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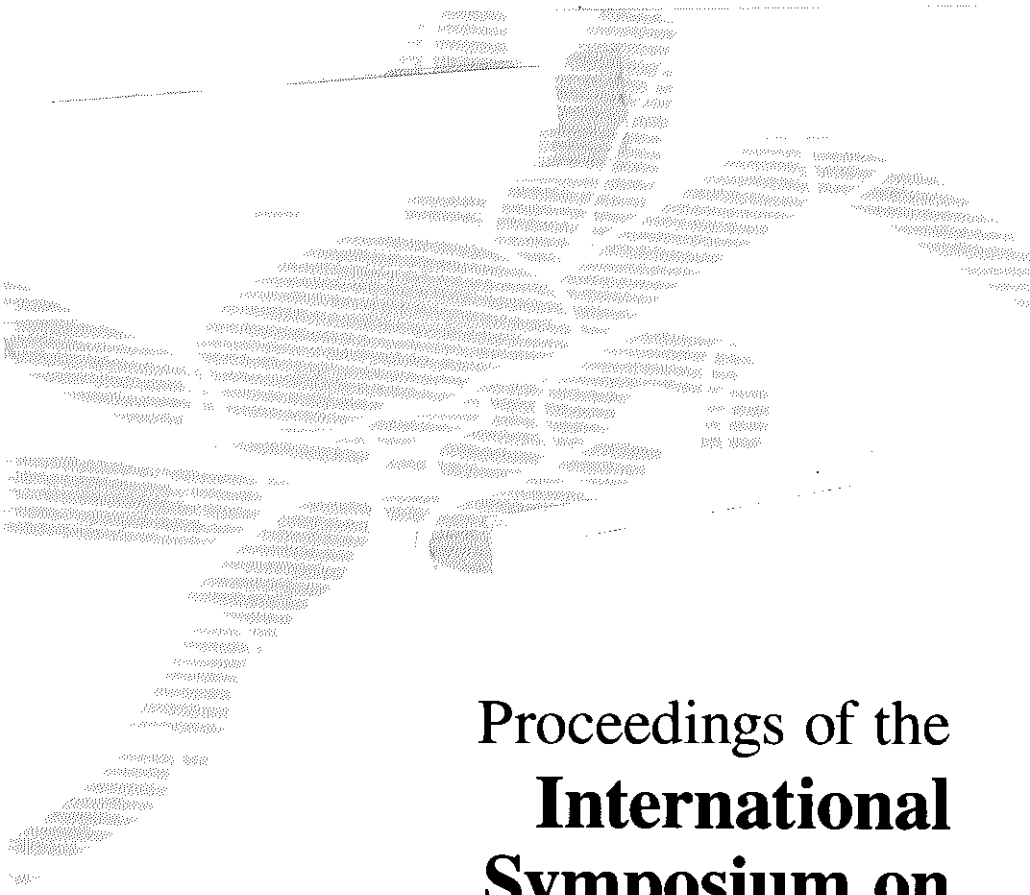

Proceedings of the International Symposium on King and Tanner Crabs

November 28-30, 1989
Anchorage, Alaska USA

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Proceedings of the **International Symposium on King and Tanner Crabs**

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Although the majority of the contributions in this book were presented at the symposium, several papers were not. Most manuscripts were provided camera-ready by the authors. Sue Keller compiled the proceedings. Ken Coyle translated and edited papers submitted by authors from the USSR. The workshop was recorded and transcribed by Gemini Reporting Services, and edited by Doug Schneider. Ruth Olson formatted many of the manuscripts, and Ingrid Nelson typeset front matter and titles. Karen Lundquist designed the cover and title page.

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Table of Contents

Our Coastal Environment: Science vs. Politics 1
John Costlow

An Overview of Eastern Bering Sea King and Tanner Crab Fisheries 9
Robert S. Otto

Tanner Crabs (*Chionoecetes opilio, C. bairdi*) of the Northwest Pacific: Distribution, Biological Peculiarities, and Population Structure 27
A.G. Slizkin

Reproduction 35

Reproductive Success of Sublegal Size Male Red King Crab with Access to Multiple Mates 37
J.M. Paul and A.J. Paul

Incubation Period, Molting and Growth of Female Red King Crabs: Effects of Temperature 51
T.C. Shirley, S.M. Shirley, and S. Korn

Fecundity and Other Reproductive Parameters of Female Red King Crab (*Paralithodes camtschatica*) in Bristol Bay and Norton Sound, Alaska 65
Robert S. Otto, Richard A. MacIntosh, and Peter A. Cummiskey

Disorders of the Reproductive Cycle in Crab Females of the Genus *Paralithodes* 91
S.A. Nizyaev and V.Ya. Fedoseev

The Size at the Onset of Maturity in Male *Chionoecetes bairdi* (Decapoda, Majidae) 95
A.J. Paul and J.M. Paul

Size at Maturity of Female Red King Crabs (*Paralithodes camtschatica*) in the Adak Management Area, Alaska 105
S. Forrest Blau

Life History 117

The Utility of Artificial Substrate Collection Devices To Determine Time and Location of Red King Crab (*Paralithodes camtschatica*) Glaucothoe Settling in Auke Bay, Alaska 119
J. Lincoln Freese and Malin M. Babcock

Behavioral Ecology of Podding Red King Crab, *Paralithodes camtschatica* 131
C. Braxton Dew

Population Biology of the King Crab *Paralithodes camtschatica* Tilesius in the North Pacific Ocean 133
V.E. Rodin

The Effect of Shell Condition on Male Snow Crab, *Chionoecetes opilio*, Weight-Width Relationships 145
D.M. Taylor and W.G. Warren

Life History Characteristics of *Chionoecetes tanneri* off British Columbia 153
G.S. Jamieson, G.D. Heritage, and N. Noakes

Review of Literature on Life Histories in the Genus *Chionoecetes* in Light of the Recent Findings on Growth and Maturity of *C. opilio* in Eastern Canada 163
G.Y. Conan, R.W. Elner, and M. Moriyasu

Longevity of Red King Crab, *Paralithodes camtschatica*, Revealed by Long-Term Rearing Study 181
S. Matsuura and K. Takeshita

Seasonal Migration of Primiparous and Multiparous Female Red King Crabs (*Paralithodes camtschatica*) 189
R.P. Stone and C.E. O'Clair

Oriented Movements of Tagged Male Snow Crabs (*Chionoecetes opilio* O. Fabr.) off the North Shore of the Gulf of St. Lawrence 193
Jean-Claude F. Brêthes and Francis Coulombe

Feeding and Growth 207

Effects of Cohort Density and Habitat on Survival and Growth of Juvenile Red King Crab, *Paralithodes camtschatica* 209
Patricia M. Rounds, Christine Brodersen, and Malin M. Babcock

Food and Feeding Habits of Red King Crab from Northwestern Norton Sound, Alaska 219
Stephen C. Jewett, Lee Ann Gardner, and Paul M. Rusanowski

Diel Feeding Periodicity of Larvae of the Red King Crab, *Paralithodes camtschatica* 233
S.M. Shirley and T.C. Shirley

Growth of Adult Male Blue Crab (*Paralithodes platypus*) 245
Robert S. Otto and Peter A. Cummiskey

Growth of Immature Southern King Crab, *Lithodes santolla*, in the Beagle Channel.....259
Julio H. Vinuesa, Laura I. Comoglio, and Gustavo A. Lovrich

Food of Early Benthic Stages of Snow Crab (*Chionoecetes opilio*) in the Southwestern Gulf of St. Lawrence.....273
Louise Lefebvre and Jean-Claude F. Brêthes

Physiological Energetics of the Snow Crab, *Chionoecetes opilio*.....283
R.J. Thompson and M. Hawryluk

A Temperature-Dependent Growth Model for Juvenile Red King Crab, *Paralithodes camtschatica*, in Kodiak, Alaska 293
Bradley G. Stevens and J. Eric Munk

Trophic Relationships of Crabs, Shrimps, and Fishes of the Western Bering Sea.....305
K.A. Zgurovsky, S.D. Bukin, A.G. Slizkin, and Ye.V. Lavrovsky

Feeding Habits of Southern King Crab, *Lithodes santolla* (Molina), and the False King Crab, *Paralomis granulosa* Jacquinot, in the Beagle Channel 315
Laura I. Comoglio, Julio H. Vinuesa, and Gustavo A. Lovrich

Mortality 327

Influence of Cold Air Exposures on Ovigerous Red King Crabs (*Paralithodes camtschatica*) and Tanner Crabs (*Chionoecetes bairdi*) and Their Offspring 329
M.G. Carls and C.E. O'Clair

Trace Metal Concentrations in Red King Crab from Norton Sound.....345
Paul C. Rusanowski, Lee Ann Gardner, Stephen C. Jewett, and Curtis A. King

A Method for Estimating Survival Rate of Male Zuwai Crab (*Chionoecetes opilio*) in the Western Japan Sea 365
Atsushi Yamasaki, Masatosi Sinoda, and Akihiko Kuwahara

Diet Influences Cannibalism in Laboratory-Held Juvenile Red King Crabs (*Paralithodes camtschatica*) 377
Christine C. Brodersen, Patricia M. Rounds, and Malin M. Babcock

Some Implications of Egg Mortality Caused by Symbiotic Nemerteans for Data Acquisition and Management Strategies of Red King Crabs, *Paralithodes camtschatica* 383
Jeffrey D. Shields, Daniel E. Wickham, S. Forrest Blau, and Armand Kuris

Brood Mortality Estimation and Role of Symbionts in Egg Mortality of the Tanner Crab *Chionoecetes bairdi* in Alaskan Waters 397
Daniel E. Wickham and Armand Kuris

Diseases of King Crab Species in Southeast Alaska
T.R. Meyers and S. Short 403

Bitter Crab Dinoflagellate Disease: Overview of the Causative Agent and Its Importance and Distribution in the Alaskan Tanner Crab (*Chionoecetes bairdi, C. opilio*) Fisheries.....405
T.R. Meyers, B. Eaton, S. Short, C. Botelho, T. Koeneman, A. Sparks, and F. Morado

Preliminary Results on the Seasonality and Life Cycle of the Parasitic Dinoflagellate Causing Bitter Crab Disease in Tanner Crabs 407
B. Eaton, C. Botelho, K. Imamura, T.R. Meyers, and T. Koeneman

Population Structure and Dynamics.....409

Population Structural Variation of the Southern King Crab, *Lithodes santolla*, of the Beagle Channel, Argentina, from 1975 to 1989.....411
D.A. Bertuche, J.G. Wyngaard, Carina E. Fischbach, and Enrique E. Boschi

A Note on Population Structure in the Eastern Bering Sea Adult Red King Crab, *Paralithodes camtschatica*.....427
K. Takeshita, Hitoshi Fujita, and Shuhei Matsuura

Effect of Hydrological Conditions on Harvest of Populations of the King Crab (*Paralithodes camtschatica*).....435
S.A. Nizyaev, V.Ya. Fedoseev, V.I. Myasoedov, and V.E. Rodin

Evaluation of Some Errors in Estimating Recruitment for the Bristol Bay Red King Crab Stock-Recruit Relationship 447
J.E. Reeves

Alternative Spawner-Recruit Specifications for Alaska Red King Crab: An Empirical Comparison 469
Scott C. Matulich, Joshua A. Greenberg, Dave B. Willis, and Ron C. Mittelhammer

Genetic Structure of Red King Crab Populations in Alaska Facilitates Enforcement of Fishing Regulations 491
James E. Seeb, Gordon H. Kruse, Lisa W. Seeb, and Robert G. Weck

Stock Assessment and Management.....503

Snow Crab Growth and Stock Size Estimations Obtained with Coded Wire Tags in the St. Lawrence Estuary 505
Réjean Dufour and Richard Bailey

A Comparison of Trawl and Pot Surveys of Red King Crab Populations (*Paralithodes camtschatica*) Near Kodiak, Alaska. 517
Jim Blackburn, B. Alan Johnson, and Dana Schmidt

An Industry Perspective on Problems Facing the Rebuilding of King and Tanner (Bairdi) Crab Stocks of the Eastern Bering Sea 533
Arni Thomson

Standardized Effort for the Kodiak King Crab Fishing Fleet 547
M.M. Johnson

Alternative Red King Crab Fishery Management Practices: Modelling the Effects of Varying Size-Sex Restrictions and Harvest Rates 551
Dana Schmidt and Douglas Pengilly

Research Perspectives on Northwest Pacific Bathyal Crustacean Resources 567
K.A. Zgurovsky, V.E. Rodin, A.G. Slizkin, and S.D. Bukin

Preserved Area To Effect Recovery of Overfished Zuwai Crab Stocks off Kyoto Prefecture 575
Atsushi Yamasaki and Akihiko Kuwahara

Development of a Fishery for *Chionoecetes tanneri* on the Continental Slope off British Columbia: Management Considerations 587
Glen S. Jamieson

The Role of Japan in King Crab Price Determination. 593
Joshua A. Greenberg and Scott C. Matulich

Importance of Bioeconomic Analysis in Managing the King Crab Industry 601
Scott C. Matulich

Workshop 611
Thomas Shirley and Scott Matulich, Moderators

Participants 627

Correct Spelling of the Scientific Name of the Red King Crab

Readers may note variations in the spelling of the scientific name of the red king crab in this symposium proceedings. Most authors were not aware of recent judgments and used an older, technically incorrect spelling of the species name. The correct spelling is now accepted as *Paralithodes camtschaticus* (Tilesius, 1815) and should be used in all future publications.

The species was first described as *Maja camtschatica* by Tilesius (1815) and nearly all subsequent crab systematists retained the original spelling of the specific epithet despite lack of gender agreement with new generic combinations, as the taxonomic placement of the species evolved to its present placement within the genus *Paralithodes*, family Lithodidae.

For proper gender and number agreement, the spelling *Paralithodes camtschaticus* should be used (personal communication, Dr. Austin B. Williams, Museum of Natural History, Smithsonian Institution). The correct spelling has been used recently in several prominent publications (Dawson, 1989; Williams et al., 1989).

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Our Coastal Environment: Science vs. Politics

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It is a pleasure, as well as a privilege, to return to Alaska, especially as part of the Alaska Sea Grant Program. A number of years ago, while serving as a member of the National Sea Grant review panel, I selected the Alaska program as one of the three that I would follow during my time on the panel. Thus, I visited here, as well as in Fairbanks, on several occasions and am looking forward to being brought up to date on progress in research on these extremely important species of crabs.

When Tom Shirley first approached me about participating in the meeting, I naturally asked for his thoughts on an appropriate topic. He suggested that certain areas of my own research would serve. As some of you are aware, one primary area of my research has focused on the development of crustacean larvae under controlled conditions in the laboratory. Initially, this was concerned largely with the impact of such natural environmental factors as salinity, temperature, light and diet. As techniques evolved, we began to combine two or more of these factors in the interest of exploring possible synergistic effects. Subsequently, these studies evolved further to include the impact of anthropogenic factors: heavy metals, pesticides, herbicides, and insect growth regulators.

In reviewing the abstracts sent to me earlier, I had the impression that many of the topics that I might address were already being considered. The program presented a very broad spectrum of topics; e.g., reproduction, life history, feeding and growth, mortality, population structure and dynamics, and stock assessment and management. It occurred to me that it might be useful to concentrate on that one basic factor which affects all of the above; i.e., the quality of the environment.

You can, quite naturally, ask why, in a symposium such as this one, I would include "Science vs Politics"? From my own experience, the quality of the coastal environment is dependent upon both the science and politics realms. "Science" is normally defined as the pursuit of knowledge, in this particular case an understanding of the natural environment and in what way a variety of factors, either independently or acting synergistically, have an impact on one or more species of organisms. Those of us in the scientific community like to pride ourselves on the exactness and discipline involved in our studies. We talk about following the "scientific method," or at least we used to, involving the development of a hypothesis, the design of an experiment to test the hypothesis, the careful accumulation and analysis of data from the experiment, and a discussion and comparison of the results relative to the original problem and hypothesis. In reality, the degree of exactness varies considerably! In the physical sciences, exactness is well established as exemplified by Boyle's Law. Unfortunately, when biological research is reviewed, it is apparent that we must accept results which may represent considerable inexactness, largely due to our present inability to fully understand all of the parameters involved in dealing with living organisms. For example, I cannot provide you this morning with a complete and accurate presentation on the overall aspects of recruitment of larvae and juveniles of any marine/estuarine invertebrate, primarily because we do not even know many of the interacting factors involved.

For the purposes of my presentation, and accepting that many of you may have different definitions, politics may be defined as the mechanism involved in providing guidelines for the management of society. I seriously doubt that anyone will claim that it is a science or that it is exact. The experimental method is rarely used and, at best, the multitude of approaches can be viewed as a variety of shades of gray rather than either "black" or "white." Incidentally, are there any members of the political community in the audience this morning? In case anyone should wonder as to my competence to speak to this point, I was privileged to serve as the elected mayor of Beaufort, North Carolina for two terms and consider myself somewhat of a student of the political process. Unfortunately, very few politicians ever enter into the realm of science! As for the scientists, you might agree that many of them practice a particular version known as "bio-politics," especially within the university systems and in relation to the art of grantsmanship! However, the issue of the quality of our coastal environment, for better or for worse, is governed by input from both the scientific community and the political community. It, too, is an issue which can be described as a spectrum of varying shades of gray.

Let us now consider two basic questions. First, in what way has the scientific community, through its research, contributed to an understanding of the quality of the coastal environment and the way in which a variety of anthropogenic changes may affect it? Second, to what degree has the political community utilized the information on these impacts within the coastal environment, which has been provided at taxpayers expense, and developed programs to intelligently manage and conserve our environment and its natural resources? To employ what is currently one of the several "buzz words" occasionally heard in our

nation's capital, how good is the "technology transfer" between the scientific community and the political community?

For a number of decades, in a large number of scientific communities throughout the world we have been accumulating vast volumes of literature describing the quality of our coastal environment and the impact of a variety of anthropogenic factors on many of the species found there. In preparation for my trip here I reviewed a number of these, some of which go all the way back to the 1960s! In 1959 the fledgling Atlantic Estuarine Research Society (A.E.R.S.), composed largely of scientists from New Jersey, Delaware, Maryland, Virginia, and North Carolina, adopted and submitted a resolutionto the Senate Committee on Interstate and Foreign Commerce endorsing President Detleve Bronk, then president of the U.S. National Academy of Sciences, and his formation of a Committee on Oceanography, and encouraging the Committee to support Senate Bill 2692, "Marine Sciences and Research Act of 1959" as introduced by Senator Warren G. Magnuson and associates. Richard C. Vetter, for many years the executive secretary of the Committee on Oceanography, circulated within the scientific and political communities a draft document, "International and National Organization of Oceanographic Activities," followed by the final version, "Oceanography 1960-1970." Planning was initiated by a number of us within the A.E.R.S. for the first national meeting on estuaries and it has been interesting to review the list of participants and presented papers at the Jekyll Island, Georgia Conference on Estuaries, April 1964. Not long thereafter, the estuarine associations, in time to represent the entire coastline of the United States, developed a federation to meet every two years, the Estuarine Research Federation. One particular document which I discovered in my files is of special interest, although unfortunately it is not dated. The authors were D.W. Hood and J.J. Goering and the title is, "Pollution Problems in the Estuaries of Alaska." It could be interesting to invite the senior author, a friend of mine for many years and now retired, to present his views on this topic in 1990! I would be remiss if I did not identify what may well have been the "spark" that led to a general public awareness of the degree to which society was beginning to alter the natural environment in a most disturbing way; e.g., the book *Silent Spring*, a milestone contribution which should be required reading for any individual interest in their environment!

A portion of my recent sabbatical leave was spent at the Plymouth Marine Laboratory, Plymouth, England. As many of you know, they have one of the finer libraries relating to marine research anywhere in the world. Within their section on marine pollution, begun approximately fifteen years ago, there are 45,000 separate publications resulting from research conducted all over the world. Have no fears, I do not intend to review even a small sample of them this morning, but it does point out that the scientific community has contributed a considerable body of information concerning the quality of the world's coastal environment and the ways in which it may have an impact on a variety of species and the functions necessary for survival.

