were then relatively modest.

The expansion period is characterized by an increasing importance of the whole fishery. Catch levels increase continuously and a slight extension of fishing area was observed up to 1977. Since then, one can state that all snow crab fishing grounds available to the fishery in the southwestern Gulf have been explored (Lamoureux, 1981). Marked increase of catch levels during this period could be partly explained by greater fishing effort, through important changes of the fishing capacity of the fleet. Also, recruitment levels were relatively high during this period (Fig. 5 and 6). These could be related to the decrease in abundance of cod stocks in NAFO subareas 4T-4Vn, as hypothesized by Bailey (1981). Since 1975, increase in catch levels exceeds the relative increase in fishing effort, thereby showing a rise in CPUE levels. CPUE levels can be considered as a valuable index of abundance. Thus, a real increase in the abundance of the crab stocks is observed in the southwestern Gulf area.

The effects of intensive exploitation of southwestern Gulf snow crab stocks were mainly observed on size structure of the populations, particularly since 1977. Between 1975 and 1977, mean size of landed crabs showed a slight increase, which corresponds to the final phase of extension of the fishing area. In addition, one could state that important arrival of new recruits during that period exceeded their removal by the fishery, thereby allowing a larger proportion to reach larger size modes. In 1977, one observes a marked increase of fishing effort in the whole southwestern Gulf, including Baie des Chaleurs and Orphelin Bank (Table 2). Since then, we note a sharp decrease in mean size of landed snow crab (Fig. 12). Moreover, data obtained at sea in 1976 and 1981 show greater relative importance of pre-recruit size classes in catch following removal of larger individuals through exploitation. Thus, through the years, removal of larger individuals by the fishery implies that snow crab fishery in the southwestern Gulf now depends almost exclusively on newly recruited individuals. We now have the following situation: relatively abundant stocks (increase of CPUE levels) composed mainly of newly recruited individuals. The success of the fishery for a given year is now intimately linked with the success of the recruitment.

Recruitment of individuals of commercial size takes place twice during the year: on a regular basis during winter (at least since 1975) and, more sporadically, in summer. Lack of precise data on landings for each of the 6 regions specified makes comparison of those two levels of recruitment impossible. However, based on its regular appearance from year to year, we could state that winter molting contributes for an important part of the annual recruitment in the southwestern Gulf snow crab stocks.

The lack of relation between exploitation intensity and proportion of soft and intermediate-shelled crab in the catch seems to indicate that the "white crab" problem may not be directly related to exploitation, but rather to the biology of the species itself. The hypothesis through which those two factors are related states that higher fishing effort, by removing larger individuals, leaves only the smaller ones with higher molting frequency, thereby increasing the probability of catching soft-shelled crab. However, one could verify this hypothesis only if molting period remains constant from year to year for the exploited molting group. Thus, if summer molting is somewhat reduced, as seemed to have happened in 1981, one would find a small proportion of soft-shelled crab in the catch, even though exploitation level is high.

Despite the lack of relationship between yearly exploitation levels and abundance of soft and intermediate-shelled crab, we observed, particularly in 1981, that the "classic" pattern of appearance of soft-shelled crab disappeared. Indeed, through the years, we observed that soft-shelled crab abundance peaked during mid-summer. In 1981, it showed a continuous decrease since the beginning of the fishing season (Table 5). In fact the exploitation-related abundance of soft-shelled crab hypothesis states that higher fishing effort, by removing larger individuals, leaves only smaller ones on the grounds.

It seems that, according to the molting group to which they belong, crabs of different size will molt at different time of the year (Ito, 1970). Thus, in a heavily exploited population where larger individuals have been removed, it is possible that incidence of soft-shelled crab be noticeably reduced during the main fishing season. The timing of molting for smaller crabs may be different but it may also be spread over a longer period of the year.

Table 5. Frequency of appearance of soft (D1) and intermediate-shelled (D2) crab for regions 1 a, 1 b and 2 during the fishing season of 1975 to 1981.

Year	Period	Percentage of D1-D2 in sample
1975	M-J	-
	J-A	58,0
	S-O	77,6
1976	M-J	40,1
	J-A	81,5
	S-O	-
1977	M-J	30,7
	J-A	60,5
	S-O	31,8
1978	M-J	44,5
	J-A	66,5
	S-O	52,1
1979	M-J	69,4
	J-A	84,2
	S-O	78,3
1980	M-J	38,3
	J-A	69,1
	S-O	-
1981	M-J	39,5
	J-A	21,6
	S-O	7,8

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The authors would like to acknowledge the assistance of Jean Dubé, Jean Lauzier, Pierrette Turcotte, Maurice Gaudet and Solange Tétreault for collecting data at sea and in ports at various time between 1975 and 1981. We also appreciated the assistance of Louise Therrien for drawing figures.

Appendix I. Criteria for determining shell hardness stage for snow crab.

Stage 1. (soft-shelled)

1) Claw easily broken by thumb pressure
2) Appendages contain mainly liquid and a small quantity of flesh
3) Color of carapace

   dorsal side : very light brown
   ventral side: usually white

4) Calcareous growth: absent

Stage 2. (intermediate-shelled)

1) Claw less easily broken by thumb pressure
2) Appendages contain less liquid; more flesh pink-colored
3) Color of carapace

   dorsal side : light brown
   ventral side: white towards pink

4) Calcareous growth: sometimes present

Stage 3. (hard-shelled)

1) Claw impossible to break by thumb pressure
2) No liquid in the appendages. Flesh of consistent structure
3) Color of carapace

   dorsal side : dark brown
   Ventral side: white-yellowish, often hairy

4) Calcareous growth: often present

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ABSTRACT

Snow crab exploitation in the southwestern Gulf of St. Lawrence started in 1968. Historical development of the fishery could be divided in two periods: a period of exploration (1968-75) and a period of expansion (1975-81). During the 1968-75 period, extension of the fishing area and learning of new techniques could explain the important fluctuations of catch levels. From 1975 to 1980 the CPUE increased gradually from 13,7 to 34,9 on fishing grounds visited by vessels from Quebec. This increase is due chiefly to the heavy input of new recruits to the fishery, but also to changes in the fishing capacity of the fleet following an increase in the size of vessels.

Between 1975 and 1980 there was a gradual decrease of the mean size of landed snow crab. After oscillations between 104 and 109 mm in 1975 and 1976, it decreases from 110 mm in 1977 to near 100 mm in 1980. The mean size decrease after 1977 was accompanied by a gradual reduction in the number of size classes above 100 mm. This is the result of a sustained fishing effort on the fishing grounds in the southwestern Gulf of St. Lawrence. Following the strict enforcement of the minimum legal size limit, smaller crabs disappear from landings after 1980.

Recruitment of individuals of commercial size through molting occurs twice during the year: regularly in winter and, more sporadically during the fishing season. Also, no relationship was found between the intensity of exploitation

and the relative abundance of soft and intermediate-shelled crab. The effects of exploitation on the abundance of soft-shelled crab and on the molting cycle during the fishing season are discussed.

Mortality Factors

Relationship Between Catches of Snow Crab, *C. Opilio* (O. Fabricus) and Abundance of Cod (*Gadus Morhua* L.) in the Southwestern Gulf of St. Lawrence

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ABSTRACT

The recruitment of snow crabs (Chionoecetes opolio) to the southwestern Gulf of St.Lawrence fishery seems to be negatively dependent on previous abundance of cod (Gadus morhua). A strong statistical relation was found when snow crab catch in a given year was correlated with the average biomass of cod present 3 to 6 years before. Snow crabs recruit to the fishery at an age of approximately 6 years old, and are subject to predation mostly during the first 3 years of their life. Increased catches of crab in recent years are explained by an improved recruitment which results essentially from a decrease in abundance of cod in the mid-70's. If the same relationship holds, catches of crab should decrease in a near future.

INTRODUCTION

Since 1967, snow crab (Chionoecetes opilio) has supported an important fishery in the southwestern Gulf of St.Lawrence (Figure 1). Exploitation has been particularly intensive since 1973, with over 60 boats fishing regularly from May to October.

It is generally accepted that this crab fishery does not affect stock fecundity nor larval production. The minumum size limit for male crabs is 95 mm (carapace width). This is approximately three molt increments (Miller and Watson 1976) above the average size at maturity of 57 mm (Watson 1970). All mature males are thus protected from the fishery and available for reproduction, for the time it takes them to grow from maturity onset to recruitment. It has been demonstrated that the males are polygamous (Watson 1972), and that the females can breed a second annual batch of eggs without further mating (Watson 1970). All these conditions are favorable to reproductive success. In fact, 99.8% of the mature females captured in research surveys in 1980 were berried. The females are too small to be exploited and their numbers are probably not smaller than under unexploited conditions. Recruitment to the fishery should then be independent of stock size. It would rather depend partly on larval survival under given environmental conditions, and partly on survival of pre-recruits, which in turn is affected by abundance of predators.

A recent study (Waiwood et al. 1980) on food habits of cod in the southwestern Gulf of St.Lawrence has indicated that brachyuran crabs (Hyas araneus and Chionoecetes opilio) are a major part of the cod diet. They accounted, by weight, for 4-38% of the total food intake depending on cod size. Calculated from the preliminary data presented by Waiwood et al. (1980), 19,255 tons of crab (7.4% of the total food) were consumed by cod in 1978 in the study area, which contained approximately 37% of the total estimated southern gulf cod population. This consumed biomass exceeds the total landings of commercial crabs from the same area.

Because cod appears to be an important predator of snow crab juveniles and could then be a major controlling factor for recruitment, an attempt was made to relate the annual yield of the snow crab fishery to cod abundance in previous years. If such a relationship were available, it could be used for the purpose of snow crab catch prediction.

MATERIAL AND METHODS

Cod in the southwestern Gulf of St.Lawrence is part of a stock which migrates between NAFO Division 4T in summer and Sub-division 4Vn in winter (Figure 1). Annual fishable biomass, as obtained from cohort analysis, was reported by Beacham (1980) for 1967 to 1979 (Table 1). Since there is no information available on fishable biomass of snow crab in the southwestern Gulf, the total catches were here used under the assumption that they are proportional to the fishable biomass.

A preliminary model for growth of snow crab in the Gulf of St.Lawrence was described by Watson (1969). It was based on observations of crabs molting in the laboratory, on modes present in the size frequencies of samples taken at sea, and on data published by Kon et al. (1968) on growth of snow crab in Japan. According to the model, it takes approximately 6 years for a crab to reach the size of recruitment into the fishery.

Consequently, a lag of 6 years was used in regressions between crab catches and the cod biomass. Since predation by cod is directed on

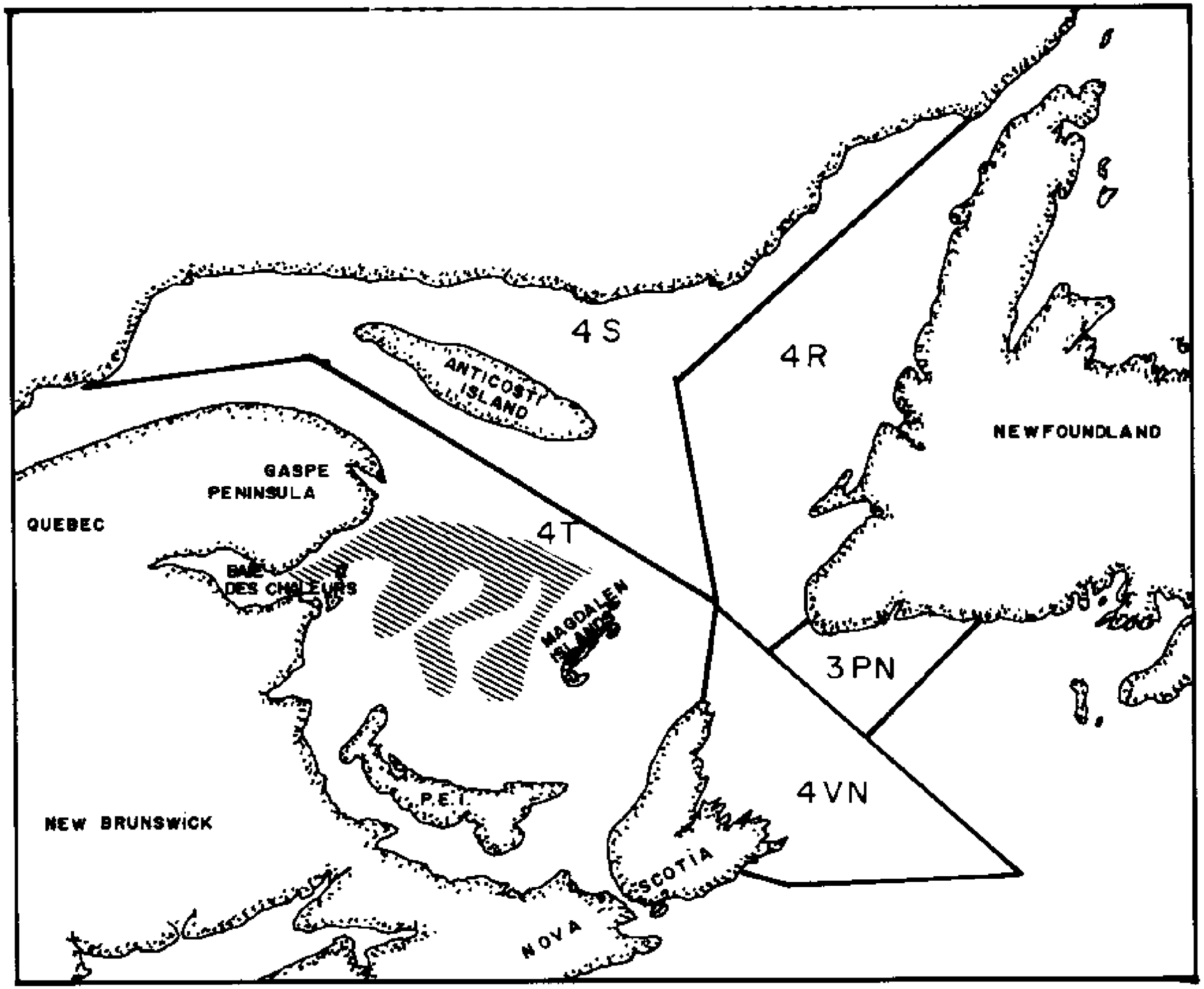

Figure 1. Gulf of St.Lawrence with NAFO Divisions and distribution of snow crab stock (hatched area) in the southwestern Gulf.

Table 1. Annual cod fishable biomass in Division 4TVn and snow crab catches from the southwestern Gulf of St.Lawrence.

Year	4TVn cod[1] fishable biomass (t)	Snow crab catches (t)
1967	171 112	158
1968	174 772	3 758
1969	188 524	7 145
1970	207 320	5 482
1971	198 512	5 388
1972	192 489	4 896
1973	152 387	6 744
1974	125 070	6 620
1975	103 255	4 630
1976	104 024	7 384
1977	122 741	9 450
1978	182 156	10 344
1979	225 909	14 908
1980	397 633[2]	14 757
1981	-	19 651

[1] = From Beacham (1980).

[2] = Projection

juvenile crabs as well as crab young-of-the-year (K. Waiwood, pers. comm.), other regressions were fitted with the averages of cod biomass over a various number of years following the initial lag of 6 years. This would tend to measure the average mortality by predation over more than 1 year. For instance, in a first regression, the 1973 snow crab landings would be related to cod biomass in 1967. In another regression cod biomass would be averaged over 4 years, with the 1973 snow crab landings related to the average biomass of cod for 1967 to 1970 inclusively.

The following exponential equation was used for the regressions:

$$y = a\ e^{-bx}$$

where y = crab catches, and x = cod biomass. Such a curve was selected because it has a positive y-intercept, representing the crab population at a maximum when cod biomass is 0. Theoretically, this would correspond to some maximum carrying capacity of the ecosystem. On the other hand, the curve never reaches the x-axis but tends to level off. Thus, increasing abundance of cod would reduce the abundance of crab available to the fishery, but never eliminate it. At low crab abundance, cod would presumably shift its predation pattern toward other available species. A change in the diet, associated with a reduction in abundance of a prey, was reported by Ponomarenko and Yaragina (1978) for Barents Sea cod, and by Waiwood et al. (1980) for Gulf of St.Lawrence cod. In absence of alternative prey, cod would probably decline in abundance.

RESULTS

Three series of six regression analyses were carried out with snow crab catch data, and different cod biomass values averaged over 1 to 6 years (Table 2). The first series was calculated with snow crab data for the years 1973 to 1979. Predicted annual catches up to 1982 were estimated with these regressions. The same calculations were repeated with snow crab data for 1973 to 1980, and 1973 to 1981 (Figure 2).

In the three series, the best regression fit is obtained with cod biomass averaged over 4 years, the coefficients of determination (r^2) being 0.89, 0.91 and 0.87 respectively. This indicates that snow crab

Table 2. Results of the regressions of snow crab catches on average cod biomass for different time periods of averaging, using the equation $Y = ae^{-bx}$, and a lag time of 6 years.

Years of snow crab data	Nb of years used in the average cod biomass	Regression parameters		r^2	Snow crab catches (t) predicted by the regression		
		a	b		1980	1981	1982
1973-1979	1	31 211	-7.37×10^{-6}	0.13	12 417	14 582	14 499
	2	74 823	-1.24×10^{-5}	0.52	18 263	20 697	18 342
	3	75 831	-1.27×10^{-5}	0.77	18 477	18 754	13 429
	4	67 644	-1.25×10^{-5}	0.89	16 372	13 650	9 304
	5	61 441	-1.23×10^{-5}	0.85	12 800	9 998	4 846
	6	67 813	-1.32×10^{-5}	0.72	10 101	5 574	---
1973-1980	1	40 306	-9.10×10^{-6}	0.36	---	16 914	16 796
	2	53 145	-1.05×10^{-5}	0.64	---	17 864	16 124
	3	55 919	-1.11×10^{-5}	0.82	---	16 497	12 322
	4	59 832	-1.18×10^{-5}	0.91	---	13 209	9 199
	5	70 832	-1.31×10^{-5}	0.88	---	10 266	4 736
	6	90 179	-1.47×10^{-5}	0.70	---	5 581	---
1973-1981	1	52 010	-1.01×10^{-5}	0.57	---	---	18 198
	2	58 626	-1.11×10^{-5}	0.76	---	---	16 745
	3	65 258	-1.19×10^{-5}	0.87	---	---	12 829
	4	78 439	-1.32×10^{-5}	0.87	---	---	9 625
	5	91 912	-1.43×10^{-5}	0.71	---	---	4 826
	6	30 846	-7.25×10^{-6}	0.14	---	---	---

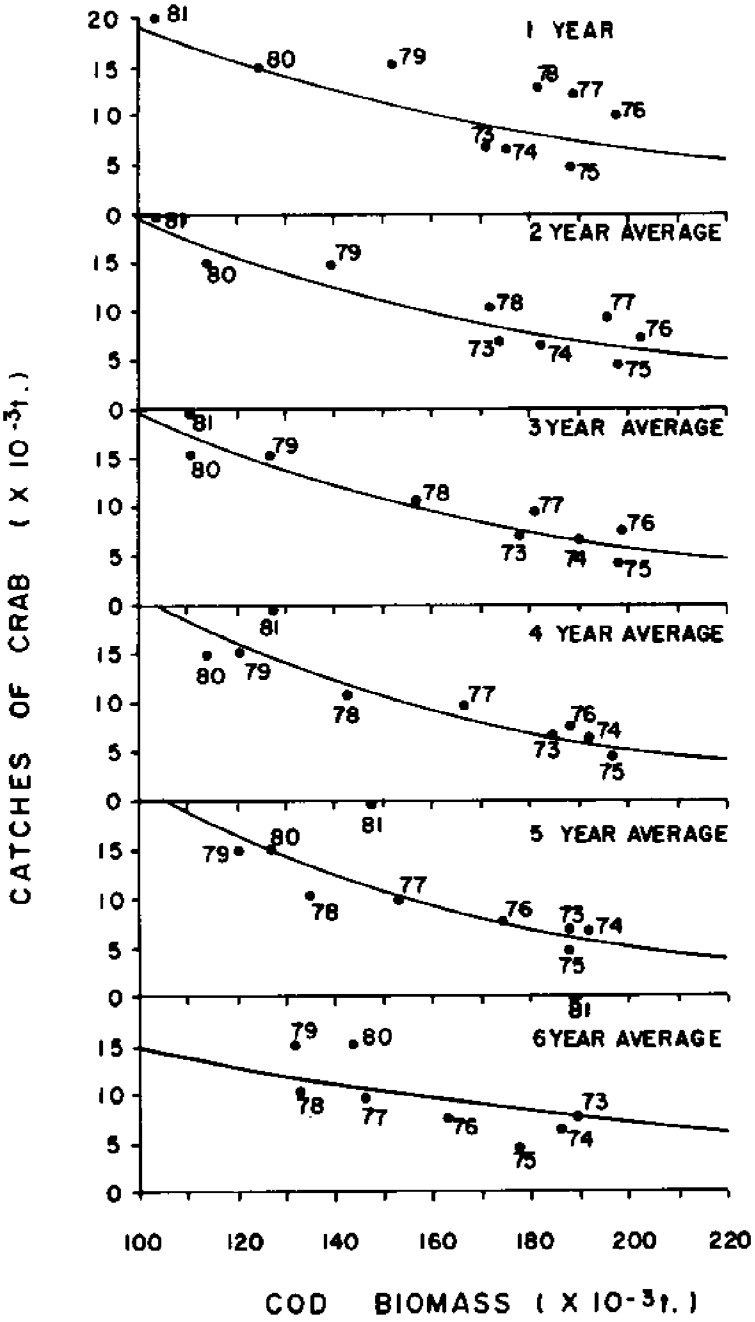

Figure 2. Relationships between annual (1973 to 1981) catches of snow crab in the southwestern Gulf St.Lawrence and average 4 TVn cod biomass.

catch in a given year seems to have been influenced mostly by the population of cod present 3 to 6 years earlier.

The 4-year average regressions in each of the three series, namely 1973-79, 1973-80 and 1973-81, predict similar crab catches for 1982 of 9,304, 9,199 and 9,625 t. The same consistency holds for the 3-year-average and 5-year-average regressions which in all cases have values for $r^2 > 0.71$. Their predicted 1982 catches are 13,429, 12,322 and 12,829 t for the 3-year averages, and 4,846, 4,736 and 4,826 t for the 5-year averages.

In the analysis using the 1973-79 crab catch data, predictions for the 1980 crab catch overestimated the actual catches of 14,757 t by 25.2% for the 3-year-average regression (at 18,477 t) and by 10.9% for the 4-year-average regression (at 16,372 t). The 5-year-average regression underestimated it by 13.3% at 12,800 t. The predictions for 1981 underestimated the actual catches of 19,651 t by 4.6% for the 3-year-average regression, 30.5% for the 4-year-average regression and 49.1% for the 5-year-average regression. Using the 1973-80 crab catch data, the predictions for 1981 were again underestimating the actual catches by 16.1%, 32.8% and 47.8% respectively for the 3-year-average, 4-year-average and 5-year-average regressions.

All regressions, particularly those with the best fit (high r^2 value), predict a reduction in the catches of crab for 1982. This reduction would be associated with the increase in cod abundance since the mid-70's.

DISCUSSION

The best relationships of crab catches to cod biomass, obtained with the average biomass of cod 3 to 6 years before the corresponding crab fishing season, suggest that predation by cod is mostly directed at crabs up to 3 years old. Predation on older crabs is probably not as important since the corresponding regressions show a decline in the coefficients of determination (Table 2). According to Watson's (1969) growth model for snow crab, a 3-year old crab is 40 to 65 mm in carapace width. This corresponds well with the observation that the largest crabs found in the cod stomachs were approximately 50 mm (K. Waiwood, pers. comm.).

The relationship between cod abundance and crab catches has remained fairly consistent in the last 3 years. According to the stable predictions for the 1982 crab catches, using the different series of regressions, the trend in the relationship between cod and crab has not changed from 1979 to 1981.

One assumption of the simple model presented here is that 1) the initial number of juveniles, or the number of larvae successfully settling on the bottom, is the same each year; or at least that 2) cod predation reduces the abundance of juvenile crabs to a number proportional to cod abundance. Although the correctness of this assumption cannot be demonstrated, evidence has been presented in the introduction suggesting at least that larval production is not reduced by exploitation of the stock.

The model also assumes that the pattern of predation on crab is stable and that the abundance of other prey species does not affect too seriously the relationship between the abundance of cod and the amount of predation on crab. Nevertheless, it is probable that a large increase in the abundance of pelagic fishes, such as herring and capelin, or a major shift in the size composition of cod would result in reduced predation on juvenile crabs. Cod seems to have a preference for pelagic prey when available (Brunel 1963; Kohler and Fitzgerald 1969). Abundance of other predators on the other hand may result in higher mortality of crabs. The relationships between cod and crab can thus be affected by outside dynamic elements. The importance of these elements will determine the goodness of fit of a direct relationship. The strong coefficients of determination found in this study are indications that these elements have been marginal or constant during the period of analysis (1973-1981). But this does not necessarily mean that the same relationship will hold as strongly in the future.

In the regression analysis, a direct measure of recruitment would have been preferable to the annual catch data. However, the necessary assumptions that the catches reflect the abundance, and that the population is composed of a significant portion of recruits seem to have some support. The catch rates reported by fishermen in the last years have increased (Lamoureux 1981), although the effort may have slightly increased too, and higher abundance is the best explanation for higher total catches. The size range of recruits in the catches is approximately 95 to 115 mm since, after one molt, the largest pre-recruit of 94 mm would increase in size by 18.6% (Miller and Watson, 1976) to approximately 112 mm. Crabs within this size range represented approximately 60% of the size composition of the catch in 1977, from 60% to 80% in 1978, and over 90% since 1979. Although it is possible that not all the crabs in that size range were recruited in the same year, their relative increasing abundance suggests that a major part of the snow crab catch in composed of recruits. The size of the catch should then be a measure of recruitment success.

The predictions of annual catches calculated with the regressions are values expected under average conditions experienced during the years considered in the analysis. These estimates will then have a statistical probability of error attached to them. For instance, the predictions for 1980 and 1981 with the 4-year-average regressions were off by 10.9% to 32.8% of the actual catch data.

In conclusion, it seems premature to use the statistical relationships between cod abundance and crab catches to predict exact yields for the fishery. However, it may prove very useful in indicating future trends in the annual catches.

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Cod Predation of Snow Crab (*Chionoecetes Opilio*) in the Gulf of St. Lawrence

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INTRODUCTION

The intricacies of a predator:prey interaction may be further complicated if either or both the predator and prey are commercially exploited. Such a situation exists in the Gulf of St. Lawrence where important fisheries exist for the cod, Gadus morhua, and its snow crab, Chionoecetes opilio, prey. Each spring, the cod migrate into the southern Gulf of St. Lawrence (NAFO Division 4T) after overwintering in the Sydney Bight (Fig. 1). In the southern Gulf, during summer and fall, cod is the major commercial groundfish with recent catches of approximately 40,000 MT (Sinclair and Maguire 1981). There has been a snow crab fishery in the Gulf of St. Lawrence since 1966 and current landings are in excess of 20,000 tons (Elner 1982).

Early investigations into the diet of 4T cod have shown that herring, capelin and flatfish were major prey items (Corbeil 1953, Powles 1958, Kohler 1964). However, Waiwood et al. (1980) and Waiwood (1981) suggest that diet composition has changed in recent years with decapods, particularly snow crab, contributing a higher proportion of the diet. Cod stomachs have been analysed on fall groundfish surveys in the southern Gulf of St. Lawrence during 1959-73 and 1979-81 (Waiwood et al. 1980; Waiwood 1981, Waiwood and Majkowski, unpublished manuscript). The object of this paper is to interpret these data with regard to the impact of cod predation on crab species in general and on snow crab in particular. Specifically we consider: historical patterns of crab predation in relation to location, variation in the contribution of crabs to the diet of cod, and predator-prey size relationships for cod-snow crab. The biomass of crab consumed by various age classes of cod (for a restricted period and area) are also estimated over the time series using data on diet composition and estimates of numbers-at-age and total food consumption-at-age.

METHODS

Geographic and year-to-year variation in the dietary contribution of snow crab were evaluated from cod stomach content data collected on groundfish surveys during 1959-73 and 1979-81. During this period, over 14,000 stomachs (non-empty) were examined. Both sampling design and procedures for stomach analysis varied during the time series. In the period 1959-63, stomach data were collected on standard, fixed-station fall surveys in the southwestern Gulf of St. Lawrence and on exploratory surveys which covered other areas in the Gulf. During 1964-70, sampling was mainly restricted to the above fixed station fall survey but, after 1971, a stratified random fall survey was added to the historic fixed-station survey. This survey was also expanded to include the entire southern Gulf. The locations of sampling stations occupied during 1959-73 and 1980-81 are shown in Fig. 2a,b. In order to standardize year-to-year comparisons in the diet of cod, we have only used data from fall cruises (September) and from a defined area (see Fig. 1). This area is approximately 9500 km^2 and corresponds to the more restricted coverage during 1964-68 as well as overlapping commercial snow crab fishing grounds.

Before 1980, stomachs were analysed at sea as a standard sampling procedure. Cod length, weight, sex and maturity were recorded. Total stomach volume was estimated by visually matching the contents with plasticine models of known volumes. The contributions of individual prey groups were estimated as parts of ten. In 1980 and 1981, whole stomachs were removed, wrapped in gauze or tied, preserved in 10% Formalin and returned to the laboratory for analysis. The total stomach contents were weighed, then sorted into taxa which were then weighed to the nearest 0.01 g. Items were identified to species level where possible. Carapace width of each crab prey was measured to the nearest 1 mm using vernier calipers.

The dietary fractions attributable to the various prey groups were calculated on a per weight basis. If only volumes were available, a density of one was assumed. The average percentage dietary contribution of snow crab was adjusted by assuming that the composition of unidentified remains (e.g. unidentified crabs, decapods or invertebrates) was not different from that of the identified fraction. Empty stomachs were not analysed.

The percentage (by weight) of crabs in the diet was calculated for different weight categories of cod each representing a specific age group. Weight categories representing ages 9-10 and 11-15 were combined. Weights-at-age for the time series were taken from Beacham (1980), and Sinclair and Maguire (1981).

The evaluation of the food biomass consumed by cod of different age-groups was based on an application of Ursin's growth theory which relates food consumption to growth (Ursin 1967). The model uses empirical growth data for cod, values for the required physiological parameters and the appropriate numbers-at-age as described and tested by Majkowski and Waiwood (1980) and Waiwood et al. (1980). Input values for the physiological input parameters of the model are presented in Table 1.

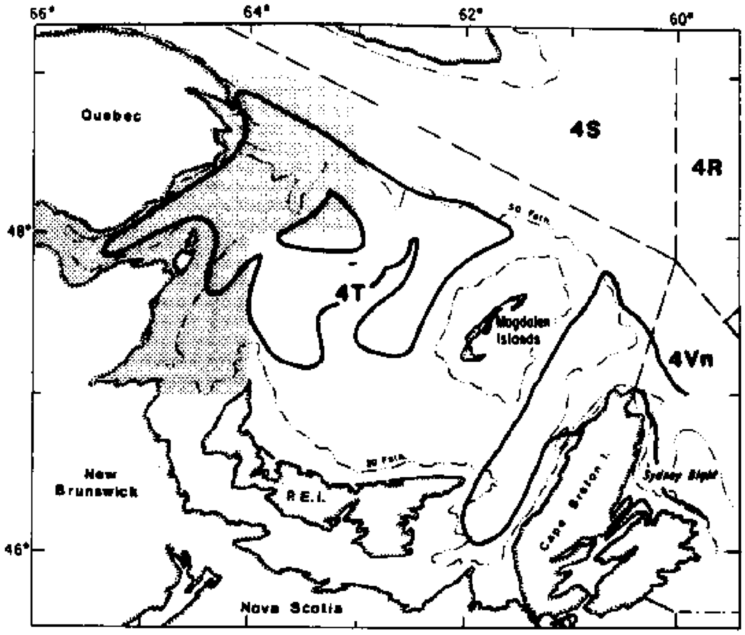


Fig. 1. Location of snow crab fishing grounds (delineated by thick, solid lines) and the defined area of study (stippled) in NAFO Division 4T, southern Gulf of St. Lawrence.

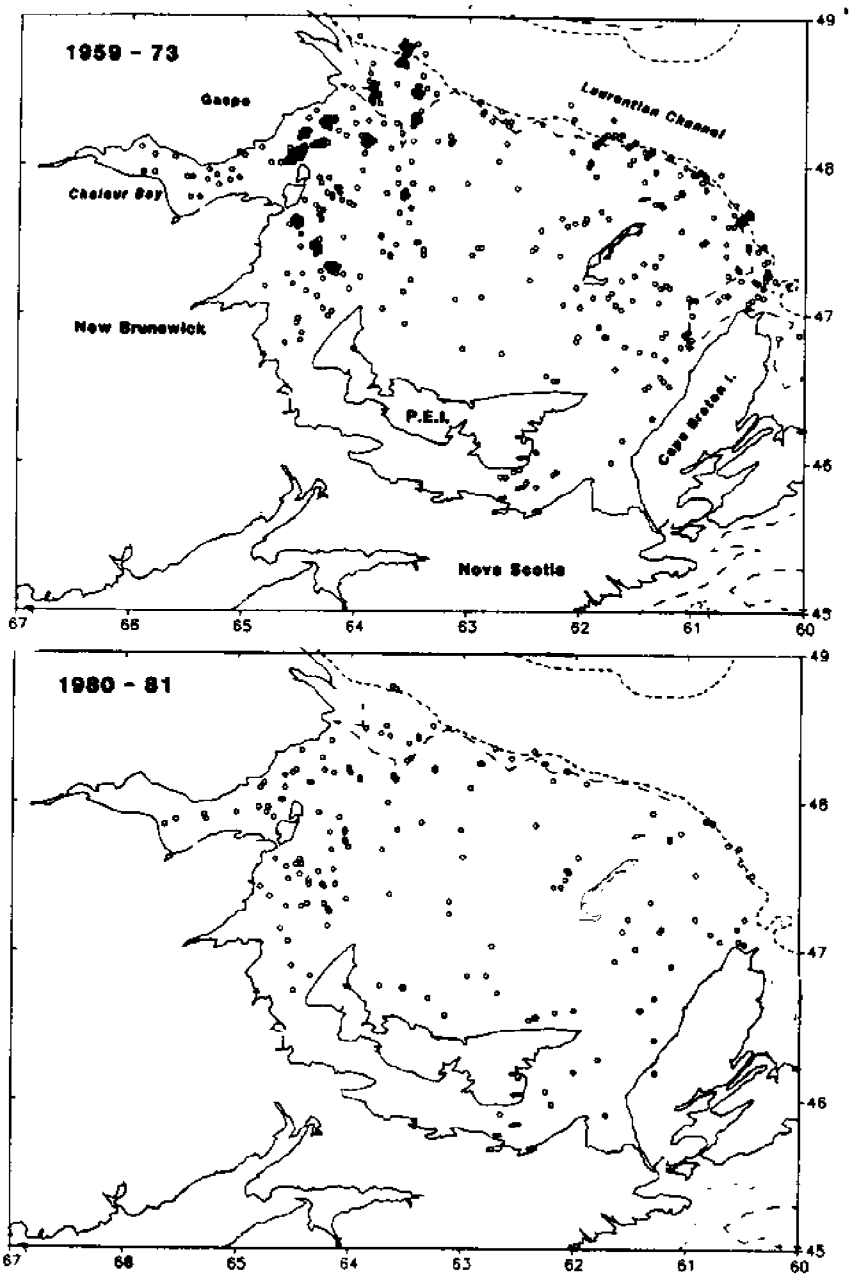


Fig. 2. Location of sampling stations for groundfish trawl surveys, 1959-73 and 1980-81.

Table 1. Physiological parameters used in the calculations of food consumption rates of cod.

Symbol	Explanation	Value	Unit	References
β_i	Assimilated fraction of consumed food	0.8	Pure number	Winberg (1956); Ursin (1967, 1979)
α_i	Fraction of assimilated food lost in feeding catabolism	0.4	Pure number	Ursin (1967, 1979); Andersen & Ursin (1977)
k_i	Coefficient of the term for fasting catabolism	1.9	g^{1-n_i}/years	Waiwood & Majkowski (unpublished data)
n_i	Exponent of the term for fasting catabolism	0.83	Pure number	Ursin (1979)
m_i	Power value of the term relating the food consumption rate to the body weight	0.56	Pure number	Andersen & Ursin (1977)
a	Coefficient of the formula relating the biomassed reproductive products spawned by a cod during the year to its body weight	0.0512	g^{1-b}	Waiwood & Majkowski (unpublished data)
b	Power value of the formula relating the biomass of reproductive products spawned by a cod during the year to its body weight	1.145	Pure number	Waiwood & Majkowski (unpublished data)
pi	Fraction of mature cod at		Pure number	Beacham (pers. comm.)
	age 3	.17		
	4	.66		
	5-15	1.0		

The average numbers-at-age ($\bar{N}_i$) in each year were calculated using the following equation from Ricker (1975):

$$\bar{N}_i = \frac{N_{oi}(1-e^{z_i})}{z_i} \qquad (1)$$

where Z_i was the sum of fishing mortality, F_i (Table 10C in Sinclair and Maguire 1981) and natural mortality (M_i) which was given the value of 0.2 for all ages and years. The starting numbers-at-age (N_{oi}) were taken from Sinclair and Maguire (1981).

The biomass of food consumed by cod in area 4T (R_{4Ti}) was calculated as the yearly food biomass minus the biomass of food eaten in area 4Vn (Sydney Bight) where the latter value was estimated to equal one third the yearly maintenance ration (see Majkowski and Waiwood 1980, 1981). The biomass of crab eaten by cod during each September (R_{hi}) and in the defined area was calculated as follows:

$$R_{hi} = pqr_i \; \bar{N}_i R_{4Ti} \qquad (2)$$

where p (= 0.125) was the proportion of the time spent in 4T represented by the month of September, q (= 0.35) was the fraction of the population inhabiting the defined area (Waiwood et al. 1980), r_i was the fraction of the food biomass represented by the crabs, $\bar{N}_i$ was the yearly average number-at-age (Table 2) and R_{4Ti} was the average food biomass eaten in 4T by cod of the i-th age. In this calculation it was necessary to assume that in September food consumption rate in the defined area was identical to that estimated for the total residence (June to December) in 4T. Since variation in total food consumption undoubtedly occurs among months and areas, differences among years in the fraction of the total population inhabiting the defined area and the values for total and individual crab biomasses consumed by cod, in the defined period and area, should be considered as approximate estimates of absolute consumption.

Table 2. Average numbers-at-age ($\overline{N}_i$) in each year calculated using equation (1) (see text for details).

	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1080	1980	1981
3	128454	120846	41249	53716	37017	54357	46661	54228	94209	84632	50487	45896	65851	27531	37737	14032	239161	71124
4	79281	102982	97320	32936	42941	29724	41747	34482	40252	72810	66755	39523	36366	46682	19699	127341	115818	194126
5	56869	59003	75740	72918	24077	30895	20827	26415	22606	25973	49948	44983	27268	22843	26353	74324	95205	87417
6	26806	36450	39851	55404	47067	14926	17705	12283	15114	13902	16243	29716	26319	15650	11202	52868	47782	65408
7	10577	14659	20593	24805	37008	25927	7548	9179	6701	9057	8248	9685	16508	13503	7652	9906	34068	30684
8	6144	4656	7882	11404	13856	19698	11977	3521	5283	3655	5152	4767	4952	8381	6048	4882	5889	21877
9	8188	2225	2735	4645	5978	6889	9622	5488	1973	3256	2012	2625	2511	2346	3766	2417	2885	3781
10	3394	3145	1246	1626	2711	3097	3232	4804	3086	1228	1957	895	1312	1198	1002	1370	1429	1853
11	1811	934	1501	746	896	1657	1554	1488	2732	1650	727	994	389	612	505	287	861	917
12	1150	673	400	854	479	505	997	710	688	1516	863	305	351	190	269	177	132	553
13	431	482	341	173	576	285	275	525	354	274	821	469	106	92	73	66	103	85
14	320	154	271	196	108	386	166	128	295	147	104	486	239	53	22	104	32	66
15	207	121	74	139	124	61	215	93	64	175	61	48	267	118	23	44	71	21

RESULTS

Contribution of Crab to Cod Diet

Figure 3a,b shows the geographic distribution of snow crab, as found in cod stomachs, from the southern Gulf of St. Lawrence for September in the years 1959-73 and 1980-81. During the period 1959-73, cod predation on snow crab appeared largely restricted to the Laurentian Channel slope edge and the area off Gaspé. In 1979-81 predation on snow crab was more general throughout the Gulf.

The dietary importance (percent of stomach contents by weight) of the three crab prey categories for eight age classes (3-10 yrs) of cod caught in the defined area in September of each sampling year are shown in Fig. 4. Generally, the prey category 'All Crabs' (composed of the rock crab, *Cancer irroratus*, in addition to majid crabs, *Chionoecetes opilio* and *Hyas* spp.) appears more important in the diet of older, and, hence, larger cod. The differences in diet attributable to predator size are even more apparent for the prey categories 'Majidae' and '*C. opilio*'. The highest dietary levels of snow crab occurred in the early 1960's and 1980-81 in cod >7 years. Snow crab was relatively unimportant in the diet of all age classes of cod between 1965-68. To determine predator:prey size relationships, carapace widths of snow crab prey were plotted against the length of their respective cod predators (Fig. 5). Generally, prey size increases with predator size; however, the variability about the regression line suggests that cod above a threshold length of approximately 55 cm are able to handle a greater snow crab size range than cod below this threshold.

Crab Biomass Consumption

Estimates of the biomasses of the three crab prey categories consumed throughout the defined area in September by the various cod age classes are shown in Fig. 6. Considerable year-to-year and age-related variation in the consumed biomasses of the various prey categories was observed. Comparisons of prey consumption patterns with diet composition patterns (Fig. 5) strongly indicate that prey biomass consumed is more influenced by the number of cod-at-age than by the respective diet composition values. Thus, the relatively small numbers of older cod with a high dependence on crab prey do not necessarily account for a larger crab consumption than more numerous younger cod with a low dietary dependence on crab. In 1981 the strong year class of age 8 cod coupled with its high reliance on snow crab appears to have resulted in a massive consumption of snow crab. September consumption, in the

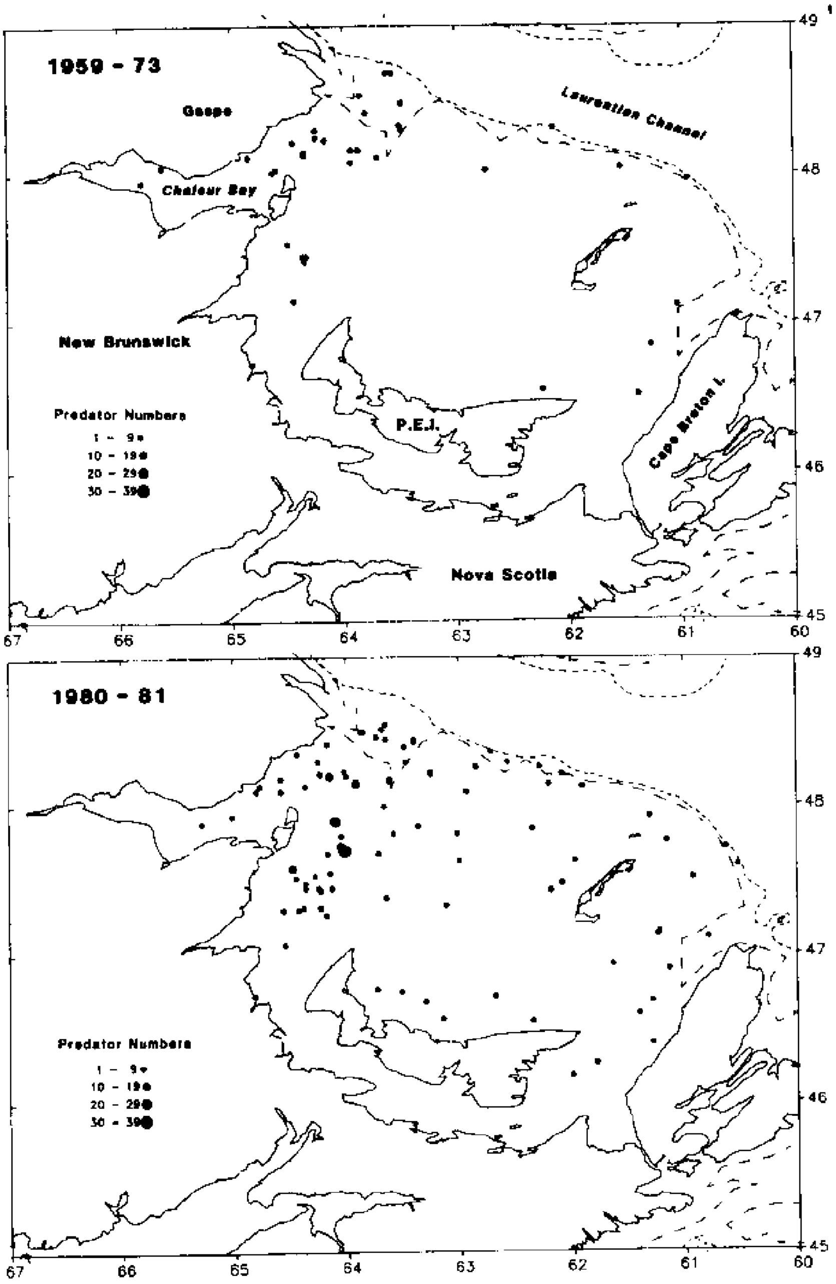


Fig. 3. Distribution of sampling stations where stomachs of cod caught contained snow crab, 1959-73 and 1980-81.

Fig. 4. Percentage of stomach contents by weight occupied by crab prey categories for 8 age classes of cod caught in the defined area in September of each sampling year.

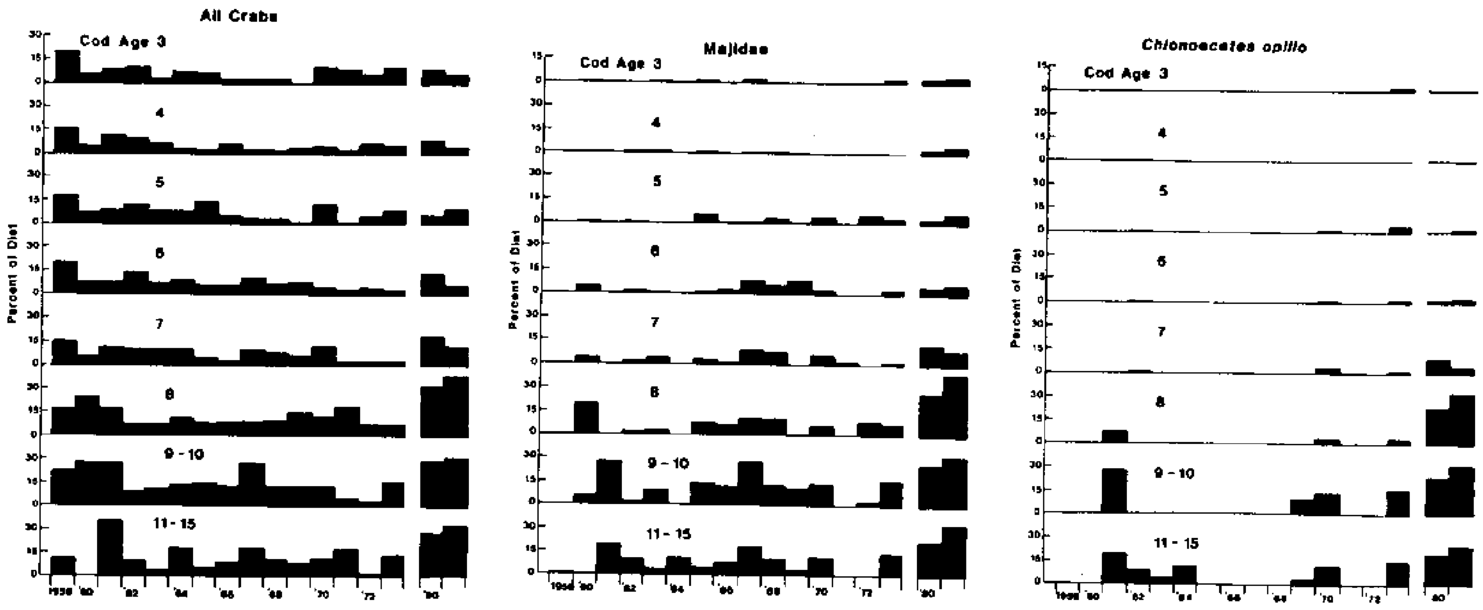


Fig. 5. Relationship between the carapace width of snow crab prey and the length of the respective cod predators.