Segments of our national government, and certain state governments, were also contributing to measures intended to at least explore the impacts of anthro-

pogenic changes in our estuarine systems. I continue to treasure the volume, *Clean Water for the Nation's Estuaries*, the proceedings of the North Carolina Public meeting held in New Bern, North Carolina on July 26, 1968. It was organized by a group that many of you here today will not recognize, the Federal Water Pollution Control Administration, the forerunner of the Environmental Protection Agency created by Act of Congress in 1970. The reason for my special interest in this volume lies in the number of letters and statements, many from representatives of major industries as well as political figures, assuring all present of their concern for the quality of the environment and the dedication of their interests to contribute to maintaining it, an assurance which has not always been totally evident in the subsequent years!

Thus, in all fairness, the political community, at least within North America, did not ignore all of this information. Beginning toward the latter part of the 1960s, individual states, as well as federal governments, became aware of the need to be concerned by the rapidly expanding development of our coastal areas and some highly significant legislation was enacted. It is with some pride that I can refer to the N.C. 113:229, originally identified as the 1969 North Carolina "Dredge and Fill Act." In extremely simple language, in perhaps half of one page, it indicates that if one of eleven identified species of marsh grass is found within an intertidal area, that area is a marsh and may not be either dredged or filled without a permit subject to public hearings. All of us can, or should be able to, identify the National Environmental Protection Act, the Coastal Zone Management Act, and the more recent Clean Water Act of the Congress of the United States.

With the information provided by the scientific community, coupled with the legislation enacted by state and federal governments, one might expect that this combination has been extremely effective in providing for the proper conservation and management of our coastal environment and that we can now turn our attentions to the more global problems such as the greenhouse effect, the origin of the cosmos, the fate of super nova, etc. There are suggestions, however, that the task has only begun, even in those areas of the world which are generally viewed as informed and intelligent.

At this point, since we are situated this morning adjacent to one type of coastal environment which is extremely specialized, it might be useful for me to briefly review another coastal environment with which I am personally involved and is quite different from that found in Alaska. An overview of the coast of North Carolina presents a broad, shallow shelf, bounded to the east by the Florida Current or Gulf Stream. As one moves toward the meeting of the sea with the land, one finds the barrier islands for which North Carolina is so famous in history. These narrow and extremely fragile strips of sand and specialized vegetation separate the ocean from the extensive bays or lagoons, expanses of water of reduced salinity due to the freshwater runoff from the low-lying land honeycombed with tidal marshes, extensive estuarine systems, and a few rivers which, in colonial days, served for transportation and a source of fish and shellfish. As one of the earliest areas settled by our European ancestors, it has been documented for three-and-a-half centuries as an area of high productivity and has

been utilized by society in a variety of ways.

Having established themselves in the low-lying areas, both on the barrier islands and on the mainland itself, the early settlers undoubtedly began to harvest the vast fisheries resources found in the shallow estuarine systems along the entire coast. This may have been followed by farming the extremely fertile areas which were cleared in the process of providing George III with "naval stores"; e.g., spars, masts, and turpentine for the insatiable demands of his mighty navy. Once the volume of the products derived from their fishing and farming exceeded their own needs, one can assume that coastal shipping followed as the beginning of commerce. At some point, considering the early use of our waterways for transportation, a variety of types of industry became established. In more recent years, with an improvement in standard of living and more leisure time, the coastal environment was discovered by tourists who came to enjoy the waters, the fishing, and the restful atmosphere removed from the stresses of large municipalities. Subsequently, having discovered the area, some of these families purchased second homes for more regular use or in anticipation of retirement. At some point, universities such as Duke developed marine laboratories in the coastal areas as adjunct campuses for teaching and research, and as our capability improved and financial support became available, this training and research moved out onto the shelf and beyond in the form of oceanographic research vessels. With a better understanding of the shelf environment, the oil industry developed the technology for offshore drilling for oil and gas, a process which is being considered off of the North Carolina coast for the first time. Almost since the beginning, various segments of our armed services have utilized portions of the coastal environment for fortifications for the protection of the society which was steadily expanding over the continent.

Thus, over the years, the utilization of our coastal environment has evolved and expanded tremendously. In 1987, the then Department of Natural Resources and Community Development of North Carolina indicated in its annual report that total revenues from all activities in the coastal area amounted to two billion dollars! It is useful to consider what amount of dollars, in the form of "principal," one would need to have invested at eight per cent per annum to yield such a return! If my calculations are correct, one would have to have invested in the range of twenty-four billion dollars! The coastal environment, therefore, represents a major contributor to the economy of the state and, if only for that reason, some consideration needs to be given to the current management and conservation programs at all levels of the government involved.

As early as the end of the decade of the 1950s, some citizens were beginning to be concerned that one or two of the established uses of the coastal environment could become dominant to the point of eliminating other, more traditional uses such as marine fisheries, or, as a result of by-products of these uses, contaminate the environment to the point that other, equally valid uses would no longer be possible. In essence, the concern focused on that point where use becomes "abuse"! A number of these uses have been the focus of studies by the scientific community and, to some degree, have been subsequently considered in legisla-

tion by both state and national governments. Let me review a few examples and then ask yourselves to what degree the research of your own scientific community has made contributions to an understanding of the impact of certain factors and how the political community with which you are, or should be involved has responded.

With the discovery of the coastal area by increasing numbers of people, some developers increased the available water-front property by dredging "finger-canals." In certain areas, both along barrier islands and on the mainland itself, areas that had been basically pristine for centuries became the sites of construction almost overnight. In the process, protective sand dunes were bulldozed, vegetation was removed, and little thought was given to storm over-wash necessary for continued maintenance of the barrier islands or the extent to which erosion would affect the property in the years that followed. In many cases, little or no attention was paid to the existing potable water supplies, adequate for small fishing communities but rapidly depleted by the influx of the expanding population. In the same way, little attention was paid to the increase in volume of sewerage and although septic tanks initially appeared to provide a solution, frequently the nature of the soil was totally inappropriate for adequate percolation. Under pressure for more refined systems for collection and treatment, economic considerations were frequently permitted to dictate the construction of facilities in areas that were totally unsuitable and discharge of the secondary treated effluents occurred into small tributaries contiguous with the estuarine systems. Whether by accident or design, all too frequently these discharges began to result in increases in the fecal coliform bacteria counts in waters previously used for centuries by shell-fishermen and closures became common, a necessary result required by the Health Department to avoid hepatitis and other human diseases. On occasion it has been argued that, considering the tremendous expanse of estuarine waters and tidal marshes in North Carolina, a "few" acres lost to closures were insignificant. In fact, in North Carolina a total of 321,000 acres of estuarine waters have been closed to shellfishing in recent years.

A second problem deals with the increase of nutrients in estuarine waters, nutrients derived from such common sources as household detergents, fertilizers routinely used in agriculture, the numerous septic tanks that continue to be used, frequently without any regular inspection, and the nonpoint runoff resulting from clear cutting of the forests. Well established by the scientific community is the result: the occurrence of algal blooms and the development of the unpleasant aroma of rotting algae followed by total depletion of oxygen from the water column and subsequent death of the organisms dependent upon oxygen.

Although still not understood, changes or additions to the water column in the past decade have resulted in increasing occurrence of unhealthy lesions on both finfish and blue crabs, two of the mainstays of the commercial fisheries in the coastal area of North Carolina. Concurrently, there appears to be an increase in numbers of "fish kills" resulting in the deaths of thousands of fish of interest to both commercial and recreational fishermen.

And finally, an example of "abuse" which is, unfortunately, of special interest and sensitivity to you in the audience; e.g., oil spills. From a number of examples over the past twenty years, it is apparent that crude oil can totally destroy an estuarine environment, eliminating for some years the more traditional uses and destroying the economic value for those who are dependent upon it for their livelihoods.

In each of these examples, at least as they relate to the laws of North Carolina, there is a common problem which is as yet not totally resolved. Since colonial days, the right of individuals to own property has been firmly established. Equally firmly established is the right of all citizens to claim the estuarine and tidal areas as part of their "public trust," held and managed for all of them by the government of the state. The major conflicts seem to develop when these two rights converge; e.g., how to prevent the results of development of private property from destroying that which is held by the state for all of its citizens.

A recent article in the Raleigh *News and Observer* indicates that a series of meetings is scheduled by the Environmental Management Commission in various locations throughout eastern North Carolina to hear citizens' views on the recently established regulation relating to "Outstanding Resource Waters." Those areas identified as "ORW's" would be subject to considerably more stringent regulations in development, protection of nursery areas, discharges, etc. I, as a scientist, will be watching the outcome of these public meetings with considerable interest, if only because they may serve as an example of how well the information developed on the coastal environment by the scientific community has been transferred to the political community.

I am relatively confident that you will agree that the scientific community has provided, in many cases and in many geographical areas of the world, conclusive evidence that the introduction of certain pollutants into the estuarine and coastal environments will cause a variety of negative results. All of us can identify a number of these examples, in the best tradition of "cause and effect."

Each of us may well have our own responses to the second question, however; e.g., to what extent has the political community with which we are involved utilized this information in the interest of providing for a cleaner environment? I, most certainly, have my own thoughts on this question as it relates to the political establishment in North Carolina! I would suggest that you, individually, review the question and then, if your conclusion finds your political establishment lacking in one or more levels or areas, make your observations known, not only to them but also to your colleagues and citizen groups to influence the desired changes.

In conclusion, the realms of science and politics need to collectively abandon their "ivory towers" and establish better mechanisms for technology transfer as it relates to intelligent management and conservation of our coastal environment. The "partnership," however, urgently needs to be expanded to include aspects of a third, dominant segment: e.g., industry. As with government, this third segment can only operate efficiently and profitably when it reflects the consensus of those

it serves. Such a partnership can be successful only if it includes the education of all of its members, especially the citizens to whom this valuable asset belongs, in the hope that as we end the twentieth century, those who follow can also enjoy those numerous benefits which we have been privileged to derive from our coastal environment.

Proc. Int. Symp. King & Tanner Crabs
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An Overview of Eastern Bering Sea King and Tanner Crab Fisheries

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ABSTRACT

The history of eastern Bering Sea crab fisheries extends back to 1930, but large-scale commercial efforts were not undertaken until development of king crab fisheries in the 1950s. Tanner crab fisheries were developed in the 1960s. Japan and the Soviet Union had large fisheries before the United States mounted a substantial effort. Foreign fisheries for king crabs ceased in 1974. Foreign Tanner and snow crab fisheries have been prohibited under the Magnuson Fisheries Conservation and Management Act since 1980. Eastern Bering Sea fisheries for red king crab (*Paralithodes camtschaticus*), blue king crab (*P. platypus*), Tanner crab (*Chionoecetes bairdi*) and snow crab (*C. opilio*) have been among the most important sources of crab in the world. Declining abundance of all stocks occurred in the 1980s and precipitated fishery closures for red king crab (1983), *C. bairdi* (1986, 1987) and Pribilof Island blue king crab (1988). These losses were partially offset by the development of fisheries for golden king crab (*Lithodes aequispina*) in the Aleutian Islands during the 1980s. The *C. opilio* fishery was a minor contribution to landings in 1980, but is now the most important U.S. crab fishery. This paper reviews changes in resource abundance and fisheries with emphasis on events of the last decade.

INTRODUCTION

Commercial fisheries for king (*Paralithodes* and *Lithodes* spp.), Tanner and snow crabs (*Chionoecetes* spp.) in the eastern Bering Sea and Aleutian Islands (EBS/AI) have long been among the world's most important sources of crabs. Comparison of regional landings with the United Nation's Food and Agricultural Organization statistics (FAO, 1989) shows that in 1987, the EBS/AI area provided 21% of the king crabs, 52% of the Tanner and snow crabs, and over 5% of all crabs in world landings. These fisheries were more important in U.S. landings (Department of Commerce, 1989), providing 87% of the king crabs, 89% of the Tanner and snow crabs, and 33% of all crabs in 1987. Fluctuations in abundance of king, Tanner and

snow crabs have caused major dislocations in the U.S. North Pacific fishing industry. While these fisheries remain important, note that they accounted for 12% of world crab landings in 1977 (Otto, 1981).

While such statistics are impressive, EBS/AI crab fisheries have undergone radical changes over the past decade. In 1978, red king crab (*Paralithodes camtschaticus*) made up 92% of the king crab landings in the EBS/AI region while blue king crab (*P. platypus*) made up the remainder and golden king crab (*Lithodes aequispina*) were only taken incidentally. By 1988, red king crab landings (44%) were no longer dominant and 50% (Fig. 1) of landings were golden king crab. In 1978, landings of all EBS/AI king crabs totaled 47,960 metric tons (t) but by 1988 they were only 9,550 t. Similarly, EBS/AI Tanner and snow crab fisheries were developed by exploiting *Chionoecetes bairdi* (hereafter, Tanner crab, Williams et al., 1989) and, as landings declined or fisheries management dictated, they later exploited *C. opilio* (hereafter, snow crab, ibid). Snow crab from the EBS are now the most important species of crab in the United States in terms of landed value, with 1988 landings worth $104 million or 27% of the value of all U.S. crab landings as compared to $10 million or 3% in 1978.

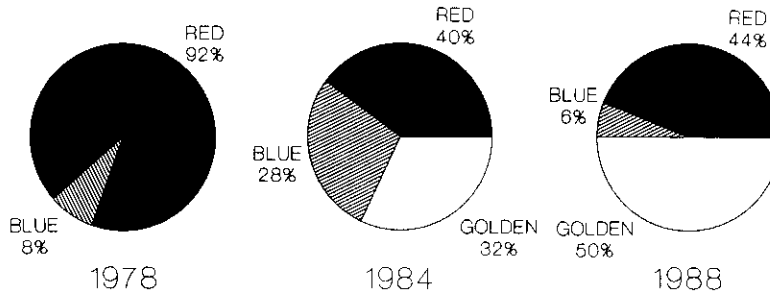

Figure 1. Relative contribution of red king crab, blue king crab, and golden king crab to landings of king crabs from the eastern Bering Sea and Aleutian Islands.

My purpose here is to provide a brief overview of king, Tanner and snow crab fisheries with emphasis on the past decade and largely regarding trends in landings or value. Interested readers should consult previous reviews (Otto, 1981, 1982; Fukuhara, 1985; Baglin et al., 1988; Alaska Department of Fish and Game (ADF&G), 1989a) for earlier historical data or more detailed accounts. I have chosen to include fisheries in the Aleutian Islands as well as the eastern Bering Sea shelf because the important development of the golden king crab fishery largely took place in the Aleutian Islands.

From the perspective of fishery management, stocks in the eastern Bering Sea and Aleutian Islands have been considered together (North Pacific Fishery Management Council, 1989) because the same fleet of vessels and the same segment of the processing industry are involved. I have not mapped the geographic distribution of various stocks in the interest of brevity. In general, my use of the term "stock" refers simply to crab inhabiting a geographic management area (e.g., areas defined in Alaska Department of Fish and Game, 1989b). Such stocks are generally delineated by the following terms: Bristol Bay (54°36' to 58°39' N. lat. and to 168° W. long.),

Pribilof Islands (immediately west of Bristol Bay), St. Matthew Island (blue king crab landings N. of 58°39' lat.), eastern Aleutian Islands or Dutch Harbor (168° to 171° W. long.), western Aleutian Islands or Adak (171° W. long. to the U.S.-U.S.S.R. convention line of 1867), and eastern Bering Sea (north of 54°36' N. lat., east of 180° W. long.). All EBS/AI crab fisheries are limited to harvest of males above a given legal size which is generally designed to allow males to breed at least once before becoming vulnerable to commercial fishing. Almost all of them are also regulated by fishing seasons designed to promote product quality and protect stocks during molting-mating seasons. King crab fisheries generally occur in the fall while the vast majority of landings in Tanner and snow crab fisheries occur in late winter or spring. A form of quota management is also employed.

A BRIEF HISTORY OF EBS/AI CRAB FISHERIES

Commercial crab fisheries in the EBS/AI region began in the 1930s with Japanese exploratory efforts in Bristol Bay (Cahn, 1948; Harrison et al., 1942; Miyahara, 1954; Kasahara, 1972). Japanese efforts were directed at Bristol Bay red king crab but did not develop a major fishery prior to World War II. About 7.6 million crab were, however, harvested in the 1930s (Miyahara, 1954). The United States began exploratory fishing in 1940, and by 1949 all major red king crab stocks in Alaskan waters were known. The distribution of blue king crabs had also been described. U.S. efforts in the EBS/AI for the years 1949-1952 were sporadic and yielded about 4,200 t. In contrast to later years, U.S. fishermen were trawling for king crabs during these years. Undoubtedly both U.S. and Japanese fishermen were aware of Tanner and snow crab resources as well, but there is little or no mention of them in early reports.

The Japanese renewed their efforts in Bristol Bay in 1953 and this stock of red king crab has been continuously exploited since, except in 1983 when the fishery was closed due to low stock abundance. The U.S.S.R. entered the fishery in 1960 and U.S. fishermen began fishing with pots in Bristol Bay in the mid-1960s while simultaneously developing red king crab fisheries in the Aleutian Islands. Fishing for blue king crabs was initiated by the Japanese in 1966 near the Pribilof Islands. Both Japanese and Soviet fisheries for king crabs in the EBS/AI region ceased in the early 1970s. Golden king crab were taken only incidentally until directed fisheries were initiated in the 1980s in response to low abundance of other king crab stocks. A history of king crab landings by species and nation is given in Table 1 for the years 1953-1978.

Japanese motherships processed Tanner crab as early as 1953 and continued to process small amounts sporadically in the 1950s as recorded in International North Pacific Fishery Commission Annual Reports (INPFC, 1956; Fisheries Agency of Japan, 1959, 1960). These processing efforts were apparently experimental and the largest pack was of 3,457 cases (48 one-half pound, 0.23 kg, cans) while the total for the five years in which Tanner crab were processed was 7,754 cases. Judging from later packing statistics the annual average landings would have been about 300,000 Tanner crab during the 1950s (Otto, 1982). Snow crab may have been processed as well during the 1950s but judging from the grounds fished almost all of the pack was probably *C. bairdi*. Directed fisheries in the EBS began in 1965 through deployment of Japanese king crab tangle nets on Tanner crab grounds. Soviet fleets followed suit but their catches of *Chionoecetes* spp. remained incidental to red king crab fishing. The Japanese developed a directed fishery for *Chionoecetes* spp. using conical pots in 1967, and this fishery continued on various grounds and under quotas negotiated through U.S.-Japan bilateral agreements until 1980. In 1980, Japanese

Table 1. Estimated annual landings of king crabs from the eastern Bering Sea and Aleutian Islands by nation and species for 1953 to 1978 (1000's t).[1]

	United States		Japan		USSR	Totals		
Year	Red[2]	Blue[3]	Red	Blue[4]	Red	Red	Blue	Grand
1953	0.91		5.16			6.06		6.06
1954	1.06		3.67			4.72		4.72
1955	0.85		3.94			4.79		4.79
1956	0.86		3.77			4.63		4.63
1957	0.27		3.88			4.14		4.14
1958	0.00		3.69			3.69		3.69
1959	0.00		4.28		0.98	5.26		5.26
1960	1.21		6.28		4.89	12.38		12.38
1961	3.22		9.90		8.55	21.67		21.67
1962	4.36		15.94		8.22	28.52		28.52
1963	9.86		16.39		9.31	35.56		35.56
1964	16.27		18.45		10.16	44.88		44.88
1965	15.36		11.07		6.16	32.59		32.59
1966	18.02		12.66	0.91	6.39	37.07	0.91	37.98
1967	18.12		9.83	1.10	3.83	31.78	1.10	32.87
1968	17.41		10.46	0.72	1.37	29.24	0.72	29.97
1969	16.95		3.06	2.49	0.85	20.87	2.49	23.35
1970	15.54		4.51	0.58	0.77	20.83	0.58	21.41
1971	17.16		1.61	0.56	0.64	19.41	0.56	19.96
1972	23.11		2.01	0.14		25.12	0.14	25.25
1973	22.40	0.58	0.56	0.02		22.96	0.60	23.56
1974	26.78	3.22	0.40	0.79		27.18	4.01	31.19
1975	30.68	1.10				30.68	1.10	31.79
1976	33.62	3.00				33.62	3.00	36.62
1977	34.05	3.47				34.05	3.47	37.53
1978	44.15	3.80				44.15	3.80	47.96

[1] U.S. data prior to 1961 and all foreign data are from Otto (1981), remainder are from Alaska Department of Fish and Game Westward Region Board Reports (e.g., ADF&G, 1989a); years are those in which the fishing season started, carry over to the next year occurred occasionally.