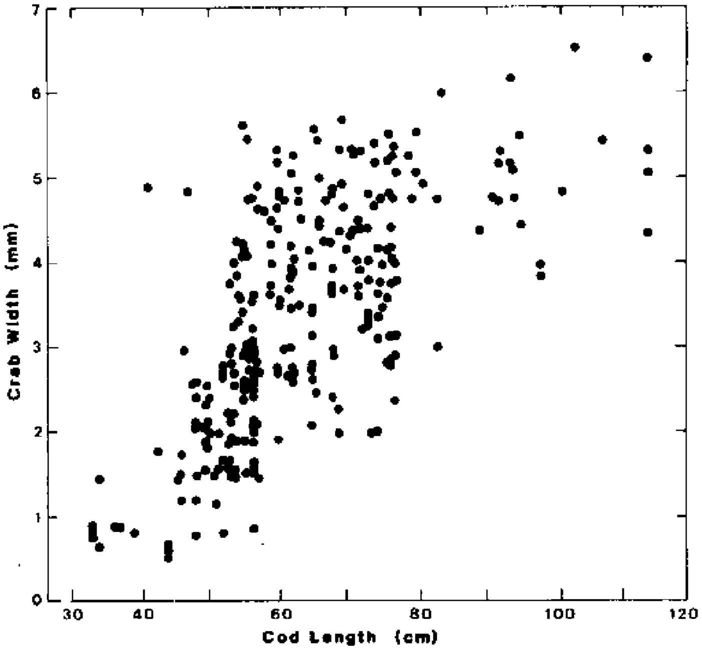
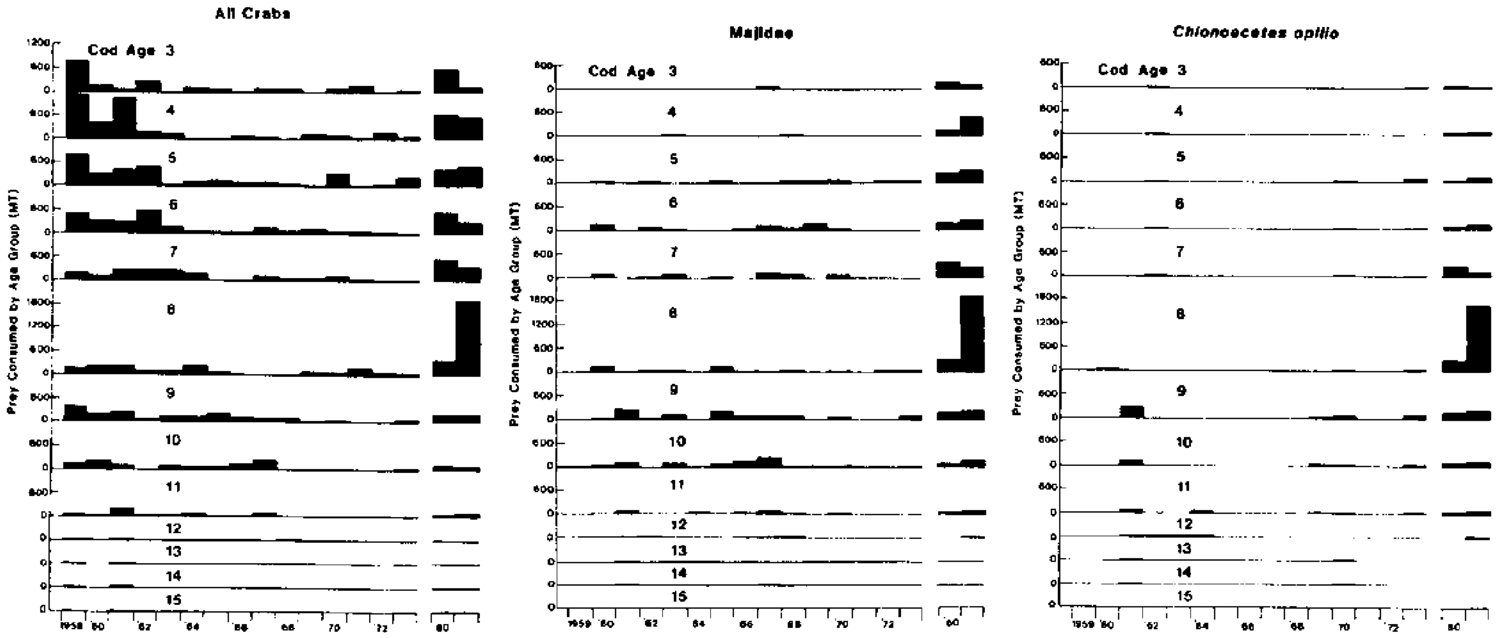


Fig. 6. Estimates of the biomass of the three crab prey categories consumed by each cod age group in the defined area for September of each sampling year.



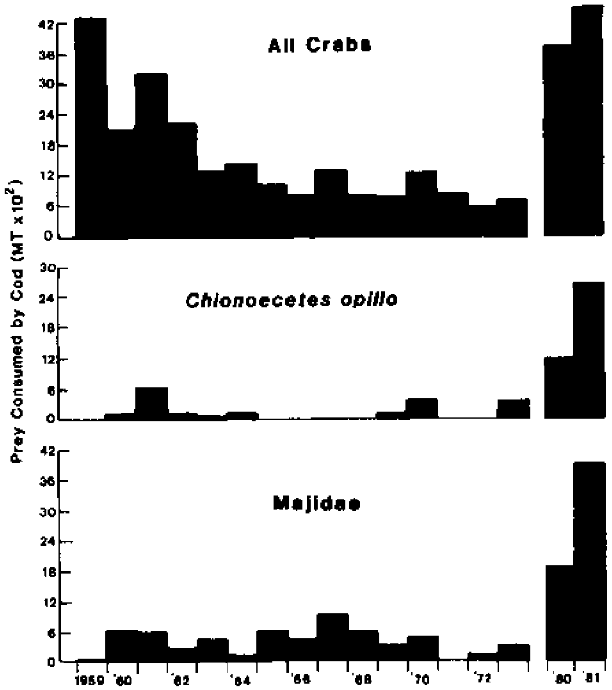
defined area, of the various crab prey categories by all age classes of cod combined are shown in Fig. 7. The biomass of snow crab consumed by cod is seen to have reached a record high level in 1980-81 compared to 1959-73. Comparison of the biomass consumption patterns for the 3 crab prey categories indicates that although consumption of the general "All Crabs" category was high during the period 1959-63, consumption of Majidae and snow crab was correspondingly low. Thus, a high consumption of Cancer crab probably accounts for the large "All Crabs" biomass eaten during the 1959-63 period.

DISCUSSION

Our findings indicate that the magnitude of cod predation on snow crab is not a simple relationship reflecting merely the abundance of the predator. The data presented demonstrate that the consumption of snow crab is profoundly influenced both by the age structure of the cod population and the dietary importance of snow crab for each age class of cod. Both cod age structure and diet composition appear to vary from year to year. Variations in the age structure of the cod population may be attributable to commercial exploitation patterns as well as environmentally-controlled fluctuations in year-class strength. The dietary importance of snow crab may be expected to vary as a fraction of changes in the availability of alternative prey species as well as the abundance of the size range of crabs that particular sizes of cod are able to handle.

If September is a typical month and our defined area is representative of the southern Gulf as a whole, snow crab do not appear to have been a major food source for cod during 1959-73. However, during 1980-81 both the dietary importance of snow crab to most cod age classes and the biomass of snow crab consumed in the defined area in September appear to have increased markedly. A major part of the increase in predation pressure on snow crab is due to the strong year class of age 8 cod coincident with their relatively high dietary dependence on snow crab. Comparison of survey sites where snow crab were found in cod stomachs reveals that, in tandem with the increased consumption of snow crab in 1980-81, there has been a broadening of the areas over which cod predation on snow crab occurs. Such a distributional change in the cod:snow crab interaction could be due either to an increase in the availability of snow crab, within the size ranges eaten by cod, or a decrease in the availability of other, more preferred, prey species. There is evidence that both phenomena have occurred simultaneously. Waiwood (1982) has shown that the dietary occurrence and population consumption by fish in general and of herring, in particular, have declined in recent

Fig. 7. Estimates of the biomass of the three crab prey categories consumed by all age groups of cod (3-15 years) combined in the defined area for September of each sampling year.



years. This would be expected given the concurrent decline in abundance in herring (Clearly 1981). The change in diet from fish to decapods has been interpreted as indicating sub-optimal feeding conditions (Daan 1973, Grosslein et al. 1980). On the other hand, catch rates in the snow crab fishery have increased consistently since 1977 (Bailey 1981) suggesting strong recruitment in recent years.

The question of the impact of cod predation on snow crab recruitment is complicated by the regulation that only male crabs of 95 mm carapace width and above can be landed. Female crabs are not fished as they undergo a terminal moult to maturity below the legal minimum size. As cod seldom feed on crabs above 70 mm carapace width (Fig. 5), they prey largely on female and sub-legal male snow crabs. The impact of such a preference on either recruitment to the crab fishery or the reproductive potential of the crab stocks is unknown. However, Bailey (1981) suggested that the recruitment of snow crabs to the fishery in the Gulf of St. Lawrence has a strong negative dependence on the cod biomass 3-6 years before. The hypothesized mechanism is that cod exert a strong control over the numbers of small crab, in a relationship directly proportional to cod biomass, and, hence, determine the numbers of crab that grow to legal size 3-6 years later. There are several weak assumptions in this model. Firstly, the consumption of snow crabs by cod is assumed to be a simple function of cod biomass. However, Fig. 7 indicates that snow crab consumption varies tremendously from year to year often being undetected in years of relatively high cod biomass. We suggest also, that crab consumption will depend on the age structure of the cod population and on the abundance of more preferred prey. Secondly, Bailey's model presumes that snow crab landings are an indicator of snow crab biomass. However, Fig. 8 indicates that crab landings in the Gulf of St. Lawrence have increased largely as the result of increased fishing effort (in numbers of traps). Since effort was not constant over the time series, catch-per-unit effort would be a more appropriate indicator of snow crab biomass. We have not found any relationship between catch-per-unit effort (catch/estimated number of traps) and previous cod biomass.

An alternative hypothesis to Bailey (1981) is that cod have not been a major influence on snow crab landings and that the 1980-81 upsurge in cod predation on snow crab is a functional response by cod to the increased availability of small crabs and a decline in preferred prey. We propose that prior to the establishment of the snow crab fishery, the Gulf of St. Lawrence snow crab stocks were in a saturated,

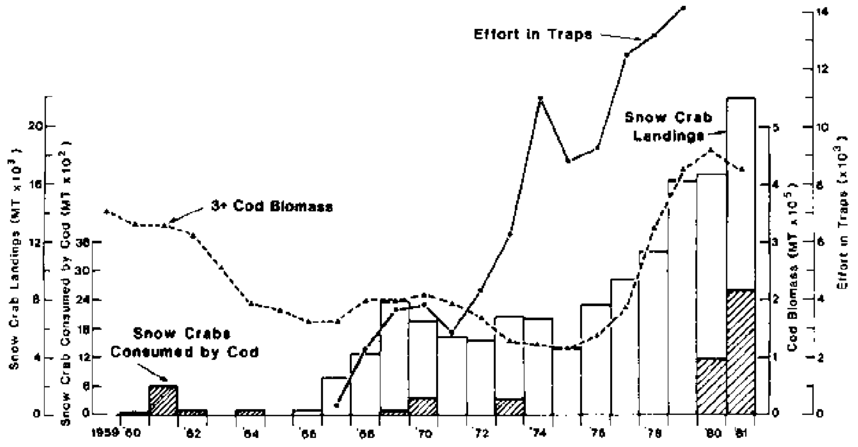


Fig. 8. Historical relationship between the biomass of cod (3-15 years) in the southern Gulf of St. Lawrence, commercial snow crab landings and fishing effort (in terms of the estimated number of traps, from Bailey (1978)) in the southwestern Gulf of St. Lawrence, and the estimated snow crab biomass consumed by cod in the defined area in September of each sampling year (note: no snow crab biomass values available for 1974-79).

'stagnant' phase with larger, old crab monopolizing niche space and, by competition, restricting the resources available to smaller crabs. If so, the growth of the smaller crabs (upon which cod feed) would have been reduced. In such a situation, cod predation on snow crab in the pre-fishery and early fishery periods would have been low and would have occurred within limited areas of the Gulf. However, once the commercial fishery started to remove the large, old crabs, interpreted to be responsible for inhibiting population growth, we hypothesize that the snow crab population was released from a 'stagnant' phase into a dynamic, high growth phase. We presume that sudden availability of space and food resources led to increased growth, greater numbers of small crab, and enhanced recruitment. In response, increased cod predation on the small 'preferred size' of crab as well as the increased numbers of soft-shelled vulnerable crab would have resulted. Such a shift is evidenced by the increase in cod predation on snow crab during 1980-81 and the broadening of the areas over which cod predation on snow crab occurs. Increases in catch rate experienced by the commercial snow crab fishery since 1977 (Bailey 1981) also suggest that crab abundance has increased over the recent post-fishery period. Furthermore, since 1977, crab catch size frequency profiles have shifted to include a greater proportion of smaller sizes; a phenomenon which can be explained both by the fishery removing larger individuals and an improvement in growth and recruitment (Bailey 1981). Given that our scenario is correct, cod predation in the post-fishery period up to 1981 has served only to crop the abundant supply of small crabs, and has had only marginal effect on crab landings. Indeed, cod predation may have enhanced the growth rate of smaller crab by decreasing intra-specific competition.

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ABSTRACT

Recent (1980, 1981) and historical (1959-1973) data on the diet of cod (Gadus morhua) from the southern Gulf of St. Lawrence are analysed with reference to the occurrence of snow crab (Chionoecetes opilio), Majidae and all crabs. The dietary contribution from each crab category varied as to cod size, geographic location, and year. Snow crab prey size increased with cod predator size. Estimates of total biomass consumed for each crab category in a defined area during September of each year show that historic levels of snow crab consumption were low compared to recent levels. We hypothesise that commercial exploitation of snow crab has stimulated increased growth and recruitment in the population and that cod have, hitherto, not impacted the snow crab fishery.

Predation on Crabs of the Genus *Chionoecetes*: A Literature Review

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ABSTRACT

Crabs of the genus *Chionoecetes* are one of the most commonly taken benthic prey in the northern Pacific Ocean, Bering Sea, and western Atlantic Ocean. Feeding studies conducted throughout their range have shown *Chionoecetes* to be prey for at least seven species of invertebrates, twenty-six species of fishes, and four species of marine mammals. All references to predation are for *C. opilio, C. opilio elongatus* and *C. bairdi*. Little is known about predation upon larval *Chionoecetes*. Dominant predators are *Chionoecetes*, king crabs (*Paralithodes camtschatica*), Alaska skate (*Raja parmifera*), Bering skate (*R. interrupta*), wattled eelpout (*Lycodes palearis*), Pacific cod (*Gadus macrocephalus*), Atlantic cod (*Gadus morhua*), sculpins (*Myoxocephalus* spp., *Hemilepidotus jordani, Malacocottus zonarus, Dasycottus setiger*), Pacific halibut (*Hippoglossus stenolepis*), and rex sole (*Glyptocephalus zachirus*). Heavy predation on commercially-important *C. bairdi* and *C. opilio* occurs in the southeast Bering Sea by the Alaska and Bering skates, wattled eelpout, Pacific cod, and four species of sculpins. Large (> 40 mm carapace width) *C. bairdi* examined near Kodiak Island were more cannibalistic than small (< 40 mm) individuals. *Chionoecetes bairdi* was the most frequently occurring species of food found in more than 4,000 Pacific cod examined near Kodiak Island. These crabs occurred in nearly 40% of the cod. The average number of crabs occurring in cod feeding on *C. bairdi* was 3.3; up to 32 crabs were found in a single cod stomach. The size of crabs from cod stomachs ranged from 1.8 to 70 mm carapace width; 78% were between 7 and 23 mm. The sex ratio of the crabs consumed was 1:1. Approximately 52% of the sculpins, *Myoxocephalus* spp., examined near Kodiak Island also contained *C. bairdi*. Nearly 23% of the crabs consumed by these sculpins were ovigerous females.

INTRODUCTION

The broad range and great abundance of the genus *Chionoecetes* are reasons this genus may receive the greatest predation pressure of any commercially exploited genus of crab. Among commercial crustaceans, it is probably second only to pandalid shrimps (genus *Pandalus*) in terms of receiving the greatest pressure from predation. The genus *Chionoecetes* is comprised of five species (*C. opilio, C. bairdi, C. tanneri, C. japonicus, C. angulatus*) and one subspecies (*C. opilio elongatus*). Their range extends from approximately 30° to 72° latitude N to depths of 2,980 m in the eastern Pacific Ocean from Bering Strait east and south through the Aleutian Islands to the United States-Mexico border, in the western Pacific Ocean from Bering Strait west and south to the Sea of Japan, in the Alaskan and Canadian Arctic, and in the western Atlantic from the west coast of Greenland to the Gulf of Maine

(Fig. 1) (Rathbun 1904, 1925; Garth 1958; Squires 1969; Watson 1969; Hosie and Gaumer 1974). Species of commercial importance include *C. bairdi* in the Bering Sea and Gulf of Alaska; *C. opilio* in the Bering Sea, Okhotsk Sea, Sea of Japan and along the north Atlantic maritime provinces of Canada; *C. opilio elongatus* in the Okhotsk Sea and Sea of Japan; and *C. japonicus* in the Sea of Japan. *Chionoecetes opilio* from the western Atlantic are commonly known as snow crabs, whereas *C. opilio* and *C. bairdi* of the eastern Pacific Ocean are known as Tanner crabs.

The following accounts of predation on *Chionoecetes* from various parts of their range have been assembled through a literature review and personal communication with various investigators. This review includes all references known to the author, however, it is not meant to be exhaustive.

GENERAL

A total of 37 predators are known to prey upon *Chionoecetes* from various regions (Table 1). The predators include at least seven species of invertebrates, twenty-six species of fishes, and four species of marine mammals. The known targets of predation are the commercially-important, shallow-water species, i.e., *C. opilio* at 5-377 m (Rathbun 1904), *C. opilio elongatus* to depths of 2,223 m (fished at shallow depths) (Garth 1958), and *C. bairdi* from shoal depths to 474 m (Rathbun 1925). Most reports on predation are on the juveniles; few reports on predation of larvae and adults exist. No reports are available on predation of the deep-water species i.e., *C. japonicus* at 411-2,745 m (Watson 1969), *C. tanneri* at 53-2,973 m (Rathbun 1925), and *C. angulatus* at 90-2,974 m (Rathbun 1925).

The habitat of juvenile *C. bairdi* in the Gulf of Alaska has been identified by SCUBA diving observations and trawling studies. Garth (1958) described the habitat of *Chionoecetes* spp. as that of green and black mud and fine gray-black sand and shell. Large numbers of early post-larval and larger juvenile *C. bairdi* near Kodiak Island have also been observed on open substrate composed of green mud and fine gray-black sand and shell material. Additional observations near Kodiak Island revealed that juveniles were occasionally found among dense patches of epiphytic growth such as hydroids and bryozoans. Larger *C. bairdi* have been observed to be partially buried in a mud-sand substrate (Powell and Jewett, pers. obser.). Trawling studies in lower Cook Inlet revealed a *C. bairdi* nursery area in which large numbers of juveniles were found among dense clusters of sponge-like material (Jewett and Feder, pers. obser).

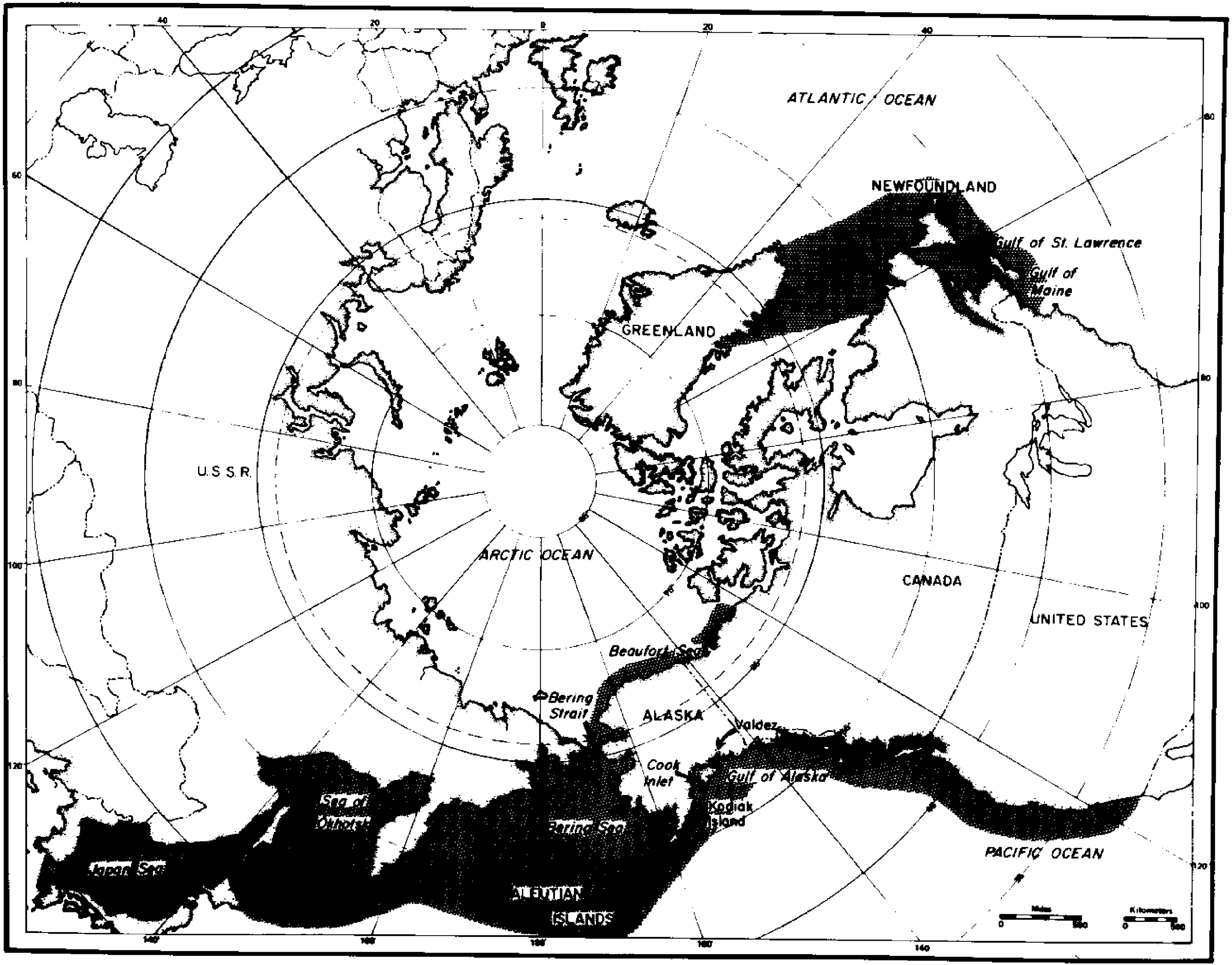

Figure 1. Distribution of the genus *Chionoecetes*

TABLE 1

PREDATORS OF *CHIONOECETES*

Predator	Study area	Prey	Importance	Reference
Chionoecetes bairdi (snow [Tanner] crab)	Kodiak Island shelf	*C. bairdi*	9.6% F^1 (1025 crab examined >40 mm CW^2) 15.8% F; 11.5% Wt.^{3} (857 crab with food)	Jewett and Feder, in preparation
			4.2% F (475 crab examined ≤40 mm CW) 4.5% F (449 crab with food)	Jewett and Feder, in preparation
	Cook Inlet	*C. bairdi*	0.6% F (715 crab examined 5-100 mm CW) 1.1% F (428 crab with food)	Paul et al. 1979
	Port Etches, Prince William Sound	*C. bairdi*	33.3% F; 10.3% Wt. (3 crab examined >40 mm-all with food)	Feder and Hoberg 1981
	Port Valdez, Prince William Sound	*C. bairdi*	6.4% F (78 crab examined) 14.3% F (35 crab with food)	Feder and Matheke 1979
C. opilio (snow crab)	Gulf of St. Lawrence	*C. opilio*	8.0% F (107 crab examined) 8.7% F (103 crab with food)	Powles 1968
C. opilio elongatus (snow crab)	Wakasa Bay, Sea of Japan	*C. opilio elongatus*	abundant (1503 crab examined = 18-150 mm CW)	Yasuda 1967
Paralithodes camtschatica (red king crab)	Kodiak Island shelf	*C. bairdi*	12.5% F (809 crab examined ≥65 mm CL^4) 14.2% F; 2.6% Wt. (713 crab with food)	Jewett and Feder 1982
	Southeast Bering Sea	*C. bairdi* and/or *C. opilio*	7.3% F (124 crab examined ≥50 mm CL) 7.8% F (115 crab with food)	Feder and Jewett 1980
	Northeast Bering Sea	*C. opilio*	8.3% F (60 crab examined >90 mm CL) 9.6% F (52 crab with food)	Hoberg et al., preparation
	Northern Okhotsk Sea	*C. opilio*	unknown (203 crab examined 70-193 mm CL)	Feniuk 1945
Cancer magister (Dungeness crab)	Cook Inlet	*C. bairdi*	<1.0% F (349 crab examined >50 mm CW) <1.0% F (251 crab with food)	Feder and Paul 1980
Lebbeus groenlandicus (shrimp)	Cook Inlet	*C. bairdi*	4.0% F (25 shrimp examined — all with food)	Feder et al. 1980
Asterias amurensis (sea star)	Southeast Bering Sea	*C. bairdi* and/or *C. opilio*	2.4% F (41 sea stars examined — all with food)	Feder and Jewett 1980
Raja parmifera (Alaska skate)	Southeast Bering Sea	*C. opilio* and/or *C. bairdi*	27.4% Wt. (85 fish = 281-1090 mm TL^5)	Mito 1974
Raja interrupta (Bering skate)	Southeast Bering Sea	*C. opilio* and/or *C. bairdi*	40.4% Wt. (779 fish = 281-760 mm TL)	Mito 1974
Bathymaster signatus (searcher)	Cook Inlet	*C. bairdi*	4.8% F (21 fish examined) 25.0% F (4 fish with food)	Feder et al. 1980
Petroschmidtia toyamensis (eelpout)	Sea of Japan	*C. opilio*	unknown	Kon et al. 1968, Ito 1968
Lycodes palearis (wattled eelpout)	Southeast Bering Sea	*C. opilio* and/or *C. bairdi*	28.4% Wt. (24 fish = 361-480 mm TL)	Mito 1974

TABLE 1

CONTINUED

Predator	Study area	Prey	Importance	Reference
Theragra chalcogramma (walleye pollock)	Bering Sea	*C. bairdi* and/or *C. opilio*	unknown	Andriyashev 1954
	Southeast Bering Sea	*C. bairdi* and/or *C. opilio* (megalopa)	<1.0% F (163 fish with food — $\bar{X}$ SL = 270 ± 145 mm)	Smith et al. 1978
	Northern Gulf of Alaska	*C. bairdi* (megalopa)	<1.0% F (253 fish with food — $\bar{X}$ SL = 344 ± 84 mm)	Smith et al. 1978
Microgadus proximus (Pacific tomcod)	Resurrection Bay, Gulf of Alaska	*C. bairdi* (megalopa^7)	100% F (6 fish examined — $\bar{X}$ SL^6 = 216 mm) 100% F (6 fish with food)	A. J. Paul, personal communication 1982
Gadus macrocephalus (Pacific cod)	Kodiak Island shelf	*C. bairdi*	26.5% F (283 fish examined) 28.4% F (264 fish with food)	Feder and Jewett 1981
			37.0% F (4277 fish examined = 330-920 mm TL) 39.5% F (4006 fish with food)	Jewett 1978
	Cook Inlet	*C. bairdi*	62.8% F (43 fish examined) 65.9% F (41 fish with food)	Feder et al. 1980
	Southeast Bering Sea	*C. bairdi* and/or *C. opilio*	10.3% F (29 fish examined — all with food	Feder and Jewett 1980
	Southeast Bering Sea	*C. bairdi* and/or *C. opilio*	18.4% Wt. (737 fish = 330–880 mm FL^8)	Mito 1974
Gadus morhua (Atlantic cod)	Gulf of St. Lawrence	*C. opilio*	7.4% Wt.	Waiwood et al. 1980
Anoplopoma fimbria (sablefish) (blackcod)	Southeast Bering Sea	*C. opilio* and/or *C. bairdi*	<1.0% Wt. (373 fish = 371-670 mm FL)	Mito 1974
Sebastolobus alascanus (shortspine thornyhead)	Northwest Gulf of Alaska	*C. bairdi*	17.2% Wt. (13 fish = 201-330 mm TL)	Mito 1974
Myoxocephalus spp. (sculpins)	Kodiak Island shelf	*C. bairdi*	39.1% F (320 fish examined) 55.0% F (239 fish with food — $\bar{X}$ TL = 580 mm)	Jewett and Powell 1979
		C. bairdi	16.5% F (103 fish examined) 23.3% F (73 fish with food)	Feder and Jewett 1981
	Cook Inlet	*C. bairdi*	30.8% F (26 fish examined) 36.4% F (22 fish with food)	Feder et al. 1980
	Southeast Bering Sea	*C. bairdi* and/or *C. opilio*	28.6% F (7 fish examined) 33.3% F (6 fish with food)	Feder and Jewett 1980
		C. bairdi and/or *C. opilio*	40.5% Wt. (64 fish = 341-600 mm TL)	Mito 1974

TABLE 1

CONTINUED

Predator	Study area	Prey	Importance	Reference
Malacocottus zonarus (sculpin)	Southeast Bering Sea	*C. bairdi* and/or *C. opilio*	36.3% Wt. (31 fish = 150-310 mm TL)	Mito 1974
Hemilepidotus jordani (yellow Irish lord)	Kodiak Island shelf	*C. bairdi*	16.4% F (535 fish examined) 17.8% F (500 fish with food $\bar{X}$ TL = 340 mm)	Jewett and Powell 1979
		C. bairdi	19.2% F (318 fish examined) 24.3% F (251 fish with food)	Feder and Jewett 1981
	Southeast Bering Sea	*C. bairdi* and/or *C. opilio*	54.1% Wt. (29 fish = 210-401 mm TL)	Mito 1974
Dasycottus setiger (spinyhead sculpin)	Northeast Gulf of Alaska	*C. bairdi*	5.8% F (69 fish examined — $\bar{X}$ TL = 96 mm) 6.2% F; 3.2% Wt. (64 fish with food)	Day et al. in preparation
	Southeast Bering Sea	*C. bairdi* and/or *C. opilio*	29.1% Wt. (44 fish = 161-290 mm TL)	Mito 1974
Ulca bolini (bigmouth sculpin)	Southeast Bering Sea	*C. opilio* and/or *C. bairdi*	<1.0% Wt. (53 fish = 271-610 mm TL)	Mito 1974
Liparis cyclostigma (polka-dot snailfish)	Southeast Bering Sea	*C. opilio* and/or *C. bairdi*	24.5% Wt. (10 fish = 480-575 mm TL)	Mito 1974
Platichthys stellatus (starry flounder)	Cook Inlet	*C. bairdi*	7.3% F (35 fish examined) 12.9% F (31 fish with food)	Feder et al. 1980
	Northeast Bering Sea	*C. opilio* (megalopa[9])	0.6% F (307 fish examined) 0.7% F (281 fish with food)	Jewett and Feder 1980
Atheresthes stomias (arrowtooth flounder) (turbot)	Southeast Bering Sea	*C. opilio* and/or *C. bairdi*	<1.0% Wt. (709 fish = 211-750 mm FL)	Mito 1974
Hippoglossoides elassodon (flathead sole)	Cook Inlet	*C. bairdi*	8.8% F (160 fish examined) 12.3% F (114 fish with food)	Feder et al. 1980
	Kodiak Island shelf	*C. bairdi*	6.5% F (246 fish examined) 9.6% F (167 fish with food)	Feder and Jewett 1981
	Southeast Bering Sea	*C. bairdi* and/or *C. opilio*	4.4% Wt. (794 fish = 151-470 mm TL)	Mito 1974
Hippoglossus stenolepis (Pacific halibut)	Cook Inlet	*C. bairdi*	32.7% F (52 fish examined) 35.4% F (48 fish with food)	Feder et al. 1980
	Kodiak Island shelf	*C. bairdi*	2 crab (1 fish examined)	Gray 1964
	Bering Sea	*C. bairdi* and/or *C. opilio*	unknown	Best 1981

TABLE 1

CONTINUED

Predator	Study area	Prey	Importance	Reference
Hippoglossus stenolepis (Pacific halibut) (cont'd)	Southeast Bering Sea	*C. opilio* and/or *C. bairdi*	<1.0% Wt. (26 fish = 341-2040 mm TL)	Mito 1974
	Far east seas	*Chionoecetes* spp.	unknown	Moiseev 1953
Lepidopsetta bilineata (rock sole)	Kodiak Island Shelf	*C. bairdi*	2.1% F (187 fish examined) 3.1% F (131 fish with food)	Feder and Jewett 1981
	Southeast Bering Sea	*C. bairdi*	10.3% Wt. (237 fish = 230-440 mm TL)	Mito 1974
Glyptocephalus zachirus (rex sole)	Gulf of Alaska	*C. bairdi*	38.0% F (300 fish examined — $\bar{X}$ TL = 231 mm) 38.8% F; 4.8% Wt. (293 fish with food)	Smith et al. 1978
	Southeast Bering Sea	*C. bairdi* and/or *C. opilio*	<1.0% Wt. (110 fish = 201-420 mm TL)	Mito 1974
Microstomus pacificus (dover sole)	Gulf of Alaska	*C. bairdi*	3.9% F (129 fish examined = 217-381 mm TL) 4.1% F; 0.3% vol. (121 fish with food)	Smith et al. 1978
Isopsetta isolepis (butter sole)	Kodiak Island shelf	*C. bairdi*	5.0% F (20 fish examined 16.7% F (6 fish with food)	Feder and Jewett 1981
Limanda aspera (yellowfin sole)	Kodiak Island shelf	*C. bairdi*	3.5% F (51 fish examined) 16.7% F (12 fish with food)	Feder and Jewett 1977
	Southeast Bering Sea	*C. bairdi* and/or *C. opilio* (megalopa)	unknown	K. Haflinger, personal communication 1982
Phoca vitulina largha (spotted seal)	East Bering Sea	*C. opilio*	rare	K. Frost, personal communication 1982
Erignathus barbatus (bearded seal)	Southeast Bering Sea	*C. opilio*	major food (397 seals examined)	Lowry et al. 1980
Odobenus rosmarus (Pacific walrus)	Northern Bering Sea	*C. opilio*	$\bar{X}$ Wt. per stomach = <1.0 (107 stomachs examined)	Fay et al. 1977
Physeter catodon (sperm whale)	USSR	*Chionoecetes* spp.	unknown	Tomilin 1957

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[1] % F = percent frequency of occurrence.
[2] CW = carapace width.
[3] % Wt. = percent of wet weight of stomach contents.
[4] CL = carapace length.
[5] TL = total length.
[6] SL = standard length.
[7] Number of megalopa per fish = 1-367; $\bar{X}$ = 98.
[8] FL = fork length.
[9] 146 megalopa in one fish.

DOMINANT INVERTEBRATE PREDATORS

Among the seven invertebrates known to prey on *Chionoecetes*, *Chionoecetes* themselves are most frequently reported predators (Table 1). Large (> 40 mm carapace width) *C. bairdi* examined near Kodiak Island were more cannibalistic than small (≤ 40 mm) individuals. Among 857 large crabs containing food 15.8% were preying on their own kind; only 4.5% of 449 small crabs containing food were cannibalistic (Jewett and Feder, in prep.). A similar frequency of cannibalism occurred in adult, feeding *C. bairdi* from Port Valdez, Alaska (Feder and Matheke 1979). Yasuda (1967) reported that *C. opilio elongatus* was "abundant" within the stomachs of adult *C. opilio elongatus*. Cannibalism has also been reported in other crabs (e.g., lined shore crabs *Pachygrapsus crassipes*, Hiatt 1948; red king crabs *Paralithodes camtschatica*, Feniuk 1945 and Kulichkova 1955; and green crabs *Carcinus maenas*, Elner 1981) but does not appear to be an important feeding strategy.

Four reports of the red king crab *Paralithodes camtschatica* preying on Tanner crabs are included in Table 1. All reports are from different geographic areas where the distribution of *C. opilio* and/or *C. bairdi* overlaps that of red king crabs. The greatest percent frequency of occurrence of predation of *Chionoecetes* by red king crabs exists near Kodiak Island where 14.2% of the king crabs ≥ 65 mm carapace length contained juvenile *C. bairdi* (Jewett and Feder 1982). The percent frequencies of occurrence of *Chionoecetes* within feeding king crabs from the southeastern and northeastern Bering Sea were 7.8 and 9.6%, respectively (Feder and Jewett 1980; Hoberg et al. in prep.).

DOMINANT FISH PREDATORS

Of the 52 accounts of fish predators taking *Chionoecetes* from various areas, 23 accounts (44%) are from the Bering Sea and 23 are from the Gulf of Alaska. Most of the information on predation of *Chionoecetes* in the Bering Sea comes from the work of Mito (1974) who examined feeding relationships among benthic fish populations in the southeastern Bering Sea. His investigation was carried out in October and November 1972 on the walleye pollock (*Theragra chalcogramma*) fishing grounds near the 200 m isobath (180-330 m). He examined the stomach contents of 25 species of fishes from 36 stations and found *C. opilio* and/or *C. bairdi* to be prey for 17 species. Tanner crabs were dominant prey for nine species, yielding between 18 and 54% of the wet weight of food for each species (Table 1).

A total of 779 Bering skates (*Raja interrupta*) were examined from 64% of Mito's stations. He found that Tanner crabs accounted for 40.4% of the total food weight of these skates. He also examined a small number (85) of Alaska skates (*R. parmifera*) and wattled eelpouts (24) (*Lycodes palearis*) and found that nearly 30% of the wet weight of food taken by each of these species consisted of Tanner crabs.

Mito (1974) examined 737 Pacific cod (*Gadus macrocephalus*), some from each of his 36 stations. The percentage of the food weight attributed to Tanner crabs was 18.4%. No other quantitative feeding data are available for Pacific cod, elsewhere, however, qualitative feeding data from the Gulf of Alaska showed that Tanner crabs are frequently taken by cod there (Jewett 1978; Feder and Jewett 1981). Cod examined near Kodiak Island in May, June and February had similar percent frequencies of occurrence of *C. bairdi* in each month examined ($\bar{X}$ = 28.4%) (Feder and Jewett 1981). In another study, more than 4,000 Pacific cod examined near Kodiak Island during June and July contained *C. bairdi* at a percent frequency of occurrence of approximately 40% (Jewett 1978). *Chionoecetes bairdi* was the most frequently occurring prey found in these cod. The average number of crabs occurring in those cod feeding on Tanner crabs was 3.3; up to 32 crabs were found in a single cod stomach. The sizes of crabs ranged from 1.8 to 70 mm carapace width; 78% were between 7 and 23 mm. The sex ratio of the crabs consumed was 1:1. The highest recorded percent frequency of occurrence of *bairdi* in Pacific cod, 66%, was found in Cook Inlet during October (Feder et al. 1980).

Atlantic cod (*Gadus morhua*) are also known to be a major predator on snow crabs (*C. opilio*) in the Gulf of St. Lawrence (Majkowski and Waiwood 1980; Waiwood et al. 1980).

Mito (1974) also found that Tanner crabs were important prey for four species of sculpins (Cottidae). The percentage of the weight of food from each of these species that was Tanner crabs was 54.1% for the yellow Irish lord (*Hemilepidotus jordani*), 40.5% for the great sculpin (*Myoxocephalus polyacanthocephalus*), 36.3% for the sculpin (*Malacocottus zonarus*), and 29.1% for the spinyhead sculpin (*Dasycottus setiger*). Frequency of occurrence feeding data on yellow Irish lords and great sculpins from the Gulf of Alaska also show that Tanner crabs are important prey there. The percent frequencies of occurrence of Tanner crabs in yellow Irish lords and great sculpins from the Kodiak Island area were 17.8 and 55.0%, respectively (Jewett and Powell 1979). Nearly 23% of the crabs that were consumed by the great sculpins were ovigerous females.

The only member of the family Cyclopteridae that contained Tanner crabs was the polka-dot snailfish (*Liparis cyclostigma*). The quantity of crabs consumed by this species was 24.5% of the food wet weight (Mito 1974).

Mito (1974) also examined six species of flatfishes (Pleuronectidae) and found Tanner crabs in five species (Table 1). Among these five species the greatest percentage of the weight of food that was attributable to Tanner crabs (10.3%) was found in the rock sole (*Lepidopsetta bilineata*).

DOMINANT MARINE MAMMAL PREDATORS

Among the four species of marine mammals that are reported to prey on *Chionoecetes* the bearded seal (*Erignathus barbatus*) is the only major predator (Table 1). Only a small proportion of the bearded seal population ranges into the southeastern Bering Sea where Tanner crabs are most abundant, thereby minimizing their impact on the valuable crab resources in that area (Lowry et al. 1979). Tanner crabs are especially important as prey of bearded seals in more northerly areas of the Bering Sea (Johnson et al. 1966; Lowry et al. 1980).

PACIFIC COD PREDATION ON TANNER CRABS

An estimate of the annual Tanner crab mortality that is attributable to Pacific cod predation is presented for the Kodiak Island area. Based upon demersal fish surveys (April-October 1973-76) Ronholt et al. (1978) estimated that the standing stock of Pacific cod near Kodiak Island was 6.9×10^7 fish. The mean size of these cod was 38 cm. In a Pacific cod feeding study near Kodiak Island (June-July 1973-75) Jewett (1978) found an average of 1.2 *C. bairdi* in the cod he examined (3,133 fish). Given the average number of crabs found in Pacific cod (1.2 crabs/fish) and an estimate of the total cod population (6.9×10^7 fish), 8.3×10^7 crabs are present in the stomachs of cod at any one time. Studies conducted on the rates of digestion in the Atlantic cod (*Gadus morhua*) suggest that various species of crustaceans are passed through the stomach in an average time of 48 hours (Tyler 1970; Daan 1973; Jones 1974). Feeding is continuous throughout the year, except for the spawning period (Tyler 1970), after which time feeding briefly intensifies (Daan 1973). Assuming a constant rate of predation for the entire year Pacific cod ≥30 cm total length empty their stomachs approximately 183 times each year. Therefore, the number of times cod empty their stomachs per year (183) times the instantaneous crab mortality due to predation by the total cod population (8.3×10^7 crabs) yields an estimate of 1.5×10^{10} crabs consumed by Pacific cod each year

183 individual cod stomach flushings/ year	x	8.3×10^7 crabs eaten by total crab pop. at any time	=	1.5×10^{10} crabs eaten annually by total cod pop.

In order to obtain an estimate of the importance of predation by Pacific cod on the total Tanner crab population an estimate of the total Tanner crab reproductive output (fecundity) is needed. Ronholt et al. (1978) estimated that the population of *C. bairdi* near Kodiak Island was 4.6×10^7 individuals. Based upon the mean crab weight from Ronholt et al. (1978), this population estimate is primarily for adult crabs. Therefore, assuming a female to male sex ratio of 2:1 (Hilsinger 1976), 30.8×10^6 adult females were present in the area. The average number of eggs per female *C. bairdi* just prior to hatching is 13.3×10^4 (Hilsinger 1976). Given the number of adult females (30.8×10^6) and the average number of eggs per female (13.3×10^4), the total fecundity is 4.1×10^{12} eggs annually. The percentage of the total number of eggs that reach adulthood is only 0.0012%

$$\frac{4.6 \times 10^7 \text{ adult crab pop.}}{4.1 \times 10^{12} \text{ eggs annually}} \times 100 = 0.001\% .$$

In other words, 99.999% mortality occurs from eggs to adults. Assuming that larval survival is only 1%, then the juvenile population is 4.1×10^{10} crabs

$$(1.0 \times 10^{-2} \times 4.1 \times 10^{12} = 4.1 \times 10^{10}).$$

Therefore, the percentage of the mortality of juvenile crabs that is attributed to Pacific cod predation is 37%

$$\frac{1.5 \times 10^{10} \text{ crabs eaten annually by total cod pop.}}{4.1 \times 10^{10} \text{ juvenile crab pop.}} \times 100 = 37\% .$$

However, the estimated annual consumption of Tanner crabs by Pacific cod (1.5×10^{10}) is actually 326 times the estimated adult crab population (4.6×10^7).

In order to more accurately address cod - Tanner crab and other fish - Tanner crab interactions the following specific data needs must be met: 1) current stock assessments of adult Tanner crabs; 2) determination of the predators of larval crabs; 3) stock assessments of dominant crab predators; 4) seasonal examination of the dominant crab predators; 5) quantification of crabs within predators; and 6) determination of the digestion rates and feeding frequencies of the major crab predators.

In a study involving the predation of snow crab (*C. opilio*) by Atlantic cod it was concluded that cod appeared to be a major controlling factor of snow crab recruitment to the fishery and subsequent catches (Bailey 1981). The conjecture is that a multispecies management approach may be practical in the context of *Chionoecetes* spp. and their dominant predators.

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The Histopathology and Possible Role in the Population Dynamics of Tanner Crab, *Chionoecetes Bairdi*, of the Fungus Disease (Black Mat Syndrome) Caused by *Trichomaris Invadens*

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The frequent occurrence of a pigmented fungus on the exoskeleton of the Tanner or snow crab, Chionoecetes bairdi, has been known for many years. The surface encrustations, commonly called black mat syndrome (BMS), are unsightly and processors are reluctant to accept crabs with the condition. The fungus was thought to be restricted to the exoskeleton and, therefore, eliminated on molting because no pigmented hyphae were seen when internal tissues of crabs with BMS were examined. Van Hyning and Scarborough (1973) identified the fungus as Phoma fimeti, a common soil fungus, from cultures of material taken from the surface encrustations. Although they noted that they never observed it in internal tissues and stated that it apparently has no deleterious effect on the crab, Van Hyning and Scarborough did postulate that in extreme cases damage to the eyes and mouth parts of females that had undergone their terminal molt could cause premature death.

Subsequently, histopathological studies have demonstrated that all crabs with the syndrome contain non-pigmented hyphae in internal tissues. In a preliminary study of 11 infected crabs, Sparks and Hibbits (1979) reported that the fungus readily perforates the cuticle, invades and proliferates in the epidermis and subepidermal layer, and then invades a number of deeper organs and tissues. They stated that heavily infected crabs are probably unable to molt and suggested that the disease is eventually fatal.

Additional study of numerous crabs with a wide range of exoskeleton involvement, and also without the syndrome, provided more information on the identity of the fungus, the probable progression of the disease and the histopathological effects on the host. The fungus proved to be a previously undescribed genus and species of marine Ascomycete and was described and named Trichomaris invadens by Hibbits et al (1981). Mix and Sparks (1980) reported that infected crabs had a marked increase in the percentage of eosinophilic granulocytes in infected crabs, and that the differential shift progressively increased as more internal organs were invaded. After examination of all organ systems of 53 C. bairdi with varying degrees of surface encrustations and internal invasion, Sparks (in press) described more fully the histopathological effects and probable progression of the disease.

Histopathology and Probable Course of Infection

Examination of fresh, unstained squash preparations of the epidermis and subepidermal tissues of crabs with external BMS clearly reveals the presence of masses of internal, unpigmented hyphae. Sections of exoskeleton and underlying epidermis and subepidermal tissues stained with Hematoxylin and Eosin (H&E) clearly show the external hyphae and fruiting bodies while the epidermis and subepidermal layer has the appearance of an amorphous, eosinophilic mass lacking all or most of the normal epithelium, muscles, nerves, connective tissue and other structures. In addition, Grocott's Methenamine Silver (GMS) preparations reveal that the hyphae readily penetrate the thick chitinous cuticle and, even in light to moderate external encrustations, proliferate to invade, destroy, and virtually replace all tissue components in the epidermis and subepidermal layer throughout the body (Fig. 1).

As the subepidermal layer becomes packed with proliferating hyphae, deeper tissues and organs are progressively invaded. The invasion occurs primarily via the connective tissue but also involves the major muscles at their attachment to the inner surface of the cuticle. Eventually, major blood vessels, the hemopoietic tissue, the spongy connective tissue wall of the heart, and the wall of the components of the digestive tract are invaded. In cases studied to date, cardiac muscle of the heart, hepatopancreas, reproductive organs, antennal gland and brain and thoracic ganglion have not been invaded. However, the ovary of crabs which have heavy infections in the connective tissue adjacent to the ovarian capsule typically contains necrotic and disintegrating ova.

Hyphae and fruiting bodies (perithecia) frequenctly occur on the external surface of the eyestalk and virtually all infected crabs have eyestalk invasion. The progression of the disease is like that in the cephalothorax with invasion and destruction of the epidermis and subepidermal layer and major muscles. Hyphae also grow along the basement membrane of the retina, then invade and destroy the retinular cells of the rhabdomes and fill up the spaces between the rhabdomes. In advanced cases, the crystalline cones are invaded and disrupted. At this stage of the infection, the architectural integrity of the retina is completely destroyed; only fragments remain in a mass of proliferating hyphae, heavy infiltration of hemocytes and, occasionally, melanized lesions.

External encrustations sometimes occur on the gill stem and lamellae and are always accompanied by invasion of internal tissues. The normal architecture of the gill lamellae is completely replaced by a solid mass of proliferating hyphae. Infections of the stem of the gill result in invasion of the connective tissue, tegmental glands and podocytes.