[2] Includes landings from Bristol Bay, eastern Aleutian Islands (Dutch Harbor), western Aleutian Islands (Adak), Norton Sound and Pribilof Islands; trawl catch prior to 1960.

[3] Includes Pribilof and St. Matthew Islands (540 t, 1977 only).

[4] Pribilof Islands only.

fisheries for *Chionoecetes* spp. were prohibited under provisions of the Magnuson Fisheries Conservation and Management Act. The Soviets left the fishery in 1971 when they ceased fishing for red king crab. Japanese landings exceeded 10 million crabs in all but two years for the period 1970 to 1980, but Soviet landings never exceeded 6.5 million crabs. United States fishermen harvested Tanner crab as early as 1968 but landings were incidental to king crab fishing until 1975. The United States did not begin a directed fishery for snow crab until 1979. A history of landings of *Chionoecetes* spp. by nation and estimated species composition is given in Table 2 for the years 1965-1978.

Note that foreign catches of king, Tanner, and snow crabs were reported through INPFC and bilateral agreements as numbers of crabs, and that the figures in Tables 1 and 2 are approximate--especially with regard to species composition. Such

Table 2. Estimated annual landings of Tanner (*Chionoecetes bairdi*) and snow (*C. opilio*) crabs from the eastern Bering Sea (EBS) and Aleutian Islands by nation and species for 1965 to 1978 (1000's t)[1]

	U.S. *bairdi*		Japan		USSR	Totals[2]		
Year	Aleutians	EBS	*bairdi*	*opilio*	*bairdi*	*bairdi*	*opilio*	grand
1965			1.02	0.05	0.69	1.71	0.05	1.76
1966			1.47	0.08	0.69	2.16	0.08	2.24
1967			8.51	0.45	3.53	12.03	0.45	12.48
1968		0.01	21.95	1.16	6.73	28.68	1.16	29.84
1969		0.46	16.72	0.88	6.25	23.42	0.88	24.30
1970		0.64	15.92	1.38	5.44	22.00	1.38	23.38
1971		0.08	12.64	1.56	3.79	16.50	1.56	18.06
1972		0.09	13.30	0.70		13.39	0.70	14.09
1973		0.14	8.57	4.03		8.70	4.03	12.74
1974	0.26	2.29	9.59	3.03		12.14	3.03	15.17
1975	0.04	3.19	4.47	3.63		7.69	3.63	11.32
1976	0.27	10.14	3.83	4.27		14.24	4.27	18.51
1977	0.56	23.34	2.95	6.85		26.85	6.85	33.70
1978	0.22	30.21	1.30	10.50		31.73	11.28	42.23

[1] U.S. data are from Alaska Department of Fish and Game Westward Region Board Reports (e.g., ADF&G, 1989); Japanese estimates are from FAO as adjusted for species composition given in Otto (1981) assuming 5% *C. opilio* in years prior to 1970 except that 1974 FAO catch data were clearly in error and 1974 catch was estimated by applying the mean weight from 1973 to the catch in number from 1974 (Otto, 1981); U.S.S.R. estimates are catch in number multiplied by the mean weight in the Japanese fishery on the basis that both fleets used tangle nets and fished similar grounds.

[2] Totals are probably near correct but species composition is approximate for reasons noted above and because there are no extant species composition data for the USSR. Grand total for 1978 includes 780 t U.S. catch of *C. opilio*.

estimates are given simply to facilitate comparison with subsequent data given below.

KING CRABS 1979 TO 1988

At the beginning of this period, EBS/AI king crab fisheries were similar in species composition to the previous decade, but by 1981 the historical dominance of red king crab was waning (Table 3). This occurred both due to declines in abundance of red king crab stocks and the development of new fisheries for blue king crab near St. Matthew Island and for golden king crab in the Aleutian Islands. The contrast in species composition from the beginning, middle, and end of this period is stark (Fig. 1). Transitions in the fishery were violent with EBS/AI landings reaching an all-time high of 74,290 t worth $149.5 million in 1980, falling to 6,650 t worth $40.2 million by 1984, and recovering somewhat in later years (Tables 3 and 4). Even with their mixed history over these years, the nominal value of EBS/AI king crab landings remained high largely because the unit value of king crabs has increased as landings declined. For example, the dockside price of Bristol Bay red king crab was $2.71/kg in 1978 and $10.00/kg in 1988. It is also noteworthy that red king crab fisheries in Dutch Harbor (eastern Aleutian Islands) as well as the whole Gulf of Alaska have been closed from 1983 onwards due to low stock abundance. Since blue and golden king crab fisheries outside the EBS/AI region are nearly negligible,

Table 3. Species composition of king crab landings (1000's t) from the eastern Bering Sea and Aleutian Islands.

Year[1]	Red[2] Catch	Red[2] %	Blue[3] Catch	Blue[3] %	Golden[4] Catch	Golden[4] %	Total
1979	57.26	95.3	2.82	4.7	0.01	0.0	60.09
1980	69.19	93.1	5.08	6.8	0.03	0.0	74.29
1981	19.53	74.1	6.22	23.6	0.60	2.3	26.34
1982	2.65	20.4	6.01	46.4	4.29	33.1	12.94
1983	1.09	9.7	5.28	46.9	4.90	43.5	11.27
1984	2.67	40.2	1.85	27.8	2.13	32.1	6.65
1985	2.50	25.7	1.34	13.8	5.89	60.5	9.74
1986	5.71	44.1	0.57	4.4	6.65	51.4	12.94
1987	6.27	54.4	0.81	7.0	4.46	38.7	11.54
1988	4.21	44.1	0.60	6.3	4.74	49.6	9.55
Totals	171.07	72.7	30.57	13.0	33.70	14.3	235.34

[1] Year in which season began, season sometimes extends into following year.

[2] Stocks contributing to landings over this time period were Bristol Bay (85%), Dutch Harbor or eastern Aleutian Islands (10%), Adak or western Aleutian Islands (3%), Norton Sound (2%).

[3] Pribilof Islands (54%) and St. Matthew Islands (46%) (see footnote 2).

[4] Dutch Harbor (15%), Adak (82%), Bering Sea (<3%) (see footnote 2).

the EBS/AI area has provided virtually 100% of U.S. king crab landings in 1983 and later years. In 1988 king crab were processed by 8 shore-based plants, 14 floating plants, and 17 catcher-processor vessels. More than 183 catcher vessels participated in these fisheries as well.

Stocks of EBS/AI king crabs show major fluctuations in abundance and hence their relative contribution to regional landings. Over the past decade landings were dominated by Bristol Bay red king crab which provided 60% of landings and 51% of the landed value of all king crabs from the region. Next in order of importance were Adak golden king crab, Dutch Harbor red king crab, Pribilof Islands blue king crab, and St. Matthew Islands blue king crab. Together, these "major" stocks have provided 93% of landings and 91% of the nominal landed value of EBS/AI king crabs in the past decade (Tables 3 and 4). The Dutch Harbor red king crab fishery has been closed due to low stock abundance from 1983 onward and there is little current information on this stock. It should be noted, however, that red king crab fisheries in both Dutch Harbor and Adak management areas were considerably larger in earlier times. A brief review of major king crab stocks with the exception of Dutch Harbor follows. Data are from the ADF&G (1989a) and from Stevens and MacIntosh (1989).

Table 4. Landed value of king crabs from the eastern Bering Sea and Aleutian Islands in millions of U.S. dollars (not adjusted for inflation).

	Red		Blue		Golden		
Year[1]	Value	%	Value	%	Value[2]	%	Total[3]
1979	124.9	95.3	6.2	4.7	0.0	0.0	131.2
1980	139.4	93.3	10.0	6.7	0.1	0.0	149.5
1981	68.6	77.0	17.8	20.0	2.7	3.0	89.1
1982	18.4	23.8	31.1	40.3	27.7	35.8	77.2
1983	7.5	10.4	34.9	48.7	29.3	40.8	71.7
1984	14.0	50.5	7.4	26.6	6.3	22.9	27.7
1985	14.5	31.7	5.4	11.9	25.7	56.4	45.6
1986	49.5	50.8	4.3	4.4	43.7	44.9	97.5
1987	54.5	61.7	5.9	6.6	27.9	31.6	88.3
1988	46.3	52.0	4.1	4.6	38.7	43.4	89.1
Totals	537.6	62.0	127.1	14.7	202.1	23.3	866.9

[1] Year in which season began hence totals are not actually annual.

[2] Zero indicates less than $50,000.

[3] Totals do not include small amounts of golden king crab from the Bering Sea for which landed value is lacking.

Bristol Bay Red King Crab

Cumulative landings from this stock represent the largest source of king crabs from U. S. waters and are second only to western Kamchatka red king crab in the history of world king crab fisheries. This stock produced the highest king crab landings in Alaskan waters for the years 1968-1982 and from 1987 to present. Despite its large contributions, the Bristol Bay stock has fluctuated widely in abundance. After a period of fishery development in the early 1950s, stock abundance apparently peaked in 1959-1960 as judged by catch per Japanese or Soviet tangle net (Otto, 1981). This peak in abundance preceded a peak in production of 29,000 t in 1964, that was followed by gradually declining catch per unit of effort (CPUE, catch per pot lift) and production through 1970-1971. From 1972 through 1978 stock abundance as measured by National Marine Fisheries Service (NMFS) surveys, CPUE and landings rose dramatically (Fig. 2).

The past decade has been the most variable in terms of stock abundance and landings. In 1979 this fishery produced 48,900 t or 70% of U. S. king crab landings. By 1980 landings reached a record 58,900 t, again 70% of U. S. landings, and 56% of world king crab landings. Survey estimates of abundance, and CPUE, however, peaked in 1978-1979 and declines were anticipated due to decreased recruitment (Otto et al., 1980). Declines in the abundance of legal male red king crab from 1980 to 1983 were far sharper than anticipated and in 1983 the fishery was closed. While large commercial fisheries undoubtedly caused some of the decline in abundance of legal males, other segments of the stock also declined sharply during this period. Declines in the population as a whole may well have been caused by epizootic diseases and increased predation as well as poor recruitment (Otto, 1986).

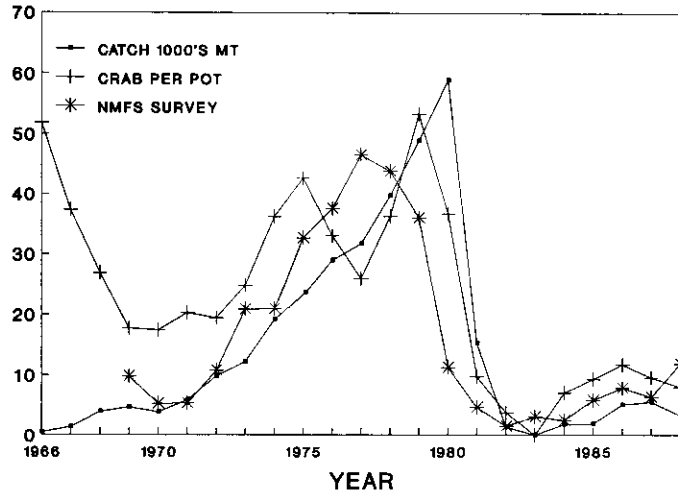

Figure 2. Comparison of U. S. commercial catch and crab per pot lift (CPUE) with NMFS survey estimates of the abundance of legal male red king crab (millions) from Bristol Bay. Note that the fishery was closed in 1983.

Bristol Bay red king crab have recovered somewhat since 1983 but average production was only 3,600 t for 1984-1988 as compared with an average of 18,600 t for the 1960s and 23,400 t for the 1970s. Reduced production from Bristol Bay is a principal reason why world king crab production fell from 104,600 t in 1980 to 39,400 t in 1983 and has since averaged 48,200 t. Currently, the stock remains at low abundance and shows no definite sign of recovery.

Pribilof Islands Blue King Crab

The Pribilof Islands blue king crab fishery was developed by the Japanese in the late 1960s. Although there had been some prior exploration of the area, development was spurred by declining abundance in Bristol Bay red king crab and decreasing quotas negotiated through U.S.-Japan Bilateral Agreements. Landings were, in part, incidental to Tanner and snow crab fisheries until the development of a U. S. fishery in 1974. All landings of blue king crab shown in Table 1 were from the Pribilof Islands until 1977 when the first landings (540 t) were made from the St. Matthew Island area. For 1966 through 1978 the contribution of this stock to EBS/AI king crab landings did not exceed 13%.

The history of the U. S. fishery and abundance estimates for legal males from the NMFS survey (Fig. 3) are inconsistent in years prior to 1978. During these early years catch tended to fluctuate with the number of vessels (e.g., 8 in 1973, 70 in 1974, and 20 in 1975); however, CPUE declined perhaps indicating that stock abundance was relatively high during the early 1970s. There is no way of corroborating this possibility since Japanese production was very low during this period and their landings were almost entirety incidental to snow and Tanner crab fishing. From 1978 onward CPUE and survey statistics are consistent and indicate stable abundance through about 1981 followed by general declines until the fishery

was closed in 1988. Landings peaked at a record 4,960 t in 1980, and there was a general decline thereafter. Reasons for these declines are obscure but perhaps parallel those for Bristol Bay red king crab. Recruitment trends in this stock have been difficult to assess due to the rocky, untrawlable habitat of sublegal males and females. As of this writing the fishery remains closed and it is unlikely to reopen in the next one to two years.

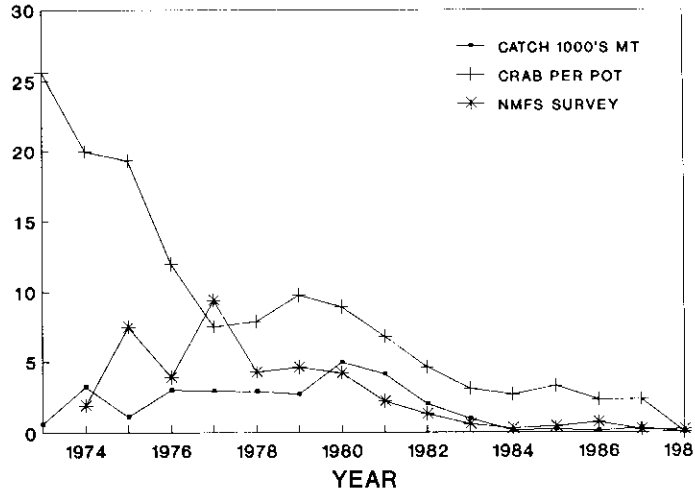

Figure 3. Comparison of U. S. commercial catch and crab per pot lift (CPUE) with NMFS survey estimates of the abundance of legal male blue king crab (millions) from the Pribilof Islands. Note that the fishery was closed in 1988.

St. Matthew Island Blue King Crab

The St. Matthew Island blue king crab fishery developed in concert with that for red king crab in Norton Sound. Although both stocks were known in the late 1940s there was little commercial interest in these until 1977. Trawls surveys conducted by the NMFS as part of baseline studies related to oil exploration (Pereyra et al., 1976; Wolotira et al, 1977) were probably instrumental in generating interest in these northern stocks. Development was somewhat hampered by the smaller average size of crab in the St. Matthew Island area and the consequently lower prices paid to fisherman. For example, the annual mean size of crab landed in the St. Matthew fishery ranged from 1.8 to 2.2 kg as compared to 3.1 to 3.7 kg for the Pribilof Islands; the price per kg paid for St. Matthew Island crab averaged 74% of that for the Pribilofs (1977 to 1987). While landings from this stock have been comparatively small, they achieved prominence due to low abundance in other areas, reaching 31% of all EBS/AI king crab landings in 1982 and 38% in 1983. St. Matthew Island landings hence contributed heavily to the dominance of blue king crabs in regional landings during the early 1980s (Tables 3 and 4, Fig. 1).

The history of catch, CPUE, and NMFS survey abundance estimates (Fig. 4) is difficult to interpret. In years prior to 1981, landings were sporadic since fishing

tended to occur as vessels returned from the brief Norton Sound fishery. Catch per pot lift was extremely variable as well, although survey estimates tended to rise slightly. From 1981 onward there has been consistent interest and effort in the fishery. In 1980, for example, less than three vessels were fishing and only one landing was made per vessel; but by 1981, 31 vessels made 119 separate landings and more that 40 vessels have fished in each year since. Catch per pot lift generally declined through the 1980s. Landings peaked in 1983 (4,300 t) and have since declined and stabilized at 460 to 600 t. Survey estimates of legal crab abundance peaked in 1982 and have been closely correlated with landings since 1983, The correspondence between survey estimates and CPUE was fairly strong from 1983 to 1987, but CPUE in 1988 was unexpectedly high. Assessment of the stock in the trawl survey is extremely difficult due to the rocky grounds in the area. Estimates of abundance probably reflect an unknown portion of the stock in any given year. Most likely, this stock will remain stable but relatively low over the next few years.

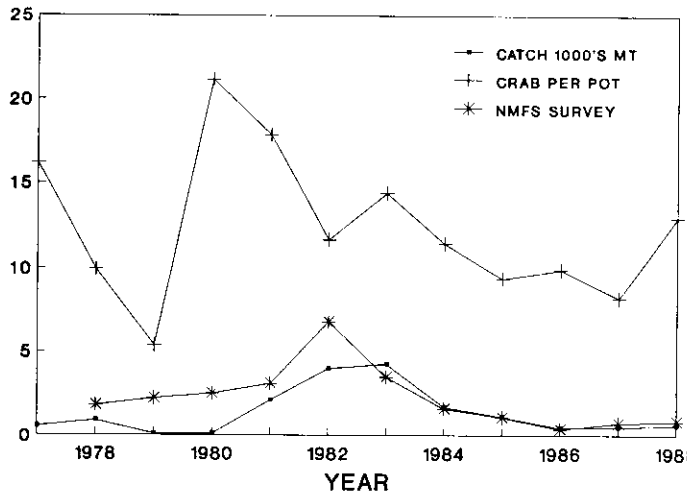

Figure 4. Comparison of U. S. commercial catch and crab per pot lift (CPUE) with NMFS survey estimates of the abundance of legal male blue king crab (millions) from St. Matthew Island.

Adak Golden King Crab

Conditions in the Adak golden king crab stock are difficult to evaluate as there have been no surveys and commercial fisheries show few definite trends (Fig. 5). Prior to 1981, catches were incidental to the Adak red king crab fishery and did not exceed 50 t in any year. Essentially, the fishery was developed in 1981 (14 vessels, 70 landings, 540 t) and 1982 (91 vessels, 501 landings, 3,600 t) as many vessels searched for alternative resources due to drastic declines in landings from Bristol Bay. Vessel effort peaked in 1983 (157 vessels, 1,002 landings, 3,700 t) with almost stable landings. Marketing conditions caused a 65% drop in price paid at Dutch Harbor in 1984 and landings decreased. Variation in CPUE and tons per landing prior to 1984 seem to be related to changes in vessel effort as many new vessels entered the fishery. In 1984, vessel effort declined to 38 vessels and has not

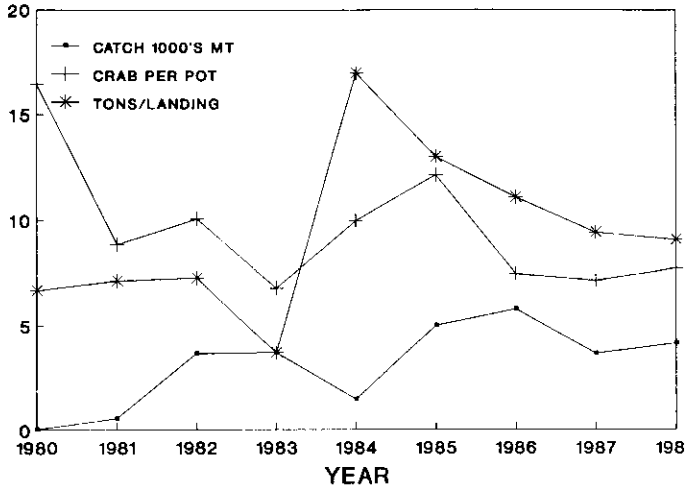

Figure 5. Commercial catch, crab per pot lift (CPUE), and metric tons per landing from the golden king crab fishery in the western Aleutian Islands (Adak).

exceeded 74 vessels in any year since. The legal size limit was decreased from 165 mm carapace width to 152 mm in 1985 which may have made more crab available to the fishery, hence leading to the high CPUE for that year. Landings peaked at 5,800 t in 1986, but landings and CPUE show no real trend for 1986 to 1988. The number of tons per landing peaked in 1984 and has tended to decline in each year since, perhaps indicating that fishermen are working harder for their catch in recent years due to increased search time or other factors unrelated to catch per pot.

Golden king crab live in deeper water and are more difficult and expensive to catch than blue or red king crabs (McNair, 1983; Somerton and Otto, 1986). For this reason golden king crab stocks were the last North American king crab resource to be developed. It is very unlikely that another king crab fishery of this magnitude will be developed again, although there is some interest in the scarlet king crab (*L. couesi*) which inhabits even deeper waters. Future increases in landings of king crabs from EBS/AI, or North American waters in general, will require recovery of stocks that are currently at low levels. While stringent management measures, including long-term closures and reduced exploitation rates, have been implemented by the Alaska Department of Fish and Game, there has been little sign of recovery of king crab stocks of the EBS/AI or in the Gulf of Alaska.

TANNER AND SNOW CRABS 1979 TO 1988

For simplicity I have confined the discussion of Tanner and snow crabs to stocks in the eastern Bering Sea (Tables 5 and 6). The contribution of the Aleutian Islands to these fisheries was minimal during the fisheries' development (Table 2) and annual landings have not exceeded 720 t (1982) in the past decade. The Japanese fishery was terminated in 1980, ending a period of Japanese crabbing in the eastern Bering Sea which had lasted 28 years.

Table 5. Species composition of Tanner (*C. bairdi*) and snow (*C. opilio*) crab landings (1000's t) from the eastern Bering Sea.

Year[3]	Tanner[1] Catch	%	Snow[2] Catch	%	Total
1979	20.60	42.2	28.20	14.6	48.80
1980	17.41	41.8	24.25	58.2	41.66
1981	13.49	36.0	23.93	64.0	37.41
1982	4.99	27.3	13.32	72.7	18.31
1983	2.39	16.8	11.85	83.2	14.24
1984	0.55	4.3	12.16	95.7	12.71
1985	1.43	4.6	29.94	95.4	31.37
1986	0.00	0.0	44.45	100.0	44.45
1987	0.00	0.0	46.22	100.0	46.22
1988	1.00	1.6	61.40	98.4	62.40
Totals	61.86	17.3	295.71	82.7	357.57

[1] Includes Japanese catch of 1,300 t in 1979 and 800 t in 1980.

[2] Includes Japanese catch of 13,600 t *C. opilio* in 1979 and 6,300 t in 1980.

[3] In some years seasons opened in November but landings were small until January of the year indicated.

Table 6. Landed value of Tanner (*C. bairdi*) and snow (*C. opilio*) crab landings (1000's t) from the eastern Bering Sea in millions of U.S. dollars (not adjusted for inflation).[1]

Year	Tanner Value	%	Snow Value	%	Total
1979	23.61	55.9	18.65	44.1	42.27
1980	19.96	64.0	11.23	36.0	31.18
1981	17.24	55.7	13.72	44.3	30.96
1982	11.67	35.3	21.43	64.7	33.10
1983	6.33	40.9	9.14	59.1	15.47
1984	1.15	12.5	8.04	87.5	9.19
1985	4.41	18.2	19.80	81.8	24.21
1986	0.00	0.0	58.79	100.0	58.79
1987	0.00	0.0	76.43	100.0	76.43
1988	4.80	4.4	104.22	95.6	109.02
Totals	89.17	20.7	341.45	79.3	430.62

[1] Japanese catch in 1979 and 1980 assumed of equal landed value to U.S. catch.

The U.S. fishery for Tanner crab had developed very quickly during the late 1970s (Table 2) and catches fell rapidly during the early 1980s, adding to economic pressures on the U.S. crab industry that accompanied declines in abundance of red

king crab stocks. While U.S. fishermen always landed a few snow crab incidentally in the Tanner crab fishery, separate statistics were not kept until 1978 when 780 t were landed by 13 vessels. The snow crab fishery developed rapidly due to the large fleet that had been capitalized by record king crab landings. In 1979, 14,600 t of snow crab were landed by 134 vessels. Landings reached 17,950 t, worth $8.31 million in 1980, but snow crab fisheries remained a sort of sideline for the fleet due to the high value of other species (Tables 4 and 6). By 1986 the snow crab fishery would become the most valuable crab fishery in the EBS/AI region. A brief review of U.S. Tanner and snow crab fisheries follows. Data are from the ADF&G (1989a) and from Stevens and MacIntosh (1989).

Eastern Bering Sea Tanner Crab

The first recorded U.S. landings of Tanner crab were taken incidentally in the Bristol Bay red king crab fishery in 1968, but landings were less than 500 t until 1974. In 1974 landings reached 2,290 t and by 1975, 28 fishing vessels had landed 3,190 t. The U.S. fishery exceeded that of the Japanese in 1976 and developed rapidly thereafter (Table 2).

By 1978, the U.S. fishery had reached a record 30,200 t, which was followed by declines in each year until the fishery was closed in 1986 (Fig. 6). Catch per pot and NMFS survey data showed nearly identical downward trends throughout this period. By 1981, the U.S. Tanner crab catch was less than that of snow crab (Table 5) and by 1982 the value of Tanner crab was less as well (Table 6). This stock was apparently increasing in abundance during the late 1960s, declining from 1969 through 1972 and rising rapidly to record high abundance in 1975 (Otto, 1981). Survey data and CPUE show that declines were nearly monotonic, but it is worth noting that the U.S. fishery developed during a period of high abundance and the decline began before catches were a large portion of the legal-size population. Since the fishery occurs in the late winter and spring, a rough rate of utilization can be

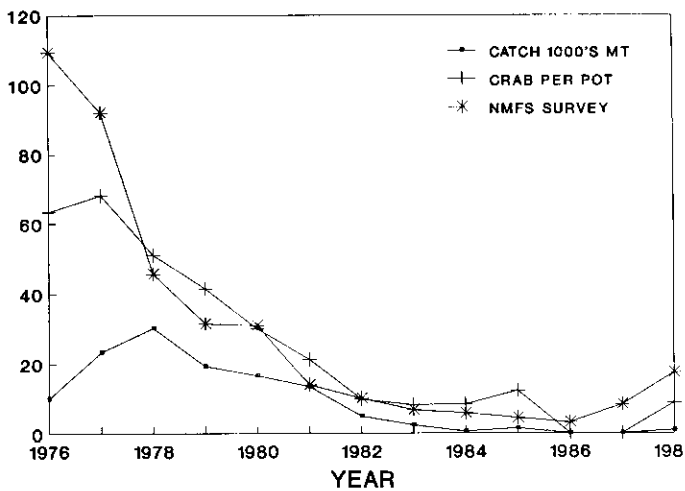

Figure 6. Comparison of U. S. commercial catch and crab per pot lift (CPUE) with NMFS survey estimate of the abundance of legal male Tanner crab (millions) from the eastern Bering Sea. Note that the fishery was closed in 1986 and 1987.

calculated relative to the previous summer's NMFS survey. For example, the combined U.S. and Japanese catch in 1977 was about 25 million crab, or 23% of the 109.5 million legal-sized crab estimated by the 1976 trawl survey (assuming that such crab are 100% vulnerable to the trawl). In 1978 the apparent exploitation rate was 30% relative to the 1977 survey. While the fishery undoubtedly caused part of the decline in abundance, it does not seem to have been the primary cause. The fishery was closed in 1986 but abundance of legal-sized crab did not begin to rise until 1987. The fishery reopened in 1988 and landings were 1,000 t. Survey estimates increased to 8.3 million legals in 1987 and 17.4 million in 1988. Preliminary ADF&G statistics indicate that the 1989 spring fishery produced 3,200 t with a CPUE of 16 crab per pot. The 1989 survey estimate was 42.3 million crab, and it appears that the eastern Bering Sea Tanner crab stock is recovering.

Eastern Bering Sea Snow Crab

Directed fishing for snow crab began in 1973 near the Pribilof Islands when quotas and fishing areas for the Japanese fleet were modified as a result of U.S.-Japan bilateral negotiations. In 1973 and 1974, 57% of the Japanese quota (by number of crabs) was for areas where snow crab is the dominant species of *Chionoecetes*. Quotas and fishing areas were adjusted over the remaining years of Japanese fishing in a manner that increased proportions of snow crab in the Japanese fishery (see Otto, 1982). These changes fostered development of U.S. fisheries, first for Tanner crab and later for snow crab, as the Magnuson Fishery Conservation and Management Act of 1976 was implemented. In 1976 the landed weight of snow crab in the Japanese fishery exceeded that of Tanner crab for the first time (Table 2). The United States did not begin landing snow crab until 1978. Due to the fishing areas assigned to the Japanese fleet, the two nations rarely fished the same grounds for snow crab. Snow crab were in high abundance in the eastern Bering Sea in the mid-1970s but declined in a manner similar to that of Tanner crab through the remainder of the 1970s (Otto, 1981) and the abundance of large (>109 mm carapace width) snow crab continued to decline until about 1982 (Fig. 7). Combined U.S. and Japanese landings increased and peaked at 28,200 t in 1979 (Tables 2 and 5) when about 49 million crab were taken.

While U.S. fishermen began harvesting snow crab during the peak year of the Tanner crab fishery (1978), development was spurred by declining abundance of Tanner crab and red king crab. Unfortunately, abundance of snow crab was also declining as the U.S. fishery developed. While in many respects similar, snow crab are much smaller than Tanner crab and command lower prices. For example, the mean size of snow crab landed by U.S. fishermen was 111 mm carapace width with a mean weight of 0.6 kg for 1979 to 1988, while corresponding statistics for Tanner crab were 149 mm and 1.1 kg. Over the same period the mean dockside prices of snow crab was $1.00/kg as opposed to $2.30/kg for Tanner crab. What they lacked in size and price, however, snow crab made up in sheer volume, and when stocks began to recover rapidly in the mid-1980s (Fig. 7) landings and value rose accordingly. In 1984 the catch of snow crab exceeded the aggregate weight of all other crabs in the EBS/AI region and by 1986 their landed value exceeded that of any other species.

Comparison of CPUE and NMFS survey estimates showed similar trends until 1984 (Fig. 7). In 1984, the minimum size snow crab accepted by processors became fixed at about 102 mm carapace width, while the mean size of landed crab was about 110 mm. By comparison, the legal size was set at 78 mm for biological reasons. I have presented survey estimates for both size categories for 1984 onwards, but

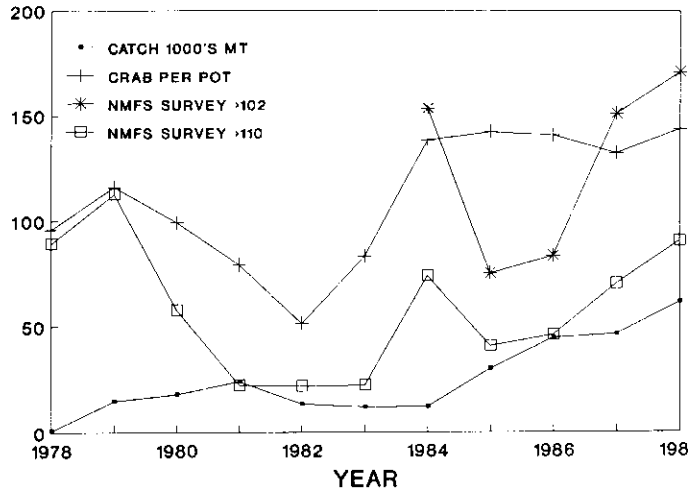

Figure 7. Comparison of U. S. commercial catch and crab per pot lift (CPUE) with NMFS survey estimates of the abundance of commercial-size male snow crab (millions) from the eastern Bering Sea. Crab of 110 mm carapace width are approximately average for the history of the fishery but processors have refused to purchase crab smaller than 102 mm in recent years.

neither corresponds well with CPUE which has remained nearly constant (Fig. 7). Through 1988, survey estimates remained high and preliminary ADF&G data for the 1989 season showed a record catch of 61,400 t with a record CPUE of 178. The 1989 NMFS trawl survey showed a 9% increase in commercial size (>101 mm) males and a 10% decrease in larger (>109 mm) males. Record landings have been achieved and superceded in every year since 1985. While abundance remains high and there is no sign of decline, one cannot assume it is stable given the past history of the stock.

CONCLUSION

The history of crab fisheries in the EBS/AI region is marked by fluctuating resource abundance and the development of new fisheries to replace those which had declined. Red king crab dominated regional crab fisheries from 1953 through 1980. Bristol Bay red king crab were most important and showed peaks in landings in 1964 and 1980. As the Bristol Bay stock declined through the 1960s, it spurred development of Japanese fisheries for Pribilof Islands blue king crab and eastern Bering Sea Tanner crab. Bristol Bay red king crab were in high abundance in the mid-to late 1970s and continued to dominate EBS/AI crab fisheries, but virtually all crab stocks in the region were in relatively high abundance during this period. The combination of high resource abundance, preferences granted to U.S. fishermen by the Magnuson Fisheries Conservation and Management Act, and favorable markets, allowed the capital generated by red king crab fisheries to be used in developing other crab resources. When all major red king crab stocks throughout Alaska declined precipitously from 1980 through 1983, fisheries for blue king crab intensified and golden king crab fisheries were developed. The snow crab fishery

came to dominate regional fisheries in the late 1980s as snow crab abundance rose and the abundance of other crab resources remained low.

The past decade (1979-1988) saw the greatest changes in resource abundance and the greatest diversification of EBS/AI crab fisheries. In 1979, 108,900 t of king, Tanner and snow crabs worth $173.4 million were landed. In 1980, these fisheries reached record landings of 115,900 t worth $180.7 million. By 1984, overall landings had plummeted to 19,400 t worth only $36.9 million. In 1980, red king crab represented 60% of landings and 77% of combined king, Tanner, and snow crab value. By 1984, red king crab were only 14% of these landings although they accounted for 38% of value, and snow crab were 63% of landings but only 21% of the value. In 1988 snow crab were 85% of landings and 55% of value while overall landings had recovered to 72,000 t worth $198.1 million.

Going into the next decade, landings will be dominated by the still abundant snow crab and the increasingly abundant eastern Bering Sea Tanner crab, with overall landings remaining at high levels. Some development of fisheries for deeper water species (*Lithodes couesi, Chionoecetes tanneri,* and *C. angulatus*) is possible but unlikely to have a substantial impact on regional landings. King crab stocks may also recover but prospects are uncertain. It is clear that the future of EBS/AI crab fisheries will depend on historically exploited stocks and their management rather than the development of new resources.

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Tanner Crabs (*Chionoecetes opilio, C. bairdi*) of the Northwest Pacific: Distribution, Biological Peculiarities, and Population Structure

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The range, distribution and formation of local populations of tanner crabs have been examined in relation to habitat on the shelf of the northwest Pacific. The association of various groups to certain environmental factors has been shown. Spatial geographical characteristics of tanner crab populations have been given.

Tanner crabs are included in a number of commercially important species which are insufficiently exploited on the shelf of the Far Eastern seas. They are widely distributed in the shelf area. The species include *Chionoecetes opilio* (Fabricius) and *Ch. bairdi* (Rathbun). Data on the distribution of these species are given in fauna reports of the Far Eastern seas and the North American West Coast (Rathbun, 1925, Sakai, 1939; Vinogradov, 1950; Kobyakova, 1937, 1958; Ushakov, 1950).

Regular standard trawl surveys conducted by TINRO for the last two decades have provided an opportunity to change our ideas of the distribution of the separate species and to study many biological problems of tanner crabs and their individual populations (Novikov, Gavrilov, 1969; Slizkin, 1974, 1977, 1978, 1982; Rodin, Slizkin, 1977; Slizkin, Myasoyedov, 1979).

Detailed data on the distribution, migrations, biology and resources of tanner crabs off the Asian Pacific coast were obtained during that study.

Ch. opilio are widely distributed. The species occurs in the Bering Sea, penetrates in the Chukchi Sea where they can be observed from Wrangell Island to Point Barrow (70°30'N) and the mouth of the Mackenzie River (Macginitie, 1955), are common in the northern Sea of Japan and penetrate up to the Korean Strait (Ogata, 1973). They are highly abundant in the Bering Sea in the Pribilof-

Table 1. Ranges and optimum summer water temperature (°C) and depth distribution (in m) of tanner crabs in the northwest Pacific.

Area	Mature			Immature			Temperature and Hatching Period	
	Low	High	Optimum	Low	High	Optimum		
Northwest	-1.8	7.2	0.9	-1.8	6.3	-0.4	-0.5	2.5
Bering Sea	20	530	115	12	300	71	Y	Y1
Sea of Okhotsk	-1.8	4.3	0.5	-1.8	3.2	-0.1	0.5	6.0
West Kamchatka	36	530	135	28	500	80	Y	Y1
East coast	-1.8	7.0	0.5	-1.8	7.2	-0.6	-1.0	10.0
of Sakhalin	18	460	166	20	510	124		Y1
Northwest Sea	-1.8	3.0	1.3	-1.8	2.5	1.3	0.0	3.6
of Japan	26	630	170	20	490	188		Y
Southern Part	1.0	5.0		0.5	3.0		9.0	12.0
	225	400	250	220	400	250		IY*
Northwest	-1.7	5.1	1.4	-1.1	5.0	1.9	-0.1	3.0
Bering Sea	15	510	89	10	355	92		IY

* from T. Ogata (1973)

Bristol area and also in the seas of Okhotsk and Japan (Tokado, 1964; Novikov, Gavrilov, 1969; Slizkin, Myasoyedov, 1979; Slizkin, 1982).

Ch. opilio occur everywhere in areas where cold intermediate water, with temperatures of -1.8°C to 7.01°C, contacts the sea bed (Table 1). *Ch. opilio* occur at water temperature up to 10°C only in the southern-most parts of the range where the water gets warm in the summer. At the same time, this species tolerates low temperature, which allows it to penetrate into low arctic regions (the Chukchi Sea). The optimum water temperature in all areas of the habitat is lower than that of *Ch. bairdi*, and the optimum temperature for immature individuals has negative values even in the summer (Table 1). These conditions occur in areas where cold intermediate water contacts the bottom.

It has been stated (Slizkin, 1974, 1977, 1982; Slizkin, Myasoyedov, 1979) that mass aggregations of *Ch. opilio* juveniles are associated with standard anticyclonic circulation. Therefore, juveniles are concentrated more to the northwest of the Pribilof Islands, in the central Gulf of Anadyr, northwest Okhotsk Sea and off east Sakhalin. In the deep water of the Sea of Japan *Ch. opilio* are widely distributed as compared to other areas (Table 1). There they are associated with

the bentho-pelagic cold water layer, homologous to the cold intermediate layer of the northern seas (Radzikhovskaya, 1965; Yarichin, 1982). Due to such a wide distribution of *Ch. opilio* in the North Pacific, they are regarded as a Pacific glacial species by Ya. A. Birshtein and L. G. Vinogradov (1953). *Ch. opilio* can be characterized as a low arctic, Pacific glacial species because of their penetration into the southern Chukchi Sea.