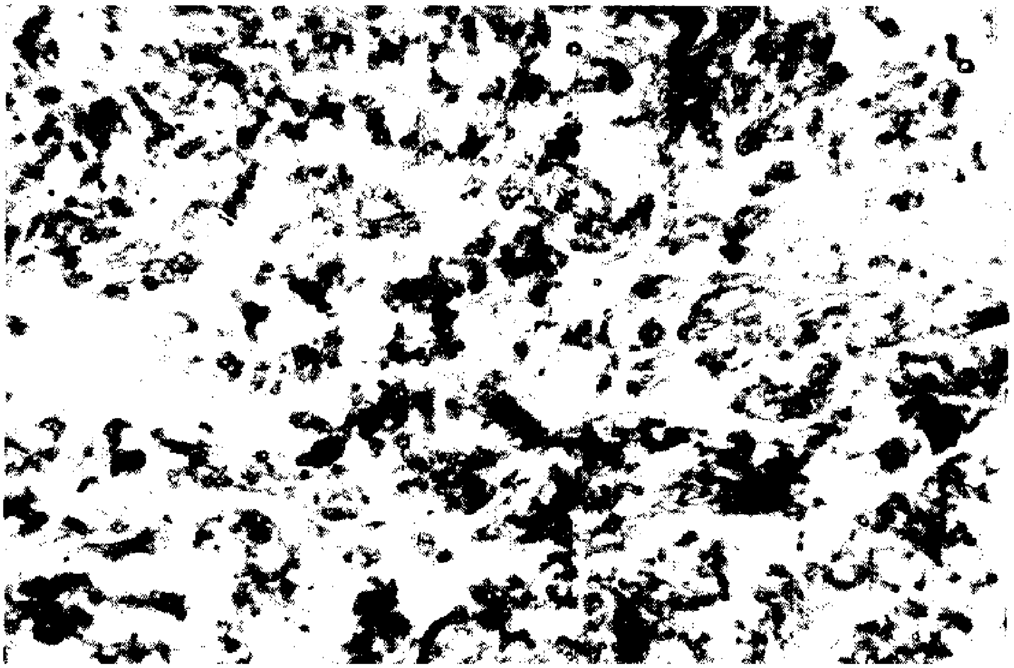

Figure 1. Subepidermal layer of C. bairdi completely filled with a mass of invasive proliferating hyphae of T. invadens. Note the total destruction of all normal tissue components. GMS. 380X.

Possible Role in the Population Dynamics

Because the new exoskeleton is produced by the epidermis and structures in the subepidermal layer, massive destruction of these tissues in a crab would prevent production of new cuticle. The affected individual would be unable to molt even though sufficient molting hormone was produced. Examination of random samples of the epidermis and subepidermal layer of crabs with moderate to heavy surface BMS reveals massive destruction of these tissues throughout the cephalothorax and eyestalk and provides strong circumstantial evidence that encrustations of this magnitude prevent molting. Support for this premise is provided by the fact that none of the more than 50 crabs without surface BMS contained any evidence of internal hyphae. These crabs were collected from the same localities as those with BMS; it seems highly unlikely that, if infected crabs could molt, none having done so would have been collected from areas of high incidence of the disease. This hypothesis, of course, should be confirmed in the laboratory. Crabs of various sizes with a range of external encrustation should be held for a sufficient time to test this hypothesis.

If the disease does, indeed, prevent molting, it would have a substantial effect on the population structure of C. bairdi and on the fishery. Infected sublegal crabs would never attain legal size and would remain in the population until removed by predation or by death from other causes. Infected immature females would not undergo their molt to sexual maturation and, therefore, would not mate and contribute to normal recruitement to the population. Histopathological studies have shown that even though invasion of the reproductive system has not been observed, developing ova in heavily infected female crabs are typically necrotic and undergoing degeneration. Supporting evidence for a serious deleterious effect on recruitement by BMS is the recent report by D.M. Hicks (this Symposium) that egg clutch size is reduced in infected female crabs and that more than 90 percent of barren females had BMS.

The widespread invasion of internal organs and tissues, accompanied by massive proliferation of hyphae and destruction of tissues, and an almost total absence of successful host defense mechanisms is also highly suggestive that BMS is a fatal disease. David Hicks' recent survey (this Symposium) and casual observations that recent declines in C. bairdi populations have been accompanied by decreasing incidences of BMS support this conclusion. Clearly, however, the potential lethality of the disease should be investigated under controlled laboratory conditions. Should it prove fatal, determination should be made of the stage of external encrustation at the time of death, the extent of internal invasion in fatal cases, and the length of time between initial infection and fatal termination.

If laboratory investigations substantiate the hypothesized lethality of Trichomaris invadens infections, past and present high incidences of infection strongly indicate that BMS is a significant cause of C. bairdi mortality. Although fishing mortality and predation are clearly of major importance, fungus disease may well have been a significant factor in recent declines in *C. bairdi* abundance.

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Tanner Crab Disease Investigations in Alaska

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INTRODUCTION

The commercial crab industry in Alaska has experienced some problems due to poor condition of tanner crab, *Chionoecetes bairdi*, also referred to as snow crab. These problems include low vigor/low meat yield crabs, soft shell, lack of ability to molt, poor growth, and the presence of shell lesions. The presence of dark shell lesions which pitted the exoskeleton, were first reported in 1960 (Bright et al.). The phenomenon was termed "rust" disease. By use of infected shells or artificial injury the disease was induced in non-infected crabs. Later the disease was shown to be caused by chitin-digesting or chitinoclastic bacteria (Sinderman and Rosenfeld, 1967). Similar lesions characterized by softening, pitting and blackening of the exoskeleton have been found in Oregon tanner crabs, *Chionoecetes tanneri* (Baross et al., 1978). Chitin-digesting bacteria were found in all lesions examined from the Oregon crabs and 47% of the isolates were found to be *Photobacterium* sp..

In 1976, the Fish Pathology Section of the Alaska Department of Fish and Game began to study the crabs to assist in finding answers to the crab disease problems. Preliminary studies involved looking at the bacterial flora and tissues of normal tanner crabs. This was followed by pathogenicity testing of common bacterial isolates on live tanner crabs.

MATERIALS AND METHODS

Baseline Study

A sample of tanner crabs was received from the King Cove area. Crab gills, muscle and hepatopancreas were homogenized in a blender and then spread on a nutrient media for enumeration and identification. Media utilized included blood agar, sea water cytophaga agar, and bromthymol blue Teepol agar which is a differential media for vibrios. Bacteria were identified using standard methods similar to those appropriate for shellfish (Grischkowsky, 1973).

Histological specimens were immediately fixed in Bouin's solution and processed according to standard procedures (Galigher and Kozloff, 1971). Hematoxylin and eosin staining was used.

Pathogenicity Testing

Adult tanner crabs, from Resurrection Bay, were maintained in sea water tanks with continuous flow at the Institute of Marine Science in Seward. There were three separate trials of the pathogenicity testing. For the first trial, the three most frequently isolated bacteria; a *Pseudomonas* sp., a coccobaccilli (*Moraxella* sp.), and a *Flavobacterium* sp. were grown separately in nutrient broths. Characteristics of the pseudomonad are Gram negative, oxidase positive, motile rod which is levan positive. It forms gray, mucoid colonies and exhibits hemolysis on blood agar. An alkaline reaction is seen in the Hugh and Leifson's O/F media. It was presumptively classified as being a "*Pseudomonas stutzeri*-like" organism but no final identification has been made. The *Moraxella* sp.is a Gram negative, oxidase positive, coccobacilli. There is no reaction in Hugh and Leifsons O/F media. The organism is sensitive to penicillin. The *Flavobacterium* sp. forms smooth, round, opague, glossy, yellow colonies. It is a Gram negative, non-motile, oxidase positive rod. No reaction occurs in O/F media.

For the first trial, four groups of crab were established. Three groups of 6 or 7 crabs were each injected with one of the bacterial cultures. Concentration of the inoculum for each crab was 10^8 - 10^9 organisms. A fourth group was injected with sterile broth. The injection site was between the left cheliped coxa and the second periopod coxa. Mortalities were monitored daily. When crabs died we performed bacterial and histological analyses of muscle, hepatopancreas, and gill tissues. We analyzed survival data using 2 x k contingency analyses and arcsine transformation for the difference of two percentages.

Procedures for the two subsequent trials were the same with the following changes: the second trial utilized only the pseudomonad and the *Moraxella* sp.; and the third trial tested the effect of lower doses and utilized a more frequent monitoring of mortality. One dose was the same as used in previous experiments, the other was one-tenth of that, both using the *Moraxella* sp. and the *Pseudomonas* sp. Crabs were checked every 6 hr for mortalities.

RESULTS

Baseline study

Bacterial counts were high, with means ranging from 1.91 x 10^5 bacteria/gm to 3.21 x 10^5 bacteria/gm (Table 1). Bacteria isolated were able to grow both at 25 C and at 5 C which is close to the water temperature in which the crab lives. Types of bacteria isolated included pseudomonads, aeromonads, flavobacteria, coccobacilli, and one *Vibrio alginolyticus*. Chitinoclastic bacteria were rarely isolated.

Histopathology indicated substantial coverage of gill filaments with debris, the presence of interlamellar myxobacteria-like organisms, bacillary involvements in musculature and open carapace lesions.

Pathogenicity testing

For the first trial, mortalities are summarized in Figure 1. All crabs injected with the pseudomonad died within 24 hours. No other statistically significant mortalities occurred although 6 of the 7 crabs in the *Moraxella* group died. Bacteria were found in the tissues of live crabs as well as dead crabs, but only the bacteria which were injected. The organisms were not transferred from one group to another. The crab gills, hepatopancreas, and muscle appeared normal with the exception of an abundance of debris on the gills of most of the crabs.

In the second trial, there were five crabs in each group. Within 24 hours all crabs injected with the pseudomonad died. Four injected with *Moraxella* died and none in the controls. Statistical analyses are summarized in Table 2. This time, both organisms were pathogenic.

Mortalities for the third trial are summarized in Table 3 and 4. Significant mortality occurred in the pseudomonad injected crabs at both dosages (Table 5). Total mortality was not significant in the *Moraxella* injected crabs but mortality for a 6 hr period was with the higher dose only. Again, death was of a very acute nature. Of the mortalities that occurred, 100% of them were within 12 hr. Injected organisms were isolated more frequently from the high dose crabs than from the lower dose ones.

DISCUSSION

Considering the relatively high bacterial counts and the open carapace lesions, which allow access to the hemolymph, it appears that the tanner crab is continuously exposed to

Table 1. Quantitative enumeration of bacteria isolated from *C. bairdi* from the King Cove area. Counts are numbers of bacteria/gram of tissue.

96 hr counts, 25 C

	Medium		
Group	BA	SWC	BTB
Normal A	2.13×10^5	5.05×10^5	2.15×10^5
Normal B	1.69×10^5	1.38×10^5	3.74×10^4
Mean	1.91×10^5	3.21×10^5	1.26×10^5

144 hr counts, 5 C

	Medium		
Group	BA	SWC	BTB
Normal A	5.03×10^5	5.46×10^5	2.83×10^5
Normal B	3.54×10^5	2.56×10^5	4.54×10^4
Mean	4.28×10^5	4.01×10^5	1.64×10^5

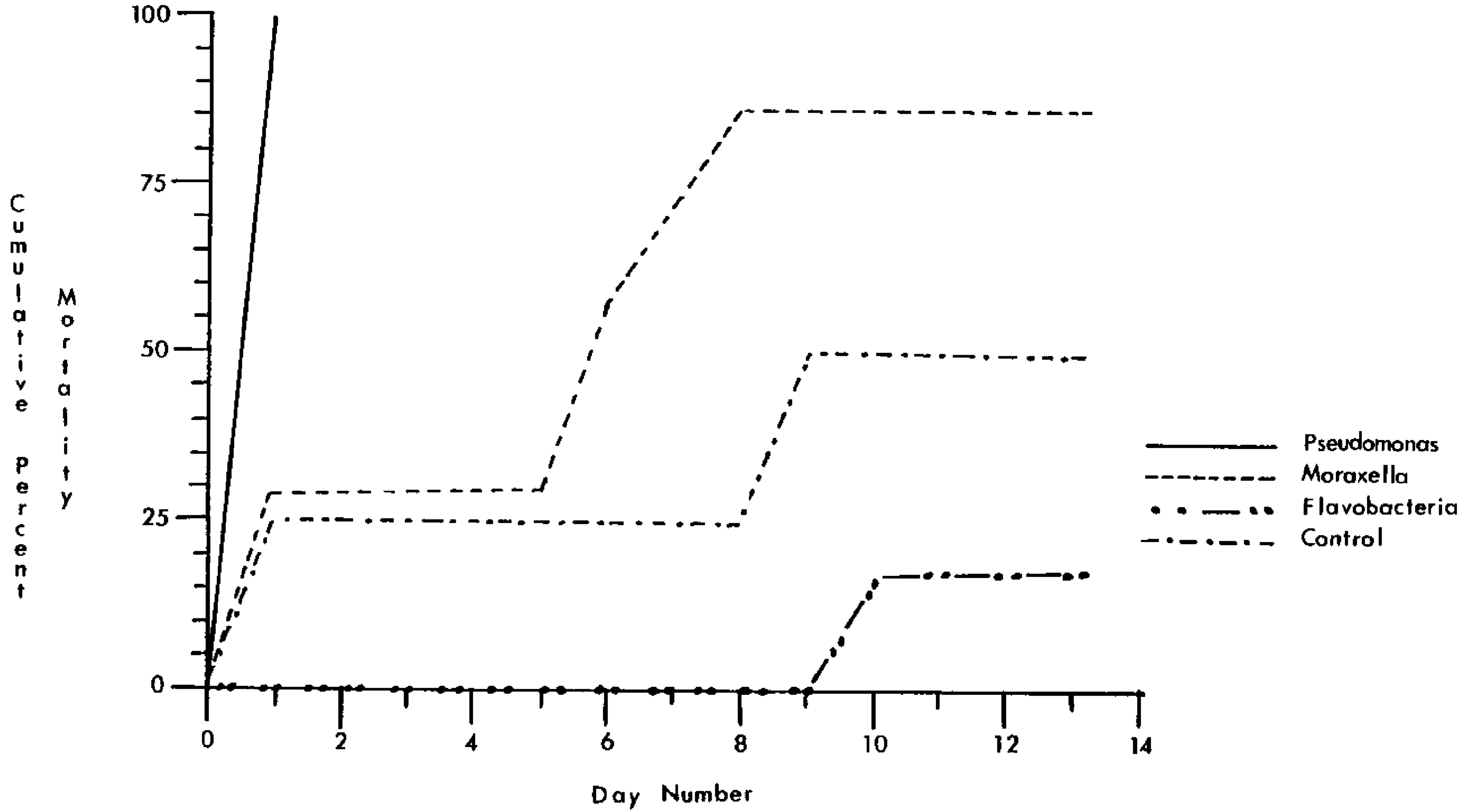

Figure 1. Cumulative percent mortality by day for pathogencity trial one of tanner crabs injected with bacterial isolates.

Table 2. Tabulation of equality of two percentages by arcsine transformation for survival of tanner crab in the second pathogenicity trial. The null hypothesis, H_o, is equality of the percentages. The alternate hypothesis, H_A, is that there was a difference in survival of the two groups.

Comparison	T_s	P	Accept H_O	Accept H_A
Pseudomonas vs Control	4.97	< 0.0003	-	control > *Pseudomonas*
Moraxella vs Control	3.50	< 0.0003	-	control > *Moraxella*
Pseudomonas vs *Moraxella*	1.45	0.0735	+	-

Table 3. Cumulative mortality per total number by 6-hr. periods for tanner crabs injected with 10 ml inoculum.

Injection group	Time (hrs.) 0	6	12	18	24	36
Pseudomonas sp.	0/10	9/10	10/10	10/10	10/10	10/10
Moraxella	0/10	7/10	7/10	7/10	7/10	7/10
Control	0/10	2/10	5/10	5/10	5/10	5/10

Table 4. Cumulative mortality per total number by 6-hr. periods for tanner crabs injected with 1 ml inoculum.

Injection group	Time (hrs.) 0	6	12	18	24	36
Pseudomonas sp.	0/4	3/4	3/4	3/4	3/4	3/4
Moraxella	0/3	1/3	1/3	1/3	1/3	1/3
Control	0/4	0/4	0/4	0/4	0/4	0/4

Table 5. Tabulation of equality testing of cumulative percentage mortality using arcsine transformation for injected tanner crabs. The null hypothesis, H_0, is that mortality was equal for both groups. The alternate hypothesis, H_A, is that mortality was not equal.

For 10^9 bacteria inoculated (10 ml):

Comparison	T_s	P	Accept H_o	Accept H_A
Pseudomonas vs Control	3.512	<0.0003	-	+
Moraxella vs Control	1.087	0.1379	+	-

For 10^8 bacteria inoculated (1 ml):

Comparison	T_s	P	Accept H_o	Accept H_A
Pseudomonas vs Control	2.96	<0.0015	-	+
Moraxella vs Control	1.61	0.0537	+	-

bacterial challenge of some type. These observations, coupled with the extensive amount of debris on the gills, may account for some of it's reduced vigor. Gill debris reduces oxygen exchange area and therefore the crabs metabolic capabilities and may limit its' dwelling range.

Both organisms tested in the second pathogenicity trial, the *Pseudomonas* sp. and *Moraxella* sp., fulfilled the requirements of a pathogenic agent. These requirements, known as Koch's postulates, include isolation of the agent from a diseased host; injection into a healthy host; expression of the disease; and reisolation of the agent.

In the third pathogenicity trial, some crabs did not die when injected with the higher dosage and others could not survive even the lower dosage, although the organisms have previously been found in healthy crabs. The susceptibility of a particular crab is probably due to a number of factors including it's overall health. Crabs injected with lower doses were able to eliminate the bacteria but it probably places considerable stress on the crab and may relate to it's susceptibility to the disease.

When death occurred, it followed injection very rapidly. This points to the possibility of a toxin being elaborated by the bacteria while it is growing in broth. Additional experimentation using washed cells or a supernatant would be useful to determine if this is the case.

Since bacteria were not transmitted from one crab to another, this raises the question of how the disease is transmitted in the wild. Perhaps bacteria are not released until the crab dies and decomposes.

At this point we know that both the pseudomonad and *Moraxella* can be lethal under certain conditions. Neither of these organisms is chitinoclastic. Darkly pigmented lesions, which may be similar to those found in tanner crab, are seen in Gulf Coast shrimp, *Penaeus actecus* and *Penaeus* setiferus. A dense population of bacteria was seen in the lesions and investigatiors were able to initiate lesions consistently with the lipolytic organisms they isolated but not always with the chitinoclastic forms (Cipriani et al, 1980). They suggested that a variety of organisms may be involved in causing the lesions. This may also be the case in tanner crabs since we also isolated a variety of organisms during a study of lesions from king crab. A combination of bacteria may be more detrimental to the crab than individual organisms.

There are several unanswered questions such as; by what mechanism are the crabs killed, what makes a crab susceptible to the disease, what is the extent and distribution of the pathogenic organisms, how is the disease transmitted and how can stocks be managed to minimize future loss.

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ABSTRACT

In Alaska, problems with the tanner crab *Chionoecetes bairdi* have included population fluctuation, reduction of return to fisherman, low vigor and low meat yield crabs, soft shell, poor growth, and the presence of shell lesions. In 1977, we began collecting data on the microflora of C. *bairdi*. Numbers of bacteria found in crabs from the King Cove area were high, 4½-5½ logarithms per gram. The bacterial counts at 5°C were equivalent to those at 25°C suggesting these isolates were active at a temperature which approaches that of crab habitats off Alaska. Most of these crabs had brown to black shell lesions thought to be caused by chitinoclastic bacteria. Microscopic examination of these lesions showed the presence of many Gram negative bacilli. Histopathology indicated substantial coverage of gill filaments with debris, the presence of interlamellar myxobacteria-like organisms, bacillary involvements in musculature and open carapace lesions. Bacteria selected for pathogenicity testing were the most frequently represented in the crabs sampled. They were "*Pseudomonas stutzeri*-like", *Moraxella* sp., and *Flavobacterium* sp.. Three pathogenicity experiments were conducted to determine which of the isolates may be involved in causing lesions, mortalities or poor crab condition. Adult crabs were maintained in seawater tanks with continuous flow. For the first experiment, the three bacterial isolates were seperately inoculated into crabs while the last two experiments didn't utilize the *Flavobacterium* sp. due to its initial lack of pathogenicity. The pseudomonad was highly pathogenic during the first experiment with acute mortalities resulting. *Moraxella* sp.produced greater mortalities than the control treatment but results were not significant. The second experiment used *P. stutzeri* and *Moraxella* sp. isolated from crabs which died in the first experiment following injections of those organisms. Both organisms were pathogenic and fulfilled requirements of a disease causing agent: being isolated from a diseased host, causing expression of the disease following injection into a healthy animal, and being reisolated from it. The third experiment tested the effect of a lower injection dose and was monitored more frequently. Significant mortality occurred in the pseudomonad injected crabs at both doses. Total mortality was not significant with the use of *Moraxella* but was at six hours with the higher dose. All mortalities occurred within 12 hr. In these investigations, the presence of large numbers of bacteria and the pathogenicity of two of these types was demonstrated but the relationship of these findings to naturally occurring mortalities and poor condition has not been established.

Abundance and Distribution of Black Mat Syndrome on Stocks of Tanner Crabs, *Chionoecetes Bairdi*, in the Northwestern Gulf of Alaska

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ABSTRACT

A total of 38,394 male and 8,160 female Tanner crab, *Chionoecetes bairdi*, were examined for the presence or absence of Black Mat Syndrome (BMS), *Trichomaris invadens*, an infectious marine fungus. Crabs were obtained by various methods from the northwestern Gulf of Alaska. The Kodiak area exhibited the highest incidence. The percent infection for males ranged from zero in most of the bays sampled to over 65.0% in some of Kodiak's offshore northeastern schools, i.e., the outer Marmot Gully. Samples from the 1981 commercial fishery indicated a higher incidence of the disease offshore than inshore for the entire 1981 commercial fishery and was highly significant at the .005 level. The Chignik and South Peninsula areas sampled showed lower infection rates for males than Kodiak. Only 4.9% of the Chignik area males caught by trawl and 0.8% of the South Peninsula area males caught by pots were infected with BMS. The incidence of BMS is higher among old and very oldshell Tanner crabs than in newshell crabs. Natural skip molting frequency may be intensified if the disease prevents ecdysis. Female Tanner crab caught in pots have the highest incidence of the syndrome; 50.1% and 34.8% of all females caught in the 1980 and 1981 Kodiak pot surveys had BMS. Egg clutch size of females may be reduced due to BMS. As much as 94.7% of all the barren females captured on the 1981 Kodiak pot survey also had BMS. The possibility that BMS may inhibit molting has management implications for the commercial fishery.

INTRODUCTION

An ascomycete, *Trichomaris invadens*, has been known to infect certain crab species of the genus *Chionoecetes*, since the Alaskan fishery began. This disease has been commonly named Black Mat Syndrome (BMS) and is found primarily on stocks of *Chionoecetes bairdi* in the Gulf of Alaska. There is evidence that it exists on *C. opilio* and *C. tanneri* from the Bering Sea and Gulf of Alaska (Figure 1), respectively (Bob Otto, personal communication). The first real description and identification of this encrusting microfungus was by Van Hyning and Scarborough in 1973 when they incorrectly identified it as a soil born microfungus, *Phoma fimeti*. Before the first identification of BMS, Ralph Brown, then a biologist for the Alaska Department of Fish and Game (ADF&G) wrote about the disease in an informational leaflet (1971). In this publication Mr. Brown cites BMS as one of the four factors contributing to the poor market conditions for *C. bairdi* at that time in the expanding fishery. Mr. Brown also conducted a limited study of the incidence of BMS on *C. bairdi* around Kodiak Island and in the Shumagin Islands. He sampled 1,000 crab from four distinct areas and found 7.0% to 75.0% of the crabs to be infected.

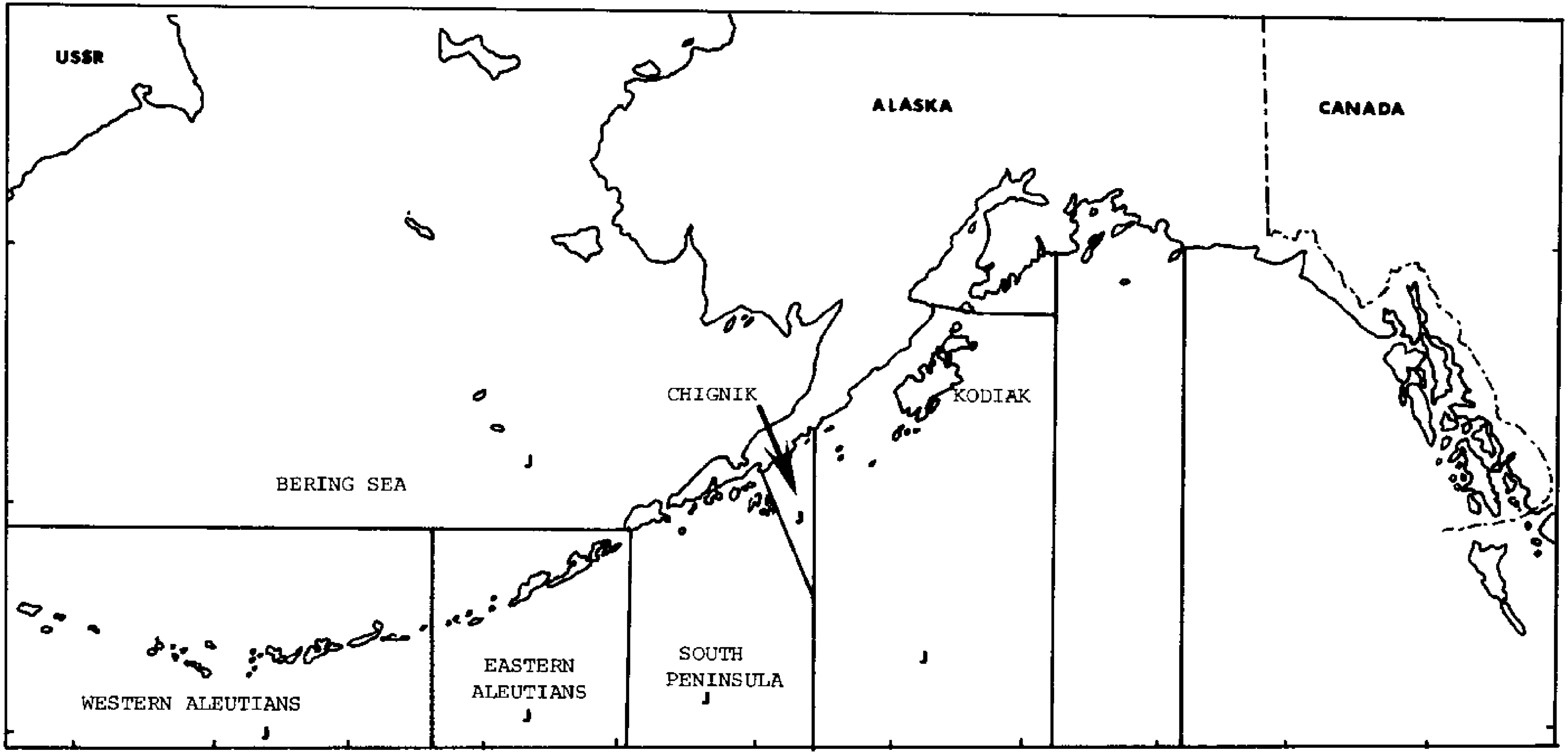


Figure 1.--Tanner Crab Management Districts of the Westward Region, Alaska.

Until recently the only known problem that this fungus brought forth was that the black tarlike nodules would break off into the crab meat while being processed, producing an aesthetically inferior product and often a reduced price to the fishermen. The disease was known to be highly area specific so it could be avoided if necessary. It is now evident from the research of Drs. Sparks and Hibbits (1978) that the fungus is debilitating, potentially a molt inhibitant and highly suspect of being fatal to the animal. This recent finding concerning the possible lethality of the disease and its potential impact on the population dynamics of the animal has led to an ongoing study on the relative abundance and distribution of BMS by the ADF&G.

MATERIALS AND METHODS

Three separate collection methods were used to sample 46,554 Tanner crabs for the presence or absence of BMS.

Initially random samples were obtained from commercial catches in Kodiak as the vessels delivered to the processors. This method of selecting legal size male Tanner crab from different areas around Kodiak Island was used in the 1980, 1981 and 1982 commercial seasons when 1,400, 7,340 and 5,743 crabs were examined, respectively. During the 1981 commercial season 103 crabs were also sampled from the Chignik area (Table 1 and Figure 1).

Another method of obtaining study specimens was from the annual ADF&G king and Tanner crab population index surveys. These samples were obtained by fishing 2.1 x 2.1 m commercial style crab pots in various research areas of the Westward Region. Collections in the Kodiak area were made during the 1980 and 1981 surveys; however, in 1980 only one of the two research vessels participating in the survey recorded BMS data. The 1980 Kodiak survey observed 4,484 male and 798 female Tanner crabs while 7,001 male and 775 female crabs were sampled during the 1981 Kodiak survey. Pot surveys were also conducted in the South Peninsula and Eastern Aleutians areas in 1981, however, only the South Peninsula survey made observations on BMS, involving 3,812 male and 303 female crabs.

The third and final source of data on BMS was from the 1980 and 1981 Tanner crab trawl surveys. Crabs were captured in bottom tows made with a 400 mesh eastern otter trawl which was towed for 30 minutes at each station fished. The 1980 survey was limited to the northern Shelikof Strait area of the Kodiak district where 3,234 male and 2,455 female Tanner crabs were sampled. The 1981 trawl survey was expanded to include the northern Shelikof Strait and Chiniak Gully areas of the Kodiak district where 2,860 male and 2,738 females were collected. Additionally the 1981 trawl survey included the Chignik district where 2,517 male (Table 1) and 1,091 female Tanner crabs were sampled. The trawl method of collecting crabs probably best samples the population as a whole as all sizes of crabs are caught whereas large males are the main size group taken in pots. The smallest crabs captured on any of the pot surveys was about 60 mm (carapace width) compared to 9 mm in the trawls.

Tanner crab were noted as having BMS if the black tarlike nodules of the fungus, *Trichomaris invadens*, were observed anywhere on the external surface.

Table 1.--Percent occurrence of Black Mat Syndrome by district and school for the 1980-82 male Tanner crab, *Chionoecetes bairdi*, sampling efforts in the Westward Region.

Kodiak Management District		1980 Comm Catch		1981 Comm Catch		1982 Comm Catch		1980 Trawl Survey		1981 Trawl Survey		1980 Pot Survey		1981 Pot Survey	
School	School No.	No.	% BM	No.	% BM	No.	% BM	No.	% BM	No.	% BM	No.	% BM	No.	% BM
Marmot Bay	5	-	-	256	1.2	451	2.2	-	-	-	-	-	-	276	1.4
Portlock	6	-	-	50	0	100	0	-	-	-	-	-	-	4	25.0
Chiniak Bay	9	-	-	51	0	176	4.0	-	-	-	-	391	21.7	137	0.7
Marmot Gully	10	100	40.0	854	18.1	457	4.8	-	-	-	-	-	-	420	33.3
Outer Marmot Gully	12	100	65.0	100	29.0	51	2.0	-	-	-	-	-	-	28	46.4
Chiniak Gully	14	-	-	805	33.0	101	8.9	-	-	90	11.1	690	53.5	296	34.8
Twoheaded	17	-	-	50	0	50	0	-	-	-	-	191	0.7	242	0.8
Ugak/Barnabas	18	200	5.0	639	1.9	600	1.3	-	-	-	-	471	12.5	960	1.8
Eastside Other	19	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Horse's Head	20	-	-	249	10.0	101	6.9	-	-	-	-	477	21.5	292	21.6
Alitak Bay	21	-	-	100	0	-	-	-	-	-	-	881	0.5	667	0.0
S. Trinity Is.	22	200	58.0	-	-	106	4.7	-	-	-	-	193	54.0	400	40.0
Compass Rose	30	200	27.0	505	24.1	688	12.4	-	-	-	-	1,150	35.5	1,761	7.7
Southwest Other	31	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ikolik/Alitak	34	-	-	503	2.8	518	2.1	-	-	-	-	40	0	676	3.8
Semidi Islands	35	200	11.5	502	6.0	214	5.6	-	-	-	-	-	-	-	-
Uyak Bay	38	100	1.0	352	3.7	199	6.0	-	-	-	-	-	-	-	-
South Mainland	39	-	-	202	11.9	250	1.2	-	-	-	-	-	-	-	-
Kupreanof/Uganik	40	100	0	706	8.3	836	4.4	-	-	-	-	-	-	842	0.6
North Mainland	41	200	30.0	1,216	5.3	766	2.6	2,922	2.3	2,309	3.5	-	-	-	-
West Afognak	42	-	-	100	1.0	79	1.3	312	1.3	461	5.2	-	-	-	-
Totals		1,400	26.4	7,240	11.3	5,743	4.0	3,234	2.2	2,860	4.0	4,484	25.2	7,001	9.6

Chignik Management District Total	-	-	103	4.9	-	-	-	-	2,517	2.5	-	-	-	-
South Peninsula Management District Total	-	-	-	-	-	-	-	-	-	-	-	-	3,812	0.8

RESULTS AND DISCUSSION

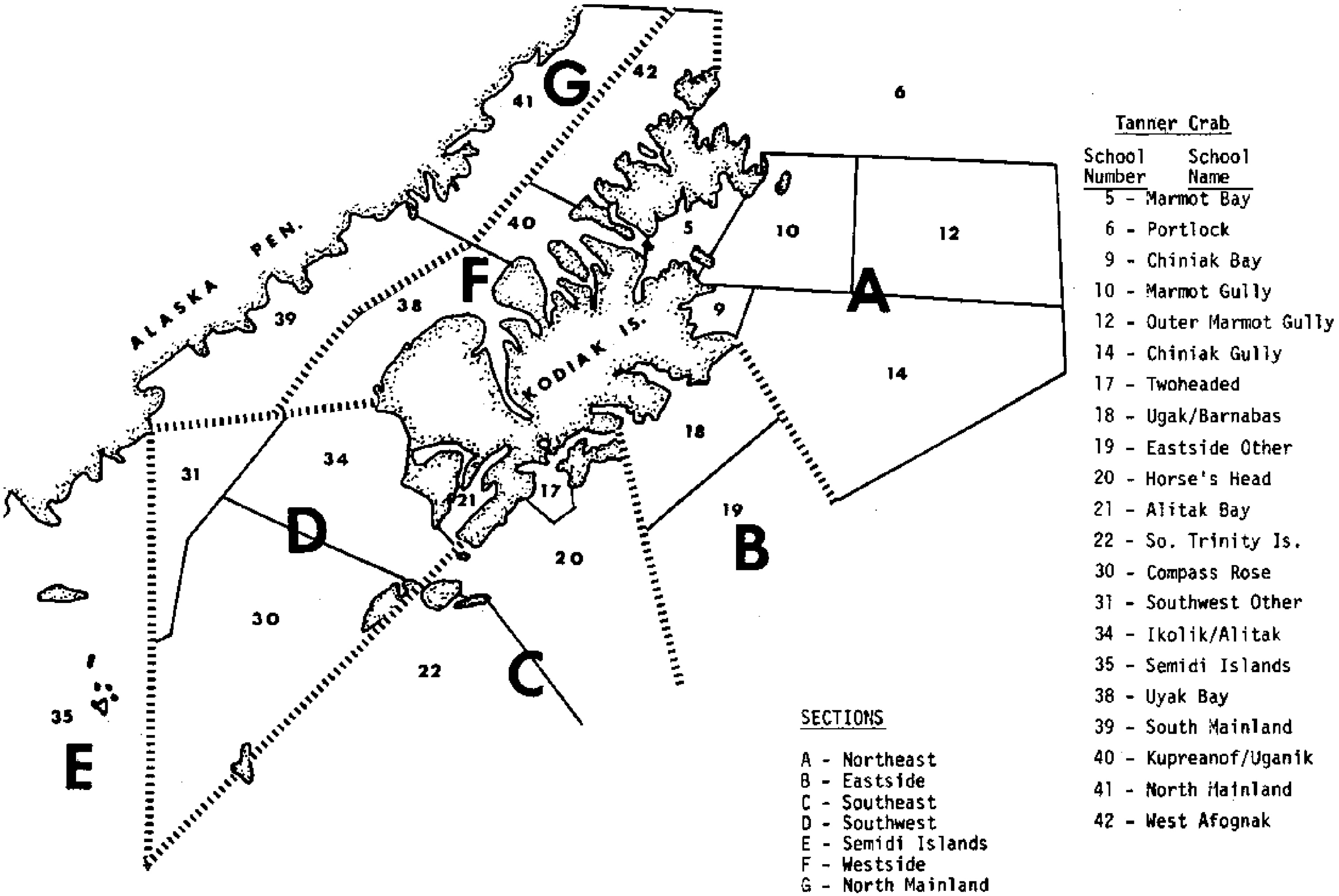
MALE TANNER CRAB

The Kodiak area can be divided into various sections and schools that comprise each section which aids the discussion of BMS incidence (Figure 2). The Northeast section of Kodiak has had a comparatively high incidence of BMS for all years sampled. Outer Marmot Gully, school 12, and Chiniak Gully, school 14, stand out as two of the highly infected schools of the Northeast section (Table 1). School 12 samples were obtained from the pot survey in 1981 and from the commercial catches in 1980, 1981 and 1982. Black Mat Syndrome was observed on 65.0% of the 100 crabs from the initial commercial sample in 1980 (Table 1 and Figure 3). Commercial catch samples from the same school in 1981 exhibited a 29.0% incidence of BMS while only 2.0% of the crabs were infected in 1982. School 12 was not heavily fished in the 1982 commercial season due to low abundance. The 2.0% BMS incidence for the 1982 commercial sample from school 12 only represented 51 crabs (Table 1). In 1981 the pot survey of school 12 produced 46.4% infected crab, but this also was a very small sample (Table 1 and Figure 7). Chiniak Gully, school 14, was also heavily infected with BMS according to all sample sources. Observations on the pot survey revealed school 14 had 53.5% infected crabs in 1980 and 34.8% in 1981 (Figures 6 and 7). The sample sizes were 690 and 296 crabs, respectively (Table 1). School 14 samples of 805 and 101 crabs from the 1981 and 1982 commercial catches showed 33.0% and 8.9% infection rates, respectively (Figures 4 and 5, Table 1).

The southern end of Kodiak Island is another area where BMS is prevalent. School 22, South Trinity Islands (Figure 2) exhibited 54.0% and 40.0% infected crabs on the 1980 and 1981 pot surveys (Figures 6 and 7). Sample sizes were 193 and 400 crabs, respectively (Table 1). A commercial catch sample from school 22 in 1980 was observed to have 58.0% of the crabs infected with BMS (Figure 3). Only 106 crabs were sampled from school 22 during the 1982 season, due to low abundance and little fishing effort. The two samples obtained in 1982 from school 22 indicated BMS occurrence was only 4.7%. School 30, Compass Rose, accounted for some of Kodiak's best fishing in 1982 but also had the highest incidence of BMS this year, 12.4% of the commercial catch sampled (Figure 4 and Table 1).

The offshore schools of the northeast and southern sections of the Kodiak area showed the highest incidence of male Tanner crabs with BMS. Other sections and schools of the Kodiak area exhibit very little disease, particularly in the bay areas (see schools 5, 17, 21 and 40, Table 1). The same predominance of the disease in offshore crabs existed for the entire Kodiak district during the 1981 commercial fishery and was highly significant at the .005 level.

The North Mainland, school 41, and West Afognak, school 42, were sampled by trawl in 1980 and 1981. In 1980, male Tanner crabs from the North Mainland were observed to have 2.3% infected crab while the 1981 survey had 3.5% (Table 1). Sample sizes from the trawl surveys were 2,922 and 2,309 crabs in 1980 and 1981 (Table 1). A commercial catch sample of 1,216 crabs from school 41 in 1981 indicated 5.3% had BMS (Figure 4). Both sampling methods exhibited a relatively low incidence of the disease in school 41.



Tanner Crab

School Number	School Name
5	Marmot Bay
6	Portlock
9	Chiniak Bay
10	Marmot Gully
12	Outer Marmot Gully
14	Chiniak Gully
17	Twoheaded
18	Ugak/Barnabas
19	Eastside Other
20	Horse's Head
21	Alitak Bay
22	So. Trinity Is.
30	Compass Rose
31	Southwest Other
34	Ikolik/Alitak
35	Semidi Islands
38	Uyak Bay
39	South Mainland
40	Kupreanof/Uganik
41	North Mainland
42	West Afognak

SECTIONS

A - Northeast
B - Eastside
C - Southeast
D - Southwest
E - Semidi Islands
F - Westside
G - North Mainland

Figure 2.--Major Tanner crab, *Chionoecetes bairdi*, sections and schools, Kodiak Management District.

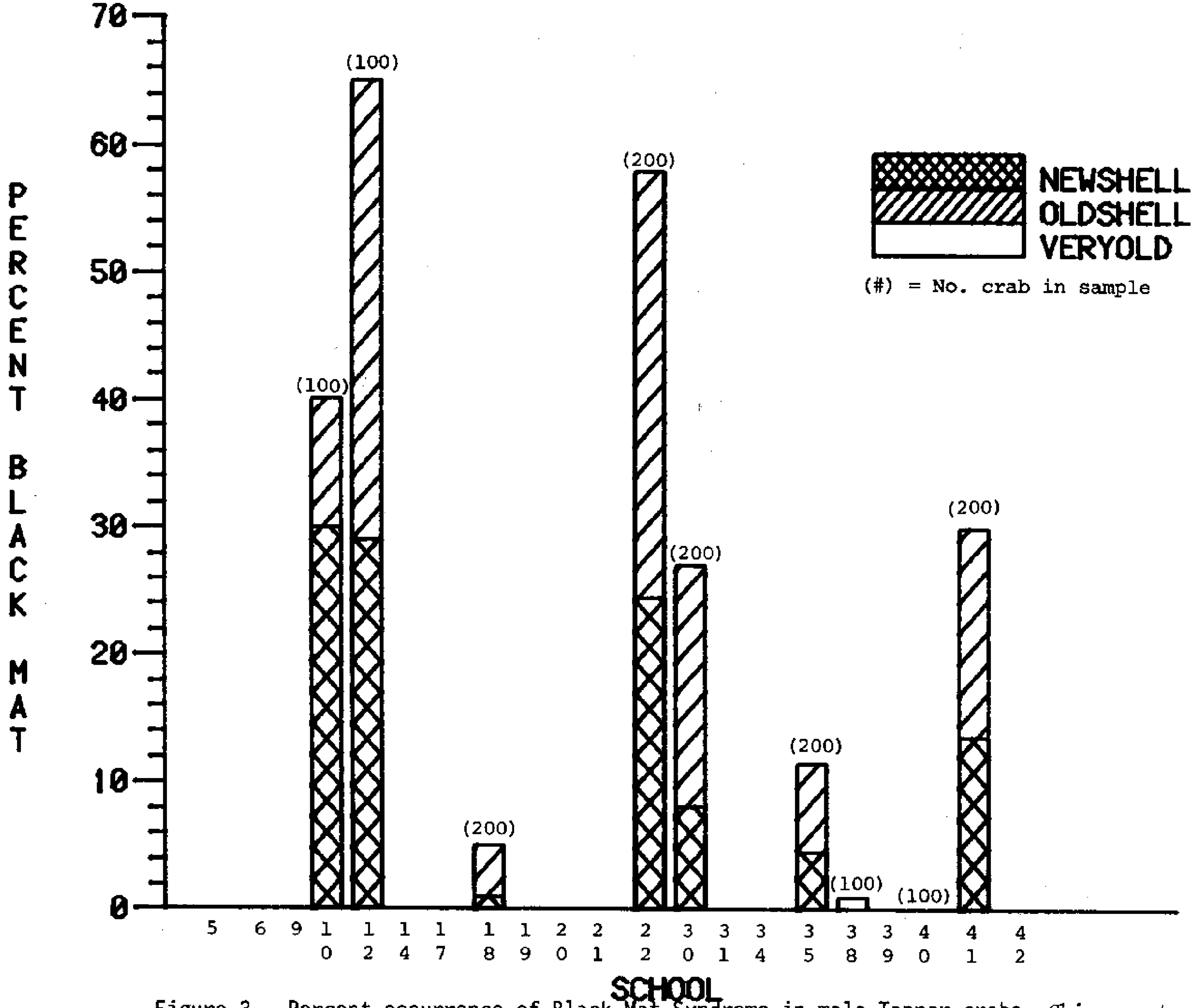


Figure 3.--Percent occurrence of Black Mat Syndrome in male Tanner crabs, *Chionoecetes bairdi*, examined during the 1979-80 Kodiak Management District commercial fishery by school and shell age.

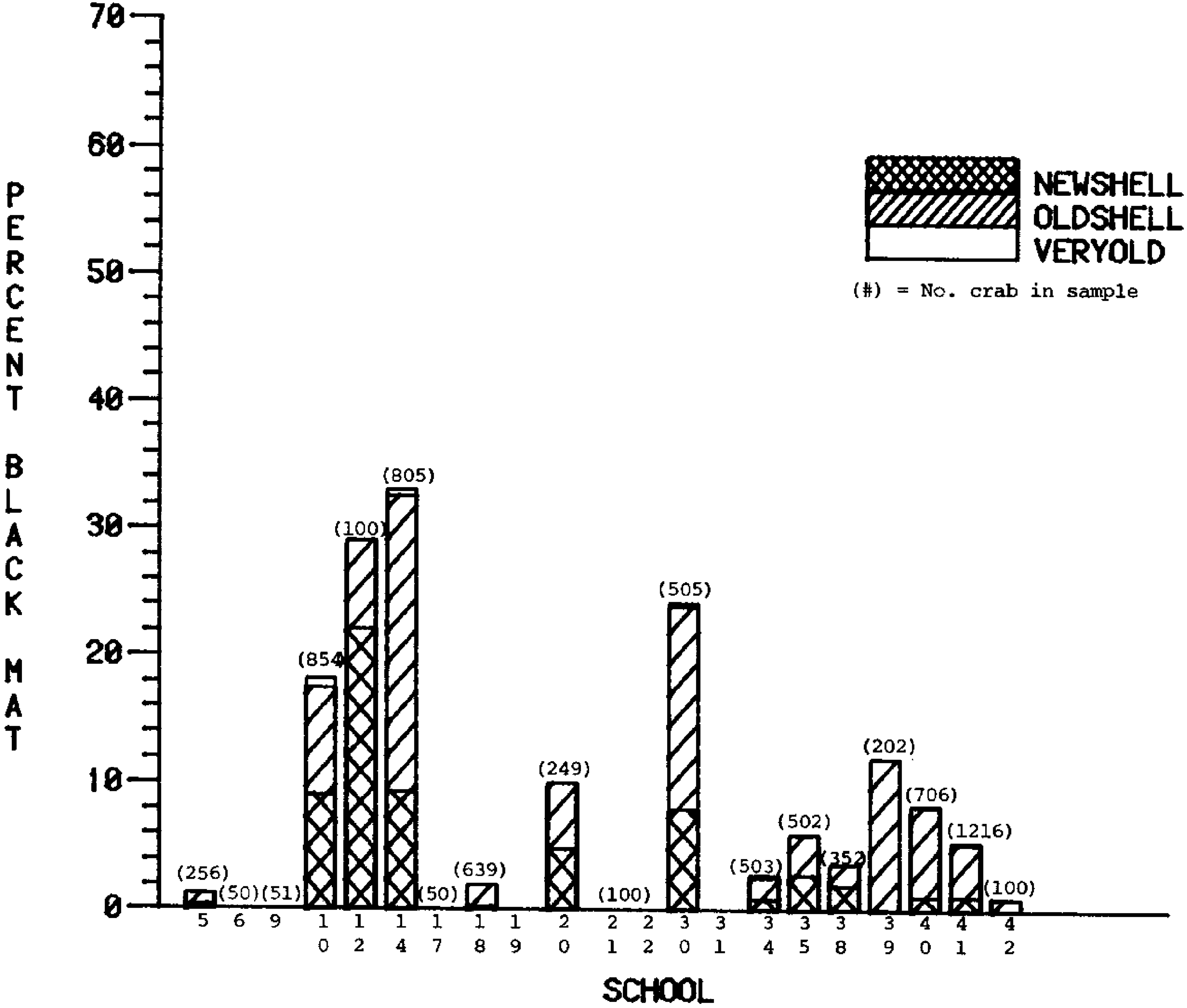


Figure 4.--Percent occurrence of Black Mat Syndrome in male Tanner crabs, *Chionoecetes bairdi*, examined during the 1980-81 Kodiak Management District commercial fishery by school and shell age.