We found that *Ch. bairdi* have a wider distribution off the Asian North Pacific coast than previously thought (Birshtein, Vinogradov, 1953; Kobyakova, 1958).

On the whole, *Ch. bairdi* are distributed eastward from the coast of Oregon (143°34' N, Hosie, 1974) northward up to the Bering Sea, and eastward to the south Kuril Islands.

Ch. bairdi are abundant in the western part of their distribution: in Olyutorskie Bay, off east and southwest Kamchatka and off the north Kuril Islands, in areas where the cold intermediate layer is not clearly expressed and is quickly transformed in spring (Arsenyev, 1968). They therefore occur both in warmer water and at greater depth than *Ch. opilio* (Table 1).

Ch. bairdi penetrate northward only up to Cape Navarin (62° N). The absence of *Ch. bairdi* north of the Anadyr faunistic barrier, the distributional boundary of arctic species southward and boreal far eastern species northward (Andriyashev, 1939), shows their boreal nature. They are mainly absent from the Sea of Okhotsk except the southern and northern Kuril Islands and southern part of West Kamchatka (Slizkin, 1974; Slizkin, Myasoyedov, 1979). Environmental conditions in the northern Sea of Okhotsk and east coast of Sakhalin are unsuitable for *Ch. bairdi*, because the temperatures of the winter remnant water layer in contact with the sea bottom remain low (Moroshkin, 1966; Chernyavsky, 1981).

Therefore, the species can be characterized as boreal by its zoogeographical characteristics and thermal habitat.

When analyzing tanner crab distribution in the northwest Pacific, it is clear that latitudinal distributional boundaries are primarily determined by temperature factors, while the formation of high abundance in any given area is a function of a group of factors: the direction of larval transport by currents, the nature of the bottom and sufficient areas for foraging are of paramount importance.

Water structure has great influence on the distribution of tanner crabs as members of the epibenthos. To be more precise, their distribution is determined by the contact of certain water masses with the sea bottom, thus causing a spotty population distribution. As a rule, these species are distributed from the depth of the summer thermocline, approximately 30-40 m, down to a depth of about 500 m (Table 1).

In other words, the habitat of an overwhelming number of tanner crabs coincides with areas where cold and warm intermediate water masses contact the bottom. Like many other benthic animals, tanner crabs have a heterotopic life cycle. That is why separate stages of their life cycle, pelagic larvae, inactive juveniles and mature migrating individuals, occur in differing habitat conditions.

Their reproductive biology is the same on the whole. They all, including the bathyl species, have plankto-trophic larvae (Pereira, 1967, Takeuti, 1968).

It is clear from the table that tanner crab larvae in the southern Sea of Japan hatch in April-early May, and off Cape Navarin in late May-early June. Surface water temperature is 0.0-12.0°C where larval metamorphosis occurs, as seen from the data in the table. In northern areas such temperatures are observed during the period of maximum summer warming and in southern areas during winter and early spring.

Pelagic larval development, requiring about two months, coincides with the phytoplankton bloom, the most favorable period for larvae. *Ch. bairdi* and *Ch. opilio* have many common morphological, physiological and reproductive features (Sapelkin, Fedoseuev, 1981); therefore hybridization takes place in areas of overlapping range (Karinen, 1982). At the same time ecological and specific distinctions are clearly traced among these species.

Nonmigrating *Ch. bairdi* juveniles are concentrated on granular bottoms (Slizkin, Fedoseyeve, 1989), 75-300 m deep (Table 1) where intermediate water with positive temperatures is in contact with the bottom. Migrating mature individuals are selectively associated with environmental conditions. Therefore, all stages of the life cycle of the species occur in positive water temperatures. They therefore have a limited distribution in the northwest Pacific.

All stages of the *Ch. bairdi* life cycle have been found around the Koryak [Kodiak?] coast, in Olyutorskie Bay of the Bering Sea, Kronotskie and Avachinskie Bays of east Kamchatka and around the northern Kuril shallows and off southwest Kamchatka. Therefore, local populations of *Ch. bairdi* inhabiting these areas can be regarded as self-reproductive. Physiological and behavioral adaptations of larvae and juveniles to vast silty and sandy bottom areas of open sea and tolerance of the juveniles to the lowest of water temperatures (Slizkin, 1978; 1982; Fedoseyev, Slizkin, 1988) are greatly conducive to the wide distribution of *Ch. opilio* in the Far Eastern seas, including the most severe northern areas. These characteristics provide the highest densities of juvenile *Ch. opilio* in areas of standard water circulation, the central part of the northern Bering Sea shelf and northwestern Sea of Okhotsk. The density of *Ch. opilio* decreases and *Ch. bairdi* abundance increases in areas of higher epibenthic water temperature along the shelf off the east coast of Kamchatka and the Kuril Islands.

Self-reproductive populations are indicated by the high abundance of juvenile *Ch. opilio* in the northwest Pacific. They are: the Anadyr-Mathew population, Korfo-Karagin, the northwest Sea of Okhotsk population, east Sakhalin and the

north Sea of Japan populations.

Moreover, relatively small semi-dependent populations have been found off Kamchatka and the Kuril Islands, and off southern Primorye (Maritime provinces). The presence of exceptionally immature crabs in the northern part of the range is attributed to the immigration of non-reproducing *Ch. opilio* populations: the northern Gulf of Anadyr, the southern Chukchi Sea, and Shelikhov Bay in the Okhotsk sea.

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Reproduction

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Reproductive Success of Sublegal Size Male Red King Crab with Access to Multiple Mates

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ABSTRACT

The reproductive potential of red king crab (*Paralithodes camtschatica*) males 80 to 139 mm carapace length was examined by placing individual males with four females and noting breeding behavior, egg clutch production and percentage of dividing eggs in each clutch.

A mating was considered successful if a male induced a female to ovulate. Males 80-89 mm carapace length were successful with 75, 38, 12 and 12% of their first, second, third, and fourth mates respectively. Corresponding values for 130-139 mm males would be 88, 78, 100 and 44% of successful successive matings.

The first females mated by males below 110 mm carapace length carried clutches in which 68-86% of the eggs initiated division. The percentage of eggs dividing in clutches of their second, third, and fourth mates ranged from 18-63%, 12-41% and 0-13% respectively depending on male size. Males over 120 mm carapace length were generally successful at fertilizing full egg clutches with two or three successive mates. But they were not always successful at getting their fourth mate to ovulate.

INTRODUCTION

The red king crab, *Paralithodes camtschatica* (Tilesius), previously supported an important commercial fishery in Alaska. Currently several areas which had active fisheries for this crab are closed to harvest because of low abundance of the

species. The reasons for the large scale population decreases are unknown, but their occurrence has increased the desire to understand the biology of the species. The current size at which 50% of male red king crab are mature, based on morphometric data, is 103 mm (Somerton, 1980). The minimum size for legal harvest is about 145 mm carapace length. Previous work demonstrated that male red king crab over 136 mm carapace length are capable of mating with up to seven females (Powell *et al.*, 1974). But for smaller males existing literature deals with only single matings. The objective of this study was to examine the ability of small red male king crab to mate repeatedly.

METHODS

The basic method used in all breeding observations was to place a single red king crab male in a tank with four multiparous females and note breeding activity when females molted. All females were carrying hatching eggs from their previous mating. In red king crab the females must molt prior to the extrusion of new eggs. Mating occurs when the female is in a soft-shell state and the female has little power to resist the male mating embrace. If mating behavior was not observed within six days of the molt, the female was placed with another male and if she then bred and extruded eggs, which initiated division, the first male interaction was considered a breeding failure. Except for eight females killed by males prior to ovulating, all other females ultimately extruded viable clutches during the observations. When breeding was observed the female was isolated after egg extrusion was completed, and held for one week to allow the eggs to develop to the four to 32 cell stage. Then a group of at least 100 eggs from each pleopod was randomly selected and examined under a microscope for cell division. The percent of dividing eggs in the pleopod subsamples were averaged to provide an estimate of what percentage of eggs in the clutch were dividing.

Then the eggs were dried to a constant weight in a convection oven at 60°C. The number of eggs in her clutch were estimated by dividing egg clutch dry weight by the average weight of one dry egg. Egg samples from 50 females were used to estimated the average dry weight of one egg. For each female 20 eggs from each of the six pleopods were removed and dried to a constant weight. After drying each group of 20 eggs was weighed on a Cahn electrobalance. Then the weight was divided by the number of eggs to estimate the averaged dry weight of an individual egg. The average dry weight of one egg was 0.00021 g (sd = ±0.000013).

Previous work demonstrated that the 10 days following the male molt is a period when males are incapable of mating (Powell *et al.*, 1972). In order to minimize this problem males used in the breeding experiments were either hard shell and captive for at least a month, or held for a minimum of two weeks after molting in the laboratory, before being placed with females. The tank size used in experiments was 800 l and the water temperature was between 4-6°C. Salinity ranged from 31-32 ppt.

For data presentation males are grouped into 10 mm size groups based on carapace length. Carapace length is measured from the right eye notch to the central portion of the rear margin of the carapace. The size range of males used included 80 to 139 mm carapace length. Females ranged from 102 to 154 mm (Table I).

RESULTS

Information associated with each of the individual breeding observation is reported in Table I. Summarizations of breeding success is outlined in Table II. Morphometric information on male carapace length and chela height and the percentage of eggs dividing in the clutch of their first mate occurs in Table III.

Both the percentage of females induced to ovulate (75%) and the percentage of dividing eggs (68%) in clutches of their first mates (Table II) suggest that not all males 80-89 mm carapace length are capable of reproducing. When allowed access to a second and subsequent females less than 18% of the eggs in the few clutches extruded initiated division. All females that failed to extrude eggs when held with these males produced viable clutches after being placed with other males. Only one male in this size range was able to fertilize all four females. One male killed 3 of his potential mates after they molted even though one extruded a clutch and the others had ripe ovaries. Eighty-eight percent of 90-99 mm males induced the first female available to them to ovulate, but only 66, 55 and 0% were successful at breeding females 2 through 4. The percentage of dividing eggs in clutches of females, bred by these size males, decreased with each successive mating (Table II). The clutches of their first mates contained an average of 86% dividing eggs. Females that were second, third, and fourth in mating chronology had egg clutches with an average of 63, 41 and 0% of the eggs dividing. One male killed two, and another one female after they molted.

Males in the 100-109 mm group induced their first mates to ovulate in 86% of the observations. Less than 42% of these males induced a second female to ovulate and only 14% bred a fourth female. Clutches of the first females bred by these males had an average of 83% of the eggs initiate division while the second, third and fourth females in mating chronology had only 39, 26, and 13% of their eggs initiate division (Table II). All males in the 110-119 mm size group induced their first females to ovulate and 90, 72, and 54% of them bred a second, third, and fourth mate respectively. The percentage of eggs initiating division in clutches of females mated to successive females 1 through 4 was 98, 74, 62, and 44, respectively (Table II). One male killed the second female after she molted but bred females 3 and 4.

Males in the 120-129 mm group mated with all four females available to them in all but one case (Table II). The percentage of eggs initiating division was typically high, 92-100% of the eggs carried by females mated third or fourth in chronology.

Table I. Observations of red king crab mating and egg production under laboratory conditions from 1986-89.

** eggs were not removed from the female.
!! female killed by male.

Male Length (mm)	Female Length (mm)	Total Eggs per Clutch	Percent Eggs Dividing	Days Between Matings for Male	Fertile Egg Clutch with Another Male
83	138	211,829	59	-	
	150	0	-	25	yes
	108	0	-	7	yes
	134	0	-	10	yes
84	137	0	-	-	yes
	130	0	-	6	yes
	118	0	-	17	yes
	141	0	-	7	yes
87	126	167,074	94	-	
	131	166,758	15	17	
	126	132,421	0	6	
	132	0	-	3	yes
87	123	126,444	92	-	
	128	101,030	40	7	
	130	0	-	19	yes
	146	0	-	5	yes
88	131	197,554	99	-	-
	153	0	-	8	yes
	133	0	-	5	yes
	145	0	-	9	yes
88	125	0	-	-	yes
	131	114,987!!	0	10	
	137	!!	0	8	
	114	!!	0	5	
88	125	142,377	100	-	
	121	161,590	96	71	
	140	250,086	98	6	
	121	135,664	99	5	
89	136	192,628	99	-	
	124	0	-	7	yes
	136	0	-	9	yes
	120	0	-	8	yes

Table I. (Continued)

** eggs were not removed from the female.
!! female killed by male.

Male Length (mm)	Female Length (mm)	Total Eggs per Clutch	Percent Eggs Dividing	Days Between Matings for Male	Fertile Egg Clutch with Another Male
90	112	74,219	99	-	
	146	254,519	99	1	
	105	64,470	95	1	
	113	0	-	13	yes
	139	0	-	6	yes
90	116	137,474	98	-	
	138	0	-	11	yes
	129	!!	-	5	
	137	!!	-	16	
90	131	145,939	99	-	
	113	135,922	98	11	
	143	0	-	18	yes
	143	0	-	4	yes
90	144	0	-	-	yes
	124	35,679	0	14	
	116	0	-	1	yes
	141	0	-	12	yes
91	138	231,673	98	-	
	140	154,684	98	20	
	161	0	-	14	yes
92	113	133,725	99	-	
	134	157,899	86	10	
	125	155,540	59	4	
	123	0	-	10	yes
94	140	228,217	86	-	
	150	0	-	4	yes
	137	0	-	14	yes
	144	!!	-	4	
94	118	179,532	99	-	
96	117	107,289	99	-	
	118	113,334	88	4	
	114	92,929	80	12	
	123	0	-	6	

Table I. (Continued)

** eggs were not removed from the female.
!! female killed by male.

Male Length (mm)	Female Length (mm)	Total Eggs per Clutch	Percent Eggs Dividing	Days Between Matings for Male	Fertile Egg Clutch with Another Male
99	110	184,932	99	-	
	143	264,163	97	16	
	145	209,308	41	9	
	144	0	-	10	yes
99	132	95,816	97	-	
	134	169,786	99	1	
	116	49,610	98	2	
	129	**	0	1	
100	116	144,127	89	-	
	127	0	-	5	yes
	124	0	-	5	yes
	127	0	-	10	yes
104	144	256,999	98	-	
	134	269,037	99	3	
	145	204,301	99	10	
	137	0	-	10	yes
105	142	330,021	99	-	
	138	0	-	3	yes
	150	0	-	8	yes
	141	0	-	3	yes
106	127	164,927	100	-	
	143	0	-	4	yes
	133	0	-	4	yes
	142	0	-	13	yes
108	120	127,175	99	-	
	120	166,286	96	2	
	127	168,589	81	17	
	133	0	-	3	yes
	153	0	-	3	yes
108	153	0	-	-	yes
	140	**	0	7	
	149	**	0	8	
	137	0	-	3	yes

Table I. (Continued)

** eggs were not removed from the female.
!! female killed by male.

Male Length (mm)	Female Length (mm)	Total Eggs per Clutch	Percent Eggs Dividing	Days Between Matings for Male	Fertile Egg Clutch with Another Male
109	131	209,038	99	-	
	145	258,607	80	1	
	149	0	-	1	yes
	154	142,457	92	10	
	141	273,065	97	3	
110	116	127,339	100	-	
	129	153,780	92	14	
	125	76,704	99	3	
	132	102,114	89	12	
112	121	131,936	99	-	
	143	10,165	83	3	
	130	154,809	86	2	
	139	0	-	1	yes
113	113	101,081	99	-	
	120	104,846	100	17	
	118	69,451	99	4	
	135	130,651	99	7	
113	140	171,363	100	-	
	106	73,346	99	6	
	141	125,357	100	14	
	128	81,339	99	8	
113	145	5,426	98	-	
	140	180,837	99	1	
	137	0	-	17	yes
	125	0	-	5	yes
114	124	266,985	90	-	
	122	147,377	99	8	
	143	283,896	40	8	
	145	0	-	9	yes
115	125	147,714	99	-	
	135	!!	0	13	
	109	53,594	96	11	
	141	161,708	20	9	

Table I. (Continued)

** eggs were not removed from the female.
!! female killed by male.

Male Length (mm)	Female Length (mm)	Total Eggs per Clutch	Percent Eggs Dividing	Days Between Matings for Male	Fertile Egg Clutch with Another Male
117	122	180,752	100	-	
	121	125,440	1	9	
	137	17,532	67	15	
	136	132,798	75	2	
118	139	290,819	99	-	
	139	324,524	97	4	
	142	0	-	10	yes
	137	231,895	99	1	
	142	253,768	83	3	
118	110	36,394	99	-	
	143	221,714	62	11	
	108	79,267	100	12	
	113	0	-	7	yes
118	119	90,174	92	-	
	121	156,438	88	16	
	125	0	-	7	yes
	130	0	-		yes
120	123	17,768	99	-	
	129	227,109	99	4	
	126	175,302	92	4	
	120	139,085	97	4	
122	132	0	-	-	yes
	153	330,988	99	16	
	143	309,614	98	1	
	145	101,541	87	1	
	147	191,551	91	7	
125	131	170,727	98	-	
	154	305,842	98	10	
	132	174,007	98	2	
	143	229,744	98	2	
	133	165,785	98	1	
	148	304,248	98	2	

Table I. (Continued)

** eggs were not removed from the female.
!! female killed by male.

Male Length (mm)	Female Length (mm)	Total Eggs per Clutch	Percent Eggs Dividing	Days Between Matings for Male	Fertile Egg Clutch with Another Male
126	125	188,126	100	-	
	109	63,222	99	2	
	132	63,954	97	3	
	133	47,521	99	3	
127	109	97,212	99	-	
	114	75,661	99	7	
	132	96,321	99	7	
	113	102,211	98	8	
128	150	241,044	98	-	
	117	126,801	99	10	
	131	103,685	99	8	
	117	22,938	100	3	
130	123	214,217	99	-	
	127	75,852	99	11	
	137	244,615	99	2	
	124	181,683	96	6	
132	138	220,918	99	-	
	125	99,394	98	5	
	123	100,952	99	1	
	141	154,131	87	4	
	116	36,505	99	17	
133	126	105,028	99	-	
	118	78,968	99	1	
	125	100,297	96	1	
	119	0	-	1	yes
135	120	158,008	99	-	
	145	0	-	2	yes
	113	113,306	66	13	
	123	147,024	62	17	
135	144	0	-	-	yes
	150	237,331	98	5	
	108	81,202	100	7	
	116	0	-	3	yes

Table I. (Continued)

** eggs were not removed from the female.
!! female killed by male.

Male Length (mm)	Female Length (mm)	Total Eggs per Clutch	Percent Eggs Dividing	Days Between Matings for Male	Fertile Egg Clutch with Another Male
135	144	41,881	92	-	
	132	!!	-	6	
	130	209,812	98	4	
	134	!!	-	6	
136	139	211,936	99	-	
	124	42,851	92	6	
	130	144,089	99	4	
	120	125,122	95	14	
137	124	187,318	100	-	
	135	194,116	99	22	
	135	62,817	100	3	
	148	0	-	1	yes
	137	0	-	22	yes
139	128	100,198	99	-	
	139	261,089	98	9	
	125	99,080	99	4	
	120	0	-	20	yes

The observations for the 130-139 mm males show that they are capable of breeding three females successfully but 5 of 9 males having access to a fourth female did not induce her to ovulate (Table I). Egg division rates averaged 87 and 76% for females first and second in chronology and 95 and 38% for the third and fourth female mated. One male killed two of his potential mates after she molted.

Typically the clutches of females were of normal size and egg count (Table I). Even clutches with low percentages of dividing eggs did not exhibit gross abnormalities in regards to clutch size. Evidently even non fertilized eggs attach normally for the most part.

The results indicate breeding intervals between successive matings could be quite short. When males over 120 mm bred females on two successive days, typically over 90% of the eggs in the second clutch initiated division.