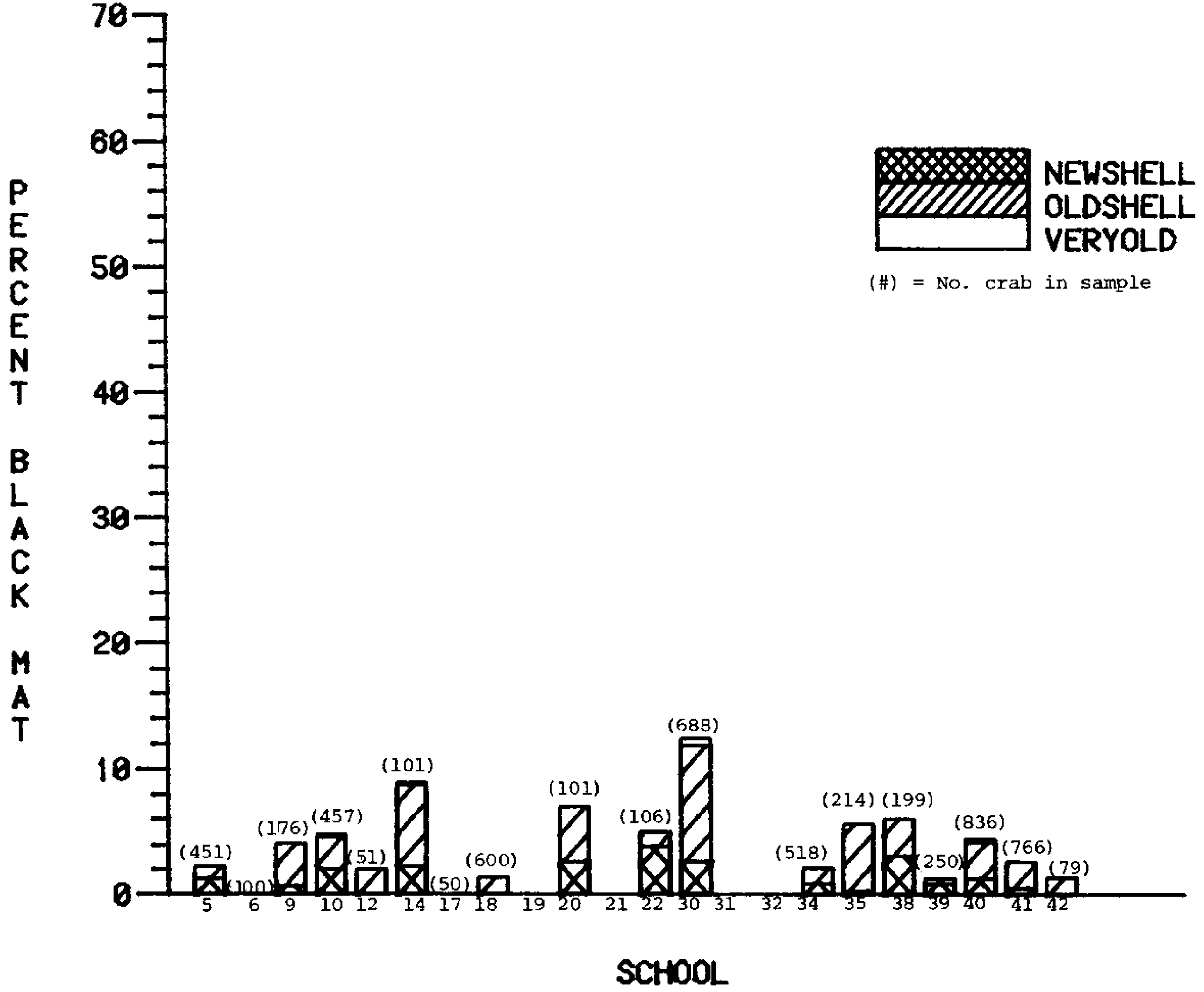


Figure 5.--Percent occurrence of Black Mat Syndrome in male Tanner crabs, *Chionoecetes bairdi*, examined during the 1981-82 Kodiak Management District commercial fishery by school and shell age.

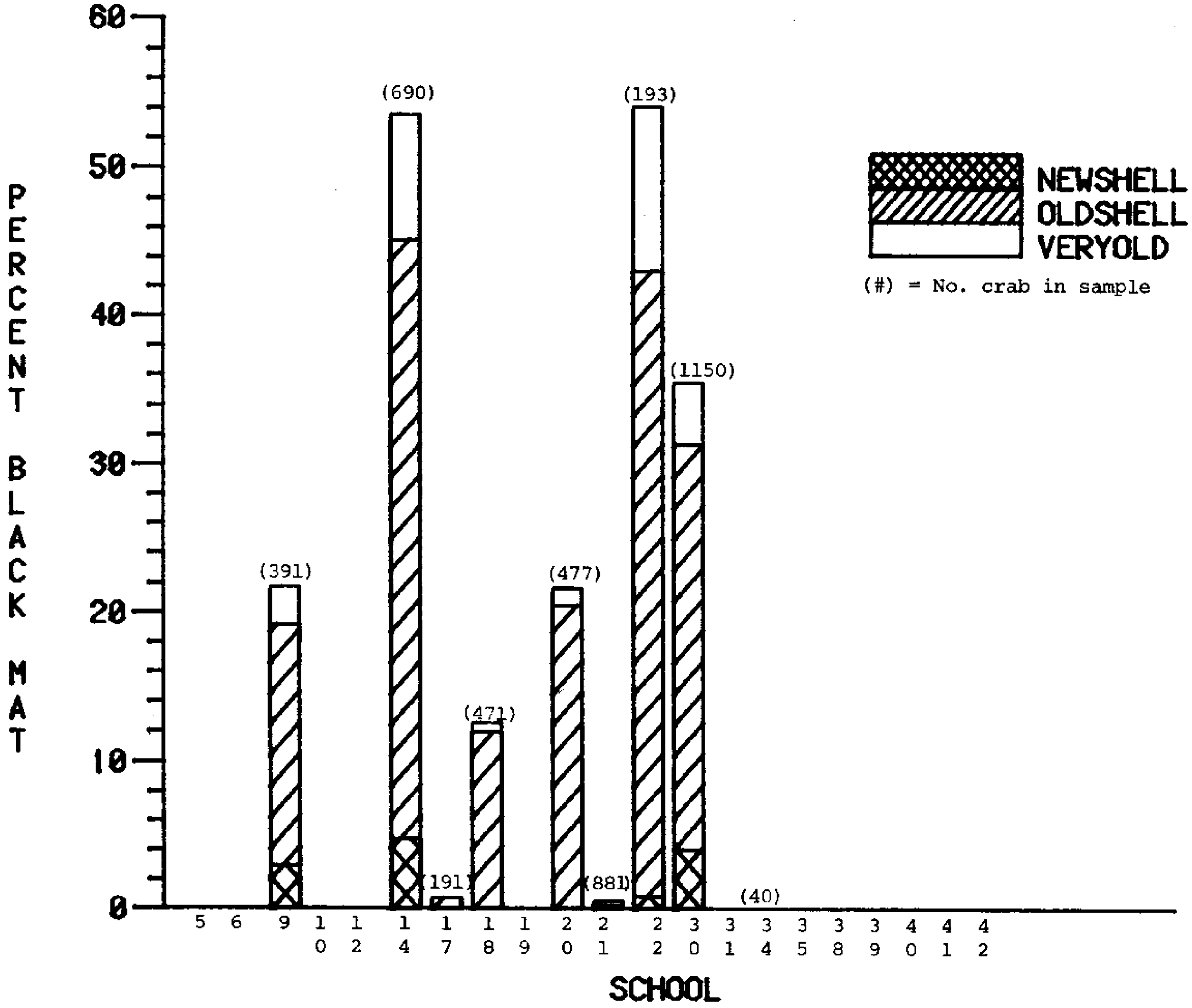


Figure 6.--Percent occurrence of Black Mat Syndrome in male Tanner crabs, *Chionoecetes bairdi,* by school and shell age, 1980 Kodiak Management District crab population pot survey.

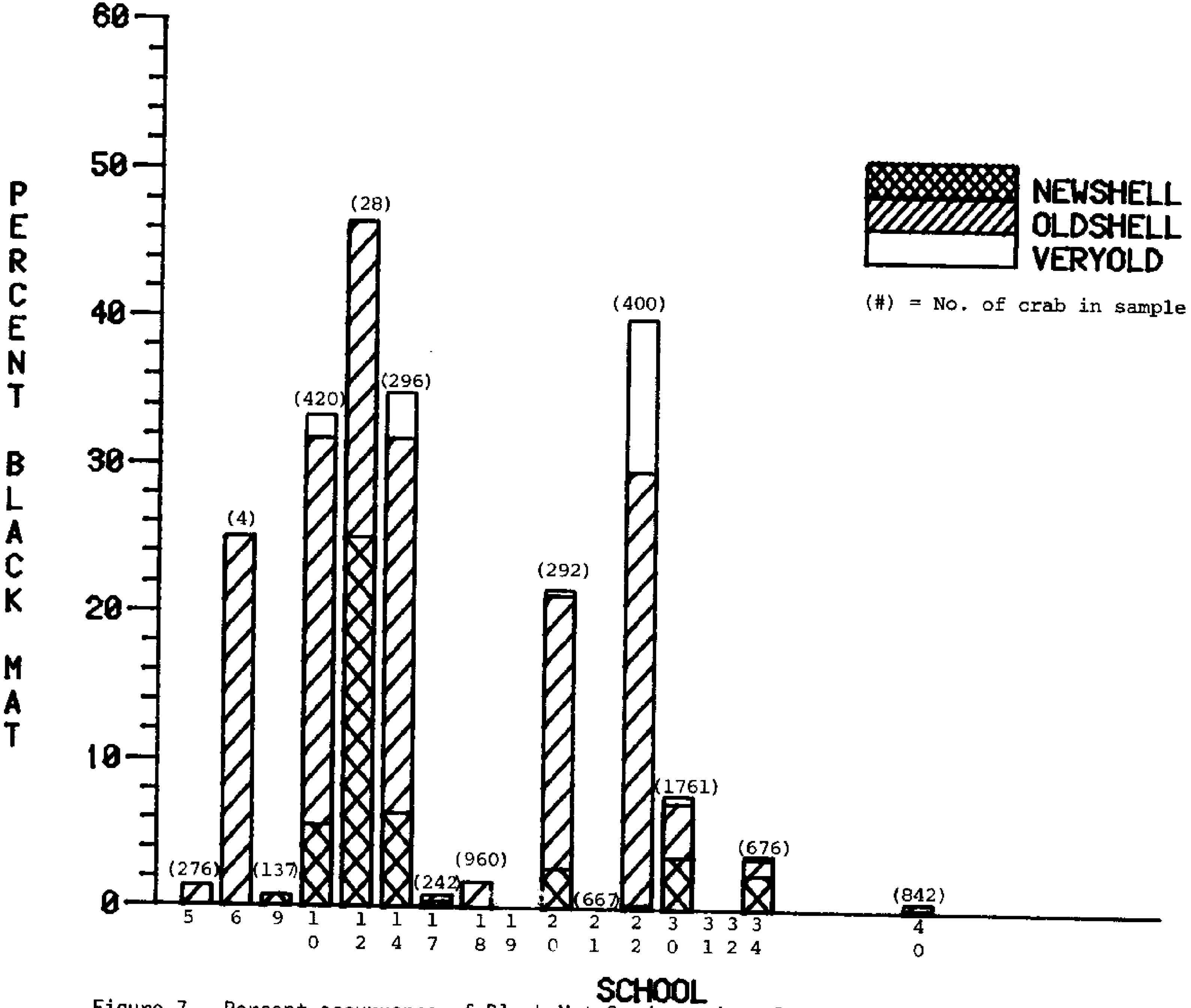


Figure 7.--Percent occurrence of Black Mat Syndrome in male Tanner crabs, *Chionoecetes bairdi*, by school and shell age, 1981 Kodiak Management District crab population pot survey.

Of the three data collection methods utilized in the Kodiak area, the pot surveys and commercial catch samples tended to show the highest incidence of infected crab. One possible reason the trawl caught crab had a lower incidence of BMS is that trawls tend to catch all sizes of crabs. About 50.0% of the crabs from the trawl surveys were less than 92 mm carapace width. These very small Tanner crabs molt so frequently that the syndrome may not have time to manifest itself. There may be other biological reasons why smaller Tanner crab do not have the same degree of infection as the larger crab. These questions need to be addressed. All sizes and sexes of crab show BMS to some degree but the old and very oldshell crabs have the highest incidence of BMS. The 1980 Kodiak trawl survey revealed 12.2% of the old-shells and 18.2% of the very oldshell Tanner crabs have BMS. Only 0.9% of the newshell crabs from the same survey had visible signs of BMS. The 1981 Kodiak trawl survey results were similar with old and very oldshell crabs having 60.2% BMS while newshells had only 1.9% BMS. It must be noted that aging Tanner crabs is somewhat arbitrary and differences between old and very oldshell crab in particular are not clear cut.

The Chignik area was sampled by trawl in 1981 and one commercial catch sample was taken during the 1981 fishery. The commercial sample from Chignik consisted of 103 crabs of which 4.9% had BMS (Table 1). The 1981 trawl survey sample of 2,517 male Tanner crabs produced a 2.5% incidence (Table 1). Old-shell crabs were found to have the highest occurrence of BMS on the 1981 Chignik survey with 71.4% of the total crabs infected. The Chignik area is not divided into schools so all data is area wide. The overall incidence of BMS in the Chignik area does not seem to be as high as it is in the Kodiak region.

FEMALE TANNER CRABS

Female Tanner crabs were studied in the Kodiak area by pots (Tables 2 and 3) and trawls in 1980 and 1981.

The Kodiak pot surveys showed a much higher proportion of the females to have BMS than any of the trawl surveys. Of the 798 female Tanner crabs captured on the 1980 pot survey, 50.1% had BMS (Table 2). The following year (1981) the pot survey showed 34.8% of the females to be infected (Table 3). The sample sizes for both years were similar. Virtually all of the female crabs that were recorded as very oldshells had BMS and as much as 94.7% of all the barren females captured on the 1981 pot survey had BMS.

The 1981 Kodiak trawl survey which sampled northern Shelikof Strait observed 8.7% of the females to have BMS. In 1981 the trawl survey again sampled northern Shelikof Strait and 9.2% had BMS. Sample sizes for the females on the 1980 and 1981 trawl surveys were 1,455 and 2,697 crabs, respectively. It is important to note a very high percentage of these infected females were either old or very oldshell animals.

The Chignik area trawl survey in 1981 made observations on 1,091 female Tanner crabs and only 1.3% were infected. The incidence of females infected in the Chignik area was similar to the percent of males found infected with BMS.

Table 2.--Number of female Tanner crabs, *Chionoecetes bairdi*, measured by exoskeletal age and occurrence of Black Mat Syndrome, in a portion of the Kodiak Management District, 1980 Kodiak Management District crab population pot surveys.

Group	Number crabs				Number with Black Mat				Percent with Black Mat			
	N	O	VO	Total	N	O	VO	Total	N	O	VO	Total
Juveniles	111	7	0	118	6	6	0	12	5.4	85.7	-	10.2
Adults	194	321	165	680	10	222	156	388	5.2	69.2	94.5	57.1
Total	305	328	165	798	16	228	156	400	5.2	69.5	94.5	50.1
% of Total	38.2	41.1	20.7	100.0	4.0	57.0	39.0	100.0				

Table 3.--Number of female Tanner crabs, *Chionoecetes bairdi*, measured by exoskeletal age and occurrence of Black Mat Syndrome, 1981 Kodiak Management District crab population pot surveys.

Group	Number crabs				Number with Black Mat				Percent with Black Mat			
	N	O	VO	Total	N	O	VO	Total	N	O	VO	Total
Juveniles	37	6	0	43	2	5	0	7	5.4	83.3	-	16.3
Adults	350	379	3	732	25	235	3	263	7.1	62.0	100.0	35.9
Total	387	385	3	775	27	240	3	270	7.0	62.3	100.0	34.8
% of Total	49.9	49.7	0.4	100.0	10.0	88.9	1.1	100.0				

SHELL AGES: N = Newshell
O = Oldshell
VO = Very Oldshell

Female Tanner crabs were also examined during the 1981 South Peninsula pot survey. Of the 303 females captured 8.9% had the disease.

Egg clutch size of female Tanner crabs are also recorded on the pot and trawl surveys (Colgate and Hicks 1982). It is interesting to note that about half of all the females recorded as having zero egg clutches, also had BMS. A relationship seems to exist between reduced egg clutch size and the extreme presence of BMS. Whether BMS causes the reduced egg clutch is not known. Egg samples and spermathecae of some heavily infected females with reduced egg clutches have been sent to interested pathologists for study.

SUMMARY

There are some important statements that can be made from this study concerning BMS:

1. There is a marked difference in the incidence of BMS for legal size males in the Kodiak district, varying from 0.0% to 60.0% between schools. To date sampling indicates the disease is more common in the Kodiak district than in the more western Chignik and the South Peninsula areas.

2. Black Mat Syndrome in the Kodiak district occurs more frequently in offshore schools than inshore schools. Most of the bays of Kodiak are virtually devoid of crabs with BMS.

3. There are differences in incidence rates between trawl caught and pot caught crabs from the same localities. In almost all cases the pot caught crabs exhibited a higher incidence of BMS than trawl caught crabs in the same region. One possible reason for this difference in incidence between the two survey methods is the size of the animals that the sampling gear selects for.

4. A high proportion of the barren female Tanner crabs captured also had BMS. Whether this barrenness is a matter of senescence or a direct cause of the BMS is yet to be explored.

5. A large percentage of the old and very oldshell age crab had BMS. A high degree of skip molting naturally exists in the Tanner crab population, but there may be a correlation between the syndrome and a greater frequency of skip molting. If so, prerecruit one crabs (115-139 mm carapace width) that had BMS might not be recruited into the fishery and the management strategy and predictive population estimation procedures would want to take this into account.

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Relationships Between Crab and Groundfish in the Eastern Bering Sea

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ABSTRACT

The study is presented in two parts: an examination of the organization of crab and groundfish communities in the eastern Bering Sea, and an evaluation of the roles and potential importance of fish predation on crab. Numerical classification analyses of bottom trawl survey data provided further documentation and elaboration of what appear to be major faunistic provinces and regional communities on the continental shelf and slope. These are interpreted as the habitat areas and species for many important biological interactions. Based on literature review, relationships between 22 benthic fish predators and 9 crab prey are summarized in the form of a food web matrix. Ten potentially important predator populations are then examined for their abundance relationships, and variations in abundance, during 1971-81.

INTRODUCTION

The major crab populations of commercial interest in the eastern Bering Sea are embedded in a complex, multispecies ecosystem composed of numerous invertebrates, fish, and marine mammals. Some of these associated species, or their products, are used as food resources; some are predators or potential food competitors; others, with no apparent trophic relationships, may interact and be members of the same ecological communities for numerous other environmental reasons.

The purpose of this study is to report the results of a new examination of the organization of crab and groundfish communities in the eastern Bering Sea and, within the context of these biological relationships, to evaluate the roles and potential importance of fish predation on crab. The examination of community organization is based upon numerical classification (i.e., "cluster") analyses of bottom trawl data from an exceptionally large sampling survey conducted in 1979. The evaluation of fish predation is treated in two steps: 1) connections between fish and crab reported in the literature are summarized in the form of a food web matrix, and 2) the relative abundance and dynamics of some of the important predator populations during the period 1971-81 are compared. Relationships between crab larvae and fish in the pelagic environment are also discussed to a lesser extent.

Another objective of the study is to bridge some of the gaps between other recent descriptions of major biological systems and their community organization, structure, and function in the eastern Bering Sea. Toward this end, efforts have been made to 1) extend the analyses of, and further detail, the recurrent species groups of fish and macroinvertebrates described by Pereyra et al. (1976: fig. IX-25) and Smith and Bakkala (1982: fig. 22); 2) provide comparisons of the major faunal domains, species groups, and large-scale distribution patterns described for the benthic invertebrate infauna (Haflinger 1981) and macrofauna (Stoker 1981; Jewett and Feder 1981); and 3) provide more detailed descriptions of the organization of the large-scale multispecies system, emphasizing groundfish and crab, so as to allow better interpretation of feeding relationships such as those described by Feder and Jewett (1981).

METHODS

Numerical Classification Analyses

Objectives of the numerical classification analyses were to 1) define areas of similar species composition on the Bering Sea continental shelf and slope, map these areas, and describe their characteristics; and 2) measure interspecific associations and define groups of species based on the similarity between distribution patterns.

Data Collection

The data that were analyzed were obtained from a bottom trawl survey conducted by the Northwest and Alaska Fisheries Center (NWAFC) in the eastern Bering Sea during 22 May to 22 August 1979. The geographic region covered by the survey ranged from Unimak Pass (lat. 54°20'N) to St. Lawrence Island (lat. 63°30'N), from inner Bristol Bay (long. 158°00'W) to the continental slope, and included a total area of about 649,000 km^2. Bottom depths that were sampled ranged from 11 to 732 m.

Of the 682 trawl samples collected by the survey, the classification analyses were applied to a subset of 566 samples that had relatively even geographic spacing: 472 of these were taken on the continental shelf (depths 11-183 m) using a 400-mesh Eastern trawl (Wathne 1977: fig. 9); and 94 hauls, taken along the continental slope (depths 183-732 m), were collected using a Nor'Eastern trawl with roller gear (Gunderson and Sample 1980: figs. 2-4). Both types of nets were used with

32 mm mesh cod end liners.

Samples and biological data were collected following the procedures described by Smith and Bakkala (1982). At each station the fishing gear was towed on the bottom for 30 min at 5.9 km/h (3.2 kn). The area of bottom "swept" by the trawl was estimated from the distance towed (determined by loran-C or radar fixes), multiplied by the effective path width (Alverson and Pereyra 1969), and was generally about 20,000 m^2. Fish and invertebrates were sorted by taxa, identified to the lowest reliable taxonomic level, weighed and counted.

Of the 287 total fish and invertebrate taxa recorded among the 566 trawl samples, only the catch data for a subset of 80 taxa was used for the grouping analyses (Table 1). Species in this subset were considered to have been reliably identified throughout the survey and occurred in at least 2% of the 566 samples. These included 62 benthic and benthopelagic fish species (and polyspecific taxa) distributed among 19 families and 18 major invertebrate taxa. Despite being a subset of the species list, the 80 taxa accounted for over 86% of the total faunal biomass.

Data Analysis

The data matrix used for classification analyses consisted of the catch data for the subset of 80 taxonomic entities at the 566 trawling sites. Catch data were used as the weight per unit area trawled. A log(*n*+1) transformation was applied to the data matrix to reduce the importance of high density values and increase the importance of low values.

The resemblance between sites or species was measured using the Bray-Curtis dissimilarity coefficient (Clifford and Stephenson 1975). To measure the resemblance between two sites (i.e., in a "normal" classification) the coefficient is computed as

$$\mathbf{D}_{jk} = \frac{\sum_{i=1}^{n} \left| x_{ij} - x_{ik} \right|}{\sum_{i=1}^{n} \left| x_{ij} + x_{ik} \right|}$$

where D_{jk} can range in value from zero (no dissimilarity) to 1 (complete dissimilarity), and x_{ij} and x_{ik} represent the transformed density values for the *i*th species (of *n* total) at the *j*th and *k*th stations.

Table 1. List of fish and invertebrates used in the analyses of species and site groups, 1979 Bering Sea trawl survey.1/

Taxon

- Agonidae
  - *Agonus acipenserinus*
  - *Aspidophoroides bartoni*
  - *Ocella dodecaedron*
  - *O. verrucosa*
  - *Sarritor frenatus*
  - Unid. agonids
- Ammodytidae
  - *Ammodytes hexapterus*
- Anoplopomatidae
  - *Anoplopoma fimbria*
- Bathymasteridae
  - *Bathymaster signatus*
- Clupeidae
  - *Clupea harengus pallasi*
- Cottidae
  - *Artediellus* spp. (7)
  - *Dasycottus setiger*
  - *Gymnocanthus* spp. (4)
  - *Hemilepidotus* spp. (3)
  - *H. jordani*
  - *H. papilio*
  - *Hemitripterus bolini*
  - *Icelus* spp. (6)
  - *Malococottus kincaidi*
  - *Myoxocephalus* spp. (10)
  - *Triglops* spp. (6)
  - Unid. cottids
- Cyclopteridae
  - *Careproctus melanurus*
  - *C. rastrinus*
  - *Liparis* spp. (13)
  - Unid. cyclopterids
- Gadidae
  - *Eleginus gracilis*
  - *Gadus macrocephalus*
  - *Theragra chalcogramma*
- Hexagrammidae
  - *Hexagrammos* spp. (2)
  - *H. lagocephalus*
  - *H. stelleri*
  - *Pleurogrammus monopterygius*
- Macrouridae
  - *Coryphaenoides pectoralis*

Taxon

- Myctophidae
  - *Diaphus theta*
  - Unid. myctophids
- Osmeridae
  - *Mallotus villosus*
  - *Osmerus mordax*
  - *Thaleichthys pacificus*
- Pleuronectidae
  - *Atheresthes* spp. (2)
  - *Glyptocephalus zachirus*
  - *Hippoglossoides elassodon*
  - *Hippoglossus stenolepis*
  - *Lepidopsetta bilineata*
  - *Limanda aspera*
  - *L. proboscidea*
  - *Platichthys stellatus*
  - *Pleuronectes quadrituberculatus*
  - *Reinhardtius hippoglossoides*
- Rajidae
  - *Raja* spp. (11)
- Scorpaenidae
  - *Sebastes alutus*
  - *Sebastolobus alascanus*
- Stichaeidae
  - *Lumpenus maculatus*
  - *L. sagitta*
  - Unid. stichaeids
- Trichodontidae
  - *Trichodon trichodon*
- Zaproridae
  - *Zaprora silenus*
- Zoarcidae
  - *Bothrocara brunneum*
  - *Lycodes brevipes*
  - *L. concolor*
  - *L. palearis*
  - Unid. zoarcids
- Caridean shrimp
  - *Argis* spp. (5)
  - *Pandalus* spp. (ca. 4)
  - *Sclerocrangon boreas*
  - Unid. crangonids

Table 1. Continued.

Taxon
Anomuran crabs
Lithodes aequispina
Paralithodes camtschatica
P. platypus
Brachyuran crabs
Chionoecetes angulatus
C. bairdi
C. opilio
C. bairdi × *opilio* (hybrid)
Erimacrus isenbeckii
Hyas spp. (2)
Oregonia gracilis
Telmessus cheiragonus
Echinoderms
Echinarachnius parma
Gorgonocephalus caryi
Strongylocentrotus droebachiensis

1/ Values in parentheses indicate the number of species possibly represented in polyspecific categories.

To measure the resemblance between species distributions (i.e., in an "inverse" classification), dissimilarity is computed using the same equation but $\underline{x}_{ij}$ and $\underline{x}_{ik}$ are the density values for the $\underline{i}$th station (of $\underline{n}$ total) for the $\underline{j}$th and $\underline{k}$th species.

Following determination of the matrix of dissimilarity coefficients between all sites or species, the categories were clustered using the group average agglomerative method (Boesch 1977). For the purpose of this study, sampling stations that clustered together as areas of similar species composition are called "site groups" and species that showed association because of similar distribution patterns are referred to as "species groups."

The data and computer programs used for these analyses were from the fisheries survey data-base system described by Mintel and Smith (1981).

Evaluation of Fish Predation

Objectives for the evaluation of fish predation were to 1) summarize observations reported in the literature of Bering Sea fish feeding on brachyuran and lithodid crabs so as to be able to appraise the various roles, prey overlaps, and potential importance of the predator/prey relationships; and 2) summarize and compare the relative abundances, and variations in abundance, of the important predator populations during recent years.

Data used to describe fish population abundance on the eastern Bering Sea shelf were obtained from the NWAFC Crab-Groundfish survey time series (Pereyra et al. 1976: Section VIII). A central 159,100 km^2 core area (Fig. 1) had been surveyed using uniform bottom trawling methods during approximately 1 June to 15 August of each year from 1971 to 1981. Field methods throughout the series have been essentially the same as those described in the preceding section.

RESULTS

Classification Analyses

Species Associations

Figure 2 shows the relationships found between the 80 fish and invertebrate taxa that were included in the analysis of the 1979 Bering Sea trawl survey. Brief interpretations of some of the associations and apparent species groups follow.

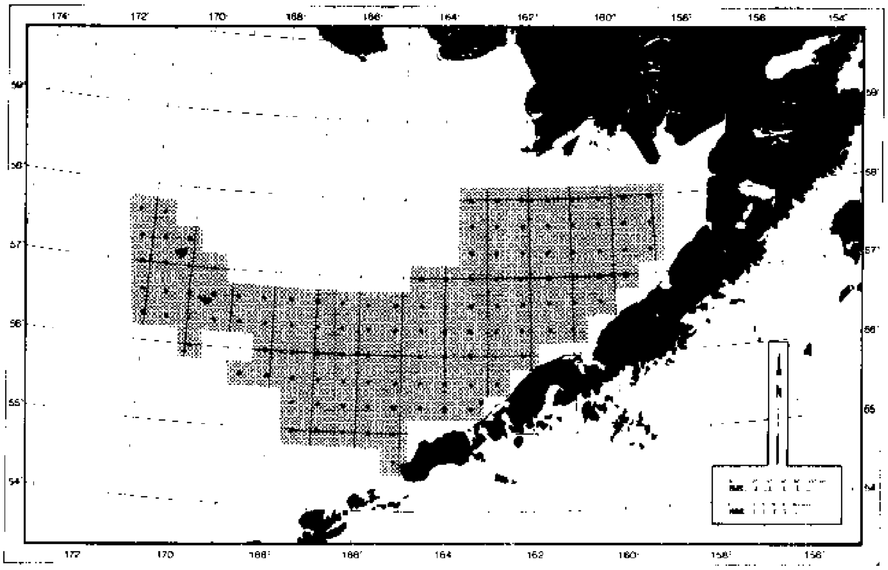

Figure 1. NWAFC index area (shaded) for annual eastern Bering Sea crab and groundfish population assessment surveys. Dots indicate routine sampling locations.

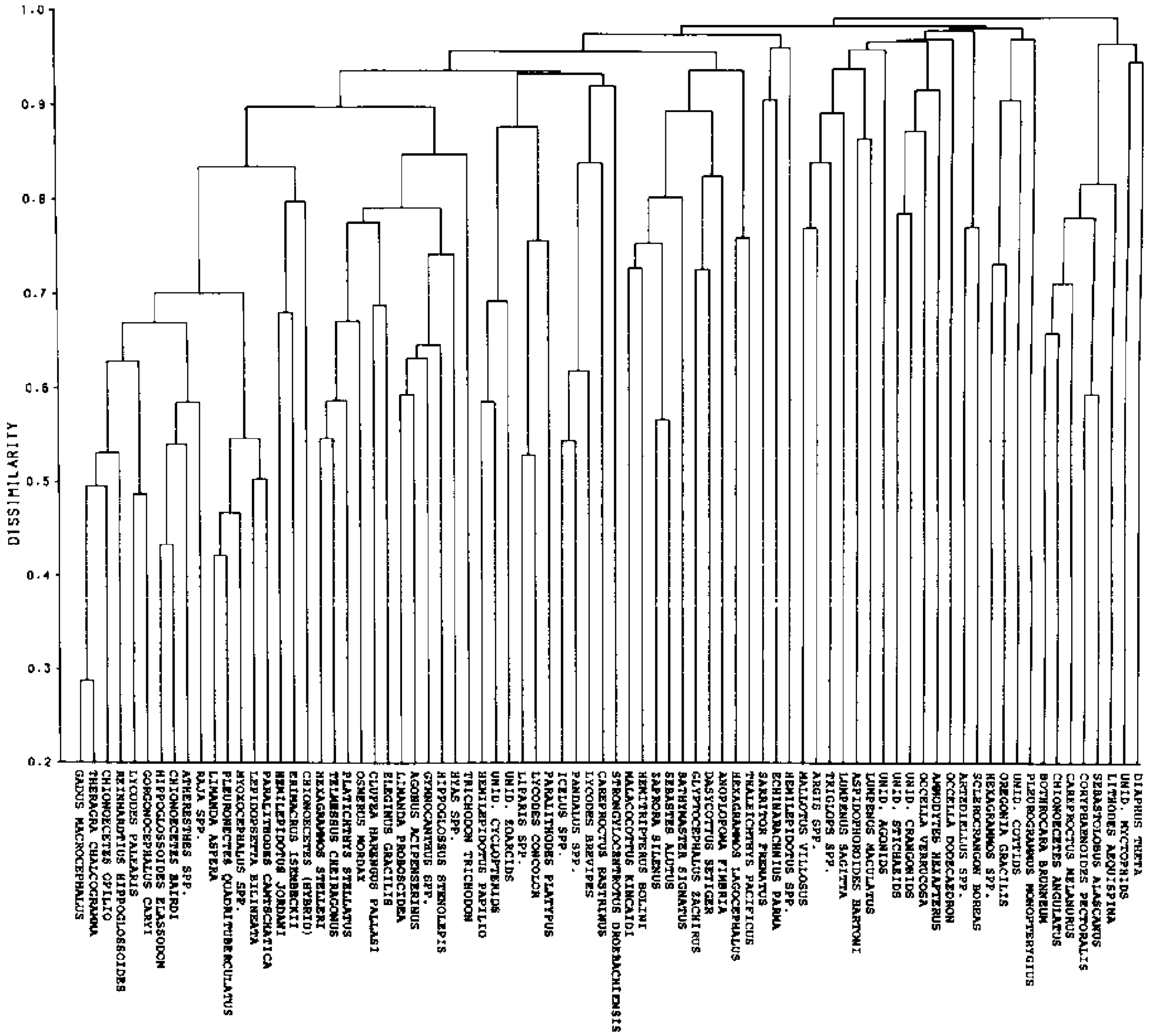

Figure 2. Dendrogram showing relationships between fish and invertebrate species based on similarity of distribution patterns, 1979 Bering Sea trawl survey.

1. The snow (Tanner) crab *Chionoecetes opilio* showed highest affinities to the following: walleye pollock, *Theragra chalcogramma*; Pacific cod, *Gadus macrocephalus*; Greenland turbot, *Reinhardtius hippoglossoides*; wattled eelpout, *Lycodes palearis*; and the basketstar, *Gorgonocephalus caryi*. This species group was broadly distributed throughout northern, midshelf regions of the study area.

2. The snow crab *C. bairdi* had highest affinities to the following: flathead sole, *Hippoglossoides elassodon*; the flatfish *Atheresthes* spp.; and skates, *Raja* spp. This group occurred primarily along the outer continental shelf.

3. Red king crab, *Paralithodes camtschatica*, showed highest affinities to the following: rock sole, *Lepidopsetta bilineata*; sculpins in the genus *Myoxocephalus*; Alaska plaice, *Pleuronectes quadrituberculatus*; and yellowfin sole, *Limanda aspera*. This species group was a dominant part of the macrofauna in the middle shelf region.

4. Korean horsehair crab, *Erimacrus isenbeckii*, had highest affinities to the following: yellow Irish lord, *Hemilepidotus jordani*; and hybrid (*C. bairdi* × *C. opilio*) snow crab. This group predominantly showed as a rare central shelf group.

5. The crab *Telmessus cheiragonus* had highest affinities to the following: whitespotted greenling, *Hexagrammos stelleri*; starry flounder, *Platichthys stellatus*; rainbow smelt, *Osmerus mordax*; Pacific herring, *Clupea harengus pallasi*; and saffron cod, *Eleginus gracilis*. This species group occurred along northern inshore regions.

6. The two *Hyas* crab species showed highest affinities to the following: Pacific halibut, *Hippoglossus stenolepis*; sculpins in the genus *Gymnocanthus*; sturgeon poacher, *Agonus acipenserinus*; and longhead dab, *L. proboscidea*. This group was also a northern coastal group.

7. Blue king crab, *Paralithodes platypus*, had highest affinities to the following: the eelpout *Lycodes concolor*; snailfish in the genus *Liparis*; unidentified eelpouts and snailfish; and the butterfly sculpin, *Hemilepidotus papilio*. This group was found in the northern, midshelf region.

8. Golden king crab, *Lithodes aequispina*, showed highest affinities to shortspine thornyhead, *Sebastolobus alascanus*; giant grenadier, *Coryphaenoides pectoralis*; blacktail snailfish, *Careproctus melanurus*; the snow crab *Chionoecetes angulatus*; and twoline eelpout, *Bothrocara brunneum*. This group occurred at continental slope depths of the study area.

Site Groups

Figure 3 summarizes the relationships observed between the 566 sampling locations on the basis of similarity of species composition. Additional characteristics of the major site groups are described in Tables 2 and 3.

To illustrate the patterns in which stations clustered, the results for this section are summarized and compared at several levels of dissimilarity. The iterative process of site clustering begins with fusing the most similar pair of stations. Through further fusion cycles additional stations, pairs of stations, or groups are then added at increasing levels of dissimilarity until all stations form a single cluster. Major site groups and their associated faunas were compared at the three values of dissimilarity shown in Figure 3: level 1, 0.75; level 2, 0.65; and level 3, 0.55.

In part, this approach represents an attempt to describe the results in terms of operational groups at different geographical scales that, on the basis of subjective analysis, seem to have biological reality. Additional, less positive, reasons were the arbitrariness of selecting a "significant" level of resemblance and the difficulty of applying significance tests between groups (Clifford and Stephenson 1975; Boesch 1977). We begin at a high level of dissimilarity, where the study area is divided into the largest site groups, and proceed in the direction of less dissimilarity to evaluate subdivisions of these groups.

At level 1, the highest level of dissimilarity, the 566 sampling locations organized into three major site groups (Fig. 4): northern coast (group 1), continental shelf (group 2), and continental slope (group 3). Species dominating the fauna of the northern coast group were (in order of relative abundance) yellowfin sole, asteroids, saffron cod, the starfish *Asterias amurensis*, and longhead dab. The continental shelf fauna was dominated by walleye pollock, yellowfin sole, snow crab (*C. opilio*), Pacific cod, and asteroids. The continental slope fauna was predominantly composed of Greenland turbot; giant grenadier; the flatfish *Atheresthes* spp.; northern rockfish, *Sebastes borealis*; and sablefish, *Anoplopoma fimbria*.

At level 2, the intermediate level of dissimilarity, the 566 stations formed five major site groups (Fig. 5): northern coast (group 1, same as at level 1); central shelf (group 2A), outer shelf (group 2Bi), St. Matthew Island (group 2Bii), and continental slope (group 3, same as at level 1). Groups 2A, 2Bi, and 2Bii were regional subsets of the extensive continental shelf group that formed at the higher level of dissimilarity, level 1. Species that dominated the faunas of the newly-formed groups were: 1) central shelf--yellowfin sole, walleye pollock, Pacific cod, snow crab (*C. opilio*), and asteroids; 2) outer

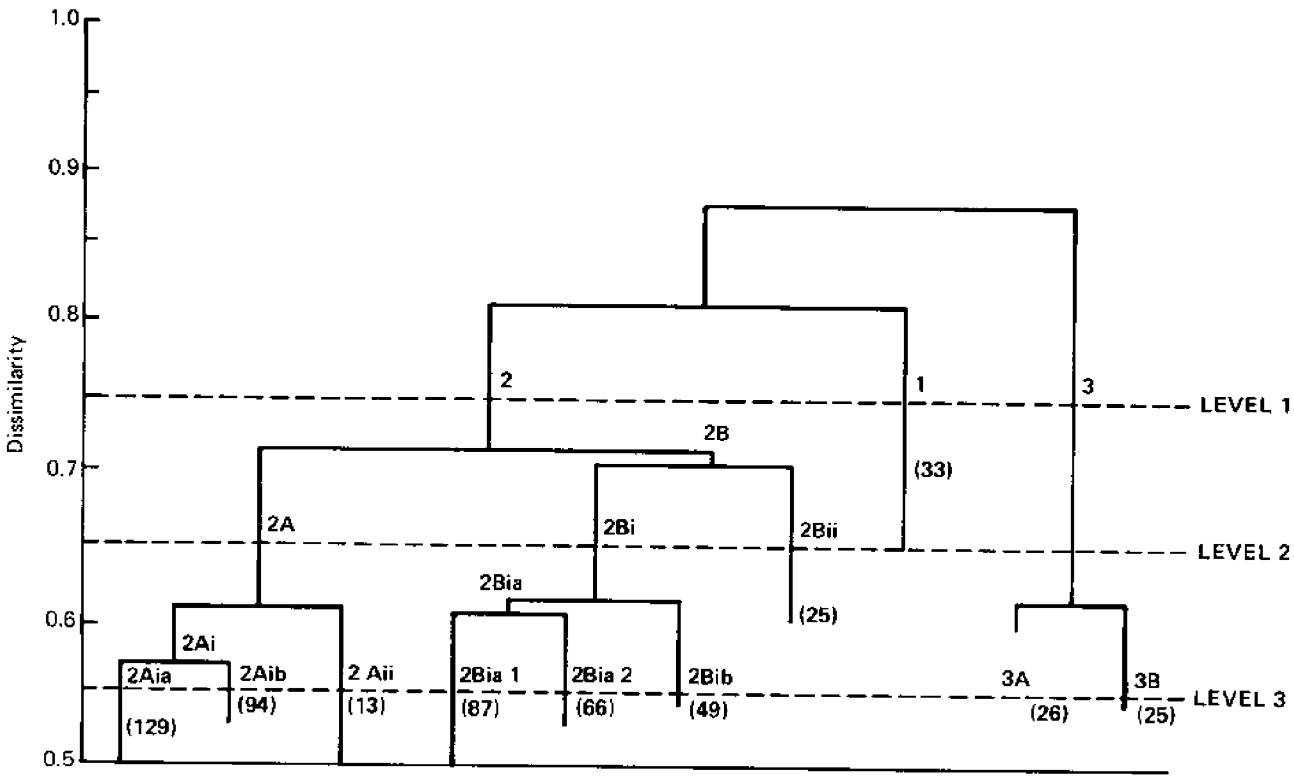

Figure 3. Schematic dendrogram showing the major site groups (areas of similar species composition) and their relationships at different levels of dissimilarity, 1979 Bering Sea trawl survey. Index numbers identify the different site groups. Values in parentheses indicate the number of stations.

Table 2. Summary of site group characteristics, 1979 Bering Sea trawl survey.

Site[1] group	Number of stations	Bottom depth (m)			Mean faunal density (kg/ha)
		Mean	S.D.	Range	
1	33	26	6	15-38	90.5
2	468	87	44	11-274	195.8
2A	236	57	17	11-93	274.7
2Ai	223	56	17	11-91	287.5
2Aia	129	66	13	40-91	307.1
2Aib	94	42	12	11-68	225.3
2Aii	13	74	12	48-93	246.5
2B	227	120	40	38-274	184.3
2Bi	202	127	37	59-274	197.0
2Bia	153	115	28	59-274	200.3
2Bia1	87	113	33	59-274	187.7
2Bia2	66	117	19	68-152	200.9
2Bib	49	166	35	99-241	118.3
2Bii	25	63	14	38-93	103.6
3	51	507	135	187-732	40.4
3A	26	417	81	187-563	41.9
3B	25	601	114	439-732	43.0

[1] See Figure 3.

Table 3. Summary of abundance relationships within the fish and invertebrate faunas of the major site groups, 1979 Bering Sea trawl survey.1/

Taxon	Site group2/ 1	2Aia	2Aib	2Aii	2Bia1	2Bia2	2Bib	2Bii	3A	3B
Yellowfin sole	41.62	84.72	91.08	8.96	0.77	7.33	--	0.55	--	--
Unid. asteroids	22.16	11.54	18.24	0.77	0.46	1.29	--	0.30	--	0.04
Saffron cod	3.97	0.41	1.22	--	--	--	--	--	--	--
Asterias amurensis	2.92	2.54	8.10	8.90	0.69	--	--	--	--	--
Walleye pollock	1.30	73.96	3.56	11.09	100.24	86.85	60.02	4.84	1.00	0.20
Snow crab (*C. opilio*)	0.31	20.13	--	36.71	38.29	13.91	0.08	36.64	0.07	0.06
Pacific cod	--	19.83	57.21	37.94	8.84	7.89	30.49	1.96	0.62	--
Red king crab	--	20.02	4.88	0.64	--	24.29	--	--	--	--
Rock sole	0.30	2.26	15.10	7.95	--	3.77	0.70	0.13	--	--
Halocynthia aurantium	--	2.16	--	22.47	--	--	--	--	--	--
Yellow Irish lord	--	0.38	0.29	22.36	--	2.82	1.56	--	--	--
Greenland turbot	--	1.56	--	1.04	8.70	1.07	0.53	3.38	19.36	18.89
Snow crab (*C. bairdi*)	--	2.24	0.41	4.91	0.92	8.79	0.72	--	0.08	--
Atheresthes spp.	--	0.42	1.04	0.28	0.19	3.07	7.17	--	8.46	0.53
Pacific ocean perch	--	--	--	--	--	--	3.43	--	0.52	--
Butterfly sculpin	--	--	--	0.31	0.90	--	--	12.48	--	--
Unid. eelpouts	--	0.70	--	--	3.57	2.66	--	8.42	--	0.08
Lycodes concolor	--	--	--	--	--	--	--	6.99	--	--
Giant grenadier	--	--	--	--	--	--	--	--	0.16	13.35
Northern rockfish	--	--	--	--	--	--	--	--	5.35	0.30
Flathead sole	--	2.15	2.43	0.60	2.36	4.87	0.48	1.24	1.08	--
Coryphaenoides cinereus	--	--	--	--	--	--	--	--	--	2.44
Sablefish	--	--	--	--	--	2.00	0.26	--	0.54	1.95

1/ Indices of abundance are given for the four dominant taxa (underlined) of each site group. Values for less abundant species are not necessarily shown. Units = mean kg/ha trawled.

2/ See Figure 3.

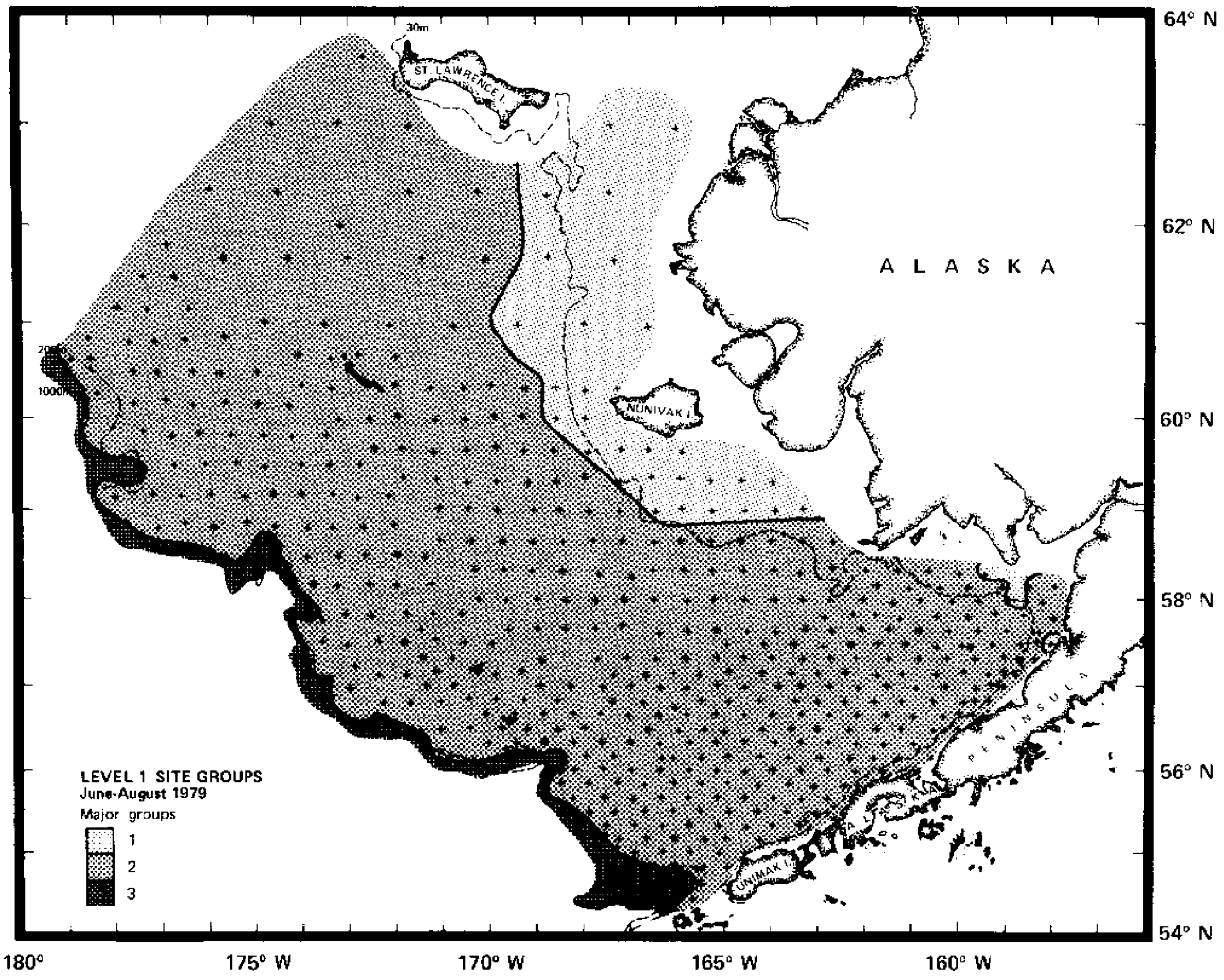

Figure 4. Map of level 1 site groups, 1979 Bering Sea trawl survey. Plus signs indicate sampling locations.