Table II. Percentage of eggs dividing in clutches of *Paralithodes camtschatica* mated successively by a single male. (Data summary from Table I, mean over standard deviation and range)

Male Carapace Length (mm)	% Eggs Dividing Mate 1	% Eggs Dividing Mate 2	% Eggs Dividing Mate 3	% Eggs Dividing Mate 4
80-89	68	18	12	12
	44	34	34	5
	0-100	0-96	0-98	0-99
90-99	86	63	41	0
	32	47	32	0
	0-99	0-99	0-98	0-0
100-109	83	39	26	13
	36	49	44	34
	0-100	0-99	0-99	0-92
110-119	98	74	62	43
	4	38	44	55
	90-100	0-100	0-100	0-99
120-129	82	98	97	96
	40	1	3	5
	0-100	98-99	92-99	87-100
130-139	87	76	95	38
	33	43	10	45
	0-100	0-99	66-100	0-96

DISCUSSION

Some existing reports state that male red king crab probably mature, like females, at around 100 mm (Powell and Nickerson, 1965; Gray and Powell, 1966) while others suggest that males attain sexual maturity at a smaller size than females (Powell *et al.*, 1972). Somerton (1980) using morphometric measurements estimated the size at which 50% of Bering Sea males were mature was 103 mm. In diver observations near Kodiak Island, Gulf of Alaska, males in grasping pairs were typically larger than 120 mm in length (Powell and Nickerson, 1965; Powell *et al.*, 1972; 1974). Our observations confirm that some males 80 to 110 mm are mature but until they are larger they cannot be counted on to breed more than one female in a season.

Most of the previous mating studies for red king crab were done with males larger than 120 mm (Powell and Nickerson, 1965; Powell *et al.*, 1974). But in one study (Powell *et al.*, 1972) males 85 to 119 mm were each mated to a single female. In

Table III. Morphometric information for male red king crab used in laboratory breeding experiments.

MALE CARAPACE LENGTH	CHELA HEIGHT (mm)	% EGGS DIVIDING IN CLUTCH OF FIRST MATE
83	24	59
84	23	0
87	22	94
87	22	94
87	25	92
88	25	99
88	25	0
88	26	100
89	28	99
90	26	99
90	26	98
90	25	99
90	26	0
91	26	98
92	28	99
92	28	99
94	26	99
94	28	99
98	28	0
99	29	99
99	29	97
100	32	89
104	31	98
105	31	99
106	31	100
108	32	99
108	32	0
109	32	99
110	32	100
112	35	99
113	36	99
113	33	100
113	32	98
114	28	90
115	33	99
117	35	100
118	35	92
118	35	99
118	35	99
120	36	99
122	36	0
125	37	98
126	39	100
127	38	99

Table III. (Continued)

MALE CARAPACE LENGTH	CHELA HEIGHT (mm)	% EGGS DIVIDING IN CLUTCH OF FIRST MATE
128	37	98
130	38	99
132	40	99
133	41	99
135	41	0
135	40	92
136	40	99
137	40	100
139	40	99

that observation three of six males 84-89 mm, bred females, but no estimate of percentage of dividing eggs in any of the clutches examined was provided. In our observations of 80-89 mm males, their first mate extruded normal appearing clutches but only an average of 68% of the eggs initiated division. One hundred percent of 18 100-109 mm males fertilized their mates in the earlier experiment (Powell *et al.*, 1972). This contrasts with only 86% of the males of this size in the present observations. Powell *et al.* (1972) reports large clutches by females mated to 100-109 mm males, but although their methods state that eggs were examined for division as a test of successful mating, the report does not mention what percentage of eggs were dividing. In the current study high percentages of the eggs of females that were not bred first in chronology did not initiate division when their mates were this size.

Several other observations exist for multiple matings with king crabs. In an early report 11 new shell males, 120-144 mm, bred 51 females that extruded full clutches but the percentage of the eggs initiating division is not stated (Powell and Nickerson, 1965). Recently molted males, just under legal size, have been reported to mate as many as 13 successive times, but their mating ability decreased after the sixth mating (Powell *et al.*, 1972). Males over 136 mm could mate up to seven times before egg viability was affected (Powell *et al.*, 1974). Several of these observations are in contrast to the present findings where males, especially those 80-110 mm carapace length, were often incapable of inducing successive females to ovulate, or clutches contained significant percentages of nondividing eggs (Table II). Perhaps some of the disparity between this report and previous studies is related to inadequate reporting of the percentage of dividing eggs in earlier studies. As is clearly shown in Table I, full clutches containing up to 100% nondividing eggs often attach to pleopods. Without careful observation these nonviable clutches could be considered viable.

In a fishery where males over 145 mm are removed from the population understanding the reproductive potential of the smaller males is important in the formulation of harvest quotas. The results of this study suggest that the onset of maturity typically occurs between 90 and 110 mm and that males of this size cannot be relied upon to fertilize more than one female in a season. Even with males in the 130-139 mm size group, not all males were successful at repeated mating. Several authors (Gray and Powell, 1966; Powell *et al.*, 1972; 1974) have noted that the size of males present in an area is not the only factor modifying breeding success. Geographic size or sex segregation, spring molting during the mating season by males, inability of males to mate for approximately 10 days after molting, and naturally occurring and fishery caused differences in sex ratios have been identified as variables that might affect the reproductive success of king crabs. To insure that the population is utilizing its full reproductive potential monitoring clutch size and viability of eggs after the mating season should be part of the management program.

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Incubation Period, Molting and Growth of Female Red King Crabs: Effects of Temperature

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ABSTRACT

In order to study temperature effects on incubation period, survival, molting and growth, five groups of five ovigerous red king crabs, Paralithodes camtschatica, of the same approximate size were gradually acclimated (<1°C per day) to experimental temperatures of 0, 3, 6, 9 and 12°C. Crabs were fed ad libitum a mixed diet twice weekly and maintained in flow-through sea water tanks until hatching and molting occurred. Temperature had no mortality effects on either the adult females or their eggs, as only a single crab died prior to egg hatching or molting, and no significant differences existed in egg mortality among temperatures. A highly significant direct relationship existed between the degree-days required for hatching and incubation temperature, with nearly three times as many degree-days required for incubation at 12 as at 3°C. Hatching occurred after 207, 225, 240 and 305 days at 12, 9, 6 and 3°C, respectively. Most crabs at 0°C molted prior to egg hatching. At the termination of the experiment (550 days), 12% of the eggs brooded by the single unmolted crab at 0°C had hatched. Crabs at all temperatures increased in carapace width upon molting after hatching, with greatest growth at 3°C and least at the temperature extremes. Mean carapace width increases (± S.E.) were 4.4±0.5, 11.9±4.3, 7.1±1.9, 8.0±1.0 and 1.4±3.2% at 0, 3, 6, 9 and 12°C, respectively. Our data demonstrate that water temperature affects hatching dates and subsequent molting and growth of of red king crabs; however, the relationship with temperature is not always direct.

INTRODUCTION

The time of appearance and maximum abundance of red king crab zoeae within a single Alaskan bay varies interannually by as much as six weeks (Shirley and Shirley, 1989, in press-c), however little is

known about the environmental regulation of larval development or hatching in red king crabs. Egg incubation temperature in some crabsis known to determine time of larval hatching (Wear, 1974; Dawirs, 1979; Nakanishi, 1987; Shirley et al., 1987) and may affect larval energy reserves, number of larval instars (Sandifer, 1973; Scotto, 1979), size of larvae (Lang and Young, 1977), synchrony with available food sources in the water column and larval survival (Shirley and Shirley 1988a, 1988b, 1989a). Incubation temperature is also known to influence sex differentiation in some crustaceans (Kinne, 1953).

Although molting and growth of red king crabs have been extensively studied in situ with tagged crabs or with caged crabs held at ambient temperatures (Bright, 1967; Grey, 1963; Matsuura and Takeshita, 1976; McCaughran and Powell, 1977; Powell, 1967), the effects of temperature on molting success and molt increment have not been examined.

Undoubtedly the long intermolt and egg incubation period of red king crabs has daunted experimental efforts and precluded testing of environmental determinants of these variables. The objectives of the present experiment were to determine the effects of temperature on survival of developing larvae and the incubating females, length of incubation period, and growth increments of red king crab.

MATERIALS AND METHODS

Ovigerous red king crabs, Paralithodes camtschatica, were collected in pots from Auke Bay, near Juneau, Alaska, in May, 1987. Five groups of 5 ovigerous red king crabs of the same approximate size, mean carapace width = 113 ± 2 mm (± one standard error), wet weight = 903 ± 35 g, were gradually acclimated (<1°C per day) to experimental temperatures of 0, 3, 6, 9 and 12°C and maintained in the laboratory at those temperatures until hatching occurred. Similar-sized crabs were used to avoid size-dependent effects in reproduction and molting events which have been documented for long-lived crustaceans (Lipcius, 1985). Crabs were held in fiberglass tanks (2.1 x 0.6 x 0.6 m) with flowing, natural seawater at a salinity of 32 ppt. Water temperature in the incubation tanks was regulated with circulating chillers and heaters and measured daily. Crabs were fed ad libitum a mixed diet of fish, shrimp, clams, mussels and squid twice weekly. Samples of approximately 100 eggs were collected and preserved in Stockard's solution (50 ml formaldehyde, 40 ml glacial acetic acid, 60 ml glycerin, 850 ml distilled water) at 14 d intervals beginning 1 June. The condition of the crab and clutch were inspected and recorded on each sampling date. New carapace width was measured after each crab molted (several days after molting to allow for carapace hardening) for determination of female growth rates at different incubation temperatures.

The incubation study was conducted from 1 June 1987 until 1 December 1988 for a total of 550 d with only one crab mortality. A carapace wound in one of the crabs in the 0°C treatment apparently admitted lethal systemic pathogens. Other superficial carapace wounds were treated monthly with Wescodyne to suppress further infection. The experiment was terminated on 1 December 1988 with a single crab remaining at 0°C because a failure in the seawater system required that it be shut down for repairs.

To detect newly hatched larvae in the flow-through incubation tanks, the drain pipes were covered with nylon mesh screen (0.500 mm^2). At least 100 stage I zoeae were collected and preserved in 5% buffered formalin. The incubation time required for hatching and duration of hatching was recorded for each temperature treatment. The number of degree-days required for hatching was calculated by multiplying the number of incubation days to the midpoint of hatching by the incubation temperature.

Statistical analyses were performed using the General Linear Model procedure (SAS, 1985). Values were considered significant if $P<0.05$ and highly significant if $P<0.01$. Means are presented ± one standard error.

RESULTS

Water temperatures in the incubation tanks were stable over the study (Table 1). The maximum temperatures were never more than 1°C over the target temperature for more than 4 or 5 d within the incubation study.

Table 1. Mean incubation temperatures (± one standard error) for temperature treatments of 0, 3, 6, 9 and 12°C. Minimum and maximum temperatures and number of days during the experiment temperatures were measured (n) are presented.

Target Temperature	Mean ± SE	Minimum Temperature	Maximum Temperature	n
0°C	0.03 ± 0.02	-1.0	1.7	537
3°C	3.01 ± 0.01	1.9	5.8	408
6°C	5.99 ± 0.01	3.9	8.7	393
9°C	8.99 ± 0.01	7.3	11.6	361
12°C	11.96 ± 0.01	8.0	12.3	425

Embryonic development

On 1 June 1987, the eggs of the experimental crabs were in developmental stage 22, about the time of blastopore formation (Nakanishi, 1987). At 3°C, stage 22 occurs 39 d after fertilization. Development proceeded linearly at all incubation temperatures, with the slope of the development curves increasing with increasing temperature. Very little variation in development existed within temperature treatments, and significant relationships ($r^2>0.99$) between developmental stage and incubation period were present for all treatments.

Embryonic development occurred continuously to stage 52, when external morphological changes were no longer detectable. In the 3, 6, 9 and 12°C incubation treatments, development appeared to proceed no further, and hatching was delayed for 28, 42, 98 and 92 d (± 13 d sampling interval), respectively. At 0°C, eggs developed linearly with no delay between completion of development and the onset of hatching. The latter statement is based on data from one

crab, as three of the ovigerous crabs at 0°C molted prior to hatching. Examination of eggs retained on the exuviae revealed that the embryos were alive and continuing to develop.

Small but significant differences ($P<0.05$) in egg mortality occurred between temperature treatments, but no relationship existed between egg mortality and temperature. Mean percent mortality during the incubation period was 2.5 ± 0.5%, 0.7 ± 0.2%, 1.2 ± 0.3%, 2.6 ± 0.5% and 2.3 ± 0.4% for 0, 3, 6, 9 and 12°C, respectively. A single flatworm but no Carcinonemertes spp., known predators of king crab eggs, were found on any clutch during the study. Other fouling organisms such as colonial protozoans and fungi were routinely observed on eggs to some degree, but were not thought to be causes of egg mortality.

Hatching was detected by the presence of larvae in the holding tanks. Larvae were first present on 24 December 1987 at 12°C (after 207 laboratory incubation days), on 12 January 1988 at 9°C (225 d), on 27 February 1988 at 6°C (240 d) and on 1 April 1988 at 3°C (305 d) (Figure 1).

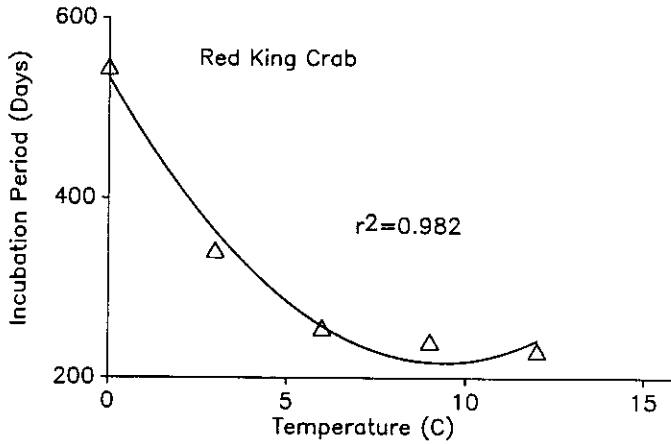

Figure 1. The number of incubation days required to attain the mid-point of hatching for female red king crabs cultured at 0, 3, 6, 9 and 12°C . Each symbol represents the mean of 5 observations except for 0°C, which is a single female which had not molted prior to hatching.

Hatching occurred over a span of 76, 29, 29 and 47 d, at 3, 6, 9 and 12°C, respectively. However, determination of the percent of eggs hatched (i.e., percentage of empty egg cases) by microscopic examination indicated that a small degree of hatching occurred before larvae were detectable in the tanks. The number of empty egg cases began to increase after 282, 226, 226 and 184 d of laboratory incubation at 3, 6, 9 and 12°C, respectively. On 2 November 1988, 6% of the eggs on the last remaining female at 0°C had hatched after 521 d of laboratory incubation, and by the day the experiment was terminated, 1 December 1988 (550 incubation days), 12% of the eggs had hatched.

A highly significant direct relationship existed between degree-days required for hatching and incubation temperature for crabs at 0, 3, 6, 9 and 12°C (Figure 2). The number of degree-days required to reach the midpoint of hatching was 1026, 1536, 2169 and 2772 for crabs at 3, 6, 9 and 12°C, respectively. Incubation time decreased 25% between crabs at 3 and 6°C, but decreased only 10% between 6 and 12°C.

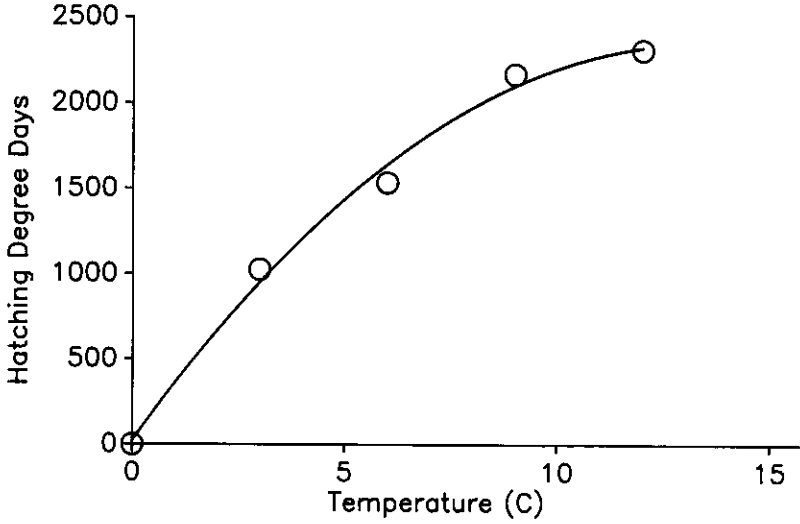

Figure 2. Number of degree-days required for hatching of red king crabs at incubation temperatures of 0, 3, 6, 9 and 12°C.

Crab growth

Crabs at all temperatures increased in carapace width upon molting after hatching. Mean carapace widths increased 4.4 ± 0.5% (mean ± one standard error, n=2), 11.9 ± 4.3% (n=5), 7.1 ± 1.9% (n=5), 8.0 ± 1.0% (n=5) and 1.4 ± 3.2% (n=3) at 0, 3, 6, 9 and 12°C, respectively (Figure 3).

DISCUSSION

Ovigerous red king crabs were reared successfully in the laboratory for up to 18 mo with only a single adult crab mortality and very low egg mortality. Only one prior experiment reared ovigerous females at high temperatures; in that study, the single ovigerous crab survived the 8°C incubation period, but none of the eggs survived (Nakanishi, 1987). In our study, hatching occurred at all incubation temperatures. Three crabs in 0°C water molted prior to the hatching of their eggs 16 mo after initiation of the study, even though the larvae were still developing normally. In the one remaining female at 0°C, eggs had just begun to hatch after 18 mo when the study was terminated.

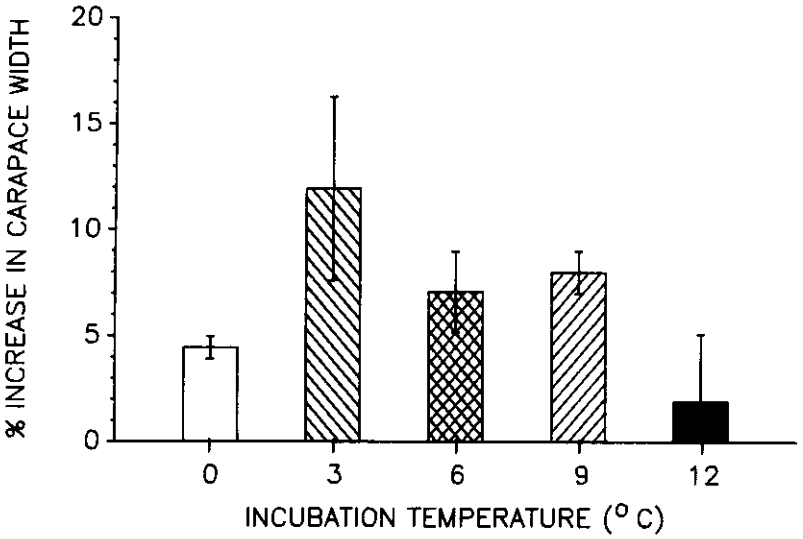

Figure 3. Female crab growth at different incubation temperatures. Growth is indicated as mean (± one standard error) percent increase in carapace width for 2, 5, 5, 5 and 3 crabs at 0, 3, 6, 9 and 12°C, respectively.

Embryonic development

Embryonic development proceeded faster at higher temperatures. Exposure to warm incubation temperatures reportedly has the greatest effect on embryonic developmental rate during the early developmental stages (Nakanishi, 1985, 1987). For larvae of the lobster, Homarus americanus, temperature determines length of incubation period, but the response to temperature varies with the age of the embryos at the time of exposure (Aiken and Waddy, 1986). The differential response may synchronize hatching among female lobsters that extrude eggs at different times within given period (Perkins, 1972). King crab embryos of similar age exposed to a range of temperatures in the present experiment displayed no evidence of hatching synchronization.