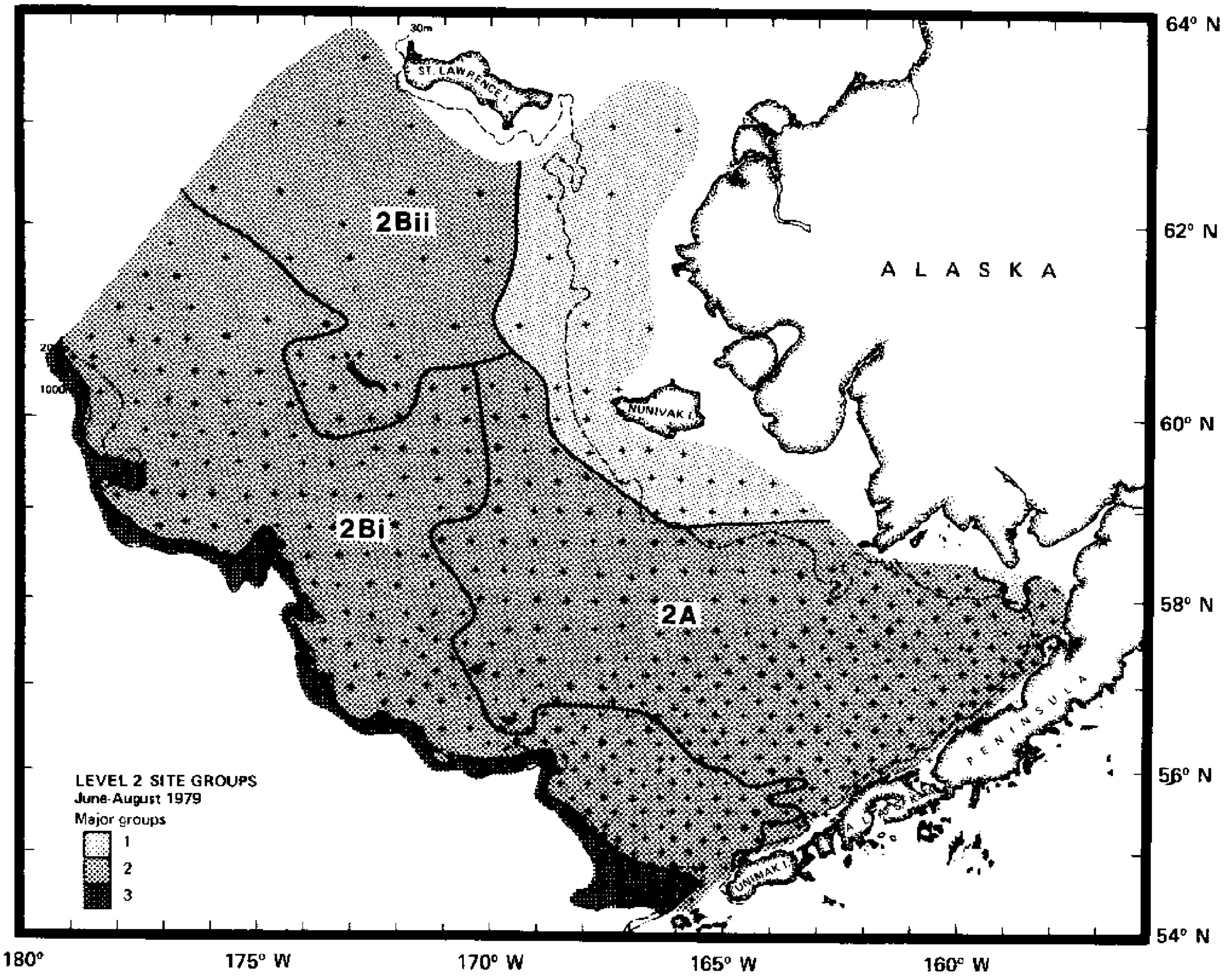

Figure 5. Map of level 2 site groups, 1979 Bering Sea trawl survey.

shelf--walleye pollock, snow crab (C. opilio), Pacific cod, red king crab, and Greenland turbot; and 3) St. Matthew Island--snow crab (C. opilio), butterfly sculpin, unidentified eelpouts, the eelpout Lycodes concolor, and walleye pollock.

Eight regional site groups were formed at level 3, the lowest level of dissimilarity (Fig. 6): middle shelf (group 2Aia), shallow central shelf (group 2Aib), Pribilof Islands (group 2Aii), northern outer shelf (group 2Bia1), southern outer shelf (group 2Bia2), deep outer shelf (group 2Bib), upper continental slope (group 3A), and lower continental slope (group 3B). Groups 2Aia and 2Aib were regional subsets of the central shelf group formed at level 2. Group 2Aii apparently represents a distinct Pribilof Islands environment. Groups 2Bia1, 2Bia2, and 2Bib were regional subsets of the outer shelf group formed at level 2. Groups 3A and 3B were apparently the result of depth zonation within the continental slope group formed at levels 1 and 2.

Species that dominated the communities of the groups formed at level 3 were (see Table 3) 1) middle shelf--yellowfin sole, walleye pollock, snow crab (C. opilio), and red king crab; 2) shallow central shelf--yellowfin sole, Pacific cod, asteroids, and rock sole; 3) Pribilof Islands--Pacific cod, snow crab (C. opilio), the ascidian Halocynthia aurantium, yellow Irish lord, and Myoxocephalus spp.; 4) northern outer shelf--walleye pollock, snow crab (C. opilio), Pacific cod, and Greenland turbot; 5) southern outer shelf--walleye pollock, red king crab, and snow crabs (C. opilio and C. bairdi); 6) deep outer shelf--walleye pollock, Pacific cod, the flatfish Atheresthes spp., and Pacific ocean perch, Sebastes alutus; 7) upper continental slope--Greenland turbot, Atheresthes spp., northern rockfish, flathead sole, and skates; and 8) lower continental slope--Greenland turbot, giant grenadier, the macrourid Coryphaenoides cinereus, and sablefish.

Fish Predation on Crab

In the Benthic Food Web

Table 4 summarizes the relationships between Bering Sea benthic fish predators and crab prey (megalops, juvenile, or adult stages) found from a review of the available literature. Following the conventions of Cohen (1978) a 1 in the matrix indicates an observed feeding relationship, a -1 indicates an inferred relationship, and a zero indicates no apparent relationship. Inferred relationships were decided on the basis of the predator's documented prey (i.e., food preferences and capabilities of food selection), and the degree of geographic overlap between predator and prey populations (i.e., contact and opportunity) as documented in the fisheries survey

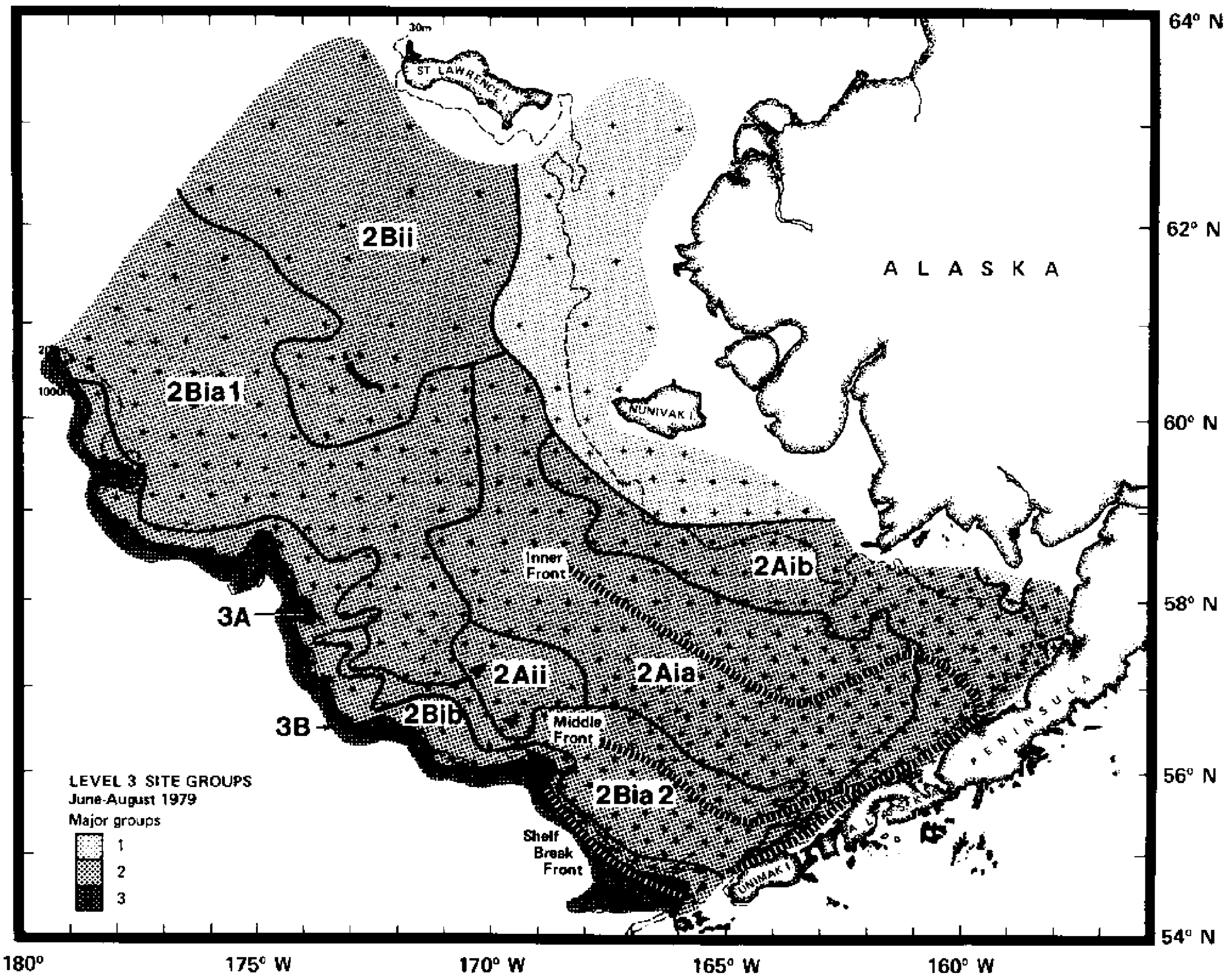

Figure 6. Map of level 3 site groups, 1979 Bering Sea trawl survey. Groups 1 and 2Bii are mapped even though they were not formed at this lowest level of dissimilarity. Superimposed are the three approximate frontal boundaries separating the major hydrographic domains described by Kinder and Schumacher (1981: fig. 4-1).

Table 4. The food web matrix of benthic fish predators and crab prey in the eastern Bering Sea.

Predator[1]	Crab prey[2]									Source
	CO	CB	HL	HC	OG	PC	PP	TC	EI	
Bathymaster signatus (B)	0	1	0	0	0	0	0	0	0	Feder (1978a)
Dasycottus setiger (C)	1	-1	0	0	0	0	0	0	0	Mito (1974)
Hemilepidotus hemilepidotus (C)	0	0	0	0	0	1	0	0	0	Jewett and Feder (1981)
H. jordani (C)	1	1	1	-1	1	0	0	0	0	Mito (1974), Jewett and Powell (1979)
H. papilio (C)	1	-1	0	0	0	0	0	0	0	Feder (1978b)
Malacocottus zonurus (C)	1	0	0	0	0	0	0	0	0	Mito (1974)
Myoxocephalus polyacanthocephalus (C)	1	1	-1	1	-1	-1	-1	-1	-1	Mito (1974), Feder (1978a), Jewett and Powell (1979), Jewett and Feder (1981)
Myoxocephalus spp. (C)	-1	1	1	-1	-1	-1	-1	-1	-1	Feder (1978b), Jewett and Powell (1979)
Careproctus spp. (CY)	1	0	0	0	0	0	0	0	0	Feder (1978b)
Liparis cyclostigma (CY)	1	0	0	0	0	0	0	0	0	Mito (1974)
Gadus macrocephalus (G)	1	1	-1	-1	-1	-1	-1	-1	-1	Mito (1974), Feder (1978a,b), Jewett (1978), Jewett and Feder (1981)

Table 4. Continued.

Predator	Crab prey									Source
	CO	CB	HL	HC	OG	PC	PP	TC	EI	
Theragra chalcogramma (G)	1	1	0	0	0	0	0	0	0	Andriyashev (1954), Smith et al. (1977), Jewett and Feder (1981)
Glyptocephalus zachirus (P)	0	1	0	0	0	0	0	0	0	Smith et al. (1977, 1978), Jewett and Feder (1981)
Hippoglossoides elassodon (P)	1	0	0	0	0	0	0	0	0	Mito (1974), Jewett and Feder (1981)
Hippoglossus stenolepis (P)	-1	1	-1	-1	-1	1	-1	-1	-1	Gray (1964), Novikov (1964), Feder (1978a), Best (1981), Jewett and Feder (1981)
Lepidopsetta bilineata (P)	1	0	0	0	0	0	0	0	0	Mito (1974), Jewett and Feder (1981)
Microstomus pacificus (P)	0	1	0	0	0	0	0	0	0	Smith et al. (1977)
Platichthys stellatus (P)	1	1	0	0	0	0	0	0	0	Feder (1978a), Jewett and Feder (1980)
Raja interrupta (R)	1	-1	0	0	0	0	0	0	0	Mito (1974)
R. parmifera (R)	1	-1	0	0	0	0	0	0	0	Mito (1974)
Sebastolobus alascanus (S)	1	0	0	0	0	0	0	0	0	Mito (1974)

Table 4. Continued

Predator	Crab prey									Source
	CO	CB	HL	HC	OG	PC	PP	TC	EI	
Lycodes palearis (Z)	1	0	0	0	0	0	0	0	0	Mito (1974)

1/ Taxonomic families shown in parentheses: B=Bathymasteridae, C=Cottidae, CY=Cyclopteridae, G=Gadidae, P=Pleuronectidae, R=Rajidae, S=Scorpaenidae, Z=Zoarcidae.

2/ Key: CO=*Chionoecetes opilio*, snow crab; CB=*Chionoecetes bairdi*, snow crab; HL=*Hyas lyratus*, blunt-nosed crab; HC=*Hyas coarctatus alutaceus*, toad crab; OG=*Oregonia gracilis*, decorator crab; PC=*Paralithodes camtschatica*, red king crab; PP=*Paralithodes platypus*, blue king crab; TC=*Telmessus cheiragonus*; EI=*Erimacrus isenbeckii*, Korean horsehair crab.

literature (Pereyra et al. 1976; Smith and Bakkala 1982).

At least 22 fish species and genera from 8 families have been observed to feed on some, or many, of the 9 major crab species. Of these, 4 fish taxa were observed or thought to feed on some benthic life history stage of all 9 crab species, 6 were recorded as feeding on two crab species, and 11 were recorded as feeding on only one.

Fish predators of crab that seem to be important because of their cosmopolitan distributions and broad diets are Pacific cod, Pacific halibut, and sculpins in the genus *Myoxocephalus*. These fish have large mouths and are large-bodied as adults. Other fish on the list may be important in more specific areas and at times of high relative abundance. For example, walleye pollock shares dominance (on a weight basis) of the outer shelf community with the snow crabs *C. opilio* and *C. bairdi*; skates (*Raja* spp.) are common, large-bodied members of the outer shelf and upper continental slope communities where they may be important grazers of epifaunal invertebrate populations; and eelpouts (particularly *Lycodes* spp.) and snailfish (especially *Liparis* spp. and *Careproctus* spp.) are most abundant north of the Pribilof Islands.

Many of the crab prey had numerous fish predators: snow crab (*C. opilio*), probably because of its small adult size and high abundance, was recorded as being fed upon by at least 18; snow crab (*C. bairdi*), 14; *Hyas* crabs, 5; decorator crab (*Oregonia gracilis*), 5; red king crab, 5; blue king crab, 4; *Telmessus* crab, 4; and Korean horsehair crab, 4. For lack of field observations, all of the relationships of the latter three crab species were inferred.

In the Pelagic Environment

Although larval (zoeae and megalops) stages of crab are potentially exposed to substantial grazing by fishes during their months in the plankton, this is an area of study that has received little attention. Potential predators include approximately 20-30 non-salmonid and salmonid fish species (Macy et al. 1978; Straty 1981), and those among the benthic and benthopelagic fishes that feed from the epibenthic layer and water column. Some of these species have large and abundant populations. A few examples of relationships that may be important follow.

Pacific salmon--sockeye salmon, *Oncorhynchus nerka*; chum salmon, *O. keta*; pink salmon, *O. gorbuscha*; chinook salmon, *O. tshawytscha*; and coho salmon, *O. kisutch*--are recognized to be major, but highly migratory and transient, components of the Bering Sea shelf pelagic community (Straty 1981). Of these, sockeye salmon has been found to feed on crab zoeae and decapod larvae (Straty 1974; Nishiyama 1974), although the significance of this linkage as a potentially large and variable source of mortality remains to be evaluated.

Walleye pollock and yellowfin sole may also be found to be important predators of crab larvae because of the dominance of their populations among the outer and middle shelf faunas; both species also seem to have the capability and opportunity for such interactions. Small planktonic crustaceans are a major part of the diet of walleye pollock, particularly of juvenile pollock (ages 1-2 yr) because of their pelagic behavior and generally higher distribution in the water column than adults (Smith 1981). Small planktonic and epibenthic crustaceans similar to crab larvae--mysids, amphipods, euphausiids, and caridean shrimp--are common prey items for yellowfin sole (Feder and Jewett 1981: fig. 69-6).

Variations in Predator Abundance

Based on the results of the literature review, 10 predator (and, in the case of yellowfin sole, potential predator) populations were examined for their abundance relationships, and variations in abundance, in the 1971-81 NWAFC Crab-Groundfish survey time series (see Fig. 1). Table 5 summarizes the mean annual abundances that were observed, also graphed in Figure 7. Brief interpretations of these results follow.

The abundance measures for the 10 populations covered 5 orders of magnitude of weight density (actually an index of catch-per-unit-effort). Throughout all years, yellowfin sole and walleye pollock exceeded all other species in abundance. Populations of intermediate abundance over the 11-yr period included rock sole, Pacific cod, flathead sole, sculpins, and eelpouts. Least abundant were skates, Pacific halibut, and searcher, Bathymaster signatus.

To aid interpretation of the time order of the observations, a run test (Tate and Clelland 1959) was applied to the vector of mean annual abundances for each population. Observations were scored as either less than, or greater than, the overall 11-yr mean. The null hypothesis was that scores occurred in random sequence.

Neither yellowfin sole or walleye pollock showed any clear trend or patterns in abundance in the time series. However, these results conflict with catch and effort statistics from the commercial trawl fisheries that indicate, for the effective fishing areas, that walleye pollock may have declined in

Table 5. Summary of indices of abundance of ten benthic fish populations that may be important predators of crab in the eastern Bering Sea, Crab-Groundfish survey time series, 1971-81.1/

Population	Year2/											Long-term mean	Run3/ test
	1971 (34)	1972 (85)	1973 (111)	1974 (111)	1975 (111)	1976 (107)	1977 (112)	1978 (116)	1979 (191)	1980 (113)	1981 (111)		
Yellowfin sole	22.5	15.9	45.2	48.3	62.4	66.7	46.0	59.8	36.5	49.6	64.8	47.06	6
Walleye pollock	59.4	19.2	29.2	27.5	21.1	46.7	37.7	47.1	48.4	30.7	81.6	40.78	7
Rock sole	3.36	4.34	8.59	12.40	10.92	11.90	5.81	8.09	4.40	11.30	12.61	8.52	4*
Pacific cod	1.47	0.77	3.69	3.40	7.00	3.04	5.84	14.78	18.42	16.62	18.11	8.47	2***
Flathead sole	4.91	3.17	3.86	7.36	6.08	6.70	5.37	4.23	4.92	4.19	6.25	5.19	4*
Sculpins	0.87	2.29	3.26	3.88	4.43	8.61	8.29	11.28	3.81	4.27	3.39	4.94	3**
Eelpouts	0.31	0.77	4.20	6.53	8.76	9.55	9.62	3.39	4.76	2.80	1.38	4.73	5
Skates	0.56	0.18	0.34	1.81	2.21	1.63	2.42	1.28	2.19	3.70	3.70	1.82	6
Pacific halibut	0.571	0.301	0.168	0.509	0.443	0.744	0.671	0.981	1.397	1.690	2.057	0.87	2***
Searcher	0.047	0.007	0.028	0.084	0.365	0.422	0.298	0.277	0.291	0.178	0.221	0.20	4*

1/ Units = mean kg/ha trawled.
2/ Values in parentheses indicate number of samples.
3/ * = $P \leq 0.20$, ** = $P \leq 0.05$, *** = $P \leq 0.01$.

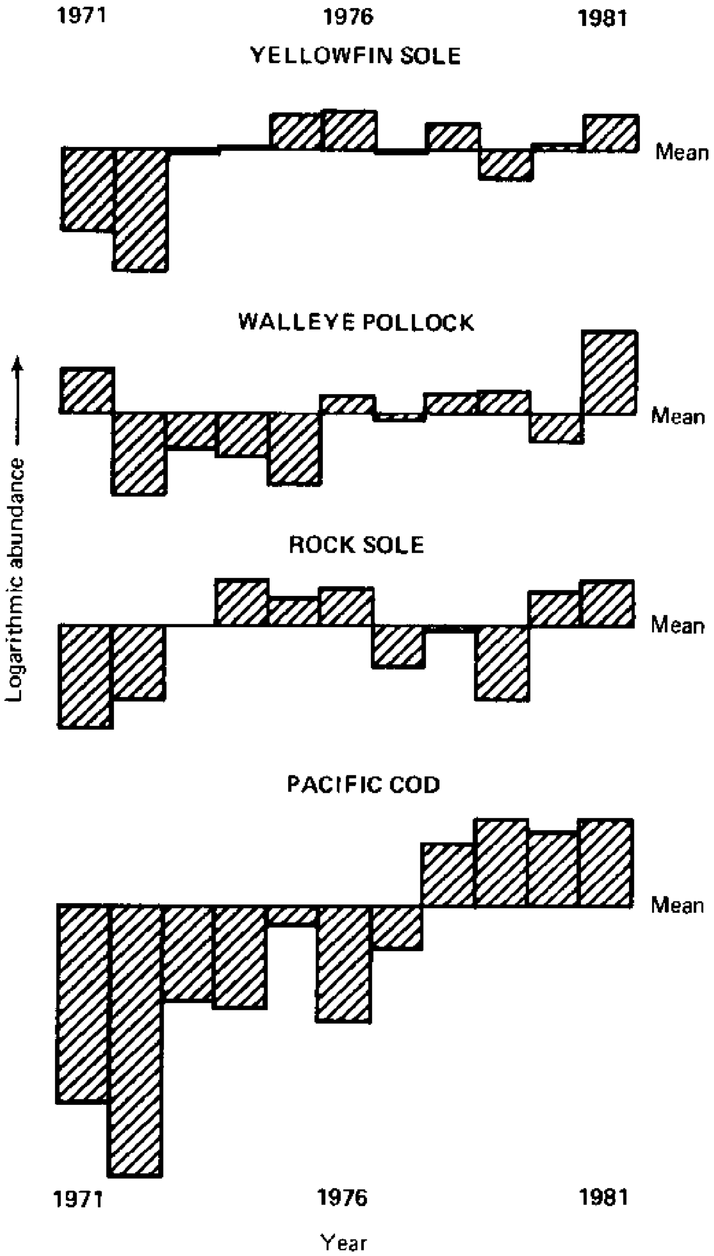

Figure 7. Variations in the abundance of ten benthic fish populations in the eastern Bering Sea, based upon the data in Table 5.

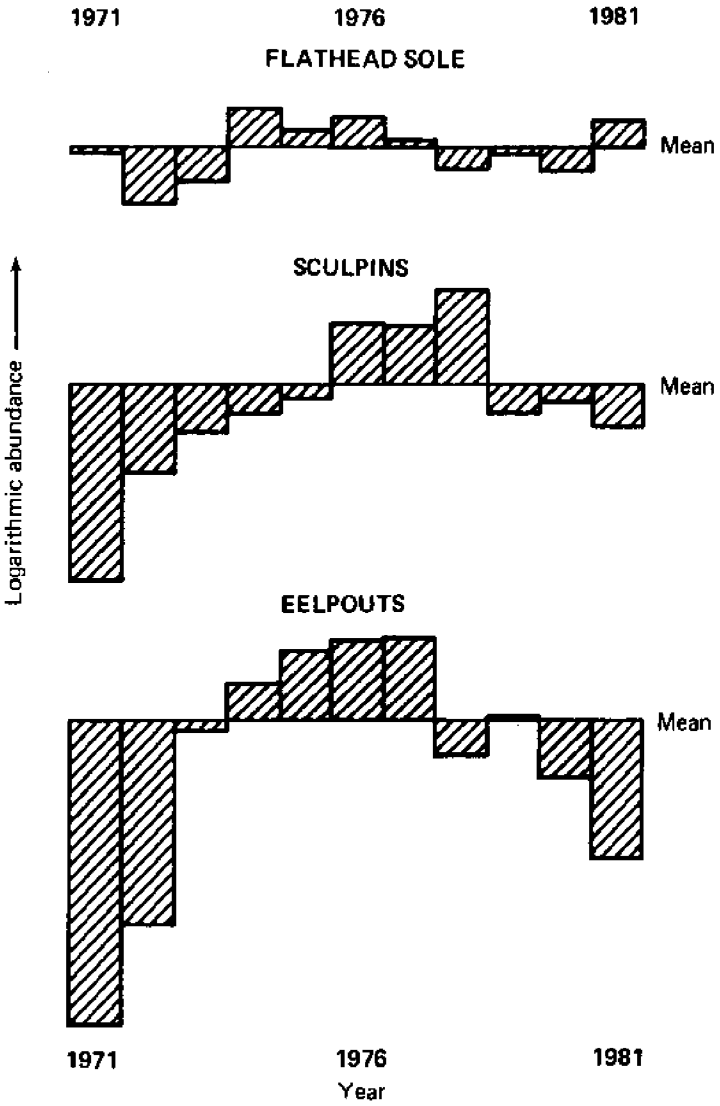

Figure 7. Continued.

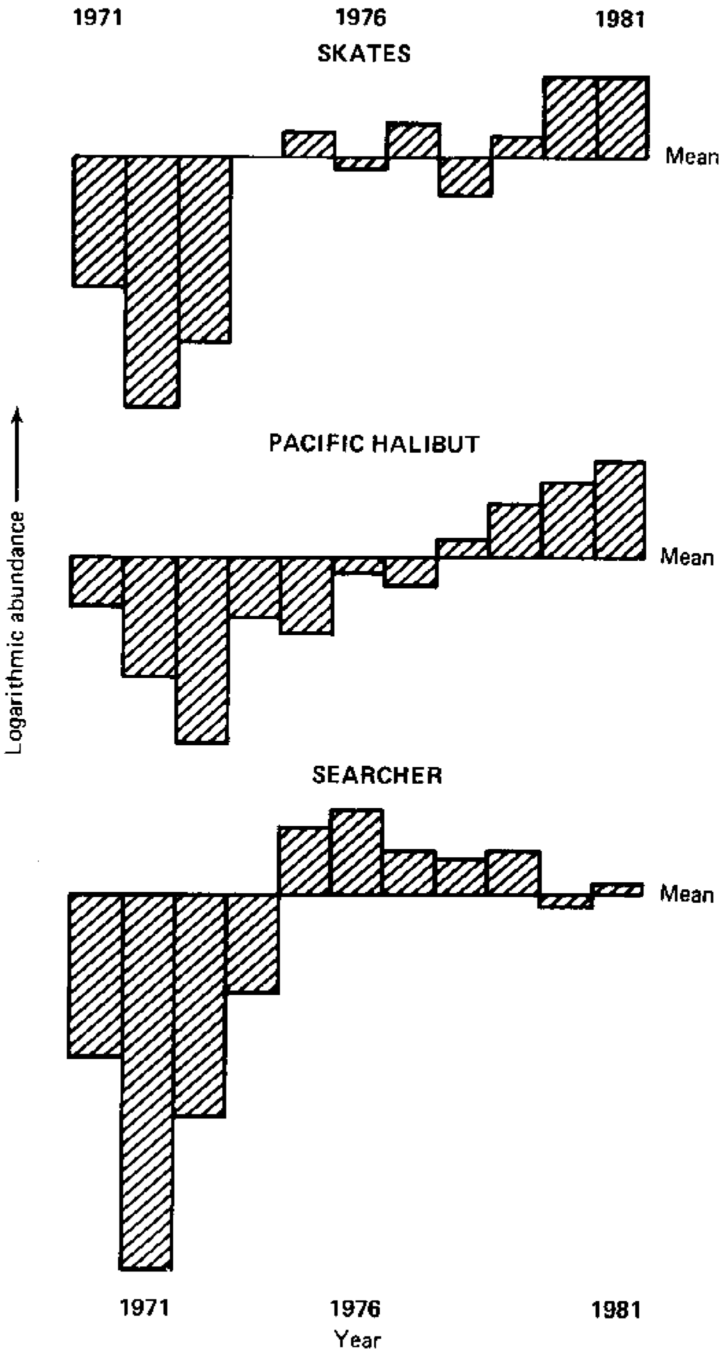

Figure 7. Continued.

abundance from 1969 to 1980 (Bakkala et al. 1981: 4) and yellowfin sole abundance may have increased during the same period (ibid, page 45).

Populations that showed fairly clear trends of increasing abundance during the 1971-81 time series were Pacific cod, Pacific halibut, searcher, and to a lesser extent, skates. The substantial increase in Pacific cod abundance that occurred from 1978 to 1981 was apparently due to the emergence of an exceptionally strong 1977 year-class (Wespestad et al. 1982).

Two composite populations showed patterns of abundances peaking near the middle of the time series: sculpins were most abundant during 1975-77; and eelpouts, 1974-77.

Rock sole and flathead sole showed patterns of abundances alternating between low and high values at intervals of 2-4 yr.

DISCUSSION

As emphasized by Wiens (1981), interpretations of community organization and large-scale patterns based on the results of a single-year survey should be viewed with some caution and skepticism because of the lack of knowledge of the importance of temporal or spatial variations. This warning seems particularly appropriate for studies of fish and epifaunal invertebrate communities in the eastern Bering Sea: because of the high latitude of the region and continental sea exposure, temporal variations of populations are likely to be accentuated by the strong climatic differences between seasons and years (Niebauer 1980) and steeply pulsed events in the biological production cycle. In addition, one major cause of spatial variation is seasonally driven population migration. During the seasonal cycle many Bering Sea fish populations appear to migrate between overwintering regions in deep water, spawning locations, and shallow summer feeding areas (Smith and Bakkala 1982).

In recognition of these considerations, a second phase of investigations has recently been examining the mean community structure and variations in community organization over multiple years. Comparable classification analyses were run on the NWAFC Bering Sea summer trawl survey data from the 4 years, 1978-81. To briefly summarize the pertinent results--although the boundaries between major site groups showed some variations, the basic communities recurred rather consistently and showed similar species composition between years (Walters and McPhail pers. commun.).

It appears, then, that the major faunistic zones and regional crab and groundfish communities described in this study have some biological reality. These results are also qualitatively similar to what are proposed to be basic hydrographic provinces (see Fig. 6) and benthic invertebrate domains (Stoker 1981; Haflinger 1981) of the eastern Bering Sea shelf.

An aspect of the food webs in these faunal areas is that there are a number of fish predators that feed on crab. The importance of these relationships to crab population dynamics--and the qualitative and quantitative changes in predation rates that result from variations in fish (and crab) population abundance--are essentially unknown, however, for lack of data. The time series illustrated in Figure 7 indicates that even though large temporal variations occur in the abundance of specific predators, some potential predators will nearly always be present for one or more life history stages of vulnerable crab species. To improve our understanding, practical steps would be to 1) more thoroughly identify the predator/prey relationships of interest, geographic areas of important contact, and seasonal timing; 2) begin to quantify predator feeding rates and resultant crab death rates (relative to other sources of crab mortality) so as to enable measures and comparisons of importance; 3) evaluate the significance of size-selective predation, where it occurs; and 4) emphasize studies of young developmental stages of crab, since it seems likely that intensity of fish predation will vary inversely to body size.

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Population Estimation

Some Problems in Assessing the Tanner Crab, *Chionoecetes Bairdi*, Population in the Gulf of Alaska and One Possible Remedy

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Introduction

The ability to accurately assess the population of a species which is the target of a commercial fishery is essential if the goal of those managing that fishery is the long-term optimum utilization of the resource. For crab fisheries this ability should include assessment of 1) the legal sized population of crabs available to the fishery annually, 2) the female portion of the population, and 3) the population of male crabs one to several years away from entering the fishery. The latter two are necessary for monitoring the reproductive health of the population and predicting future recruitment trends. Making adequate early predictions of recruitment can be important to an industry which is capital intensive and a high risk venture.

Since 1973 the Department of Fish and Game (ADF&G) has assessed the annual abundance of a number of Tanner crab, *Chionoécetes bairdi*, stocks in the Gulf of Alaska. The method uses king crab pots to sample both Tanner and king crab on a single survey. Sampling design and methodology was primarily concerned with surveying king crab stocks due to the greater value of the king crab as compared to that of Tanner crab and the earlier development of the king crab fishery. Unfortunately, funding for crab assessment work has fluctuated significantly forcing the department to prioritize the crab stocks it could assess from year to year. Because of this, a number of Tanner crab stocks have received little, if any, effort on the annual crab assessment surveys. After several surveys a number of problems with the application of the method to Tanner crab became apparent from the data. Whether due to the locations fished or the fishing characteristics of the pots, few female Tanner crabs are captured on the pot surveys. Similarly few crabs two or more molts away from attaining legal size are captured. More importantly prerecruit crabs are not captured in predictable numbers on successive pot surveys. Thus, information on two of the three main groups of crabs we need data on is poor or lacking using the current pot assessment method. We do seem to obtain usable data on the relative abundance of legal size crabs from the pot survey; at least the harvest levels derived from the relative changes in the abundance of legal crabs seem to be borne out during the commercial fishery (in terms of catch per unit effort over the course of the fishery).

In the late 1970's a heightened interest developed in the possible use of trawls to assess crab stocks in the Gulf of Alaska. Using trawls had proven to be a successful method of assessing crab stocks in the Bering Sea by the National Marine Fisheries Service (Reeves 1979). However, much of the continental shelf in the Gulf of Alaska is untrawlable and it was assumed that surveying crab stocks with trawls would be unfeasible. Upon examining the historic Tanner crab fishing grounds and the available hydroacoustic data (IPHN 1964) it became evident that a sizeable portion of the Tanner crab habitat might be accessible to trawls. Tanner crab tend to inhabit relatively soft bottom areas.

An experimental program was initiated in 1980 to test the feasibility of using trawls to assess the abundance of Tanner crab stocks in certain areas of the Western Gulf of Alaska. Funding was increased in 1981 and the survey effort was expanded. The following is a preliminary evaluation of the experimental trawl program.

Methods

The 1980 trawl survey was limited to northern Shelikof Strait between the Kodiak Archipelago and the Alaska Peninsula. In 1981 the areas surveyed included northern Shelikof Strait, Chiniak Gully, the Semidi Islands region and the entire Chignik Management District (Figure 1). Sampling took place in late June to early July in 1980 and from mid-July to mid-August on the 1981 surveys.

Samples were collected with a 400 mesh eastern otter trawl. Each station consisted of one 30-minute tow. Station selection was based on a systematic grid pattern and tows were placed at the center of a station unless bottom or weather conditions dictated that it be placed off center. The number of tows made per stratum during the 1981 survey in northern Shelikof Strait was determined by optimal allocation (Cochran 1977) prior to the survey. The allocation was based on the legal size male component of the 1980 survey catches.

Upon retrieval of the net, all Tanner crabs were separated by sex, counted, aged, and in most cases, measured (carapace width for both sexes and abdominal width for juvenile females). Observations were made on egg clutch size (as percent fullness of the brood chamber). Upon returning to Kodiak catches were standardized to 1.85 km tows. Population estimates were generated for various Tanner crab size groups using the area swept technique for stratified data (see Appendix).

Using the resulting population estimates, predictions were made for the number of legal size crabs that would be available during future commercial seasons. These predictions assumed an annual natural mortality rate of 20%. Because of the high incidence of skip molting in prerecruit one Tanner crabs (115-139 cm CW) predicting recruitment to legal size (≥ 140 mm CW) is not straightforward. In order to take skip molting into account the following formula was used to define subsequent recruitment:

$$\text{Recruitment Coefficient (RC)} = \frac{\text{Newshell } \male\text{'s 140-164 mm}}{\text{Newshell } \male\text{'s 140-164 mm} + \text{Oldshell } \male\text{'s 115-139 mm}}$$

$$\text{Recruitment} = \text{RC} \times \text{A}$$

where A = population estimate of 115-139 mm males times 0.72 (or 1-1/2 years survival with an annual mortality rate of 20%).

RC = recruitment coefficient (from above).

Results and Discussion

Sampling intensity and Tanner crab catch data are summarized for each of the areas surveyed on the 1980 and 1981 trawl surveys (Table 1). Since northern Shelikof Strait is the only area for which we have more than one year's data, only the results from that area will be discussed herein.

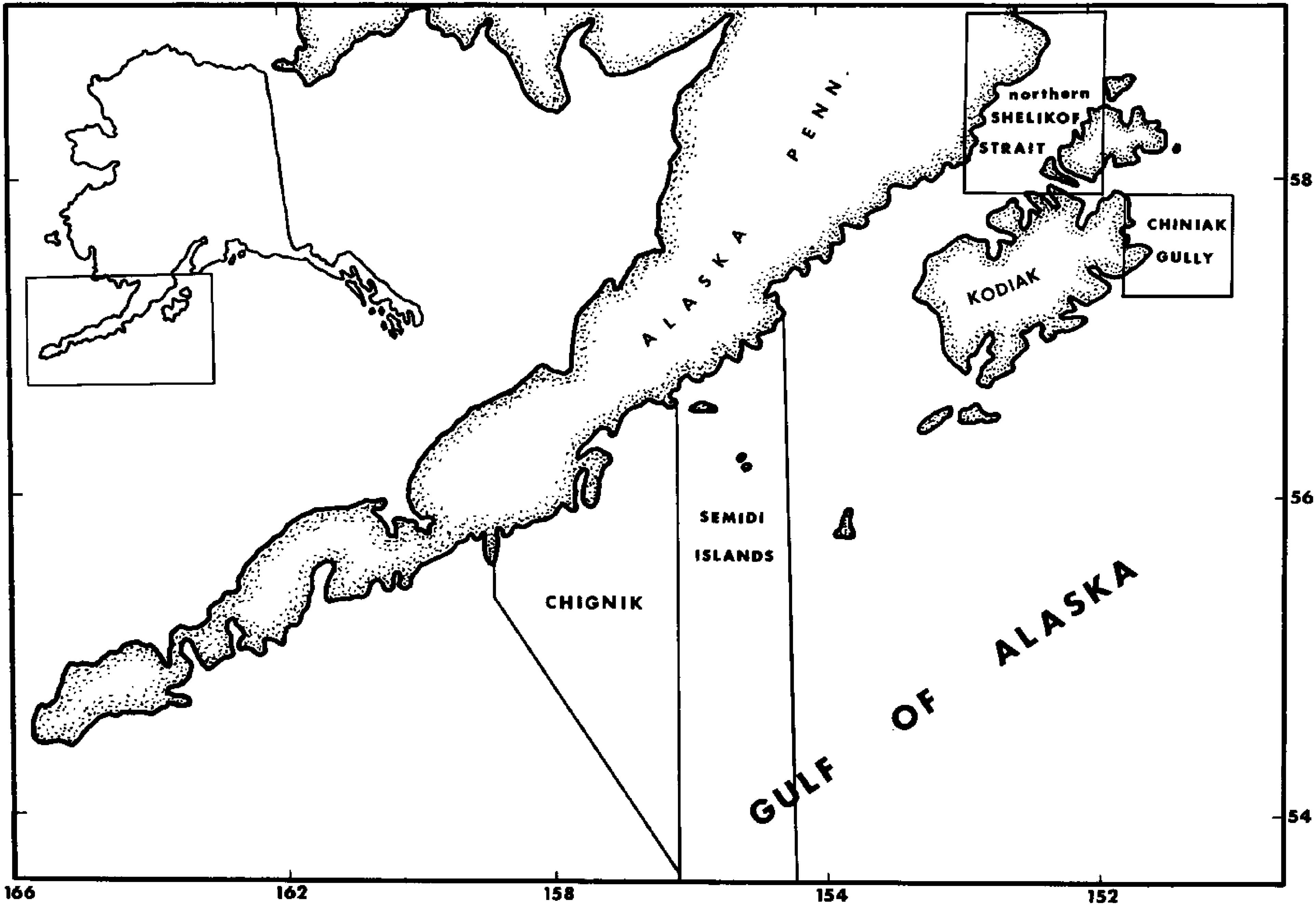

Figure 1.--Four areas of the western Gulf of Alaska in which Tanner crab, *Chionoecetes bairdi*, trawl surveys were conducted during 1980 and/or 1981.

Table 1.--Summary of sampling effort and total Tanner crab, *Chionoecetes bairdi*, captured on the 1980 and 1981 trawl surveys in the Kodiak and Chignik areas.

Area	Year	No. Tows	Sampling Intensity (km^2/tow)	Total Males	Total Females	Total Crabs
Kodiak:						
Shelikof Strait	1980	44	106	3,466	3,161	6,627
Shelikof Strait	1981	25	163	1,790	1,793	3,533
Chiniak Gully	1981	10	61	67	29	96
Semidi Islands	1981	3	-[1]	-	-	-
Chignik:	1981	55	205	1,656	704	2,360

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[1] none of the tows were successful

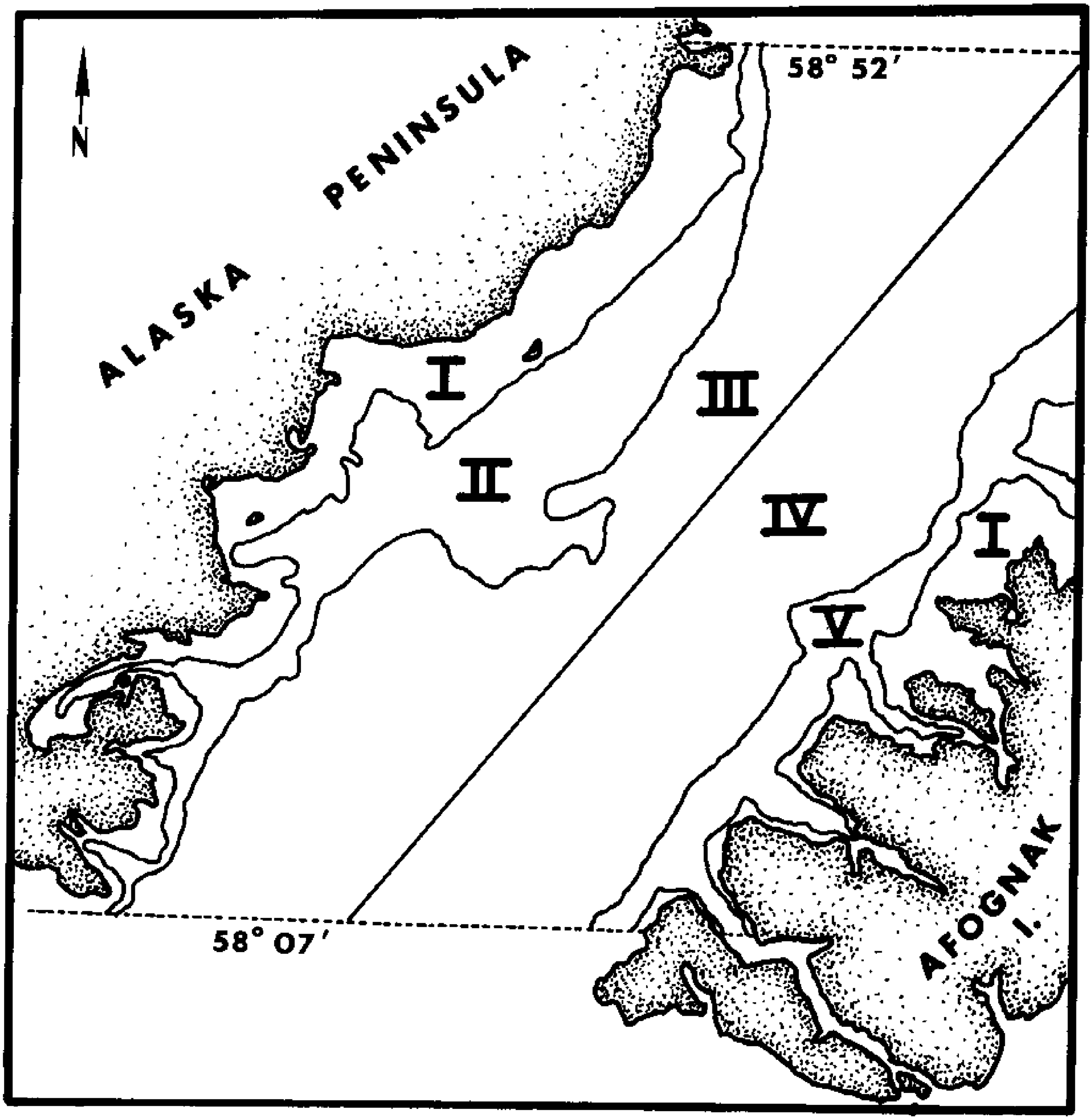
Table 2.--Number of male Tanner crabs, *Chionoecetes bairdi*, captured per 1.85 km by size group and percent total male catch in northern Shelikof Strait, 1980 and 1981 Kodiak area trawl surveys.

	1980		1981		Percent of legals	
Size Group, mm	No.	%	No.	%	1980	1981
≥ Fours, ≤ 69	1,232	35.5	400	22.3		
Threes, 70-91	647	18.7	463	25.9		
Twos, 92-114	549	15.8	330	18.4		
Prerecruit Ones 115-139	672	19.4	349	19.5		
Recruits Newshell 140-164	230	6.8	183	10.2	63	74
Postrecruit Ones Old and Very Oldshell 140-164	122	3.5	35	2.0	33	14
Postrecruit Twos ≥ 165	14	0.4	30	1.7	4	12
Total Legal ≥ 140	366	10.6	248	13.9		
Total Male Crabs	3,466	100.0	1,790	100.0		
No. of Tows	44		25			

The waters sampled on the two northern Shelikof Strait surveys lie between 58° 07' 00" and 58° 52' 00" North latitude, west of the 152° 30' 00" West longitude to the Alaska Peninsula (Figures 1 and 2). This represents an area of approximately 5,650 km^2. Strata were selected on the basis of depth and whether a station was located in the eastern or western half of the strait (Figure 2). The latter criterion was based on the apparent paucity of Tanner crabs of any size on the eastern side of the strait indicating a lack of suitable habitat. During both surveys tows were not made in Stratum I. Most of this area is unsuitable for trawling due to a combination of vessel draft, bottom type and proximity to land. Forty-four and 25 tows were completed on the 1980 and 1981 surveys, respectively. In 1980 the area considered surveyed comprised 4,652 km^2 or 82% of the potential habitat. This represented one tow per 106 km^2. The area considered in 1981 was 4,064 km^2 or 72% of the potential habitat. Thus, sampling intensity was one tow per 163 km^2. Stratum V was dropped from the 1981 survey because no legal size crab were caught in the three tows made in that stratum in 1980. The allocation of samples among strata should have resulted in a 1981 survey which was comparable to the 1980 survey.

A total of 6,627 Tanner crabs were captured on the 1980 survey while 3,533 crabs were caught in 1981. Of these, in 1980, the male portion of the catch was 3,466 crabs or 52% while males accounted for 1,790 individuals or 51% of the total catch in 1981. Females comprised 3,161 crabs or 48% of the 1980 catch and 1,743 individuals or 49% of the catch in 1981 (Table 1). The proportions of the various size groups of male crabs was similar in both survey years with two exceptions (Table 2). The drastic reduction in the number of males $\leq$ 69 mm CW in 1981 was probably due to the growth of 56 mm to 69 mm CW crabs (the prerecruit four component) in 1980 into the subsequent size group (70 mm to 91 mm CW or prerecruit threes) in 1981 which can be clearly seen in the width frequency distribution from the two surveys (Figure 3). Another possibility is that the reduction in the proportion of the 1981 catch that was $\leq$ 69 mm CW was partially due to sampling bias introduced by allocating stations among strata on the basis of the legal size portion of the 1980 catch alone. These types of observations on small size Tanner crabs are not possible with our current assessment program using pots.

Within the legal size crab groups, the proportions changed significantly between surveys. The proportion of legal size crabs that were recruit and postrecruit two crabs increased from 1980 to 1981 while the proportion of legals that were postrecruit one crabs showed a decline (Table 2). The latter change does not seem to be related to differences in tow locations as all areas which produced good numbers of postrecruit one crabs in 1980 were fished in 1981. It may be due to the fact that the percent of postrecruit one crabs in the 1980-81 commercial fishing season doubled from that observed in the 1978-79 and 1979-80 fishing seasons. If fishing was particularly heavy on this group last year in relation to the legal size male population as a whole and there was poor recruitment to legal size the previous year, the result would have been the observed decline in the proportion of legal size postrecruit one crabs on the 1981 trawl survey. Of course, the change could



Stratum I - Shore to 36.4 m depth contour (east and west sides of strait)
Stratum II - 36.5 m to 146.1 m depth contours west of midline of strait
Stratum III - 146.2 m depth contour east to midline of strait
Stratum VI - Midline of strait east to East 201.0 m depth contour
Stratum V - East 201.1 m depth contour east to 36.5 m contcur

Figure 2.--Area of northern Shelikof Strait in which trawl surveys were conducted in 1980 and 1981 with strata used in population estimations.

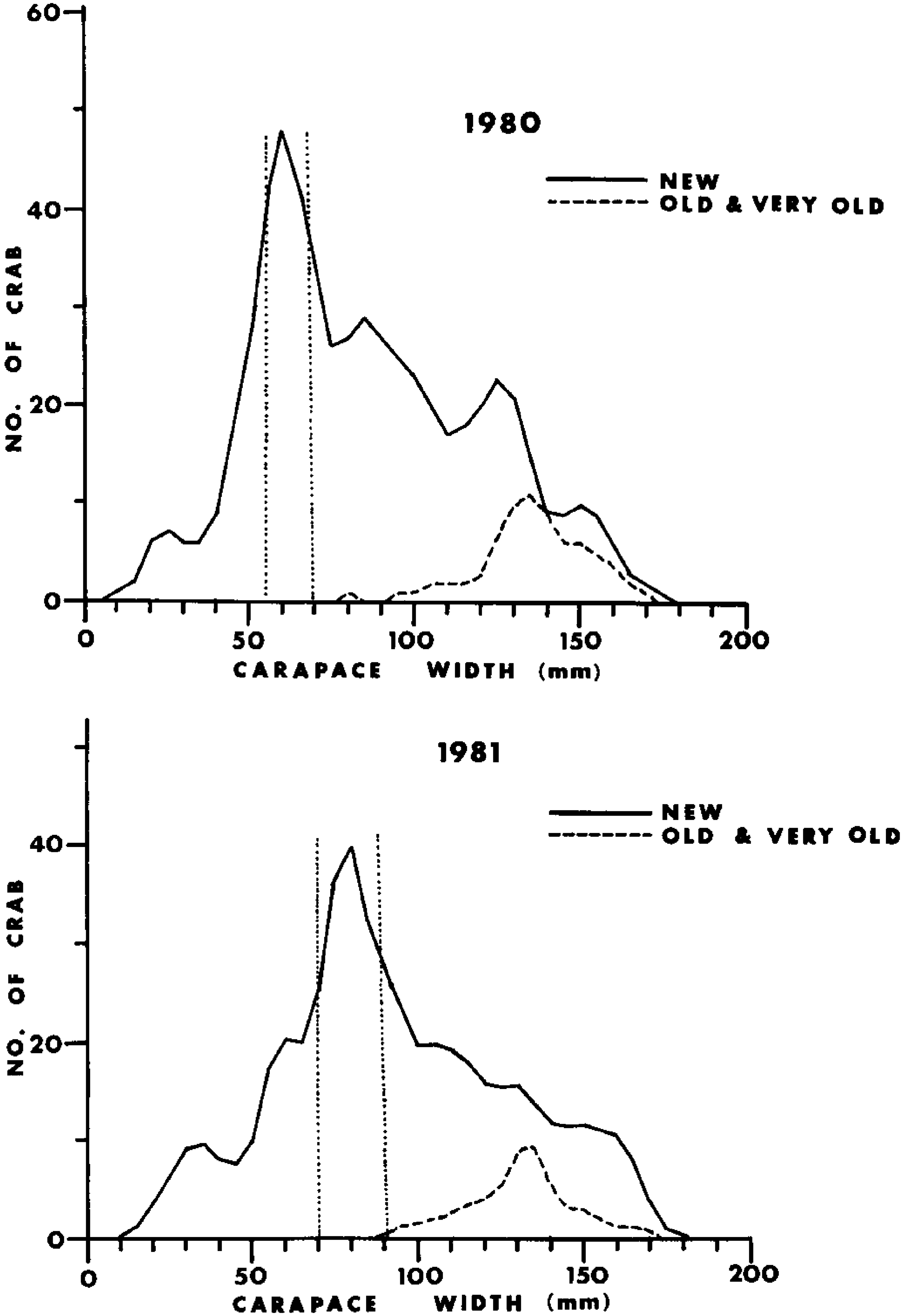


Figure 3.--Width frequency of male Tanner crab, *Chionoecetes bairdi*, captured on 1980 and 1981 trawl surveys in northern Shelikof Strait.

have different origins such as heavy recruitment to legal size after the 1980-81 fishery coupled with a high natural mortality rate in the postrecruit one group for some reason. Another possibility could be the growth of postrecruit one crabs into the postrecruit two group in 1981. This may have been responsible for some of the 19% decline in the proportion of legals that were postrecruit one crabs in 1981 and can be seen in the corresponding increase of 8% in the proportion of legal size crabs that were postrecruit two crabs in 1981 (Table 2).

Observations on the reproductive health of the female population were accomplished by examining the relative egg clutch size of the adults measured. In northern Shelikof Strait females with full egg clutches (90% to 100% full) accounted for 53.5% and 68.9% of the total adult females measured on the 1980 and 1981 surveys, respectively (Table 3). However, if those females that carried partial egg clutches are included, 94.8% of the 1980 survey females measured had egg clutches and 94.7% of the 1981 survey females measured had egg clutches. There was no significant difference in the percent of females that were barren on the two surveys. Of the adult females with no egg clutches, 30% had active ovaries in 1980. Barren adult females captured in 1981 were saved, but unfortunately, a few were lost and we haven't any data from those stations. However, the majority of the barren females (64 of 71 individuals) came from one tow. Among those individuals, 14% had active ovaries and 85% had inactive ovaries. All of these individuals either had old sperm in their spermathecae or empty spermathecae and old grasping marks showing that none of them had mated after the spring hatching of the previous year's eggs. We do not know whether oldshell or very oldshell barren females that seem to have active ovaries can produce viable eggs if mated.

Population estimates were calculated using the standard area swept technique for stratified data (Table 4). The estimates are not presented for comparison, but to show that, for the most part, the percent errors (See Appendix) around the estimates from both surveys are within an acceptable range for management purposes (about 25%). In comparison to the pot method of population assessment it should be noted that since we don't know the effective fishing area of pots, Tanner crab population estimates cannot presently be derived from the pot method of assessing the population alone. Of course, such estimates can be generated using an effective mark/recapture program (as in the case of king crab). However, we have not been able to develop such a program for Tanner crab.

In order to form a preliminary judgment of the effectiveness of the trawl method we made several predictions of future populations from the 1980 survey data and checked these predicted population levels against the results of the 1981 trawl survey, and Leslie population estimates (in Ricker 1975) generated from the 1980-81 and 1981-82 commercial fisheries. The comparisons are made for the North Mainland section of northern Shelikof Strait which is comprised of the strata west of the midline of the strait (Figure 2). The North Mainland section was used due to our having good fishery performance data from that area. It should be pointed out that 94.3% of the legal size (≥ 140 mm) males captured on the 1980 trawl survey were from the North Mainland section while 94.6% of the same group were captured there on the 1981 survey. In order to have a time reference all comparative estimates have been generated for the start of the 1980-81 or 1981-82 commercial

Table 3.--Number of adult female Tanner crab, *Chionoecetes bairdi*, measured and percent fullness of egg clutch in northern Shelikof Strait 1980 and 1981 trawl surveys.

Survey		Percent fullness of egg clutch						Percent with eggs
		0	1-24	25-49	50-74	75-89	90-100	
1980	Number	47	20	32	128	190	480	
	% Total	5.2	2.2	3.6	14.3	21.2	53.5	94.8
1981	Number	71	25	25	63	235	927	
	% Total	5.3	1.9	1.9	4.6	17.4	68.9	94.7

Table 4.--Population estimates for female and various size groups of male Tanner crabs, *Chionoecetes bairdi*, in northern Shelikof Strait 1980 and 1981 Kodiak area trawl surveys.

	Population estimate (number of crabs) ± percent error	
Size Group (mm)	1980	1981
Juvenile females	7,112,474 ± 16.2%	6,581,276 ± 25.7%
Adult females	5,110,674 ± 40.6%	6,584,877 ± 23.9%
Total females	12,223,148 ± 20.0%	13,166,152 ± 23.1%
≤ 69 males	4,844,729 ± 19.4%	3,048,454 ± 20.5%
70-91 males	2,729,541 ± 17.4%	3,493,208 ± 32.6%
92-114 males	2,109,003 ± 23.1%	2,429,040 ± 19.3%
115-139 males	2,560,491 ± 25.5%	2,086,921 ± 21.0%
Male Recruits Newshell 140-164	822,573 ± 25.1%	1,105,582 ± 32.2%
Male Postrecruit Ones - Old and Very Oldshell 140-164	455,611 ± 29.4%	216,075 ± 29.2%
Male Postrecruit Twos ≥ 165	53,601 ± 38.5%	160,255 ± 27.0%
Total legal ≥ 140 Males	1,364,771 ± 20.4%	1,521,526 ± 26.9%
Total Males	13,602,350 ± 11.8%	12,580,950 ± 16.8%

fishing seasons (February in both years). The population of legal size crabs expected at the start of the 1980-81 fishery was estimated to be 1,158,627 ± 21.2% (Table 5, #1). The upper limit of the estimate is 1,404,256 crabs. A Leslie population estimate generated from the 1980-81 fishing season revealed 1,536,182 crabs at the start of the season (Figure 4a and Table 5, #2). This estimate is 24.6% higher than the midpoint of the trawl derived estimate (8.6% higher than the upper limit). This suggests that the 1980 trawl survey estimate of the total legal size crabs was from 9% to 25% too low. As has been suggested by previous work in the Bering Sea (Fugita and Takeshita 1981), population estimates derived from trawl data probably need to be refined by using catchability factors since the net probably does not capture 100% of the crabs it encounters on a tow. Suggested catchability factors in the Bering Sea have ranged from 0.3 to 0.6 (Fugita and Kawasaki 1981) which are lower catch rates than the 0.7 shown by the fishery performance data and the trawl survey estimate from northern Shelikof Strait. It should also be noted, however, that population estimates derived from fishery performance data are frequently erroneous.

The population of legal size crabs expected at the start of the 1981-82 commercial season was estimated to be 1,295,626 ± 28.1% from the 1981 trawl survey (Table 5, #3). The preliminary Leslie population estimate from the season data revealed 1,268,000 crabs at the start of the fishery (Figure 4b and Table 5, #4) which is very close to the midpoint of the survey derived estimate (2.1% lower than the midpoint). These estimates would suggest that we do not need to apply a catchability factor to the 1981 trawl survey estimate of legal size crabs. Since the trawl estimate was actually lower than the Leslie estimate, though only slightly, it might suggest that the effective net width (path swept) of 12.19 m used to calculate the population estimates in 1981 was smaller than the actual path swept. This would tend to inflate the population estimates derived from that survey. We definitely need to conduct gear mensuration work to determine how our net fishes under various circumstances before we can come to any definitive conclusions regarding population assessment using trawls in the Gulf of Alaska. The Leslie estimates calculated from the 1980-81 and 1981-82 commercial fisheries are encouraging in that they compare quite well with the expected populations derived from the respective trawl surveys. It is interesting that both Leslie estimates were generated using five comparable weeks of fishery data and fishing effort was essentially the same both seasons (23,081 and 23,047 pot lifts, respectively). Such comparable data are probably unusual and we cannot rely on obtaining such information on an annual basis.

Fishery managers are keenly interested in the extent of recruitment of sublegal individuals into the commercial fishery. Thus, we wanted to compare the population of prerecruit one (115mm - 139 mm) crabs in 1980 with the population of recruit (140mm - 164 mm, newshell) crabs in 1981. However, we cannot measure the growth of the prerecruit one crabs directly because of the common phenomenon of skip molting in these, and larger, crabs. We used a recruitment coefficient (Table 5, #5) which estimated the proportion of prerecruit one crabs that had molted into the recruit class prior to the 1980 survey. The recruitment coefficient was then applied to the population estimate of prerecruit one crabs in 1980 to determine the number of crabs that could be expected to molt into the recruit class for the 1981-82 fishery.

Table 5.--Factors and population estimates used to evaluate the predictive capability of the trawl survey method of assessing the Tanner crab, *Chionoecetes bairdi*, population in one area of the Gulf of Alaska.

Reference no. (from text)	Factor/Population Estimate (for North Mainland stock)
1	Total legal crab (≥ 140 mm CW) from 1980 survey = 1,158,627 ± 21.2%
2	Leslie estimate of legal crab (≥ 140 mm CW) at start of 1980-81 commercial season = 1,536,182
3	Total legal crab (≥ 140 mm CW) from 1981 survey = 1,295,626 ± 28.1%
4	Leslie estimate of legal crab (≥ 140 mm CW) at start of 1981-82 commercial season = 1,268,000.
5	Recruitment coefficient generated from 1980 survey = 0.56.
6	Recruit crab (newshell, 140-164 mm CW) in 1981 from 1980 survey data (using recruitment coefficient) = 938,886.
7	Recruit crab (newshell, 140-164 mm CW) in 1981 from 1981 survey data (using survey population estimate) = 992,270 ± 31.5%.
8	Total legal crab (≥ 140 mm CW) expected at start of 1981-82 season from 1980 survey estimate minus 1980-81 commercial catch plus recruitment (using 1980 recruitment coefficient) = 1,246,752.
9	Recruitment coefficient generated from 1981 survey = 0.69.

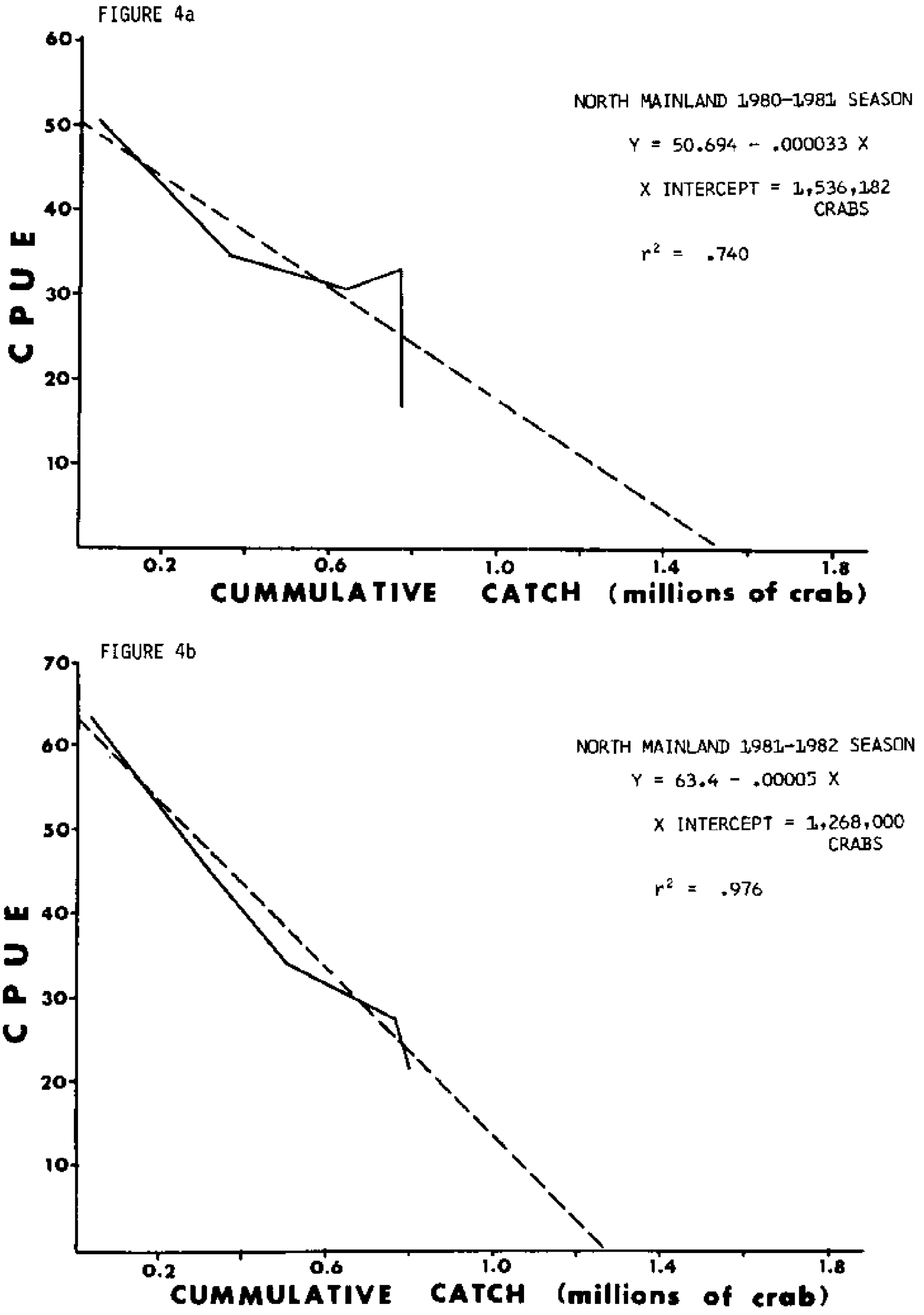


Figure 4.--Leslie population estimates for legal size Tanner crabs, *Chionoecetes bairdi*, from a) 1980-81 commercial catch data, and b) 1981-82 commercial catch data.

The resulting number of recruits was 938,886 crabs (Table 5, #6). For comparison the population estimate of recruit crabs at the start of the 1981-82 fishery from the 1981 trawl survey was 992,270 crabs (Table 5, #7). Since we do not know how precise our recruitment coefficient is, the agreement between these figures is encouraging.

Looking at the total legal size crab population in the North Mainland section of northern Shelikof Strait, we deducted the number of crabs caught during the 1980-81 commercial fishery from the population estimate of total legals derived from the 1980 trawl survey and added the expected recruitment as calculated from the 1980 survey (see above). The resulting population estimate of legal size crabs at the start of the 1981-82 fishing season was 1,246,752 crabs (Table 5, #8). Notice how close this estimate is to both the estimate derived from the 1981 trawl survey (1,295,626 crabs) and the Leslie estimate calculated from the 1981-82 commercial fishery (1,268,000 crabs) (Table 5, #3 and #4). It would be convenient if the crude recruitment coefficients we use to calculate recruitment prove acceptable and we are looking forward to the 1982 survey in order to test the recruitment coefficient derived from the 1981 trawl survey data (Table 5, #9).

Conclusions

Tanner crab stocks have been assessed using pots since 1973 in certain areas of the Gulf of Alaska. It has become apparent that the pot method of population assessment does not provide adequate informaiton on females and prerecruit Tanner crabs.

An experimental trawl program to assess Tanner crab populations in the Gulf of Alaska was initiated by the ADF&G in 1980. The survey was repeated in northern Shelikof Strait in 1981 and was expanded to other areas that year. The results of the two population assessment surveys in northern Shelikof Strait using trawls are encouraging. A large portion of the crab catches was comprised of females and prerecruit two (and younger) males. Neither of these groups are captured by the current population assessment program using pots in significant numbers. Population estimates from the trawl survey data compare well with estimates derived from the commercial fishery and with expected growth of particular crab size groups. Recruitment predictions calculated from the prerecruit one male population estimate using a recruitment coefficient to take skip molting into account seem to be confirmed by subsequent survey and commercial fishery data.

More work needs to be done before definitive conclusions can be made regarding the effectiveness of trawls as a population assessment method in the Gulf of Alaska. We particularly need to conduct gear mensuration work and define the catchability of Tanner crabs under varying substrate conditions. We also need to continue surveying areas of the Gulf of Alaska which are more complex in terms of bottom topography than northern Shelikof Strait (the Chignik Management District is an excellent example). Such sampling will provide the data necessary to decide whether we can apply the trawl method to most of the Gulf of Alaska Tanner crab stocks.

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APPENDIX

For stratified data the population estimate is:

$$PE = \frac{6076 \cdot C_T \cdot A_T}{W}$$

where PE = population estimate in numbers of crabs
6076 = number of feet in one nautical mile
C_T = mean catch per mile
A_T = total area surveyed in miles squared
W = effective net width in feet

For stratified data, the mean catch, C_T, is "weighted" to reflect the criteria of each of the particular strata selected in the following manner:

$$C_T = \frac{\sum_{i=1}^{h} C_i \cdot A_i}{A_T}$$

where C_T = mean catch
C_i = mean catch from the i^{th} stratum
A_i = area of the i^{th} stratum
A_T = total area
h = number of strata

The standard error of the mean catch, $s.e._T$, is derived from stratified data as follows:

$$s.e._T = \sqrt{\sum_{i=1}^{h}\left[\left(\frac{A_i}{A_T}\right)^2 \cdot \frac{s.d._i^{\,2}}{n_i}\right]}$$

where $s.e._T$ = standard error of the mean catch
$s.d._i$ = standard deviation of the i^{th} stratum
A_i = area of the i^{th} stratum
A_T = total area
n_i = number of tows in the i^{th} stratum
h = number of strata

The standard error of the mean catch was then used to calculate the percent error.

$$\text{Percent Error} = \frac{s.e._T}{C_T} \times 100$$

where $s.e._T$ = standard error of the mean catch
C_T = mean catch

ABSTRACT

The chief problem facing management biologists involved with the Gulf of Alaska Tanner crab, *Chionoecetes bairdi*, commercial fishery is with accurately assessing the crab population. Joint king/Tanner crab population assessment surveys using crab pots have been conducted in areas of the Gulf of Alaska since 1973. Although the pot method of assessing the population seemed to work satisfactorily for king crab, the pot surveys have not produced the data needed to estimate future Tanner crab recruitment or monitor the female portion of the population.

A program to evaluate the use of trawls in assessing Tanner crab populations in the Gulf of Alaska was initiated in 1980. Trawl surveys were conducted in northern Shelikof Strait in 1980 and 1981. Preliminary results from the surveys are encouraging. The portion of the male catch that was two or more molts (< 92 mm CW) away from attaining legal size averaged 51% of the male crab captured on the two surveys. This seems to be providing data necessary to estimating future recruitment trends. Size frequency relationships and population estimations from the surveys and data from the subsequent commercial fisheries tend to confirm the trawl survey method as a viable means of assessing the Tanner crab population in northern Shelikof Strait. We need to do more research in such areas as gear mensuration, Tanner crab catchability and the perennial problem of shell aging to determine what refinements should be applied to our survey method on population estimating procedures.

Tanner Crab Population Abundance and Its Relationship to the Commercial Fishery in the South Peninsula Area

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ABSTRACT

Fluctuations in the abundance of male Tanner are discussed. According to population surveys starting in 1974, the population of legal male Tanner crabs was fairly stable from 1974 to 1977. Survey catches of legal males at that time averaged over 20 crabs per pot. Abundance of pre-recruit males peaked in 1976, then started a five year decline. Starting in 1978 the population of legal males declined as a result of poor recruitment. A one year lag time between the decreasing pre-recruit and legal populations was noted. By 1980 the legal male population was down to approximately 10 percent of its pre-1977 level. Since the commercial fishery exploitation rate was relatively low prior to 1979, commercial CPUE did not begin declining until the year after the survey CPUE started to drop. Since that time commercial and survey CPUE have fluctuated in a similar manner.

INTRODUCTION

South Peninsula District includes all waters south of the Alaska Peninsula bounded by the longitude of Scotch Cap light on the west and bounded on the east by a line from Kupreanof Point to Castle Rock and extending southeast from Castle Rock (Figure 1).

Tanner crab (Chionoecetes bairdi) fishing in the area started in 1967 with a commercial harvest of 5,000 pounds. Catches steadily increased until the 1973-74 season when 9.5 million pounds were landed. Since that time catches have fluctuated between 3.3 and 11.2 million pounds (Table 1). Currently about 65 vessels participate in the fishery, catching 3 to 6 million pounds total.

Management of this fishery is carried out from Sand Point, a city of about 800 persons. Data collected during an annual population indexing survey as well as commercial fishery performance data are used to estimate relative population size and determine optimum harvest levels.

This paper illustrates how Tanner crab populations have fluctuated in the area and how that fluctuation has affected the commercial fishery.

MATERIAL AND METHODS

Abundance of Tanner crabs is estimated from data collected during annual surveys of the area which started in 1974. Crabs are captured in 7 foot by 7 foot crab pots. Pots are fished in strings of three in the bays and strings of ten in open ocean areas. Spacing of pots is approximately one-fourth mile. Stations are oriented generally east-west according to an established grid pattern (Donaldson and Hicks, 1980). Pots are baited with herring only and are retrieved the day after setting, weather permitting.

All crab measurements are of carapace width, measured to the nearest millimeter. Male crabs less than 138 millimeters are considered sub-legal pre-recruits. Males 138 millimeters and greater are considered to be legal size.

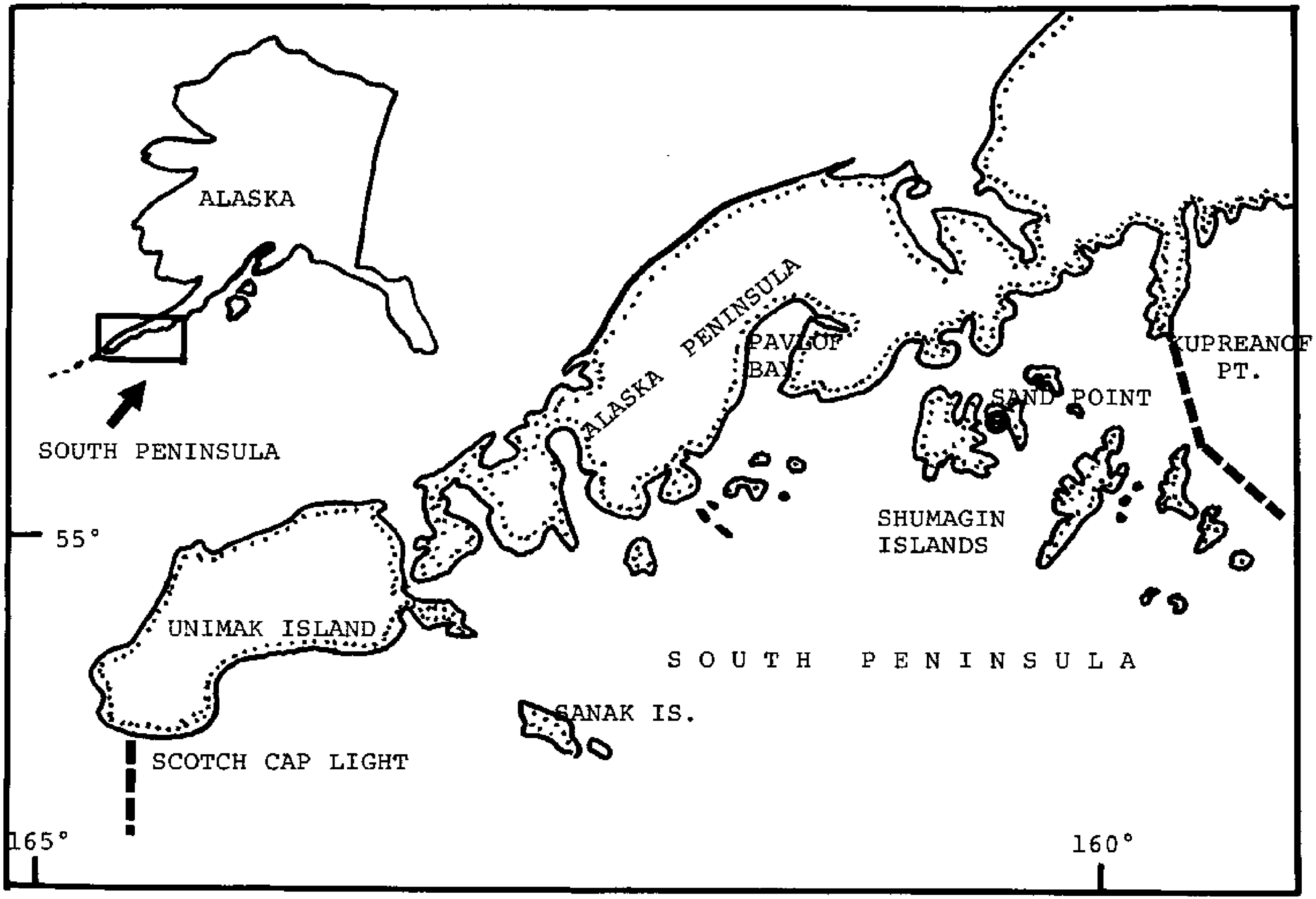

Figure 1. South Peninsula Tanner crab district.

Table 1. Commercial Tanner crab catch statistics in the South Peninsula area 1973-74 through 1980-81.

Season	Crabs Caught	Pounds Caught	Pots Lifted	Avg. Wt.	Avg. Width	CPUE
1973-74	3,981,135	9,503,366	70,047	2.4	152.5	57
1974-75	2,053,530	5,195,800	38,153	2.5	153.7	54
1975-76	4,434,381	11,201,941	59,377	2.5	153.8	75
1976-77	2,524,565	6,773,838	63,143	2.7	157.4	40
1977-78	2,847,948	7,446,270	70,587	2.6	155.5	40
1978-79	3,267,122	8,684,408	82,374	2.7	158.1	40
1979-80	2,581,544	6,961,251	96,989	2.7	156.1	27
1980-81	1,274,539	3,294,106	59,560	2.6	155.7	21

Table 2. Summary of monthly Tanner crab catch data for South Peninsual District 1979-80 season.

Month	Crabs Caught	Pounds Caught	Pots Lifted	Average Weight	Average Width	CPUE
November	48,161	141,946	1,982	2.9	160.5	24
December	21,357	64,071	1,170	3.0		18
January	357,714	1,015,829	10,911	2.8	162.6	33
February	579,657	1,610,656	20,242	2.8	159.8	28
March	867,529	2,331,962	35,307	2.7	157.5	25
April	533,116	1,406,871	20,650	2.6	157.1	25
May	174,010	389,916	6,727	2.2	152.6	26

Commercial catch sampling is carried out as the vessels unload their catch. Catch-per-unit-effort is recorded as crabs per pot lift and is determined from operator interviews and fish tickets. Size and age composition of the commercial catch are determined from samples of 50 crabs taken from each vessel. Interviews and catch samples are obtained for as many deliveries at as many locations as possible.

RESULTS AND DISCUSSION

Average catch per pot of sub-legal males (Figure 2) on the survey provides the basic data for predicting population fluctuations. Because of gear selectivity, the sub-legals captured will generally be recruited to the fishery the following year (Donaldson and Hicks, 1980; Donaldson, et. al., 1981). During the years of the survey, the sub-legal population reached its peak abundance in 1976. Subsequently the sub-legal population declined, reaching its current low level in 1978. Presently this population is about 15 percent as large as it was in 1976.

CPUE of legal males on the survey (Figure 2) began to decline in 1978, one year after the sub-legal CPUE declined. With little recruitment to offset natural mortality and removals by the commercial fishery, the legal population decreased steadily until 1980. Legal male Tanner crab abundance reached a low of about 10 percent of its 1974 level.

Performance of the commercial fishery has reflected the declining population trends noted on surveys. Commercial CPUE (Table 1) started at 57 crabs per pot for the 1973-74 season and has declined steadily. As a result of relatively low exploitation rate prior to 1979, the commercial CPUE has declined more slowly than the survey CPUE. In 1975-76 increased CPUE was probably the result of an artificially low harvest the previous year due to extended price negotiations. Lowest commercial CPUE of 21 crabs per pot in 1980-81 corresponds to the lowest levels of catch and population abundance.

First indications of any recovery for the stock came in 1981. Slight increases in abundance were noted both on the survey and during the fishery. In addition reports of very large numbers of sub-legals were received from fishermen in many areas. As a result of this increased abundance, commercial catch was allowed to increase by 40 percent, approximately half of the estimated 86 percent population increase.

Results of commercial catch sampling have revealed a relationship between abundance of pre-recruit crabs in one year and the average size of commercial crabs the following year. With increases in abundance of pre-recruits in 1976, for example, the average size of the 1977-78 commercial catch declined by over 2 millimeters and one-tenth pound (Table 1, Figure 3).

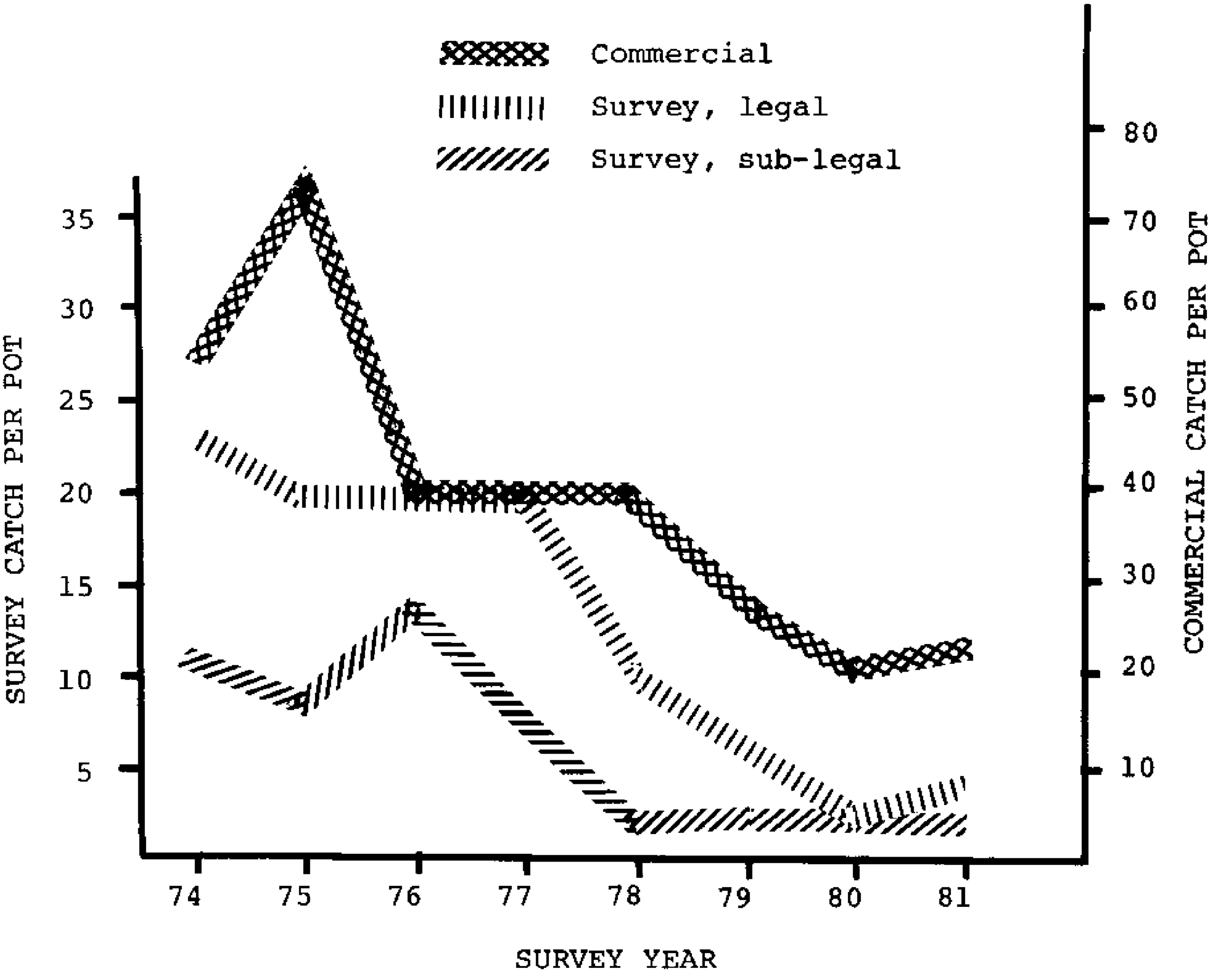

Figure 2. Survey and commercial CPUE, 1974 through 1981.

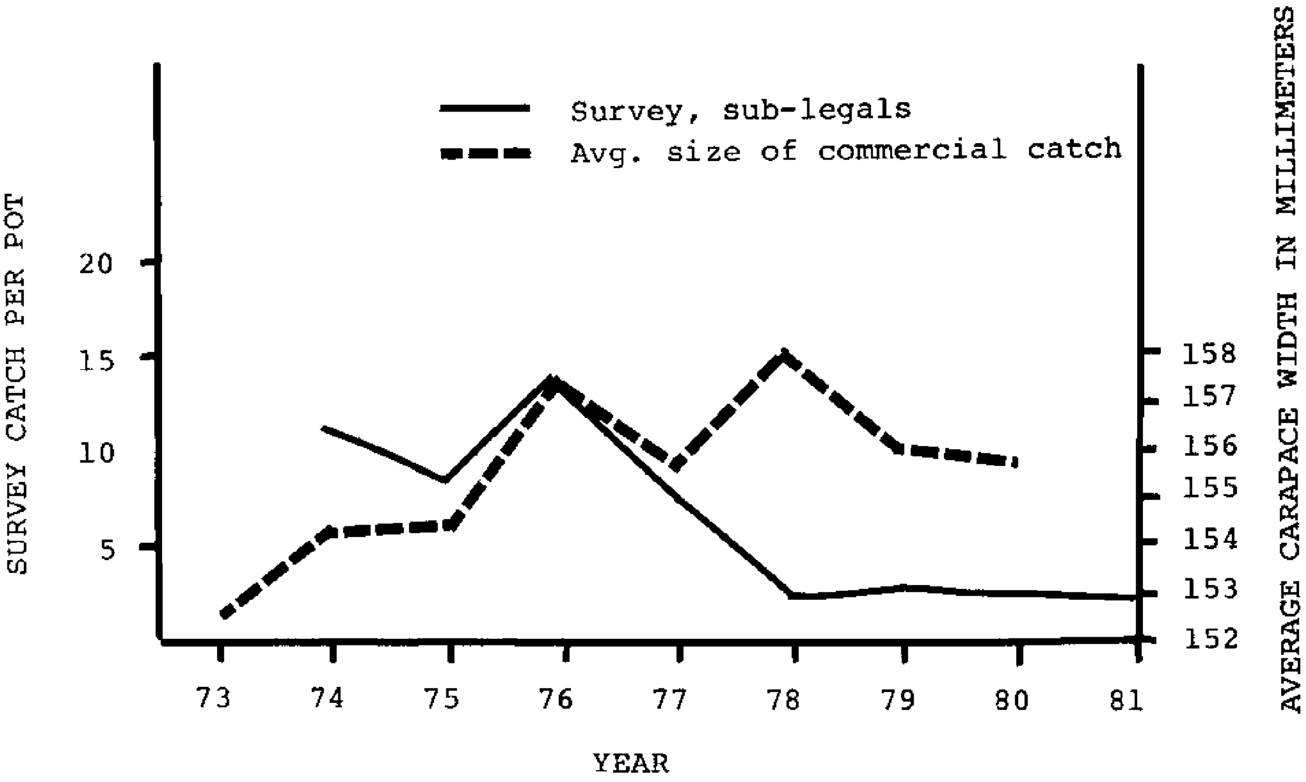

Figure 3. Comparison of survey CPUE for sub-legals with average size in commercial catch.

Average size of crabs harvested during the 1979-80 season should have increased based on the decreasing pre-recruit population in 1978. Average width and weight by month for the 1979-80 season (Table 2) shows the average size was quite large early in the season. Average size of crab was 2.8 pounds and 160.9 millimeters for the first four months of the season (November through February). These crabs were primarily post-recruits with some areas containing as low as 10 percent recruit crabs.

By May the average weight had declined to 2.2 pounds and catches were primarily of recruit crabs. Crabs recruited during the 1977 season would have passed through three seasons in the fishery. A very low average weight at the end of the 1979-80 season as well as the low population abundance in 1980 indicated the 1977 year class which supported the fishery must have been harvested or died due to natural causes.

Starting with the 1980-81 season, the Tanner fishery became heavily dependent on annual recruitment. This was demonstrated in 1981 when the harvest was boosted, partially as a result of improved recruitment. Emergency order closures which allowed greater carry over of post-recruits also contributed to this improving fishery.

Utilizing the relationship between average size of catch and recruitment, it is possible to speculate about the population prior to the 1974 survey. Average carapace width for the 1973-74 season was 152.5 millimeters, smaller than in any subsequent year. Pre-recruits must have been relatively more abundant in 1972 than in subsequent years. As a result the legal population in 1973 must have been larger than in 1974, when survey CPUE was at its highest level. Commercial catch-per-unit-effort data supports this speculation. CPUE during the 1973-74 season was 57 crabs per pot lift, slightly higher than the 54 crab per pot in 1974-75.

Sub-legal male Tanner crabs have apparently been declining in abundance, at least since 1972. Current low levels of abundance for legal males are the result of low survival rates causing poor recruitment. Although this trend may have started as early as 1972, it became most apparent in 1977 when the sub-legal male population began to decline severely.

In order to help slow the decline and prevent biological damage to the stock, the commercial fishery has been closed by emergency order for the past three seasons. Current survey data and fishermen's reports indicate recruitment may improve again next season. Therefore, stable or increasing harvest is expected.

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Characteristics of *Chionoecetes* Fisheries

State, Federal and International Regulation of Tanner Crab Harvests in the Bering Sea

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STATE, FEDERAL AND INTERNATIONAL REGULATION OF TANNER CRAB HARVESTS IN THE BERING SEA

The primary harvest areas for tanner crab operations in the Bering Sea extend into the area of the high seas well beyond national sovereignty. Traditionally, the area of the high seas beyond the three mile territorial sea has been subject to fisheries regulations only through the voluntary, cooperative agreements of parties interested in preventing of overfishing so as to assure a sustained harvest opportunity for their fishermen. In addition, individual countries such as Japan, the Soviet Union and the United States have established and enforced their own controls on national vessels. For example, the Japanese management program established quotas and provided that ripe female crab were not to be retained. The government's role was primarily restricted to a limited entry program for Japanese national vessels that involved the issuance of permits to the distant water vessels. The Minister of Agriculture was responsible for issuing permits, but seasons and other conditions of the fishery were largely established by mutual agreement with the fishermen. Thus, seasons were directed towards times of the year that maximized the fullest meat content, a particularly important goal for a crustacean that does not produce as much meat as the larger king crab.

Although individual states of the United States have not historically extended their local regulations beyond the three-mile limit of the territorial sea, Alaska has not hesitated to regulate the activities of U.S. residents who land catches of tanner crab at Alaska processing facilities. In particular, since the inception of the king crab fishery in the late 60's and the subsequent development of the tanner crab fisheries, the state has imposed conservation regulations on the harvest through the powers and authorities granted to the Alaska Board of Fisheries pursuant to AS 16.05.251(a). This section provides that the board may establish harvest levels, seasons, areas of fishing, and methods and means.

Until passage of the Magnuson Fishery Conservation and Management Act, 16 U.S.C. § 1801 et seq., the United States government did not regulate domestic fishing on the high seas. Instead, U.S. efforts focused on regulating harvests of foreign vessels through cooperative international agreements. The MFCMA, however, established, for the first time, a system of regulatory controls that not only apply to foreign vessels, but also have the potential for regulating the fishing of all U.S. vessels in a Fishery Conservation Zone extending from the territorial sea at the three-mile designation to the edge of the Zone at 200 miles. At the same time, the State of Alaska has continued to enforce fishing regulations that govern U.S. fishermen.

Alaska's legal authority has been exercised in this area beyond three-miles for more than a decade under the local police power authority embodied in the United States Constitution. Since the constitution does not specifically provide that this power extends beyond territorial limits, there has been considerable dispute over the years regarding the state's actual authority to manage fishery resources beyond three miles. However, two important decisions of the Alaska Supreme Court have considered state jurisdiction affecting fisheries management matters beyond three-miles and both have concluded that such controls are legitimate police power functions. In addition, a three judge federal court panel spelled out conditions that, if applied to the king crab fishery, would allow extra territorial state jurisdiction over that species.

In Hjelle v. Brooks, 377 Fed. Supp. 430 (1974), the three judge panel of the U.S. District Court in Anchorage enjoined enforcement of state regulations in the area beyond three-miles. The ruling came at a preliminary stage in the proceedings, and suggested that the fishermen's group would prevail in invalidating existing extraterritorial regulations. In addition, it did not appear that continued fishing would jeopardize the sustained yield of the resource. The panel acknowledged the possibility that a pending trial on the merits might establish a legal nexus between the king crab resource and the associated fishing activities to state interests. If so, this would justify the state's regulations. However, before that issue could be decided, the state adjusted the shellfish regulations to provide for a seaward biological influence zone beyond three miles. The new regulations emphasized the nexus between extraterritorial fishing interests in conserving the resource. 5 AAC 34.001 et seq.

These new regulations were challenged in State v. Bundrant, 546 P.2d 530 (Alaska 1976) and reviewed by the Alaska Supreme Court. That decision remains today as the legal articulation of extraterritorial jurisdiction over fisheries matters by states. In summary, the court concluded that Alaska has a legitimate interest in king crab and in the king crab fishing industry that justifies extraterritorial regulation of crabbing. This case was appealed to the United States Supreme Court, but the court declined to review pending a final decision. On remand, the state district court found difficulty with ambiguities in the state's definition of the Bering Sea fishing area, and dismissed the charges because the area was not clearly described. State v Uri, Alaska District Court No. 71-12228 (Feb. 28, 1977). Since the regulatory area had been redefined by the Alaska Board of Fisheries, the case was not appealed. In addition, the fishermen had not received any windfall benefit for deliveries of crab taken from the closed area.

The Bundrant case was decided on January 19, 1976. Just four days earlier, on January 15, 1976, the king crab fishing vessel F/V AMERICAN EAGLE was seized in Pelican and charged with violating state regulations in an area beyond the territorial sea near Dutch Harbor. Again, the fishermen challenged the state's authority to adopt extraterritorial regulations but the state supreme court did not reverse its earlier opinion in the Bundrant case. The AMERICAN EAGLE case presented a different situation from the Bundrant violations because evidence gathered by state and federal investigators from the Alaska Department of Fish and Game, the state's Division of Fish and Wildlife Protection, United States Coast Guard, National Marine Fisheries Service and an international fisheries observer indicated more than $100,000 of king crab had been taken in a five-day operation. See F/V AMERICAN EAGLE v. State, 620 P.2d 657, (Alaska 1980). This forfeiture decision was appealed to the United States Supreme Court but the court declined to accept the appeal due to a lack of a "substantial federal question". See 102 Supreme Court 85 (1982).

The United States Supreme Court did not indicate a specific reason for rejecting the vessel owners' appeals. However, possibly a primary reason for not reviewing the state's supreme court's decisions regarding extraterritorial regulation on crab fisheries was the fact that on March 1, 1977, the Magnuson Fishery Conservation Management Act went into effect. That law makes it unnecessary for states to establish the resource and industry nexus between extraterritorial fishing and state interests in order to justify extraterritorial regulations over fisheries. In 16 U.S.C. § 1856 the Act provides that "(N)o State may directly or indirectly regulate any fishing which is engaged in by any fishing vessel outside its boundaries, unless such vessel is registered under the laws of such State." (Emphasis added). In the future, therefore, it will not be necessary to establish these factual nexi, but the state's regulations will be applicable to vessels that are registered under its laws.

There is one possible intervening factor that might preempt such continued state regulation of its vessels beyond three miles. Since federal law is the supreme law of the land under the U.S. Constitution, states are not able to enact legislation or adopt regulations that prevent the application of federal rules. Accordingly, the general counsel to the National Oceanographic and Atmospheric Administration has opined that as long as state regulations affecting fishing beyond three-miles do not conflict with federal regulations in the FCZ, state controls must be followed by all vessels registered under the laws of that state. NOAA General Counsel for Fisheries opinion dated January 29, 1981. In such conflict cases, the United States Supreme Court has indicated that if the conflicting state regulations are so contrary to the federal rules that their operation is impossible, the state laws must fail. Ray v. ARCO, 435 U.S. 151 (1978). State regulations that are not inconsistent with federal laws will be allowed to coexist, and can be enforced by the state. The exact degree of inconsistency that is required before a state regulation is invalidated is not capable of being reduced to precise formula but is the subject of a case-by-case analysis. Further, the background of the provision regarding vessels registered under the laws of a state in § 1856 is unclear and a state could argue that this section affirms a state's historical responsibility to regulate all its vessels no matter what federal law provides.

These conflicts and ambiguities in existing federal/state authorities render determining which regulatory agency has authority over U.S. crab vessels as difficult as speciating C. bairdi and C. opilio hybrids. It leads to considerable, and often unnecessary, confusion when dissimilar or seemingly conflicting regulations are adopted by the respective agencies since only the court can officially determine which rule should prevail. It can also generate unnecessary animosity toward the responsible fisheries agencies by fishermen who are affected directly by the conflict.

In order to avoid uncertainty in a situation where two agencies have been granted management authority, the North Pacific Fishery Management Council has been establishing a procedure in the king crab fishery where the state, council and U.S. Secretary of Commerce are considering a federal framework plan that approves the state's regulations. The result would be a single set of regulations that can be enforced by both state and federal agencies.

Whether this procedure will ultimately result in measures sufficient to establish an orderly, efficient tanner crab fishery in Alaska will depend on whether or not fishermen can be convinced that the regulations will assure a sustained yield harvest, and fair, equitable fishing opportunity for all participants. The best way to assure such cooperation and understanding will be for the federal and state governments to evidence sincerity in a cooperative approach that will eliminate duplication and conflicting regulations. Such a foundation will allow the regulatory agencies, and the fishermen, to focus on fundamental responsibilities of management and harvesting the resource on a sound biological basis.

Characteristics of the Snow Crab, *Chionoecetes Opilio*, Fishery Off Cape Breton Island

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INTRODUCTION

Exploitation of the snow crab resource around Cape Breton Island, Nova Scotia, Canada, was started in 1966 by inshore boats from Cheticamp operating in the 'gully' region off the NW coast (Fig. 1). Offshore boats from the provinces of New Brunswick and Quebec began to fish in the same area soon after. Between 1977 and 1979, landings rose markedly in phase with effort and the expansion of the fishery to approximately 180 inshore vessels operating around most of the Island's coast (Table 1).

Between 1976 and 1978, six inshore areas were defined around Cape Breton Island (Fig. 1) for exclusive exploitation by inshore boats under 45 ft (13.7 m) in length. One hundred and fifty snow crab licenses were issued to inshore boats to fish these areas in 1981. Additionally, 28 licenses were allotted for inshore boats to fish area 7 off the SW coast; area 7 is also open to the New Brunswick and Quebec offshore snow crab fleets.

Currently, the Cape Breton Island fishing season for snow crab is approximately 9 weeks in duration, extending from mid-July through September in most areas. The relatively short season is in contrast to the remainder of the Atlantic snow crab fishery (Elner 1982) and in accord with the goal to develop this particular fishery as a stable, supplementary fishery with a large number of participants. Total Allowable Catch (TAC) restrictions, enforced in several areas since 1979, have been in an attempt to maintain a large, stable stock (based, where possible, on a strategy of permitting only the harvest of biomass equivalent to the calculated growth and recruitment additions for the previous year) until population parameters can be modelled to permit more optimal exploitation. Other measures, such as division of TAC's into individual boat quotas and strictly limiting the number of licenses in an area, promote an equitable distribution of resource benefits among the fishermen.