Changes in incubation temperature from 3 to 6°C (near the mean annual bottom water temperature of Auke Bay, 3 to 4°C) resulted in a 25% increase in incubation time. Similar 3°C increases above 6°C resulted in only 5% increases in incubation time. Shifts in water temperature near the average bottom water temperature apparently have greater affects on incubation time than temperatures exceeding the natural benthic water temperatures. During the spring and early summer months (February or March through June) of 1985 to 1989 in Auke Bay, Alaska, the average water temperature at 40 m depth varied by 1.5°C (Shirley and Shirley, 1988b, 1989a, 1989b). Average annual surface temperatures (measured daily for the entire year) varied by approximately the same amount (B. Wing, personal communication). Slight shifts in environmental temperatures about the mean could therefore have significant effects on the time of hatching (Shirley and Shirley, 1988c). Changes in hatch time may result in temporal asynchrony between newly hatched king crab larvae

and the abundance of their planktonic food sources, which may affect survival of the larval year class (Shirley and Shirley 1988b, 1989a, 1989b, in press-c).

Nearly three times as many degree-days were required for incubation at 12°C as at 3°C (Figure 2). These data suggest that more is involved in the onset of hatching than simply the number of degree-days of egg incubation. At 6, 9 and 12°C, hatching did not occur immediately after completion of morphological development of the embryos, but was delayed up to 3 mo. Although development was complete, yolk was present which sustained the embryos through the period before hatching. At 0 and 3°C, there was little or no delay in hatching after completion of development. Many species require external environmental cues to initiate hatching (Forward, 1987; Forward et al., 1987; DeVries and Forward, in press). Hatching of king crab eggs occurred during the winter months of late December, January and February at 12, 9 and 6°C, respectively. Changes in bottom water temperatures and salinities, and light levels and abundance of planktonic organisms during these months are minimal, particularly when compared to changes in environmental variables occurring near the natural hatching period in March to May (Bruce et al., 1977; Coyle and Shirley, in press; Laws et al., 1988). The lack of changes in environmental variables or absence of other potential hatching cues may cause a delay in larval release at the higher incubation temperatures. Eggs incubated at ambient temperature in the laboratory for several months hatch at the same time eggs hatch in the field (unpublished observations). In many crab species hatching is a highly synchronous event occurring over a narrow time span. The synchrony of hatching is thought to be controlled by enzymes released by the eggs in some species, while controlled by pheromones released by the brooding female in other species (Forward and Lohmann, 1983; Rittschof et al., 1989; DeVries and Forward, in press). Production or function of enzymes may be impeded by altered temperatures.

The length of incubation at 3°C, 321 d (282 d to hatch + an estimated 39 d from day of fertilization to beginning of study), was comparable to that in Nakanishi's study, 330 d (1985, 1987). Larvae survived well at 3°C and 6°C, but not at 9 or 12°C. Survival of larvae released at elevated temperatures was also reported to be low by Omi and Mizushima (1972, 1980). Nishimura (1935) described optimum temperatures as being between 1.3 and 5.9°C for king crab hatching. Although eggs developed satisfactorily at 0°C in our study, three of four ovigerous females molted before hatching began in the remaining crab approximately 19 mo after fertilization.

Egg incubation temperature influenced rate of embryonic development, hatching date, larval survival and larval morphology. Low crab mortality and normal embryonic development were measured over a wide range of temperatures. Only a small percentage of larvae which hatched at warmer temperatures were observed swimming in the water column. However, larvae hatched at ambient temperature tolerated elevated temperatures in a range of salinities for 96 hr (Shirley and Shirley, 1989c). The pre-zoeal stage may be more sensitive to water temperature than other larval stages, or the larvae may have had insufficient energy reserves after hatching at the higher temperatures to permit normal swimming activities.

A noteworthy finding of the incubation study was the variation in length of egg incubation with different incubation temperatures. The date of first appearance of king crab larvae in the water column of Auke Bay from 1985 to 1989 varied considerably, with the earliest appearance on 8 March 1988 and the latest appearance on 19 April 1985, with differences in hatching dates related to variations in water temperature (Shirley and Shirley 1988b, 1989a, 1989b, in press-c). Laboratory hatching of eggs incubated at 3°C occurred on 27 February and at 6°C occurred on 1 April. In the same year the incubation study was initiated (1987) laboratory hatching of red king crabs at ambient temperature occurred very close to the natural hatching time and persisted for about the same length of time of king crabs in Auke Bay (Shirley and Shirley 1988b, 1989a, 1989b) (Figure 4).

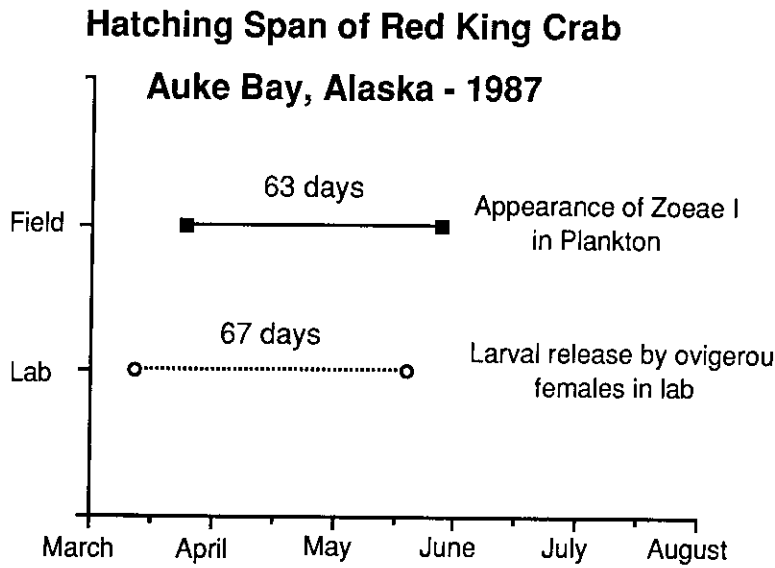

Figure 4. Comparison of the hatching span of king crabs at ambient temperature in the laboratory (Shirley and Shirley, 1988c) and in Auke Bay in 1987 (Shirley and Shirley, 1989a).

Shifts in hatching date caused by small variations of water temperature could affect larval survival if larval release does not coincide with sufficient abundances of planktonic food. Larval king crabs must feed within the first 4 d after hatching in order to successfully molt to the next larval instar (Paul and Paul, 1980), emphasizing the need for critical timing of larval release and availability of food for survival of larvae and recruitment to the benthic crab stage. Interannual variation in the survival rate of red king crab larvae in the plankton was small in Auke Bay from 1985 to 1989, but was related to the availability of prey items in the form of phytoplankton from the spring bloom and copepodites (Shirley and Shirley 1989a, in press-a, b, c).

Crab growth

Twenty three of the 25 experimental crabs molted. One crab at 0°C died early in the experiment and another had not yet molted by the termination of the experiment. We have not yet observed a "skip molt" in king crabs among any of our experiments except among crabs parasitized with rhizocephalans (Hawkes et al. 1986a, 1986b, 1987). However, molting is often poorly synchronized and spread over long time periods in the laboratory, even when the crabs are of similar sizes and are reared at the same temperature. All crabs except those at 0°C molted after their eggs hatched, however the time between hatching and subsequent molting varied greatly, both between and within temperature treatments.

Maximum average growth of the ovigerous females, calculated as the percentage increase in carapace width from premolt to postmolt, occurred at 3°C. The molt increment was generally inversely related to temperature, except for those at 0°C which also grew less than those at 3°C (Figure 3). The molt increment of the crabs at 3°C was similar to that reported for female blue king crabs by Hawkes et al. (1987). A large variation in molt increment occurred within the temperature treatments and one crab at 12°C decreased in size with molting, suggesting that molting is either not directly controlled by growth requirements or that normal molting control was altered by experimental temperatures. In adult American lobsters, molting and growth are thought to be distinct processes that should be kept conceptually distinct (Nelson et al., 1988a,b).

Although a few exceptions have been reported, the intermolt period and the molt increment of crabs generally decrease with increasing temperature; the former effect predominates such that the overall result is an increase in growth rate with temperature (Hartnoll, 1982, 1985).

The precocious molting (prior to hatching of their eggs) by the ovigerous females at 0°C indicates that the molting and reproductive cycles are independent, even if normally synchronized. A hormone associated with ovary maturation, presumably GSH (gonad stimulating hormone), causes suspension of the molt cycle in female homarid lobsters, ensuring ample time for complete embryonic development before completion of premolt by the female at temperatures normally experienced in the field (Aiken and Waddy, 1980). At abnormal temperatures, asynchrony of the cycles may occur.

Although molting in king crabs may be at least partially synchronized by photoperiod, the females at elevated temperatures molted up to several months earlier (late winter and early spring) than their counterparts in the field, while those at 0°C did not molt until September or October, 17 to 18 mo after their collection from Auke Bay. There is no convincing evidence that photoperiodism is in direct control of molting in homarid or palinurid lobsters (Aiken, 1980; however, see Nelson et al., 1988a, b for indirect effects of photoperiod upon molting) and the influence of light on molt increment, intermolt period and molt timing is considered to be highly variable among crustaceans (Aiken, 1980; Hartnoll, 1982). Since molt timing was inversely related to rearing temperature, water temperature must be considered the principle variable controlling molting in king crabs.

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Fecundity and Other Reproductive Parameters of Female Red King Crab (*Paralithodes camtschatica*) in Bristol Bay and Norton Sound, Alaska

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ABSTRACT

The fecundity of female red king crab (*Paralithodes camtschaticus*) from two eastern Bering Sea populations, Bristol Bay and Norton Sound, is described and compared. Bristol Bay embryo clutches, collected both post-extrusion and pre-hatch, show that embryos decrease in number and increase in size over the incubation period. The most common clutch symbionts found during the course of embryo counts were amphipods and turbellarian flatworms and their eggs. Only three of the 243 clutches examined from Bristol Bay contained nemertians, which are known to cause significant embryo mortality in king crabs from other Alaska populations. The size at maturity of females from the Pribilof Islands, Bristol Bay, and Norton Sound populations is 102.1, 88.8 and 71.4 mm respectively. Reproductive season timing and clutch size distribution of females from the Bristol Bay and Norton Sound populations are described and compared.

INTRODUCTION

The eastern Bering Sea supports three concentrations or populations of red king crab, *Paralithodes camtschaticus* (Fig. 1). Populations are separated by areas where red king crab rarely occur. The Bristol Bay population has supported one of the largest fisheries for this species in the world (Otto, 1981, 1990), while the smaller Norton Sound population has supported minor commercial harvests since 1977 (Powell et al., 1983). The Pribilof Islands population is found west of 168° 00' W. long. and south of 58° 39' N. lat., and supports small harvests taken incidentally to blue king crab (*Paralithodes platypus*) fishing. The National Marine Fisheries Service (NMFS) has conducted standardized trawl surveys in Bristol Bay and the Pribilof Islands area on an annual basis since 1972 and in Norton Sound triennially since 1976. These surveys are designed to provide estimates of population size and structure, but also provide data on reproductive parameters.

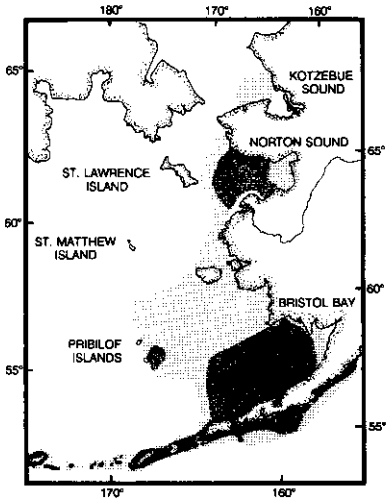

Figure 1. Distribution of three red king crab populations in the eastern Bering Sea (dark shading), and adjacent areas where they rarely occur (light shading).

One important objective of crab fishery management in Alaska is to maintain the reproductive potential of each harvested population (North Pacific Fisheries Management Council, 1989). One aspect of reproductive potential, fecundity, has been described for the Bristol Bay population (Takeuchi, 1967; Rodin, 1970, 1985) and several other red king crab populations (Haynes, 1968; Marukawa, 1933; Matsuura et al., 1972; Sato, 1958).

We report here on red king crab fecundity in Bristol Bay from early (June) to late (February) in the incubation period, and compare fecundity in the Bristol Bay population with that of Norton Sound. Clutches were also examined for embryo size, embryo profile area, and the prevalence of clutch symbionts. Size at 50 percent maturity (SM50), reproductive season timing, and clutch size distribution are described using 15 years of NMFS summer trawl survey data. Our intent is to provide some of the information necessary to quantify the reproductive status of king crab populations.

MATERIALS AND METHODS

Fecundity, Embryo Size and Profile Area, and Clutch Symbionts

Fecundity samples were collected on eight different NMFS cruises between the years 1982 and 1985 (Table 1.) Seven cruises were bottom trawl surveys in June, September, and February and one was a July crab pot fishing survey. Multiple June Bristol Bay and September Norton Sound samples were collected to increase the sample size and size range of females sampled. Our intent was to continue sampling in a multi-year framework until 10 clutches had been collected in each 5 mm size group of ovigerous females. We restricted collections to those females with "full" clutches because these were by far the most usual case (see below) and hence represented the typical situation. Collections will hereafter be referred to by an

Table 1. Collection data for female red king crab captured for determination of fecundity in Bristol Bay and Norton Sound.

Collection	Date	Gear	Number of Clutches	Size Range mm
Bristol Bay				
BB-6-82	6/ 7-6/16/82	Trawl	28	81-114
BB-6-83	6/ 8-6/15/83	Trawl	48	81-132
BB-6-85	6/ 9-6/27/85	Trawl	34	87-112
BB-7-85	7/ 7-7/ 8/85	Pot	40	81-136
BB-9-82	9/13-9/15/82	Trawl	82	79-130
BB-2-83	2/16-2/22/83	Trawl	74	80-130
Norton Sound				
NS-9-82	8/14-9/11/82	Trawl	70	65-118
NS-9-85	9/16-10/1/85	Trawl	36	67-103

area-month-year label as in: BB-6-82 (Bristol Bay, June, 1982) and NS-9-85 (Norton Sound, Sept, 1985). All samples collected from June to October had last extruded embryos in late winter or spring of the same year, while those collected in February last extruded in late winter or spring of the previous year. Late winter collections provide some information on the loss of eggs within the population during the course of embryogenesis.

Fecundity was measured as the number of embryos attached to a female. In the field, pleopods with attached embryos were excised from females and placed in formalin diluted to 10 percent with seawater. Each clutch was air dried to a constant weight and, after removing pleopods and setae, weighed to the nearest 0.1 mg. Two subsamples of about 250 embryos each were randomly selected, weighed and counted. Fecundity was estimated by dividing the total weight of embryos by the average of the two estimates of individual embryo weight that were obtained from subsamples. If the mean embryo weight in the two subsamples differed by more than 5 percent, an additional pair of subsamples was taken to replace the first.

The number of embryos per female was assumed to be a constant proportion (A) of carapace length (millimeters) raised to a power (B). Parameters were estimated using ordinary least-squares regression after both variables were transformed to natural logarithms. Comparisons among collections were made by ANCOVA (Computer program BMDP1V; Engleman, 1979). Ordinary linear regressions on untransformed data were also computed to facilitate comparison with fecundity data given by other authors.

Embryo size was estimated from random samples of 10 formalin preserved embryos from 10 females in all but the NS-9-82 collection. The length (longest axis) and width (perpendicular to longest axis) of each embryo was measured to the nearest 0.05 mm with an ocular micrometer. Geometric mean size (millimeters) of each embryo was calculated as the cubic root of length x width x width.

Measurements of embryo profile areas were made to determine relative stages of embryonic development (Matsuura and Takeshita, 1985). Six embryos from 10 egg

masses were profiled from the BB-9-82, BB-2-83, and NS-9-85 collections. These formalin preserved embryos were transferred to Bouin's Fluid for at least a month before profiling to increase visibility of the embryo. The percentage of the lateral view of the egg occupied by the embryo (as opposed to yolk) was obtained by tracing the projected image on paper and weighing the drawn parts to the nearest 0.1 mg. Embryos in all June and July samples were insufficiently developed to warrant profiling (see Nakanishi, 1987).

Most clutches were examined for the presence of symbionts. Clutches were rinsed in fresh water in a pan then spread out on a plate to dry. Wet embryos on the four large pleopods and the pan containing the rinse water were visually examined for foreign organisms under bright light without magnification. Massed embryos were teased apart and examined for about a minute. In many cases, organisms had washed out of the mass and into the bottom of the pan. This was not a quantitative search, and the percentage of the clutch or number of embryos examined is unknown. The size threshold for discovery of a foreign organism was probably about 1 mm. The terms prevalence (proportion of infested individuals in the host population) and mean intensity (mean number of symbionts per infested host) are from Margolis et al., 1982.

Analysis of NMFS Trawl Survey Data Base

The NMFS trawl survey data base was used to describe the following reproductive parameters in both Bristol Bay and Norton Sound females: size at maturity, reproductive season timing, and clutch size distribution. In addition, the data base was used to describe female size at maturity in the Pribilof District. Table 2 summarizes the trawl survey data sets used in these analyses.

One or two vessels fishing an eastern otter trawl were used for the NMFS trawl surveys. Trawl tows are of 1/2 hour duration and most tows are 1.4 to 1.8 nautical miles long. In Bristol Bay, tows were made at the centers of squares defined by a 20x20 nautical mile grid, while in Norton Sound, a 10 mile grid (or in one limited area a 15 mile grid) was used. Tows in most of the Pribilof District were made at 14 nautical mile intervals. If the trawl catch was too large to permit the measurement of all crabs, a random sample was selected for measurement in the field and an appropriate sampling factor applied before data analysis. Female red king crab from each catch were measured for carapace length (CL, nearest millimeter from rear of right eye orbit to median posterior of carapace; Wallace et al., 1949), and classified into one of the following categories: (1) immature (no embryos or empty embryo cases); (2) uneyed embryos (attached embryos lacking eye spots); (3) eyed embryos (with dark eye spots); (4) empty embryo cases attached to pleopods; and (5) mature without embryos or embryo cases. In this paper, mature females are defined as having embryos or embryo cases, categories 2-4 above. Crab in category 5 are seldom found and are not reliably separable from immatures, so this category is included with immatures, below.

Size at maturity was characterized by fitting a logistic curve to the proportion of females that were mature, for data grouped by 5 mm carapace length intervals. Curves were fit by the method of Somerton (1980) using weighted nonlinear regression and the Levenberg-Marquardt algorithm (ZXSSQ; International Mathematical and Statistical Library, 1984). Weights in this method are equal to the inverse of binomial variance at each size. Collections were compared on the basis of the size at which 50 percent of the females would be expected to carry embryos or empty embryo cases (SM50) as computed from fitted curves.

Field data also included scoring of ovigerous females for relative clutch size on a six point scale (1) trace to 1/8 full, (2) 1/4 full, (3) 1/2 full, (4) 3/4 full, (5) full, and (6) overfull. Over the period 1975-1989, "overfull" was rarely and inconsistently used so it has been combined with the "full" category below. Clutch size was described in two ways. First, by calculating the percentage of ovigerous females in each of the 5 clutch fullness categories by year. Secondly, by calculating the clutch size distribution by 5 mm carapace length interval for each year then calculating the mean for all years combined.

Bristol Bay

Data from 15 years of summer trawl surveys, 1975-1989, were included in the analysis of reproductive features (Table 2). We chose to begin the analysis with the 1975 data rather than 1972 data because there seemed to be inconsistencies in coding during early years. Surveys were not identical in areal extent, but in each year essentially the entire range of females was covered. Although inclusive dates of summer trawl surveys were May - August, most data (70% of all females caught) were from June (Table 2). In some years, after the standard survey was completed, survey vessel(s) returned to Bristol Bay to make additional duplicate tows to augment survey information or in the conduct of comparative fishing experiments. Most of the crab caught after June were taken at stations that duplicated the standard survey pattern.