The major concentrations of snow crab around Cape Breton Island are in area 1; 57% (913.4 MT) of the total (1611.4 MT) snow crab landings for Cape Breton Island were caught here in 1981. The 'gully' in area 1 has probably produced a higher sustained mean catch per unit of effort (CPUE) than any other known snow crab ground in Canadian waters. In comparison, since 1980, fishermen on the Atlantic side of Cape Breton Island (areas 2-6) have been largely confined to exploiting scattered low-density pockets of snow crab.

Fig. 1. Snow crab management areas around Cape Breton Island.

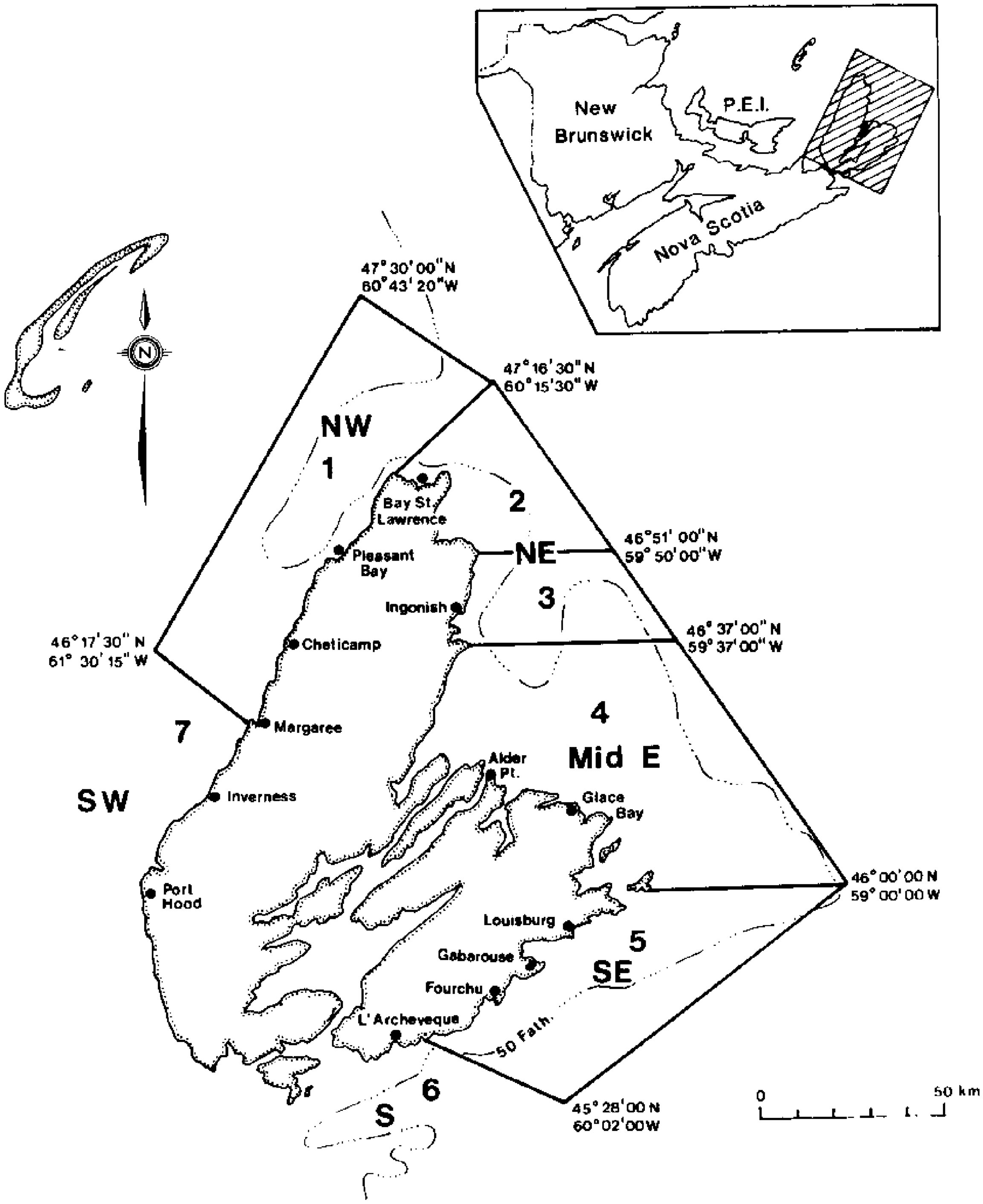


Table 1. Snow crab landing statistics, by management areas, for Cape Breton Island, 1977-81.

Area	Year	No. of boats licensed (participating)	Kg landed log books	Kg landed sales slips statistics	Effort in traps hauled from log books (trap type)	Mean CPUE (kg.trap haul^{-1})
1	1977	8(8)	-	-	-	-
	1978	14(14)	1,941,000	-	26,301 (1.5x1.5x0.5 m)	73.80
	1979	27(27)	1,390,765	1,390,106	20,436 (")	68.05
	1980	27(27)	1,104,783	1,157,998	12,360 (")	89.38
	1981	27(26)	795,751	913,442	13,413 (")	59.33
2&3	1978	36(36)	192,228	-	17,258 (1.2x0.9x0.8 m)	11.14
	1979	48(34)	262,250	293,106	*25,660 (")	10.22
	1980	48(39)	181,003	186,605	*17,499 (")	10.34
	1981	49(28)	816	35,910	32 (1.5x1.5x0.5 m)	25.50
4	1979	38(38)	507,569	624,029	10,546 (")	48.13
	1980	38(26)	39,800	181,241	827 (")	48.13
	1981	37(11)	6,545	61,476	315 (")	20.78
5	1978	15(15)	250,076	-	4,531 (")	55.19
	1979	25(23)	682,731	679,504	14,747 (")	46.30
	1980	26(24)	324,786	395,855	7,341 (")	44.24
	1981	26(10)	81,819	90,463	2,835 (")	28.86
6	1979	8(6)	27,351	24,868	1,880 (")	14.55
	1980	11(9)	69,136	58,586	5,246 (")	13.18
	1981	11(5)	20,350	15,896	1,316 (")	15.46
7	1979	15(13)	212,800	213,326	4,449 (")	47.83
	1980	25(23)	494,980	519,248	10,242 (")	48.33
	1981	28(26)	365,386	494,221	7,554 (")	48.37

*These estimates include boats from area 4 fishing in area 2 and 3.

Inshore boats exploiting the snow crab resource around Cape Breton Island are generally 9.2-13.7 m in length. Traps are set singly on soft, mud bottom at depths ranging from 48-256 m and are usually hauled daily. The most commonly used traps are 1.5 x 1.5 x 0.5 m steel frames covered in 76- to 131-mm mesh, with two fishing heads. However, Japanese-type conical traps and wooden traps predominate in NE Cape Breton. Regulations limit the maximum number of traps per boat to 30.

Regulations for all Atlantic snow crab fisheries confine exploitation to male crabs of 95 mm carapace width (CW) and above. This size is well above the 80 mm CW size of 100% maturity for males (Watson 1970). Female crabs are effectively excluded from the fishery as they undergo a terminal molt to maturity below the legal minimum size limit. Most mature females examined during the 1981 season were berried, indicating that the reproductive potential of the stock is being maintained.

Since 1977, the Cape Breton Island fishery has been monitored through sales-slips, port and at-sea catch sampling, and fishermen's log records. Tagging programs have been carried out around the Island since 1978 to determine commercial stock biomass, exploitation rate, movement and growth. Utilizing the various monitoring data, annual stock assessments have been produced by Bailey (1978) and Elner and Robichaud (1980, 1981).

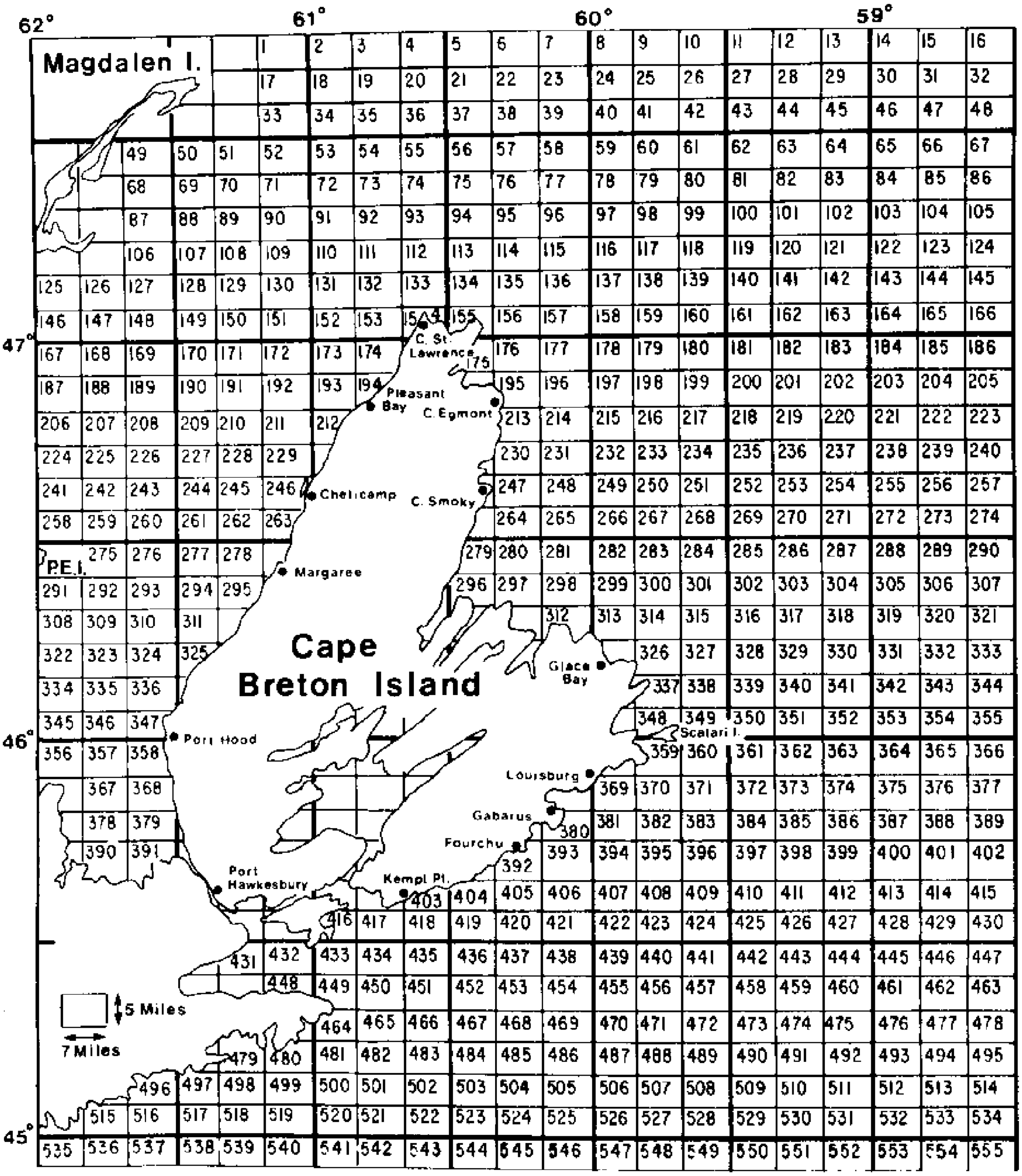
Based on the annual stock assessments, this study compares the snow crab fishery and stock dynamics in area 5, representative of east coast, Atlantic-side grounds, with area 1, representative of the west coast, Gulf-side grounds. Areas 1 and 5 are comparable in that they have similar numbers of licensed snow crab boats: 27 boats vs 26 boats, and a similar area: 2750 km^2 vs 2059 km^2.

METHODS

Since 1978, Cape Breton Island snow crab fishermen have been required to maintain logbooks (Elner 1982). To improve trap location information, fishermen were given grid maps (Fig. 2) in 1980 and 1981 and requested to indicate the grid number(s) corresponding to their fishing area(s).

Biomass estimates were made by Leslie analysis, plotting cumulative catch (x-axis) at weekly intervals against mean CPUE (kg$\cdot$trap $haul^{-1}$), from logbook data (Ricker 1975). The slope of the linear regression gives an estimate of the catchability (q) of the gear. The intercept of the regression line on the x-axis gives an estimate of the total biomass (B_0) above legal minimum CW available

Fig. 2. Grid map utilized by Cape Breton Island snow crab fishermen to indicate trap positions in their logbooks.



for the fishing season. Assuming that natural mortality is not significant during the relatively short fishing season (i.e. a type I fishery, Ricker (1975)), the rate of exploitation (u) is given by:

$$u = \frac{Y}{B_0} \quad \ldots\ldots\ldots\ldots\ldots (1)$$

where Y is the total catch.

If q is assumed to be constant throughout the fishing season, it is possible to calculate the biomass (B_t) present at any given time, knowing the CPUE value at that time, from:

$$\frac{CPUE_t}{q} = B_t \quad \ldots\ldots\ldots\ldots\ldots (2)$$

Equation (2) makes it possible to estimate biomass increases from growth and recruitment, through molting, during the fishing season. Significant molting periods are detectable by in-season rises in mean CPUE and simultaneous increases in the observed frequency of soft-shelled crabs in commercial catch samples.

Ricker (1975) gives a detailed account of possible sources of discrepancy in Leslie analyses.

Tag returns from mark-recapture studies were analyzed by Leslie and Peterson techniques to provide supplementary biomass and exploitation rate estimates (details of the various tagging studies are given by Bailey (1978), Elner and Robichaud (1980, 1981)).

In area 5, a total of 2010 male snow crabs of legal size and above were marked with spagetti tags and released prior to the 1979 fishing season. A spagetti tag consists of a coded, yellow vinyl tube tied around the carapace of the crab. Although spagetti tags are not retained through ecdysis, they can provide short-term information on population size, exploitation rate, and movement.

In area 1, 3951 crabs were marked with spaghetti tags in 1978. Prior to the 1980 fishing season, 2500 and 251 crabs of legal size and above were marked with t-tags and spaghetti tags, respectively. The t-tags were injected through the posterior suture line and designed to be retained through ecdysis (however, none of the tagged crabs recaptured to date appeared to have molted and grown). In 1981, 3005 crabs of legal size and above were tagged with a modified t-tag. Fishermen were relied upon to return all the tagged crabs found. A reward was offered the finder for each tag returned with details of how, where, and when the capture was made.

Port and at-sea samples of commercial landings have been taken through the fishing season in each area since 1977 to assess catch size-frequency distribution and shell condition.

RESULTS

The catch rate for the 1981 season in each grid area fished by inshore boats around Cape Breton highlights the differences between the east and west coast of the Island (Fig. 3).

NW Cape Breton Island (Area 1)

A quota of 1,406 MT was set in area 1 during 1979, based on an assessment of biomass addition during the previous season. Similarly, based on the assessment of the 1979 season, a quota of 980 MT (80,000 lb/unit x 27 boats) was set for the 1980 season. This quota was subsequently raised to 1224 MT following high catch rates in the initial weeks of the season. The 1981 quota, based on inter- and intra-season biomass additions in 1980, was placed at 1002 MT but was not reached due to poor market conditions and a consequent reduction in fishing effort.

Port and At-Sea Sampling

Mean carapace widths from port and at-sea sampling of commercial catches since 1977 are compared in Fig. 4. Mean carapace widths in the at-sea samples are smaller than corresponding port samples as the at-sea samples include measurements for all sizes of male crabs trapped, before culling of crabs of sublegal size. No sustained trends are apparent in either the at-sea or port samples.

Fig. 3. Distribution of fishing effort and catch rates around Cape Breton Island during the 1981 season, as derived from logbook data.

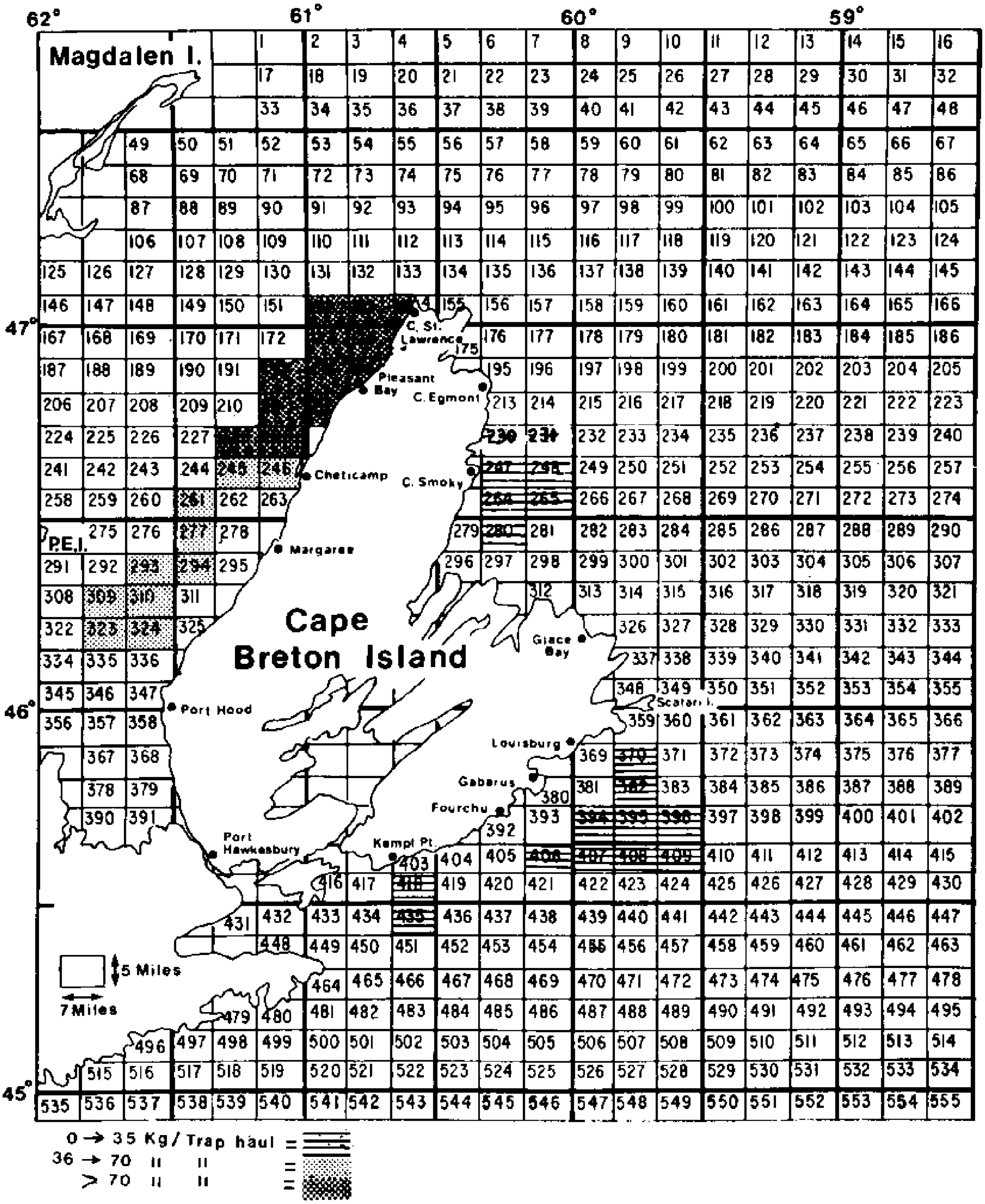


Fig. 4. Historical monthly mean carapace widths for male snow crabs from port and at-sea sampling of commercial catches in area 1, NW Cape Breton Island.

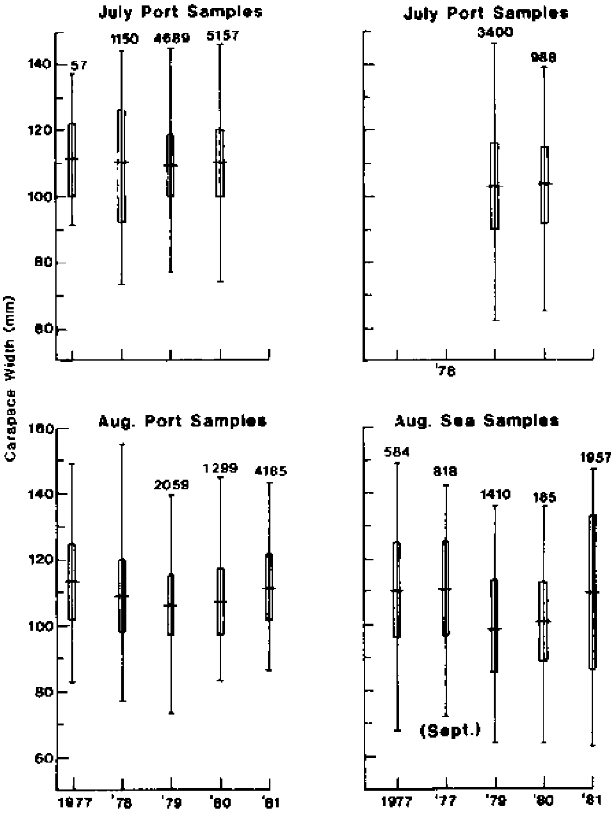
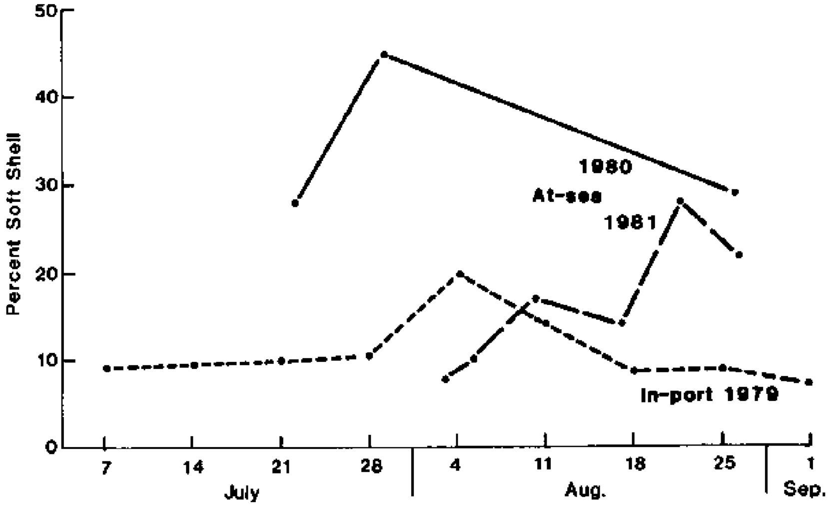


Fig. 5. Historical percent frequency of occurrence of shell states for male snow crabs in commercial catches for area 1, NW Cape Breton Island.



At-sea observations on the shell condition of crabs in commercial catches during 1981 (Fig. 5) showed an increase in the frequency of occurrence of soft- and intermediate-shell states towards the end of August, indicating that molting was occurring and, hence, a pulse of growth and recruitment was coming into the system. However, catch rates (Fig. 6) failed to show an obvious synchronous rise to reflect a significant biomass pulse into the commercial stock. In contrast, molting peaks detected during July-early August in 1979 and 1980 did appear to influence catch rates.

Logbooks

As an example of how logbook data (Fig. 6) were analysed by the Leslie method, the following is the treatment of 1981 data from area 1: CPUE declined steadily throughout the fishing season and a linear regression through all data points gives an estimate, at the intercept on the x-axis, of the total available stock of commercial-size crabs (Bo) for the season as 1,689.7 MT (95% confidence limits: 1452 and 2084 MT). Subtracting the total 1981 catch (Y) for area 1 (795.8 MT, as derived from logbooks) from Bo gives the amount of commercially available stock left on the grounds at the end of the 1981 fishing season as 894 MT. Assuming that natural mortality was not a significant factor during the fishing season, the exploitation rate (u) in 1981 was 47% (95% confidence limits: 55% and 38%) and the instantaneous rate of fishing mortality (F) was 0.63 (0.80-0.46).

During the first week of the 1981 fishing season in area 1, the mean catch rate was 78.54 kg per trap haul, giving an estimate for the then available stock (B_1) as 1649.8 MT (from $B_1 = CPUE_1/q$). Given that 1688.7 MT was B_0, the total available stock for the season, then, subtracting B_1, the net stock increase from growth and recruitment during the season can be estimated as 39.9 MT. The biomass increase represents only 2.4% of the initial available biomass (B_1) and is 380 MT less than observed during the same period in 1980.

Based on the 1980 Leslie analysis of logbooks for area 1, 733 MT of commercial stock was estimated to remain on the grounds at the close of the fishing season. Thus, a substantial stock difference of 917 MT (124.8% of the stock left at the end of 1980) is presumed to have been added to the fishing grounds between the end of the 1979 season and the opening of the 1980 season. Table 2 summarizes the area

Fig. 6. Historical trends of catch rate over cumulative catch in area 1, NW Cape Breton Island, from logbook data, showing Leslie regression lines.

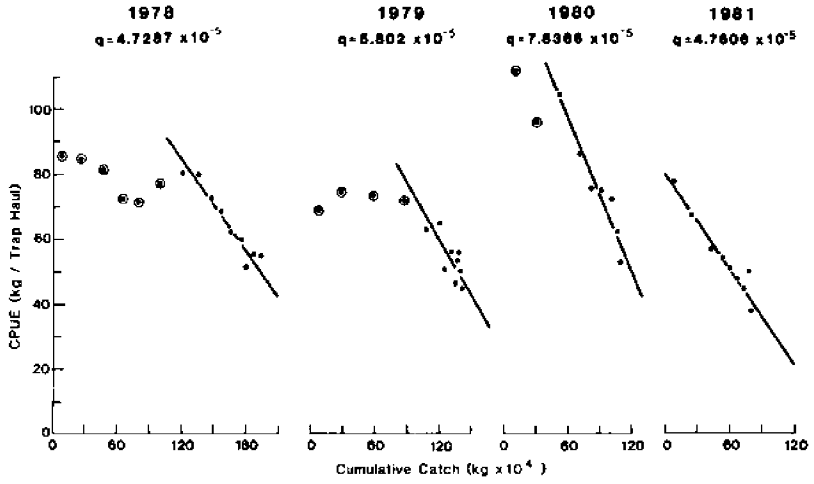


Fig. 7. Historical trends of commercial snow crab biomass over time, from logbook data, for area 1, NW Cape Breton Island, 1978-81.

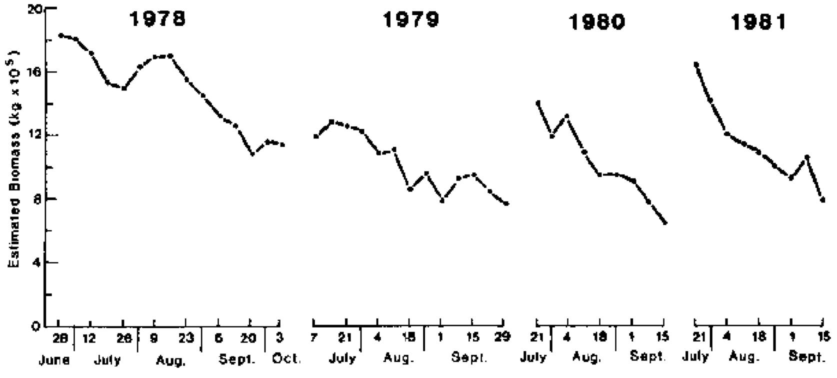


Table 2. Biomass and catch estimates (MT) for the area 1, NW Cape Breton Island snow crab stocks, 1977-81.

		1977	1978	1979	1980	1981
1) Biomass at start of season	:		1,827	1,449	1,418	1,650
2) Growth and recruitment during season	:		1,189	790	420	40
3) Total exploitable biomass (1+2)	:		3,016	2,239	1,838	1,690
4) Catch (logbook-derived) (exploitation rate)	:	516	1,941 (64%)	1,391 (62%)	1,105 (60%)	796 (47%)
5) Biomass at end of season	:		1,075	848	733	894
6) Growth and recruitment between seasons	:		374	570	917	
Management-imposed TAC:		-	-	1,406	1,224	1,002

1 biomass history since 1977 from Leslie estimates based on logbook data and shows that the 1980/81 interseason biomass increase is 347 MT more than the interseason increase in 1979/80. However, on balance, the large interseason biomass pulse in 1980/81 is offset by the smaller in-season pulse in 1981 compared to previous years.

Figure 7 shows the available biomass in area 1, for fishing seasons 1978-81 and illustrates the year-to-year stability of the stock despite considerable landings (Fig.8).

Tagging

A summary of analyses of tag returns in 1978, 1980 and 1981 is presented in Table 3. Generally, biomass, exploitation rate, and catchability parameters estimated from tagging data are similar to those estimated from logbook information.

SE Cape Breton Island (Area 5)

A preemptive quota of 943 MT (80,000 lb/unit x 26 boats) was set in area 5 during 1980. In the 1981 season, a quota of 41 MT (3,477 lb/unit x 26 boats), equal to an estimated between-season biomass pulse in 1979-80, was imposed in an effort to stabilize the rapidly diminishing stock.

Port and At-Sea Sampling

Comparison of catch size-frequency distributions since 1978 indicate a trend for increasing mean CW (Fig. 9). Overall, the trend may reflect a lack of recruitment into the stock and an increasing dependence by the fishery on older animals.

The low incidence of soft-shell crabs (Fig. 10) suggests that molting and subsequent growth and recruitment was not prevalent during either the 1980 or 1981 fishing seasons. No obvious molting pulses are detectable in catch rate data from 1978-81 logbooks although there was a high incidence of soft-shelled crabs in September 1979.

Logbooks

Because of the depressed nature of the fishery in 1981, only 10 out of the 26 licensed fishermen in area 5 set their traps. A biomass estimate, by Leslie analysis of logbook

Fig. 8. Historical trends of catch by weekly period, from logbook data, for area 1, NW Cape Breton Island, 1978-81.

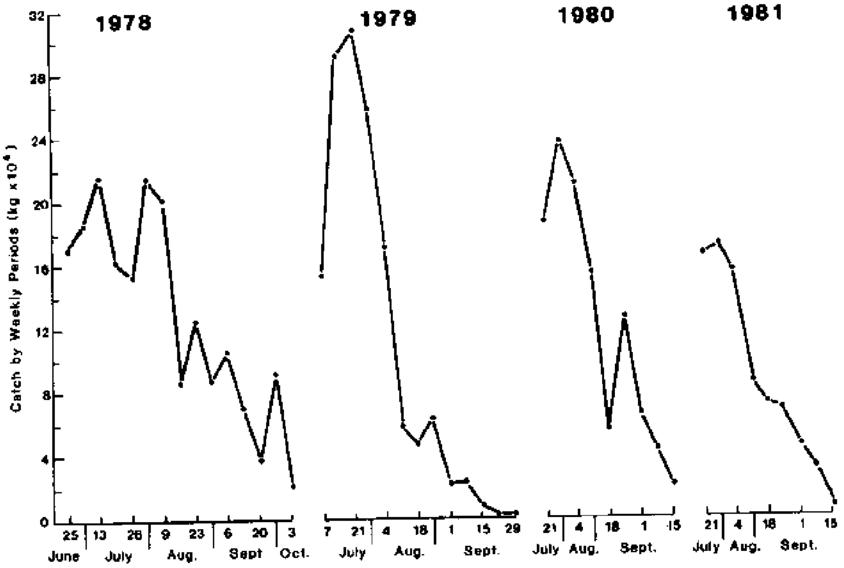


Fig. 9. Historical monthly mean carapace widths for male snow crabs from port and at-sea sampling of commercial catches in area 5, SE Cape Breton Island.

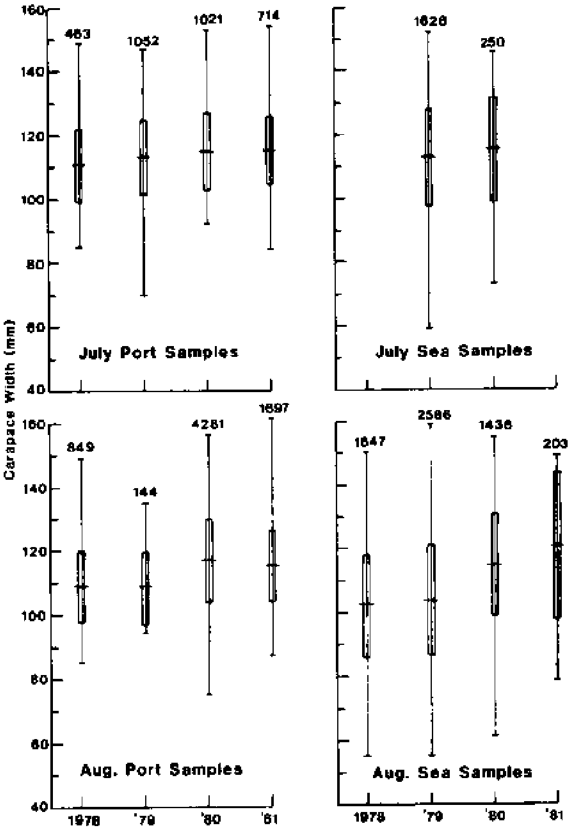


Table 3. Summary of information from tagging studies carried out in area 1 and area 5, Cape Breton Island.

		No. crabs tagged	No. crabs recaptured	Exploitation rate (95% confidence limits)	Peterson estimate of biomass (MT)	Catchability (q)
Area 1	1978	3,951	1,777	65.3%	1,751	4.100×10^{-5}
	1979	-	119	54.7% (27.3-88.5%)	-	4.456×10^{-5}
	1980	2,500	369	48.1% (25.2-65.7%)	2,378	5.051×10^{-5}
	1981	3,005	1,351	45.0%	2,032	-
Area 5	1979	2,010	1,444	64.5% (42.9-80.4%)	1,069	6.733×10^{-5}
	1980	-	167	48.7% (64.5-0%)	653	9.357×10^{-5}
	1981	-	19	-	-	-

Fig. 10. Historical percent frequency of occurrence of shell states for male snow crabs in commercial catches for area 5, SE Cape Breton Island.

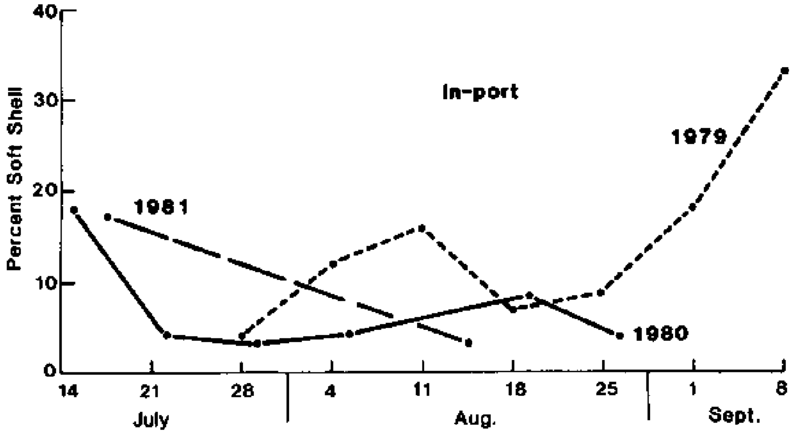
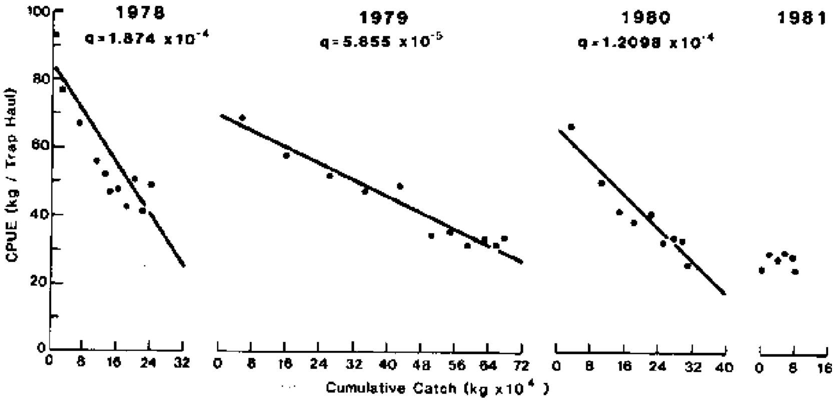


Fig. 11. Historical trends of catch rate over cumulative catch in area 5, SE Cape Breton Island, from logbook data, showing Leslie regression lines.



data is impractical as the catch rates remained at a constant low level throughout the fishing season (Fig. 11); hence, no measurable decrease in commercial biomass was apparent. The phenomenon possibly reflects the collapsed nature of the stock and is due to the small numbers of fishermen continually moving their gear from crab 'pocket' to crab 'pocket' to sustain their catch rates; hence, the stock was never sufficiently depleted to register a decline in CPUE. The possibility that CPUE was sustained by continual growth and recruitment equal in magnitude to the harvest is obviated by the lack of soft-shell crabs in the catch samples.

By using the 1980 catchability (q) value of 1.2098×10^{-4} and the initial CPUE, an estimate of biomass at the start of the 1981 season of 213 MT is obtained. This biomass estimate is 5 MT lower than the commercial biomass estimated to remain on the fishing grounds at the end of the 1980 season. This would indicate that there was no significant growth and recruitment in the commercial stock between the 1980 and 1981 seasons.

Comparison of CPUE during the last 4 years of commercial fishing (Fig. 11) indicates that present catch rates are among the lowest ever experienced. Estimated biomass (Fig. 12) and catch by weekly period (Fig. 13) since 1978 also reflect the collapsed nature of the area 5 snow crab stock. The history of the area 5 fishery is summarized in Table 4.

Tagging

Biomass and exploitation rate estimates from the 1979 tagging study in area 5 are presented in Table 3 and compare favorably with estimates derived from logbook data.

DISCUSSION

When area 5 and adjacent east coast areas of Cape Breton Island were opened to snow crab fishing in the late 1970's, exploitation was based, no doubt, on accumulations of virgin biomass. Initial catch rates and landings were high. However, within four fishing seasons catch rates and the commercial biomass in area 5 has collapsed, as have the fisheries in the remaining four eastern areas. In contrast, although exploitation in area 1 has been continuous since

Fig. 12. Historical trends of commercial snow crab biomass over time, from logbook data, for area 5, SE Cape Breton Island, 1978-81.

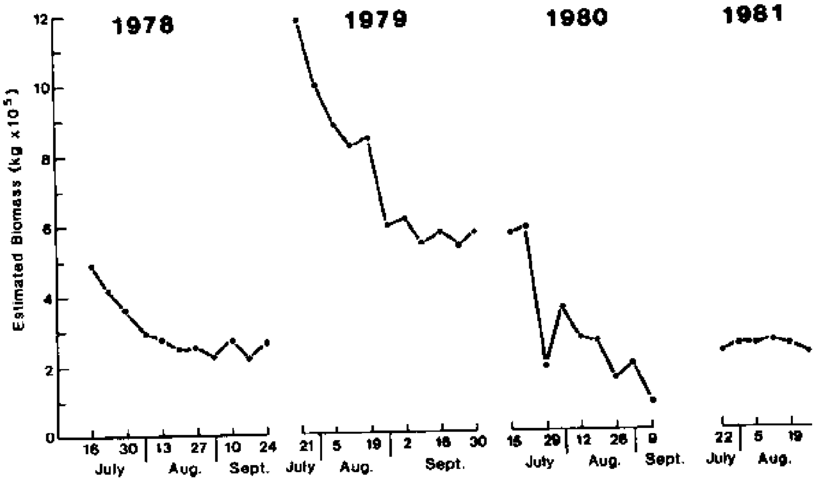


Fig. 13. Historical trends of catch by weekly period, from logbook data, for area 5, SE Cape Breton Island, 1978-81.

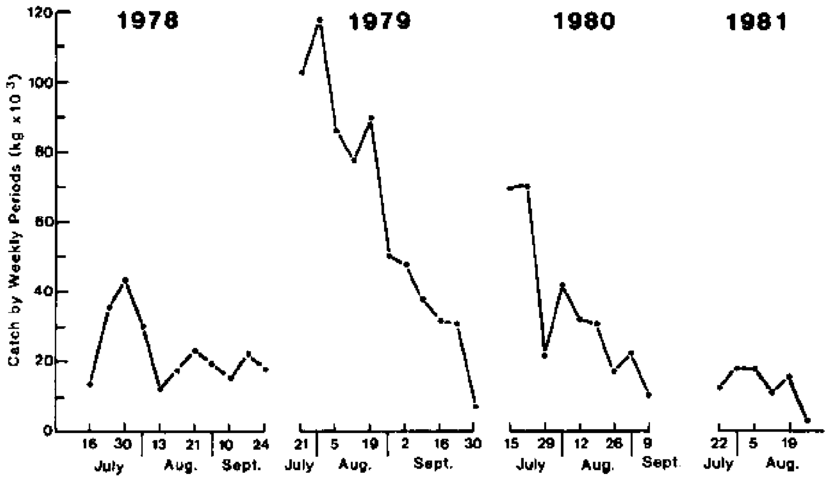


Table 4. Biomass and catch estimates (MT) for the area 5, SE Cape Breton Island snow crab stocks, 1978-81.

	1978*	1979	1980	1981
1) Biomass at start of season :	440	1,185	543	213
2) Growth and recruitment during season :	-	-	-	-
3) Total exploitable biomass (1+2) :	440	1,185	543	213
4) Catch (logbook-derived) (exploitation rate) :	250 (57%)	683 (58%)	325 (60%)	82 (38%)
5) Biomass at end of season (3-4) :	190	502	218	131
6) Growth and recruitment between seasons :	995	41	-5	
Management-imposed TAC:			943	41

*With caution

1966, the catch rates and commercial biomass have remained relatively stable since monitoring began in 1978. The substantial differences in historical landings between areas 1 and 5 appear more remarkable given that the areas are of approximately equal size, have had similar numbers of fishermen, and are separated by less than 160 km of landmass. Furthermore, with the existing, generally adhered to, minimum legal CW of 95 mm, the number of snow crab eggs being released annually into the Atlantic is assumed to equal pre-fishery levels and, hence, decreases in egg production are unlikely to be a factor in the collapse.

Evidence from stock assessments over 4 years indicates that area 5 and the remaining east coast snow crab grounds are unproductive in terms of growth and recruitment. Possibly, the eastern areas, being at the southern edge of known commercial snow crab concentrations in the Atlantic, represent marginal grounds in terms of habitat. Thus, although comparisons of biomass, growth and recruitment levels, as well as catch rates and size frequencies for area 5 reveal apparent recruitment failures, it may be that the situation represents the normal pattern of growth. Thus, the eastern Cape Breton Island snow crab grounds were probably built up over time through trickles of movement, growth, and recruitment. Such a scenario would account for the initially high catch rates and landings on the grounds, the lack of resilience of the stocks to exploitation, and the subsequent devastation of biomass and catch rates after only a few fishing seasons.

In contrast to the east coast, the management by 'stable-stock' policy appears to have succeeded in area 1 on the west coast. The magnitude of overall annual biomass additions in area 1, although variable in periodicity, have appeared relatively large and consistent since 1978. This consistency, despite high exploitation rates of 47-64%, has conferred resilience to the area 1 stock and has facilitated management. Given that stability has been achieved in area 1 at the expense of curbing effort and landings, the long-term sustainable yield for the fishery appears to be approximately 1,000 MT per annum.

Between 1978 and 1980 biological advice for a cautious approach to exploitation of snow crab stocks was ignored, due mainly to the initially high catch rates. Now, the biological problems are compounded by excessive potential effort threatening future prospects for recovery in the fishery. In 1982, management acknowledged that the general strategy for snow crab exploitation in Atlantic Canada was not applicable to eastern areas of Cape Breton Island. As the reproductive potential of the resource is protected by minimum size regulations, management has dropped catch controls for the east coast areas and, from 1982 onwards, plans to allow fishermen to exploit snow crabs on a largely opportunistic basis.

In summary, the Cape Breton Island experience highlights the problems associated with attempting to optimize a fishery without adequate biological information on recruitment patterns. To avoid similar problems in the future, elucidation of the various mechanisms governing success of the various snow crab life history stages and the eventual magnitude of recruitment pulses into the fishing grounds must become a prime research concern.

ACKNOWLEDGMENTS

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Biology of a Leech Ectocommensal on the Spider Crab, *Chionoecetes Opilio*

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ABSTRACT

Commercial crab (Chionoecetes opilio) meat from Newfoundland, Canada is often contaminated with dark, ovoid cocoons of the marine leech, Johanssonia arctica. The latter is an ectocommensal organism on the crab. It feeds in the blood of several species of marine fish but uses the crab as a substrate for cocoon deposition. Cocoons occur mainly on the first and second pairs of walking legs of recently molted crabs with hardened shells. Although C. opilio is widely distributed in the N.W. Atlantic, the leech's distribution appears more restricted as it lives at -1 to 2°C. Heavy fishing pressure in an area 5-8 km east of the Avalon peninsula resulted in a reduction of large old crabs and increased numbers of molting animals in summer. Coincidentally, leeches and cocoons have also increased in this area. Contamination of crab meat with cocoons probably occurs during processing.

INTRODUCTION

At least four ectocommensal organisms are associated with the spider crab, Chionoecetes opilio, in Newfoundland. These include a leech, Johanssonia arctica (Meyer and Khan 1979), a turbellarian platyhelminth (Fleming and Burt 1978) and an unidentified barnacle and bioluminescent polychete (Khan, unpublished data). The leech is the most prevalent organism, occurring primarily on the first and second pairs of walking legs of intermolt crabs (Khan 1982 in press). The leech feeds on fish and not on the crab, which is used as a substrate for cocoon deposition and dispersal. Cocoons, which contain fertilized eggs, are deposited on the ventral surfaces of the legs. The initial golden-brown colour becomes progressively darker with age and following emergence of the young, the empty cocoons remain for varying periods. Commercial crab meat, during processing, invariably becomes contaminated with cocoons. The present study provides information on the distribution and prevalence of the leech and the factors which affect its incidence.

MATERIALS AND METHODS

Leeches were obtained from spider crabs caught in Japanese conical and large square (1.8x1-8x0.8m) traps as well as gill nets. In Newfoundland, the depth varied from 170 to 350 m (water temperature, -0.1 to ˉ2.0°C) while in the Gulf of St. Lawrence, it extended from 95 to 160 m (-0.3 to 4.0°C). Muddy bottom prevaled in most areas. Observations from 1972 to 1981 were made as often as possible (monthly) on research vessels or commercial catches shortly after arrival in port and included shell dimension, shell condition (vide Miller 1975), leech and cocoon abundance.

In a study, conducted in Conception Bay to determine leech and cocoon prevalence on crabs at varying depths, Japanese conical traps were used (Miller 1975). The latter were set at approximately 60, 120 and 180 in groups of 6, each trap was about 35 m apart. Shell condition, carapace width, leech and cocoon abundance were recorded for each crab. Bottom temperatures were also determined.

DISTRIBUTION ON CRABS

Leeches were observed initially on spider crabs as well as on toad crabs (Hyas coarctatus) and occasionally on lobsters (Homarus americanus), bivalve shells and stones. More leeches were observed on recently molted crabs with a hardening carapace (Table 1, stages II and III), than on newly emerged or older crabs that were darker and sometimes encrusted with barnacles. The majority (70%) of leeches attached to the ventral, femoral surfaces of the first and second pairs of walking legs than on the other appendages (Table 2). Moreover, the leeches appeared to frequent the second pair of legs (42%) in contrast to the first leg (28%) or other appendages. This was also reflected in the abundance of cocoons, as approximately 60% were deposited on the same second pair of legs while about 88% of the total were attached to femoral surfaces of the first two pairs of legs. No cocoons have ever been observed on the internal surface of the exoskeleton.

Table 1. *Prevalence of the leech, *J. arctica* and its cocoons on the crab, *C. opilio*, at different stages of carapace hardness. (n=100)

Stage No.	Carapace Condition	$\bar{x}$ Leech Number	$\bar{x}$ Cocoon Number
I	Newly emerged	5.4 ± 2.1	0
II	Recently emerged	15.2 ± 10.7	55.6 ± 46.1
III	Hard, pale red shell, no barnacles	22.5 ± 20.0	139.4 ± 134.3
IV	+Hard, dark shell with barnacles	13.3 ± 10.1	175.0 ± 146.2

*Sample taken approximately 170 m deep, 5-8 km off St. John's in 1974-75.

+More than 70% of the cocoons were empty.

Table 2. Prevalence of the leech *J. arctica* and its cocoons on the appendages of the spider crab, *C. opilio*.+

	Claw	*Appendages Walking Legs			
		1	2	3	4
$\bar{x}$ no. leeches	2.6	9.0	13.8	5.6	1.6
$\bar{x}$ no. cocoons	0	45.7	102.3	13.9	6.0

+Data based on 110 crabs taken in February 1981 in Conception Bay, Newfoundland at 185 meters; water temperature was -0.5°C.

*Includes both pairs.

GEOGRAPHICAL DISTRIBUTION

Leeches were observed on the legs of crabs taken from several areas adjacent to coastal Newfoundland, Labrador, Nova Scotia (Table 3) and the estuary of the Gulf of St. Lawrence. The greatest number of leeches were observed on crabs taken in Conception Bay and 5 to 15 km east of St. John's (East Avalon). Crabs in other areas with substantial numbers included Bonavista and Notre Dame Bays. Fewer leeches and cocoons were observed on crabs in White, Fortune and Placentia Bays and off the Labrador coast. Numbers were extremely low off Cheticamp, Nova Scotia and south east Newfoundland. No leeches or cocoons were observed on crabs at Port au Chois area (northern Gulf of St. Lawrence).

While samples were being obtained from commerical catches, it was noted that fewer leeches and cocoons occurred on crabs as the distance from shore increased. They appeared more abundant on crabs taken from the "Cordelia deeps", an area, 5-8 km offshore from St. John's, that was heavily fished for the last 8 years. Estimates of the crabs sampled indicate that leeches and cocoons were most abundant on crabs 5-8 km that at 15, 50 or 85 km offshore (Table 4). Moreover, the number of leeches and cocoons were substantially greater on crabs taken in 1981 than in 1974 (Table 5).

TEMPERATURE EFFECTS

Crabs, harbouring leeches, were held in the laboratory in a flowthrough system in ambient sea water to ascertain the effect of temperature on survival. Both crabs and leeches were active at -1.0 to 2.0°C. The crabs fed regularly when offered fish and some survived for periods up to 3 years when the water temperature was kept cold (~1°C) continuously. Despite regular feeding and continual low temperature, however, only two of the several hundred crabs held over the years, molted in the laboratory. The leeches fed on the blood of fish and subsequently attached to the crabs. Both leeches and crabs became progressively less active when the ambient temperature exceeded 4°C. Adult (>15 mm) leeches did not feed or deposit cocoons and many died within a month at 4-5°C. After holding crabs over winter in the laboratory for the last 10 years at the ambient (-1.0 to 2.0°C) from November through May, it has been observed that mortality is still high as the sea water temperature rises to 5°C or more despite the long period of acclimation (5-6 months) and gradual rise subsequently of the ambient water temperature in late spring. Small (50-80 mm) hard shell crabs survived longer than all other stages or sizes (>80 mm).

Table 3. Prevalence of the leech, *J. arctica*, and its cocoons on the spider crab, *C. opilio*, from coastal areas of eastern Canada.

Area	Depth	Temp. °C	$\bar{x}$ Crab size	$\bar{x}$ Leech no.	$\bar{x}$ Cocoon no.
East Avalon	176	0.3	104.7 + 8.0	22.5 + 9.1	116.7 + 67.1
Conception Bay	200	-0.1	90.8 ± 11.6	45.0 ± 17.0	191.3 ± 87.3
†Trinity Bay	225	-0.1	103.4 ± 8.6	7.4 ± 4.2	37.1 ± 12.1
†Bonavista Bay	220	-0.1	104.7 ± 7.1	17.4 ± 6.2	74.2 ± 23.2
Notre Dame Bay	139	0.1	117.3 ± 12.0	8.4 ± 6.1	51.0 ± 29.8
†White Bay	330	-0.2	114.1 ± 17.0	1.2 ± 0.8	21.7 ± 9.3
Hawke Channel	240	0.4	98.9 ± 8.5	1.1 ± 0.9	12.1 ± 9.2
Port au Choix	175	4.5	99.6 ± 11.8	0	0
Cheticamp, N.S.	129	4.2	123.4 ± 10.5	0.4 + 0.3	0.2 + 0.2
Fortune Bay	180	0.1	90.6 ± 12.0	6.2 ± 4.1	43.2 ± 17.1
Placentia Bay	170	-0.9	107.6 ± 11.4	5.1 ± 3.2	112.0 ± 49.2
†Southeast Nfld.	190	0.9	80.3 ± 21.0	2.1 ± 1.6	8.9 ± 6.3

†Temperature estimate based on information provided by Fisheries and Oceans.

Table 4. Prevalence of leeches and cocoons of *J. arctica* on the spider crab, *C. opilio* at varying distances from St. John's, Nfld. Samples were obtained during August 1981 at depths 175-210 m.

Distance offshore (km)	$\bar{x}$ Leech no.	$\bar{x}$ Cocoon no.
5 - 8	42 ± 28	300 ± 185
15	20 ± 13	116 ± 47
50	23 ± 15	117 ± 33
85	4 ± 2	23 ± 14

Table 5. Prevalence of the leech, J. arctica, and its cocoons on crabs[+], taken 5-8 k- off St. John's in August 1974 and 1981.

Date	$\bar{x}$ Leech No.	$\bar{x}$ Cocoon No.
1974	6.4 ± 2.3	116.1 ± 95.9
1981	42.1 ± 27.6	300.0 ± 185.2

[+] Data based on stages II and III crabs.

To determine whether temperature affected leeches to the same extent in nature, collections were made at various depths in Conception Bay. Generally the crabs were less abundant, progressively smaller, older and harbored fewer leeches and cocoons at shallow (60 m) depths than at intermediate (120 m) or deeper (180 m) levels during the winter (Table 6). In summer, no leeches or cocoons were observed on crabs taken at 60 m (WT=8.2^{o}C), while few were observed at 120 m but were numerous at 180 m. While cocoons were observed on crabs taken at 60 m (WT=2.5^{o}C) in November no leeches were present. However, both leeches and cocoons were present on crabs taken at 120 and 180 m and the numbers were slightly greater than in February and June.

DISCUSSION

Results from the present study provide evidence of increasing abundance of leeches and cocoons on spider crabs collected 5 to 8 km northeast of St. John's over an 8-year period. It is known that the leeches deposit their cocoons on recently molted crabs and rarely on old crabs especially when encrusted with barnacles (Khan 1982). In the population of crabs exploited commercially since 1973, the fishery concentrated on the older animals. Landings in this area have increased from 473 to 6,870 metric tons between 1974 and 1979 (Taylor 1981). From records of Fisheries and Oceans, it was estimated that the percent of recently molted crabs (1973-74) in a normal catch was less than 10 percent during summer. In newly exploited areas soft shelled crabs constitute 5-10 percent of the catch (Brothers 1976). As the fishing pressure increases, however, it removes most of the large, old crabs and results in a significant reduction in size (Watson and Simpson 1969). Coincident with this change occurs an increase of molting crabs up to approximately 60 percent (Miller and O'Keefe 1981). Presumably, as a population becomes depleted by fishing pressure, more food becomes available and increased feeding is reflected in a greater percentage of molting animals. This increase of molting crabs provides the leech population with additional sites for cocoon deposition which previously was unavailable. Consequently, leeches and cocoons have increased on crabs in commercially exploited areas. The prognosis for the future is for increasing numbers of leeches and cocoons on the spider crab in areas of continual high exploitation.

Since the majority of J. arctica have been observed on spider crabs, it can be assumed that the distribution of the leech probably coincides with that of its symbiote. From reports of observers on Federal and Provincial Fisheries' surveys for spider crab stocks (unpublished observations), it appears that J. arctica is distributed up to 170 km east of the Avalon Peninsula but rarely to the south of this area.

Table 6. Effect of depth and temperature on the distribution of the leech, *J. arctica* on the spider crab, *C. opilio*[+].

Date	Depth (m)	Temp	$\bar{x}$ crab size	$\bar{x}$ leech no.
10. 3.81	60	-0.1	56.5 ± 3.4	1.4 ± 1.2
10. 3.81	120	-1.5	76.9 ± 12.0	11.6 ± 7.0
10. 3.81	180	-1.2	94.2 ± 13.2	37.7 ± 16.2
10. 6.81	60	2.3	47.8 ± 14.4	0
10. 6.81	120	0.2	62.1 ± 17.1	4.1 ± 2.3
10. 6.81	180	-0.7	91.8 ± 16.3	45.0 ± 16.7
22.11.81	60	0.9	49.1 ± 17.4	0
22.11.81	120	-1.0	96.1 ± 8.2	20.5 ± 9.7
22.11.81	180	-1.0	113.8 ± 4.3	49.3 ± 14.2

[+] n = 25

Along the northeast coast, the distribution follows the 183 m depth contour line to approximately 120 m depth of the coastline and also along the Labrador coast as far north as Hawke Channel up to 125 km offshore. The distribution in the Gulf of St. Lawrence is limited to the Cheticamp area, north and south of Anticosti island in the vicinity of the 183 m depth contour and in shallower areas in the estuary of the St. Lawrence River (Bailey, personal communication). In areas where bottom temperatures exceed 5°C during summer months, survival might be low as temperature appears to be a major limiting factor. Since C. opilio is the main substrate for attachment and cocoon deposition, it is likely that the absence of C. opilio (Watson and Simpson 1969) can be correlated with that of J. arctica. Such areas include the southern Grand Bank, St. Pierre Bank, the region between Hermitage Bay and Port aux Basques, and the Scotian Shelf. Overall distribution in the N.W. Atlantic might be limited by the 4-5°C summer isotherm.

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Data Needs and Management Workshop

Data Requirements for Tanner Crab Management, as Suggested by the Bristol Bay King Crab Management Model

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INTRODUCTION

The red king crab (Paralithodes camtschatica) fishery in Alaska has developed over the last three decades into a highly valued United States fishery operated by technically modern harvesters and processors. The fisheries are managed with a combination of regulatory measures, including prohibition on the landing of females, minimum size limits, and catch quotas. Production centers are located at Kodiak Island and in the Bristol Bay section of the eastern Bering Sea, where Japanese and Russian fisheries predominated until their exclusion in the early 1970s. Distribution of production for 1981 is shown in Figure 1A. Historical production from the main areas is shown in Figure 1B. During the 1960-1979 period, most production came from Bristol Bay, especially during the 1970s, when production around Kodiak dropped significantly. The catch of red king crab in Bristol Bay dropped markedly in 1981, thus tending to equalize production from the two main areas.

The National Marine Fisheries Service has monitored the condition of the Bristol Bay red king crab stock annually since 1968. This trawl survey provides a continuing series of abundance estimates by sex and size, which is important to the management of the stock. The abundance trends estimated from the surveys are shown in Figure 2 (inset). The increase in stock during the mid-seventies was the result of several strong year-classes. The current drop in stock abundance is associated with weak recruitment.

This report describes a model for management of the Bristol Bay red king crab stock and its application. The model has been jointly adopted by the Alaska Board of Fisheries and the North Pacific Fishery Management Council as part of the Fisheries Management Plan for Bering Sea and Aleutian Islands king crab stocks (NPFMC 1982). In presenting this model, emphasis is placed on its use for identifying high priority research areas for biological management. Data requirements pertaining to aspects such as unit stock definition, multiple-species management, predictions of future production, and socioeconomic factors will not be covered. Rather, the model deals with establishing quotas, exploitation rates and minimum size limits for male crabs on an annual basis, taking into account data on spawning stock and recruitment, the effect of male removal on reproductive success, and abundance of harvestable stock.

DESCRIPTION OF THE MODEL

The king crab management model is based on three main components: (1) a spawner-recruit relationship, (2) effects of male removal on female fertilization, and (3)

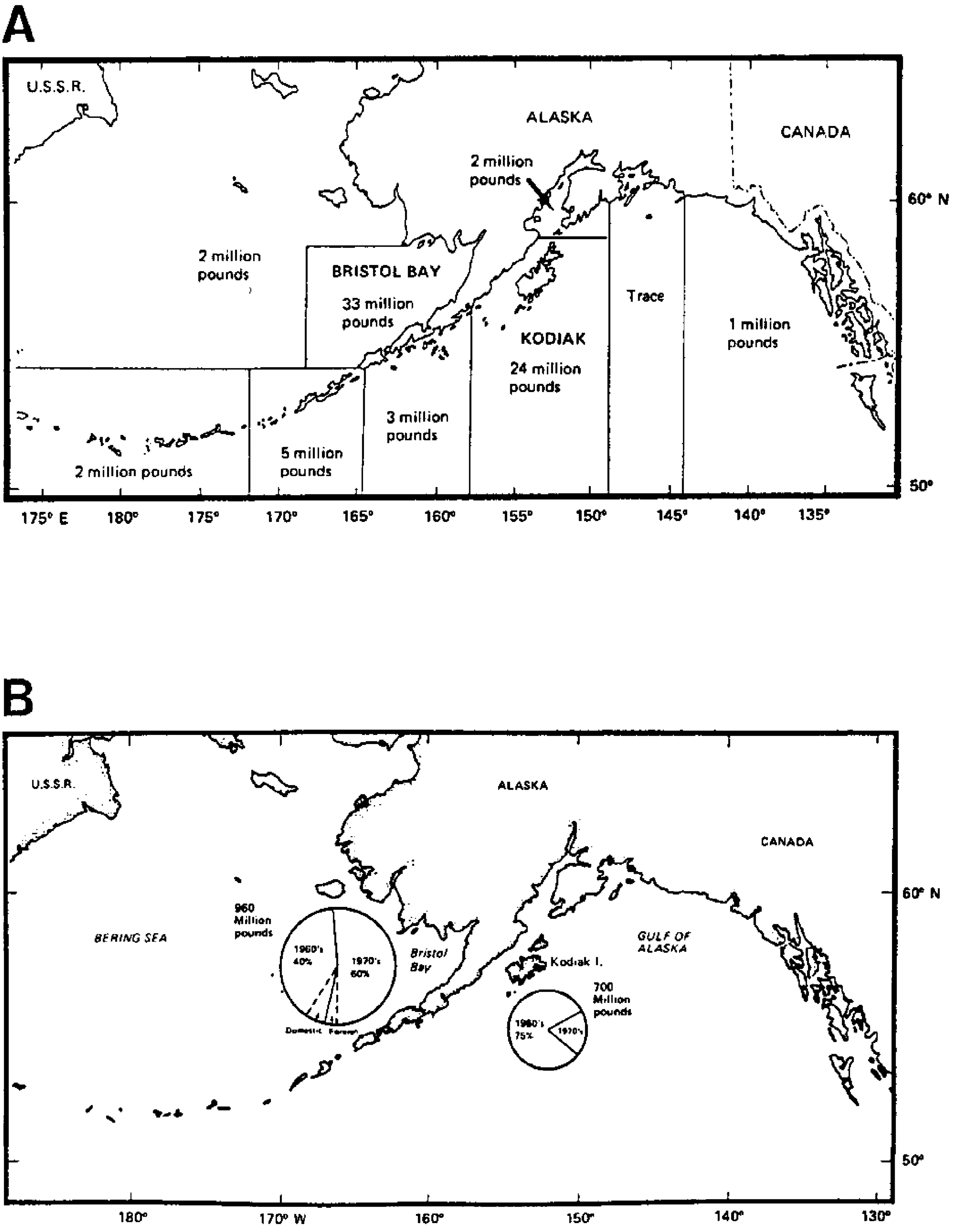

Figure 1 A.--Distribution of Alaskan production of red king crab in 1981.

B.--The 1960-79 historical production for the primary fisheries for Alaskan red king crab

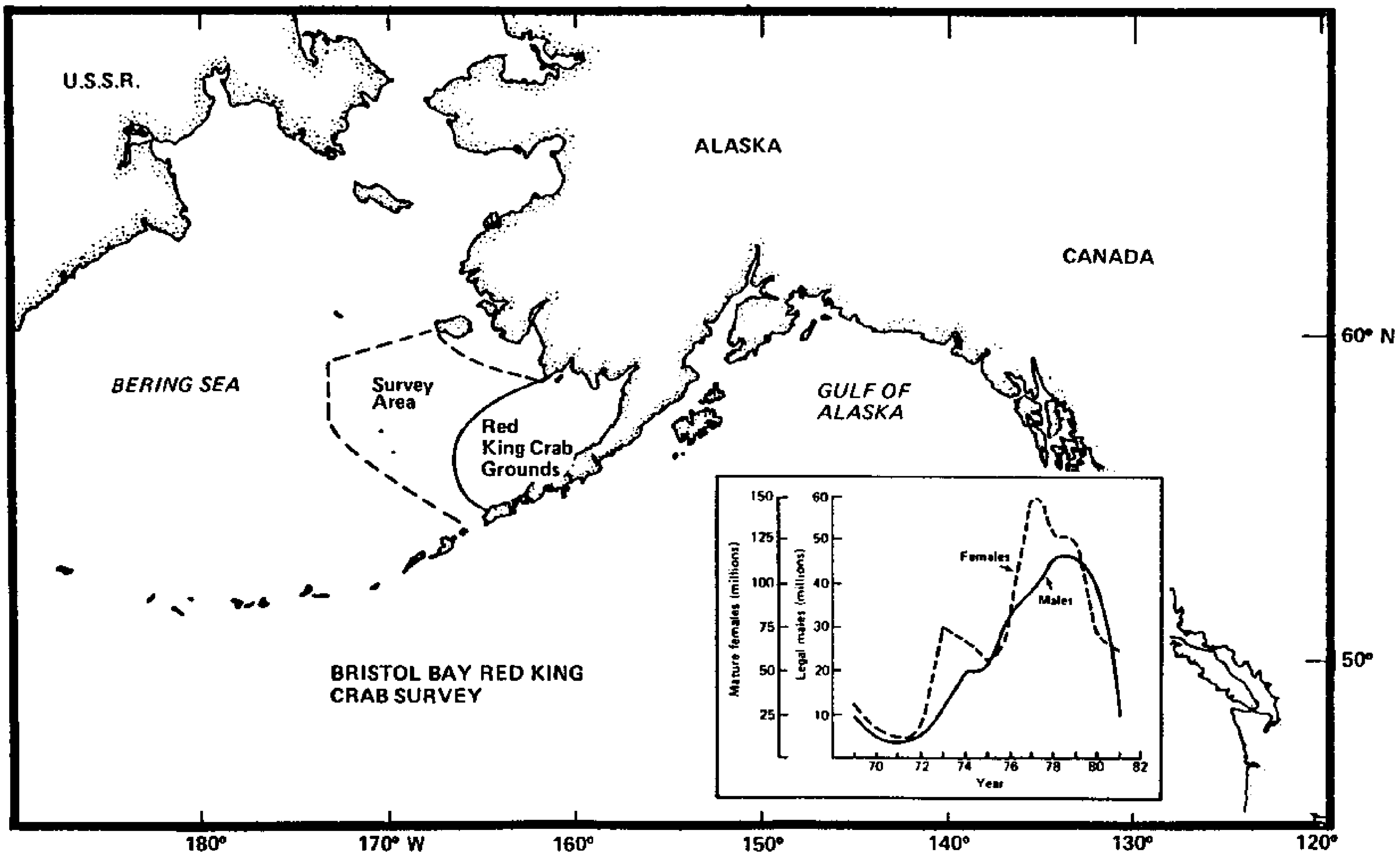

Figure 2.--Survey region for Bristol Bay red king crab and resulting estimated trends in abundance.

determination of quotas based on spawning stock condition. The model assumes that a spawner-recruit relationship exists, at least in the lower part of the range of stock abundances. A further requirement is the concept that there is a minimum level of fertilized female stock which is required for successful reproduction and future recruitment to the harvestable stock. This threshold level is used to determine the intensity of harvest. The removal of male stock will influence reproduction since the fertilization rate of females may decline as the minimum size limit on males is lowered and/or the rate of exploitation is increased. Thus, the allowable catch will fluctuate depending not only on the abundance of harvestable stock but also on the abundance of fertilized females relative to the threshold abundance. These three components are now discussed in more detail.

The Spawner-Recruit Relationship

Theoretically, the spawner-recruit relationship can take many forms, but from a practical management standpoint, two basic forms can be distinguished: (1) where recruitment drops off at high spawning stock densities (Figure 3A), and (2) where recruitment is independent of spawning stock density above a certain level (Figure 3B). Within these two basic forms, the spawner-recruit relationship can still theoretically take on a variety of shapes, but again for practical management considerations, the most probable curves can be limited to a few (numbered 1, 2, and 3 in Figure 3). The vertical dashed lines represent spawning stock levels which will, on the average, produce the highest recruitments, i.e., the spawning level to be maintained, as far as possible, by management. The solid straight replacement line represents the abundance of recruits that will maintain (or replace in the future) the current level of spawning stock.

The spawner-recruit data at hand for red king crab in Bristol Bay (Figure 4) suggests that we are dealing with a curve similar to form A1 of Figure 3. Here, abundance of 5-year-old males is related to abundance of fertilized females six years earlier. The six-year lag is used because mated females carry fertilized egg clutches for approximately one year prior to releasing hatched larvae. Male crabs recruit to the fishery at age 8 or 9, but recruit to survey trawl gear at age 5 consistently enough to provide at least a reliable index to relative abundance from year to year. Abundance estimates of age 5, rather than age 8, males are used to provide additional data for the spawner-recruit relationship.

A fit of the Ricker (1954) model to the Bristol Bay data available through 1981 (again, Figure 4) indicates that a maximum in recruitment occurs at an abundance of 20 million

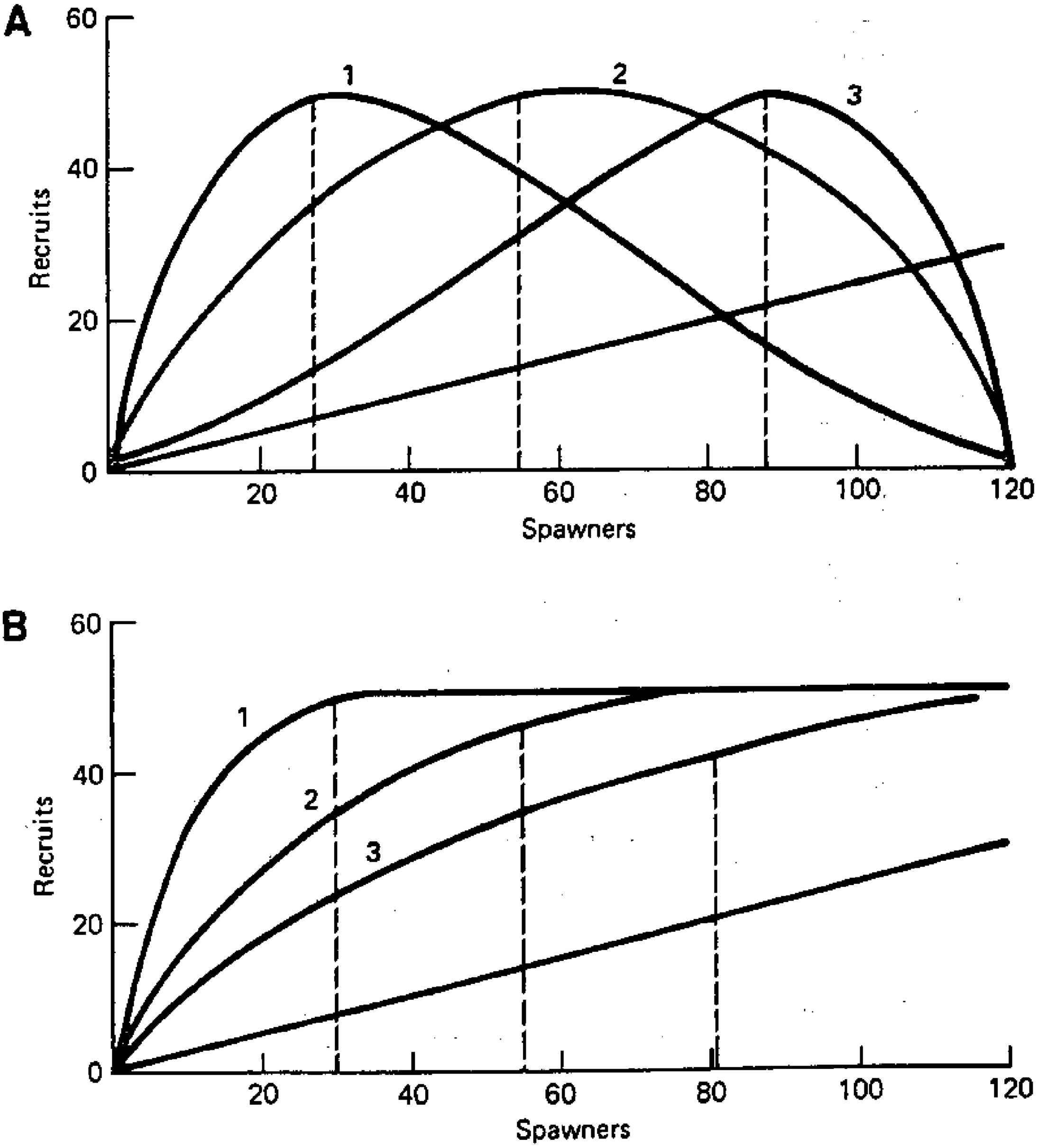

Figure 3.--Examples of possible spawner-recruit curves: A, dome-shaped and B., asymptotic.

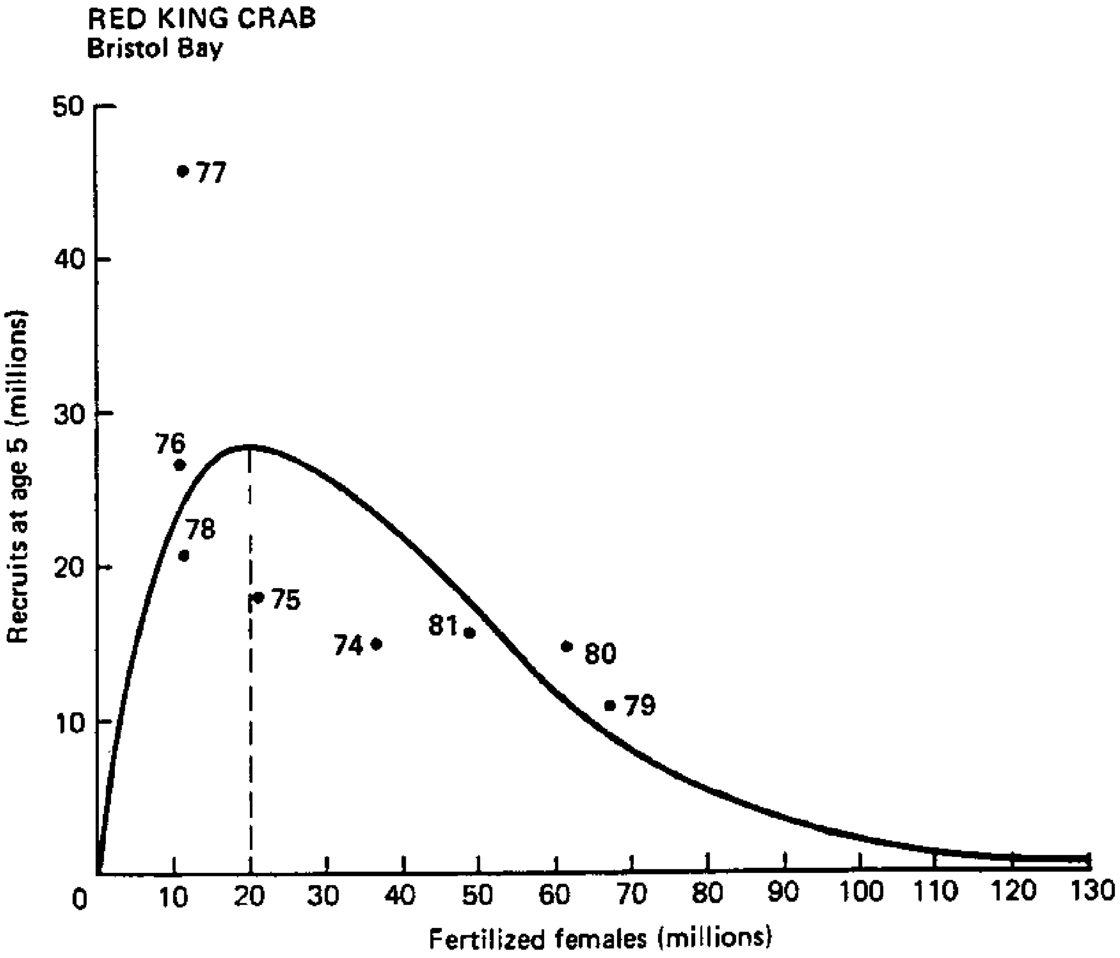

Figure 4.--Spawner-recruit relationship for Bristol Bay red king crab using survey estimates of abundance for 1968 through 1981.

fertilized females. However, at this relatively early stage of knowledge, other forms of the king crab spawner-recruit relationship cannot be ruled out. In fact, it may be expected that as annual points are added to the data the estimates of the fertilized female stock producing maximum future recruitment may change. As time goes on, the shape of the relationship may also change.

In order to anticipate these potential changes, estimates of recruitment one and two years into the future are attempted from survey estimates of abundance of 3- and 4-year-old males (Reeves 1982). When, for example, such estimates for 1982 and 1983 are added to the 1968-81 data and the Ricker model fit to the new data set, a different estimate of the fertilized female stock which maximizes future recruitment is obtained. The results of such an analysis are shown in Figure 5 (dashed curve) and indicate that the fertilized female stock which maximizes recruitment may increase in the next few years. The inclusion of projected recruitment estimates in the analysis enables a range to be established for the spawning stock level which maximizes future recruitment.

This range may be defined as the threshold region. In the case of the Bristol Bay king crab stock, the main function of the spawer-recruit analysis is to estimate this threshold region. When the spawning stock is within this region, there may be a higher probability of obtaining strong recruitment in the future. More importantly, however, this region represents a zone of caution which, when occupied by the spawning stock, should signal the need for precautionary management measures to prevent weakened future recruitment. Thus, at this stage of knowledge of the Bristol Bay king crab resource, the spawner-recruit relationship must be considered a precautionary model delineating the spawning stock threshold rather than a prognostic model for recruitment.

Effect of Male Removal on the Spawning Stock

The single-sex fishery for king crab can be expected to impact the reproductive potential of the stock by altering the ratio of mature males to mature females. Information exists (Powell, James and Hurd 1974) indicating that males are polygamous, but data on sex ratios required for mating and fertilization of all mature females under various natural conditions are lacking. Powell, Shafford and Jones (1973) have further pointed out that the size ratio of mature male to mature female may be an important factor in mating and fertilization of the female stock since mating pairs observed under natural conditions were usually characterized by male size dominance. Powell's studies have shown that, in partially controlled underwater environments, successful mating

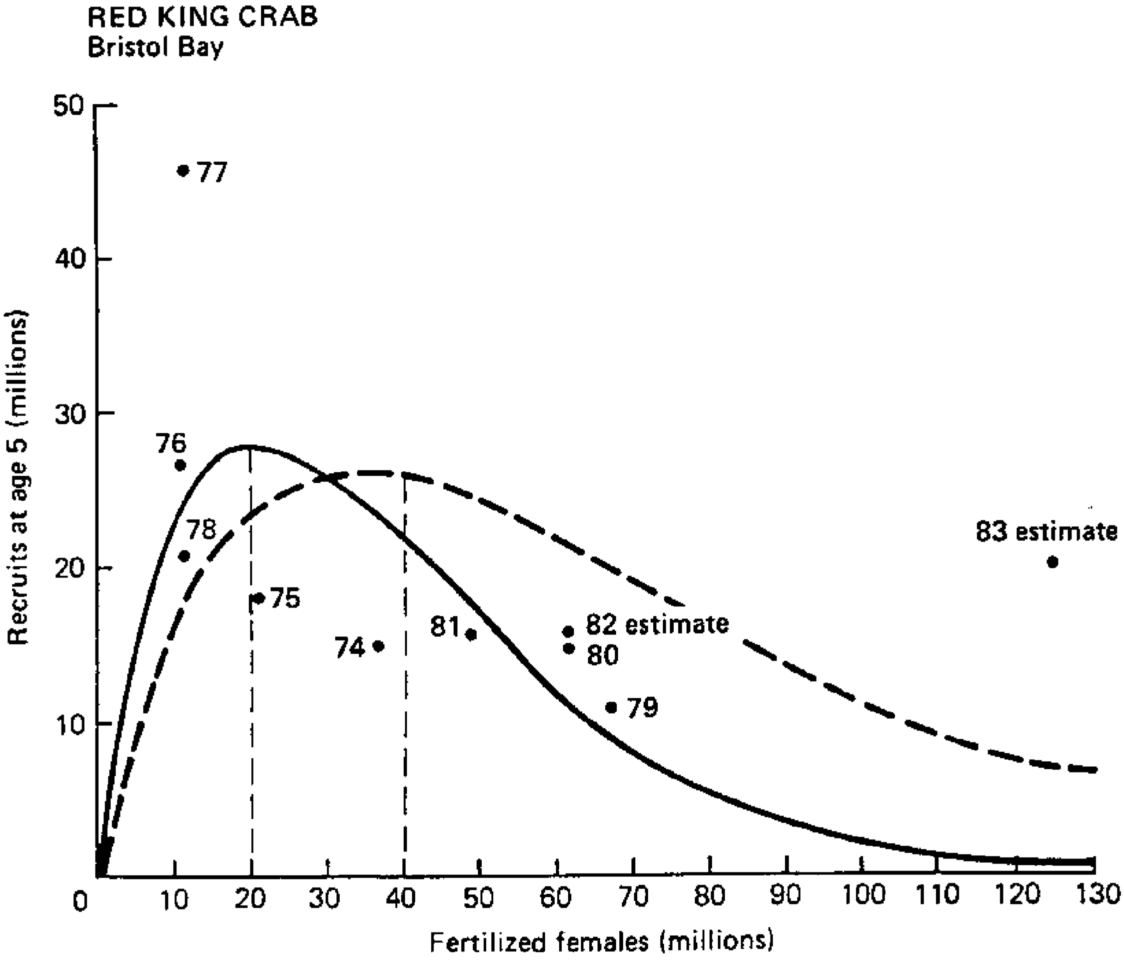

Figure 5.--Spawner-recruit relationships for Bristol Bay red king crab using (1) the 1968-81 survey data and (2) the 1968-81 data plus estimates of recruitment for 1982 and 1983.

and fertilization can result from female:male sex ratios as high as 10:1 and male:female size ratios of less than 1. However, the extrapolation of these results to conditions on the mating grounds in any given year remains a problem.

As a starting point in the study of this problem, a simulation modeling exercise was conducted employing the model of Reeves and Marasco (1980) and incorporating Powell's data. Fertilization of mature females was modeled as a theoretical function of the ratio of mature males:mature females and the mature male:mature female weight ratio during the mating season. Percent fertilization declined when the sex ratio exceeded 4:1 and when the weight ratio dropped below 1.7 (Figure 6). The effect of a range of exploitation rates and minimum size limits on the fertilization rate of females was then simulated, providing a theoretical matrix of fertilization rates as a function of exploitation rate and size limit (Table 1). The lower portion of Table 1 depicts a matrix of spawning stock sizes, obtained by scalar multiplication of the fertilization rate matrix by the estimated abundance of mature females in any given year. The scalar used to derive the spawning stock matrix is the estimated abundance of mature females on the spring mating grounds, projected using growth and mortality data from estimates obtained from the research survey of the previous summer (summer of 1981 in the example of Table 1).

The line superimposed on the spawning stock matrix corresponds to the upper boundary of the threshold region determined from the spawner-recruit analysis. The upper boundary was chosen as a cautious estimate of the spawning stock threshold level, in light of the relative paucity of spawner-recruit data and the apparent propensity of the relationship to change with time. Elements of the matrix above the threshold line are considered safe spawning stock levels relative to the threshold region, as are their corresponding exploitation rates and minimum size limits.

Annual Allowable Catch Based on Spawning Stock Condition

Estimates of potential catches in any given year are based on area-swept estimates of abundance from research surveys conducted each summer. As indicated in Table 2, estimated selection curves in the form of percentages available at various minimum size limits and estimated average weight per crab are applied to numerical estimates of abundance of male crabs by size groups. The result is an estimate of the poundage of crabs available on the grounds for a range of size limits. A range of annual exploitation rates is applied to abundance values for each minimum size limit. This gives a matrix of yields as a function of size limit and rate of exploitation (Table 3). Superimposition of the

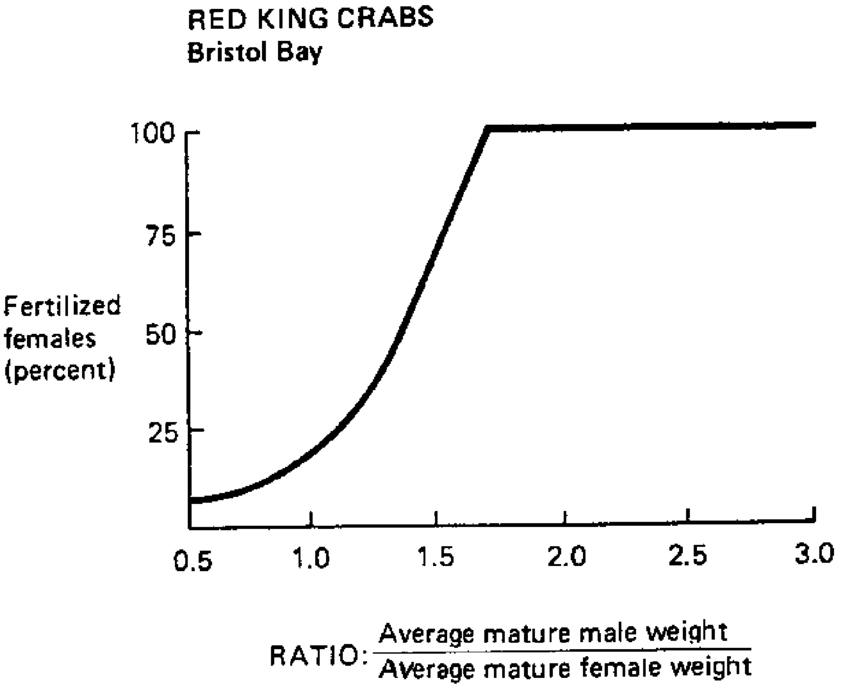

Figure 6.--Theoretical relationship between the rate of female fertilization and the size ratio of males to females during the mating season.

Table 1.--Estimated rate of female fertilization (top) and female spawning stock (bottom) as a function of minimum size limit and rate of exploitation for Bristol Bay red king crab.

Size Limit (inches)	Exploitation Rate							
	.3	.4	.5	.6	.7	.8	.9	1.0
Estimated Percent Fertilized Females								
7.00	100	100	100	100	98	97	95	93
6.75	100	98	97	96	92	90	87	85
6.50	100	96	96	96	86	82	79	76
6.25	93	89	85	81	78	74	72	67
6.00	86	82	77	73	70	66	64	59
5.75	81	77	72	68	65	62	60	55
5.50	77	73	68	64	61	57	55	50
5.25	72	68	63	59	56	53	51	46
Estimated 1982 Spawning Stock (Millions of Fertilized Females)								
7.00	53	53	53	53	52	51	50	49
6.75	53	52	51	51	49	48	46	45
6.50	53	51	51	51	46	43	42	40
6.25	49	47	45	43	41	39	38	36
6.00	47	43	41	39	37	35	34	31
5.75	43	41	38	36	34	33	32	29
5.50	41	39	36	34	32	30	29	27
5.25	38	36	33	31	30	28	27	24

Table 2.--Data used for estimation of the yield matrix for Bristol Bay red king crab.

Carapace length group (mm)	Average weight (lbs)	Estimated abundance for 1981 season (millions of males)	Percent available at minimum size limit of: 5.25"	5.50"	5.75"	6.00"	6.25"	6.50"	6.75"	7.00"
100-119	2.7	9.3	50	35	20	0	0	0	0	0
120-129	3.6	6.1	100	90	80	50	20	0	0	0
130-139	4.5	4.6	100	100	100	100	80	50	20	0
140-149	5.4	3.5	100	100	100	100	100	100	80	50
150-154	6.2	1.5	100	100	100	100	100	100	100	100
155-159	6.9	0.9	100	100	100	100	100	100	100	100
160-164	7.6	0.7	100	100	100	100	100	100	100	100
165-169	8.2	0.6	100	100	100	100	100	100	100	100
>169	8.9	0.5	100	100	100	100	100	100	100	100
Total Pounds Available			106.0	100.1	94.3	82.9	72.4	62.0	52.2	42.5

Table 3.--Estimated yield matrix (millions of pounds) for Bristol Bay red king crab in 1981.

Size Limit (inches)	Exploitation Rate							
	.3	.4	.5	.6	.7	.8	.9	1.0
7.00	13	17	21	26	30	34	38	43
6.75	16	21	26	31	37	42	47	52
6.50	19	25	31	37	43	50	56	62
6.25	22	29	36	43	51	58	65	72
6.00	25	33	41	50	58	66	75	83
5.75	28	38	47	57	66	75	85	94
5.50	30	40	50	60	70	80	90	100
5.25	32	42	53	64	74	85	95	106

spawning stock threshold line on the yield matrix serves to define a set of biologically safe catches. The choice of yields within the upper part of the matrix is based on non-biological considerations, while yields below the threshold line are to be pursued only at some potential risk to the reproductive maintenance of the stock. However, associated with these potentially riskier positions in the yield matrix is the greater likelihood of obtaining additional information on the effects of higher yields on the reproductive capacity of the stock.

Delineation of the reproductive threshold region is a key element of the model. The position of this region within the long-term range of spawning stock sizes can be expected to change annually until such time as the spawner-recruit relationship becomes well defined and reasonably stable. Accordingly, that portion of the yield matrix considered as biologically safe can be expected to vary from year to year as new data are added to the spawner-recruit relationship, until stability is achieved.

The female fertilization rate matrix is another key element of the model but is largely theoretical at the current state of knowledge regarding the effects of fishing on fertilization. Empirical deviations from these theoretical rates, which are expressed as functions of minimum size limit and exploitation rate, can also cause shifts in the position of threshold line within the yield matrix. Thus, the biologically safe region also can be expected to change as information regarding the fertilization rate matrix is added to the model. New information will be more readily obtained if regulations allow variation in size limit and rate of exploitation from year to year. However, even without such flexibility, information on within-cell variation (for any given size limit-exploitation rate combination) will be obtained.

DATA REQUIREMENTS FOR THE MODEL

Examination of the foregoing model elements leads to the delineation of parameters which must be accurately estimated if the model is to be successfully applied to management of the resource. The key data requirements may conveniently be divided into stock and fishery parameters.

Stock Parameters

Abundance (or indices of abundance), growth, and mortality estimates are of course essential to the assessment of any stock-fishery interaction. In the context of the king crab model, abundance information by size, and in some cases by age, is required for the spawner-recruit relationship, the spawning stock matrix, and the yield matrix. Growth and length-weight information are needed to determine abundance of recruits for the spawner-recruit relationship and for converting the yield matrix to a weight basis. Information on growth and natural mortality is required to project research survey abundance estimates to expected abundance during the next mating season.

The single-sex nature of the crab fisheries necessitates additional focus on the important reproductive parameters. Maturity schedules for females by size are required for the spawner-recruit relationship and the spawning stock matrix and should also be obtained for males for more detailed studies of the fertilization rate matrix as a function of mating size and sex ratios. Mating behavior as it affects, and is affected by, such factors as required sex and size ratios and timing of the molt between sexes, is important to determination of the fertilization rate matrix. Clutch size and viability are also key parameters to this matrix.

Fishery Parameters

Selection curves for minimum size limits of interest are required to obtain estimates of the exploitable population, which forms the basis of the yield matrix. Annual estimates of the rate of exploitation are required to determine the current position within the yield matrix. Recent events in the Bristol Bay king crab fishery have indicated that an additionally important fishery parameter may be the so-called handling mortality, incurred by the capture and discard of the non-marketable part of the catch. Such mortality of female and sub-legal males may be a function of minimum size limit and exploitation rate and in turn may affect the fertilization rate matrix by altering required sex and size ratios. Handling mortalities exerted on females will have additional implications for the spawning stock matrix.

While major aspects of king crab life history may differ from those of tanner crab, the general features of their respective stocks and fisheries are similar enough that the king crab model may serve as a guideline for data required for the management of tanner crab stocks. Table 4 provides a summary of parameter requirements, organized by major model components.

FUTURE MODEL STUDIES

The deterministic nature of the king crab management model is clearly unrealistic. Future work should include studies on the stochastic properties of model parameters. Such studies should lead to a better perception of the model's ability to discriminate between the results of

Table 4.--Parameter estimates required for the Bristol Bay red king crab management model.

Parameter	Model Component Spawner-recruit relationship	Fertilization rate matrix	Spawning stock matrix	Yield matrix
Abundance	x		x	x
Growth	x		x	x
Natural mortality			x	
Maturation	x	x	x	
Mating behavior		x		
Clutch size		x		
Selection				x
Exploitation rate				x
Handling mortality		x	x	

different management strategies, e.g., the magnitude of change required in the minimum size limit on exploitation rate to significantly change the rate of female fertilization or level of spawning stock abundance. Presumably, as random error measure is incorporated into the model, cells of each component matrix could to some degree become indiscriminate from adjacent cells, thus simplifying and, at the same time, making the matrix more realistic.

Beyond the incorporation of stochasticity, specific environmental parameters should be examined for their interaction with the model. The spawner-recruit analysis should include oceanographic, climatic, and ecosystem variables, such as temperature, currents, wind, predation, and competition. It is highly probable that several factors other than spawning stock abundance are affecting the recruitment process. Environmental factors may also affect the rate of female fertilization to an equal or greater extent than fishery removals.

Abundance estimates are highly important to the mode. Thus, it is desirable that these annual estimates be verified by other independent or semi-independent methods. Several analyses could be performed for Bristol Bay king crab. Catch-effort analysis by Leslie-DeLury techniques, catch composition analysis by virtual population methods, sex or size ratio analysis using change-in-ratio techniques, and tag release-recapture studies could provide the needed verification.

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Workshop Summary

WORKSHOP ON DATA NEEDS FOR MANAGEMENT

The workshop was led by a panel of symposium participants consisting of: Richard Bailey and Robert Elner (Department of Fisheries and Oceans, Canada), Steve Jewett (University of Alaska, U.S.), Jerry McCrary (Alaska Department of Fish and Game, U.S.), Robert Otto and Jerry Reeves (National Marine Fisheries Service, U.S.), and Dave Somerton (University of Washington, U.S.). The panel's initial comments were in response to a presentation by Jerry Reeves (this symposium) on data requirements for the management of crab fisheries based on the experience with the red king crab (*Paralithodes camtschatica*) fishery of Bristol Bay, Alaska. Following initial discussions, audience members from Canada, Japan, and the United States were asked to comment upon data needs for management.

Several points were raised on the economic components of management of the *Chionoecetes* fisheries. One person stated that in Alaska management has tended to be conservative and that user groups have not been asked just what kind of fishery they want in terms of economics. Another stated that we need to optimize the economics of the industry since crab is not a major source of protein and is more vulnerable to market fluctuations. All agreed that the economic side of the fishery management equation is important. However, the predominant opinion was that our job as biologists is to provide the information necessary to manage the fishery from a biological perspective. A number of individuals pointed out that most research biologists are not sufficiently familiar with fishery economics to give informed opinions on management from the economic perspective. It was suggested that any future symposium on *Chionoecetes* should include fishery economists to broaden our perspective on management.

Discussion followed on a number of areas which various individuals felt should be targeted for future research. A consensus seemed to agree that more work is needed on the juvenile portion of *Chionoecetes* populations: what is their lifestyle and what environmental factors are of primary importance to the survival of year classes. Some individuals emphasized describing substrate preference for juvenile crabs as an important area of study. Careful definition of stocks was considered important for increasing our ability to manage the fisheries accurately. We also need to obtain better information on mortality factors and the frequency of the molt if we are to understand the structure of *Chionoecetes* populations, particularly future recruitment and the length of time recruits remain in the fishery. Development of a permanent tag was seen as critical for obtaining the necessary data.

A considerable amount of time was spent on the predation component of natural mortality, especially predation by cod. Data suggest that, from egg extrusion to the adult stage, over 99 percent of the crabs are lost through a variety of factors. Cod predation may account for as much as 37 percent of this mortality. In order to better understand these predator/prey relationships, it was felt that we need to examine crab predation seasonally and work on digestion and feeding rates of major crab predators. Related comments indicated the need to define the role of competition with other crab and fish species.

Some individuals expressed an interest in monitoring physical parameters in the environment more closely on a continuing basis. It was generally agreed that this research was needed but difficult to justify to funding agencies on a cost effective basis.

The point was also raised that we could put considerable effort into studying the environment and the lifestyles of juvenile Chionoecetes and find that we know much about factors we cannot do anything about. The suggestion was made that we prioritize our research efforts so that we first obtain data that can be used directly in our annual management strategies, with less initial effort on aspects of Chionoecetes biology that are more remote from the fishery.

It was suggested that refining basic population assessment of the adult and near-adult portions of the population is what fishery managers need most urgently from the research community.

Regionally, interest was expressed in varying aspects of *Chionoecetes* biology. In Japan, the egg clutch incubation period in *C. opilio* was considered to be a high priority for future work, while in maritime Canada more work is needed on the molting cycle in *C. opilio* due to the perennial "soft crab" problem in the commercial fishery. In Alaska, aside from population estimation, interest was expressed in defining the role of disease, particularly black mat syndrome in *C. bairdi* (and *C. opilio*) population dynamics.

The remainder of the workshop session was devoted to compiling a prioritized list of research objectives for those working on the biology of the genus *Chionoecetes*. The resulting list is presented below. All items on the list are considered to be areas where knowledge needs to be acquired. Each item was rated by group consensus as high, medium, or lowest priority in regards to the need for immediate study relative to the other items on the list.

It was also recognized by the group that the priority categories are mutually exclusive, and that significant interactions between the items of the categories probably exist.

Research Needs *Chionoecetes* spp.

High Priority	Medium Priority	Low Priority
Growth-Molting Frequency	Predator-Prey Relations	Fishing Mortality
Disease (Pacific area only)	Fishing Mortality (Pacific)	Environmental Factors Affecting Mortality
Mortality Estimation	Stock-Recruitment	Molting Season (Pacific only)
Molting Season (Atlantic only)	Stock Delineation	Multispecies Management
Development Permanent Tag	Energetics	
Biomass Evaluation	Mating Behavior	
Distribution, Migration Juveniles	Incubation Period	
Forecasting		
Incubation Period (Japan only)		

The following list of management considerations was also identified by the group and when more fully explored may modify the above list of research goals.

Management Considerations

Management Goals

Economics Restraints (costs-benefits)

Implementation of Biological Management

Enforcement

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