To analyze reproductive season timing, a June time-window was established within which the percentage of mature crab carrying eyed embryos or empty embryo cases was determined. This June window served the dual purpose of including most of the summer data in a reasonably narrow time frame (Table 2), and excluding most duplicate tows that tend to destroy the systematic distribution and intensity of sampling effort. June data were also used in analysis of SM50 and clutch size distribution. Because of an earlier than usual survey starting date, however, the 1980 SM50 and clutch size analysis included May as well as June data to augment a very small June sample size (Table 2). The summer clutch size analysis in all years included only females with uneyed embryos in order to restrict the analysis to one year class of embryos. The clutch size analysis for 1976 data excluded one large catch in which 58 percent of the females with uneyed embryos caught had very soft shells and small clutches. We believe that these females had either not completed extrusion or had lost substantial numbers of eggs during capture. Clutch size distributions were also analyzed from limited surveys conducted in September of 1972, February of 1983 and January-February of 1985. These analyses gave some insight into the relative timing of reproduction in primiparous and multiparous females, and the nature of anomalous timing observed in the 1982-1983 reproductive cycle.

Norton Sound and Pribilof District

Each of the five surveys covered essentially the entire range of the Norton Sound population. Because data bases are small, and because only one year class of embryos was ever found in a survey, all data (Table 2) were included in the analysis of SM50, reproductive season timing, and clutch size distribution.

In 1975-1989 summer trawl surveys and the 1983 winter survey, a total of only 182 female crab were caught in the Pribilof District. Females were caught in 13 of the 15 summer survey years, and the maximum number caught in a single year was 84. Because of the small sample size, these combined data were used only for the analysis of SM50.

Table 2. Summary of female red king crab measured and caught in NMFS eastern Bering Sea and Norton Sound crab surveys.

Year	All Data Dates	All Data Meas	All Data Caug	June Data Meas	June Data Caug	Mature June Meas	Mature June Caug	Uneyed June Meas	Uneyed June Caug
Bristol Bay - Summer									
1975	6/ 1-7/ 1	2139	4731	2135	4727	1259	2111	1126	1828
1976	5/30-8/ 9	2981	6217	1290	3769	776	2896	674	2652[1]
1977	5/25-6/27	4178	7517	2615	3536	2017	2564	2009	2556
1978	5/20-7/16	3948	4932	965	1354	818	1152	816	1149
1979	5/26-8/20	4665	7811	3483	6479	2768	4665	2711	4586
1980	5/15-7/15	1390	3063	65	65[2]	61	61	50	50[3]
1981	5/23-7/20	4098	4638	1461	1461	1119	1119	1000	1000
1982	5/29-6/28	2066	4050	2014	3998	1254	1733	314	584
1983	6/ 7-7/ 1	945	1038	944	1037	262	274	223	235
1984	6/10-8/10	1943	5922	787	4593	371	876	344	837
1985	6/ 8-7/30	415	415	412	412	256	256	251	251
1986	6/ 3-8/ 5	371	372	357	358	176	176	105	105
1987	5/28-6/29	1019	1156	1014	1151	592	609	583	600
1988	6/ 3-8/ 6	550	795	503	748	432	671	395	624
1989	6/ 4-8/14	554	703	501	605	382	454	188	258
Bristol Bay - Fall and Winter									
1982	9/13-9/15	2190	3176						
1983	2/14-2/20	570	1085						
Pribilof District - All Seasons									
1975-1989	2/22-8/ 3	182	182						
Norton Sound - Fall									
1976	9/ 2-10/ 6	181	183						
1979	8/ 1- 8/ 5	28	28						
1982	9/ 5- 9/11	265	265						
1985	9/16-10/ 1	151	151						
1988	8/16- 8/23	218	218						

[1] Females from Haul 34 (2093 crab) were excluded from analysis because 58% were soft shell and had not reliably extruded their entire clutch.

[2] Because of the small June sample size, the 1305 females measured/2978 females caught between 15 and 31 May were included in the size at 50% maturity analysis.

[3] Because of the small June sample size, the 217 females measured/809 females caught with uneyed embryos between 18 and 31 May were included in the clutch size analysis.

RESULTS AND DISCUSSION

Size at Maturity

Estimated size of Bristol Bay red king crab at SM50 for the years 1975-1989 ranged from a low of 85.3 mm in 1985 to a high of 92.0 mm in 1983 (Table 3). The 15 year mean SM50, calculated from pooled data is 88.8 mm. In a different analysis of the same data base, MacIntosh et al. (1979) calculated the SM50 for Bristol Bay (including the Pribilof District) in the years 1975-1979 to be 90, 90, 89, 88, and 86 mm, respectively. None of these values vary more than 2.6 mm from the currently calculated values. Historically, however, SM50 may have been higher in Bristol Bay as both Wallace et al. (1949) and Weber (1967) report values in the 95-100 mm range.

Table 3. Carapace length (CL) at which 50 percent of red king crab females bear embryos or empty embryo cases in three eastern Bering Sea populations: Bristol Bay, Norton Sound, and Pribilof District.

Year	Parameters[1] A	Parameters[1] B	Size (CL)	Variance	Size (CL) Range mm
Bristol Bay					
1975	0.106E+13	-0.314	88.2	0.08	42-157
1976	0.613E+ 9	-0.229	88.5	0.49	57-160
1977	0.148E+12	-0.292	88.2	0.13	17-157
1978	0.831E+23	-0.603	87.5	0.37	27-162
1979	0.623E+14	-0.359	88.6	0.11	17-162
1980	0.826E+13	-0.341	87.3	0.25	27-147
1981	0.364E+12	-0.303	87.7	0.24	47-147
1982	0.657E+10	-0.254	88.9	0.14	52-142
1983	0.601E+11	-0.270	92.0	0.10	42-137
1984	0.553E+14	-0.353	89.7	0.10	62-137
1985	0.987E+16	-0.432	85.3	0.17	62-127
1986	0.490E+14	-0.351	89.7	0.72	57-137
1987	0.351E+14	-0.345	90.3	0.06	47-132
1988	0.462E+12	-0.303	88.6	0.21	17-132
1989	0.118E+ 8	-0.185	88.1	0.53	22-132
All	0.126E+12	-0.288	88.8	0.05	17-162
Norton Sound					
1976	0.193E+07	-0.220	65.7	1.51	19-101
1979	0.284E+23	-0.714	72.4	0.21	16-101
1982	0.202E+22	-0.700	70.1	0.04	19-118
1985	0.683E+12	-0.369	73.9	0.16	16-103
1988	0.279E+14	-0.426	72.6	0.04	37-103
All	0.243E+11	-0.335	71.4	0.03	16-118
Pribilof District					
All[2]	0.142E+14	-0.297	102.1	0.62	48-190

[1] $Y = \frac{1}{1 + Ae} BX$; X = carapace length, Y = percent.

[2] All data consists of 182 females caught and measured in the years 1975 through 1989.

Hsu (1987), using data from the NMFS trawl survey data base, calculated SM50s for Bristol Bay females ranging from 89 to 98 mm for the years 1972-1985. The average of Hsu's values is 92.4 mm or 3.6 mm larger than our average. The method he used to fit the logistic equation and how data were weighted are not entirely clear. He also used a slightly different definition of "gravid females" than we have used here. Hsu's presentation of results suggests that he obtained parameters of the logistic curve by linearly transforming the logistic function and performing linear regression. In our analysis, linear transformation and regression are used to obtain approximate values of parameters that are used as initial values by the Levenberg-Marquardt iterative regression routine. Calculation of the SM50 from our initial values frequently resulted in a larger value than that obtained from the final fit.

In Norton Sound, the SM50 ranged from 65.7 mm in 1976 to 73.9 mm in 1985

(Table 3). The five year mean SM50 (from pooled data) was 71.4 mm. Powell et al. (1983) estimated the SM50 visually from a plot of 1933 crab caught in June and July of 1981. That value of 68 mm is within our range of values and is less than 4 mm smaller than our 5 year mean. In the Pribilof District, a SM50 of 102.1 mm was calculated from the 182 females caught and measured during the 15 year period 1975-1989.

Norton Sound red king crab mature at smaller sizes than those in populations to the south (Fig. 2). Further, there are significant differences in SM50 for the three populations studied (Table 3). Norton Sound females mature at smaller sizes than any other known population of red king crab while Pribilof females mature at sizes comparable to those in the northern Gulf of Alaska (100-105 mm, Powell and Nickerson, 1965; Wallace et al., 1949). Bristol Bay females mature at sizes similar to those for Adak (89 mm; Blau, 1990). Somerton and MacIntosh's (1983) estimates of SM50 in female blue king crab are 81 mm for the St. Matthew Island area and 96 mm for the Pribilof Islands. Somerton and Otto's (1986) estimates of SM50 for female golden king crab (*Lithodes aequispina*) are 98 mm for the eastern Bering Sea north of 58° 30' N, 100 mm for central areas and 111 mm for the area south of 54° 15' N.

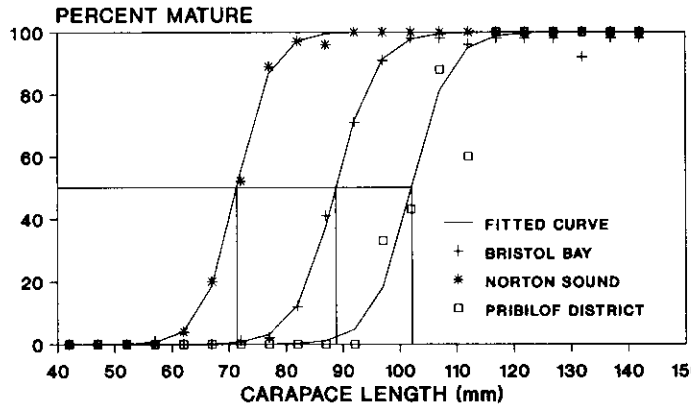

Figure 2. Female estimated size at 50 percent maturity (SM50) in three eastern Bering Sea red king crab populations.

Since the northernmost population studied has the smallest SM50 in all three species of Bering Sea king crabs, one is tempted to assume that SM50 is inversely correlated with latitude and simply a reflection of temperature. The Pribilof Islands, however, are at approximately the same latitude as Bristol Bay and, according to Ingraham's (1983) values of mean monthly temperature, the Pribilof Island area is somewhat colder than Bristol Bay. Although the values of SM50 are nearly identical for Bristol Bay and Adak, the Adak area is considerably south of Bristol Bay and warmer according to Ingraham's data. Powell et al. (1983) showed that the average growth increment for adult male red king crab was 12.5 mm for Norton Sound as compared to approximately 16 mm for Bristol Bay (Weber and Miyahara, 1962). There are no growth increment data for the Pribilof Islands area, but male crab landed in commercial fisheries averaged 162-176 mm in carapace length from the Pribilof Islands and from 145 to 151 mm for Bristol Bay (1980-1983 data; Alaska Department of Fish and Game (ADF&G), 1984), despite identical legal size limits in both areas.

While Ingraham's data show that Norton Sound is a much colder environment than the Pribilofs or Bristol Bay, it appears that temperature is not the only cause for differences in SM50 among areas. Differences in growth rate probably are involved, caused by differences in temperature regimes as well as other habitat characteristics such as the availability of food or the quality of the diet available.

Fluctuations occurred in SM50 estimated from collections in different years within Norton Sound and Bristol Bay (Table 3), but were small relative to the differences observed between populations. Deviation about the overall mean are no larger than 4 percent for Bristol Bay (1985) and 8 percent for Norton Sound (1976). As Somerton (1981) points out, SM50 may change within a population for biological reasons and is also subject to measurement error. The relative abundance of a cohort one instar smaller than the mean size at maturity and changes in mortality or growth rates can influence the value of SM50 within the population. Within our data, sample sizes are usually large (Table 2) and variance of SM50 values are less than 1.0 mm with the exception of the 1976 Norton Sound collection (1.5 mm). We do not believe that the observed fluctuations are a reflection of the precision of estimates. Estimates could be biased if there are differences in the spatial distribution of juveniles and adults of the same size that cause juveniles to be less available to the trawl. For example, if such juveniles were found closer to shore and underrepresented in the survey, the estimate of SM50 would tend to be smaller than its true value. It may be advisable to use several years of data and possibly different methods of collection in characterizing SM50.

The largest fluctuations in SM50 in Bristol Bay occur after 1982. From 1982 to 1983 the estimated abundance of females greater than 89 mm CL declined from 54.8 to 9.7 million while those less than 90 mm declined from 77.2 million to 24 million (Stevens and MacIntosh, 1989). Increased mortality may have led to the high value of SM50 observed in 1983. Stevens and MacIntosh's data also suggest that juvenile females were either in low abundance or unavailable to the trawl in 1985 and 1986, perhaps accounting for some of the fluctuations observed for those years. Trawl survey estimates show that the mean abundance of females greater than 89 mm CL was 88.7 million for the years 1975-1982 but only 12.9 million for the years 1983-1989. For females less than 90 mm, corresponding figures are 47.7 million for 1975-1982 and 16.7 million for 1983-1989. SM50 values may be less stable in small populations than they are in large populations.

Timing of the Molting and Mating Season

In an individual red king crab, hatching, molting, extrusion of eggs and fertilization all take place in less than 20 days (Marukawa, 1933; Powell and Nickerson, 1965), while the collective reproductive activity of all primiparous and multiparous females in a population may take place from as early as January to as late as July. Figure 3 shows the extent to which reproductive activity was completed in June of each survey year in Bristol Bay. The greater the percentage of mature females still carrying eyed embryos or empty embryo cases, the later reproductive activity occurred. The values for females greater than 99 mm are intended to exclude most primiparous females, all of which would be expected to have mated and extruded embryos before June. In 11 of the last 15 years, at least 80 percent of all females greater than 99 mm had completed reproductive activity for the season (Fig. 3).

The assumption that all females with eyed embryos or empty embryo cases have yet to molt and extrude a new clutch of embryos is implicit in the discussion above. Available evidence suggests that this is a reasonable assumption in all survey years

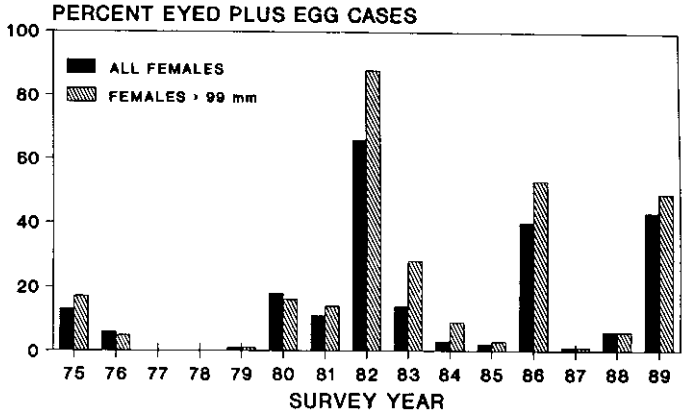

Figure 3. Percent of mature female red king crab caught in NMFS trawl surveys in June carrying eyed embryos or empty embryo cases. Mature females greater than 99 mm carapace length are roughly equivalent to multiparous females.

prior to 1982. In June 1982, 66 percent of all females captured and 88 percent of those greater than 99 mm had not yet extruded. By September, corresponding figures were 19 percent and 44 percent, showing that a substantial portion of mature females, particularly larger females, failed to molt, mate and spawn in 1982. Unspawned females carried only empty egg cases in September. In February 1983, 13 females with empty egg cases made up only 6 percent of the 197 multiparous females captured. Examination of the ovaries of these 13 showed 11 that were small and in the process of reabsorbing eggs that normally would have been spawned in 1982. No such females were captured in June 1983. The standard population estimate of mature females (> 90 mm CL) fell from 54.8 million in June 1982 to 9.7 million in June 1983 (Stevens and MacIntosh, 1989) indicating that the above anomaly in reproduction was accompanied by a high rate of mortality. Since this decline (82%) represents the net effect of recruitment and mortality, the mortality rate was likely higher than indicated by population estimates.

Despite the above situation, females that did spawn in 1982 appeared to be carrying normal percentages of partial clutches of new eggs in September or eyed eggs in February 1983 (Table 4). In 1982, 22 percent of all mature females and 32 percent of mature females greater than 99 mm still had eyed embryos in June, indicating that hatching was late, although the degree of reproductive activity cannot be assessed for the population. There are three additional years in which a substantial percentage (≥20%) of all molting and extrusion activities were not complete in June. Data are not available to describe the fate of late-spawning females in years since 1982. In view of the 1982-1983 observations it does not seem reasonable to extrapolate spawning success or the degree of reproductive activity in the population in years when late spawning occurs and no follow-up data are available.

The combination of females failing to spawn and a high mortality rate leads us to suspect that an epizootic disease was present in the Bristol Bay population from 1981 to 1983. Part of the mortality rate, however, might be explained simply by late molting since predators rarely take adult king crabs except during molting (Livingston, 1988) and predators may be more abundant or active in red king crab habitats during summer months. It is also possible that senesence was involved since

Table 4. Red king crab embryo clutch size distribution from NMFS trawl surveys in Bristol Bay and Norton Sound.

Area	Year	Clutch Size (%) Trace to 1/8	1/4 Full	1/2 Full	3/4 Full	Full
Bristol Bay - Summer	1975	1[1]	0	10	1	89
	1976	6	13	16	17	49
	1977	0	0	1	5	94
	1978	0	0	4	23	73
	1979	0	0	3	8	89
	1980	0	0	4	12	84
	1981	0	0	2	16	81
	1982	0	0	2	29	68
	1983	0	0	1	2	97
	1984	0	2	23	16	59
	1985	0	0	4	12	84
	1986	0	0	2	16	82
	1987	0	0	0	3	96
	1988	1	1	3	1	94
	1989	1	1	5	11	82
	Mean	1	1	5	11	81
Bristol Bay - Fall	1982	0	2	0	2	96
Bristol Bay - Winter[2]	1983U	0	0	0	3	97
	1983E	1	1	2	6	91
	1985U	0	0	0	1	99
	1985E	2	0	1	1	97
Norton Sound	1976	1	4	20	23	51
	1979	0	11	0	0	89
	1982	1	0	3	1	94
	1985	0	0	0	0	100
	1988	1	2	3	10	83
	Mean	1	3	5	7	83

[1] Percentages may not add to 100% due to rounding error.

[2] U, E are for clutches with uneyed (new) and eyed previous year's) embryos.

the larger females present in 1982 may have been part of the same cohorts that supported record fisheries from 1977 through 1980. Sparks and Morado (1985) found that 7 percent of 44 females collected in the fall of 1982 and 6 percent of 36 females collected in the winter of 1983 were infected with a microsporidan of the genus *Thelohania*. These were the first confirmed observations of microsporidan infection in Bristol Bay. A viral disease was also present at a prevalence of 2 to 8 percent during the same period. Hypothetically a disease would have to be present in 1981 to affect spawning in 1982 and both diseases were present in 1983. Unfortunately, there is no information concerning the etiology of either disease and we do not know if the above prevalences are representative. Viral, and particularly microsporidan diseases are known epizootics in other crustaceans.

Previous investigations of spawning in Bristol Bay have also shown substantial variation in timing. Observations taken aboard Japanese factory ships were the most complete and frequently indicated substantial spawning activity extending into June (reviewed by Weber, 1967). The Fishery Agency of Japan (1956) reported that mating occurred throughout June in 1954 and from late May to early June in 1955. For 1960 to 1965, the spawning period was reported as extending past June 15 in 1960, 1961, 1962 and 1964 (Fishery Agency of Japan, 1967) and the reported duration of the spawning period ranged from 26-54 days. The end of the spawning period was considered as the point in time when about 50 percent of the females carried "new eggs" (Fishery Agency of Japan, 1964; Fig. 44). Korolev (1964) reports that hatching began in mid-April and ended in mid-June in 1960. Our data occasionally show females with eyed embryos during the last week of June and agree with Japanese data in this respect. While Japanese data are not entirely comparable to ours, they show large proportions of females carrying eyed embryos or egg cases during June in most years. Our data indicate that this was atypical for 1975 to 1981. From 1982 onwards high percentages of females carrying the previous years embryos occur in four of eight years.

Late hatching within the population may affect subsequent year class strength. Paul et al. (1989) indicate the diatom genera *Thalassiosira*, *Skeletonema* and *Chaetoceros* were abundant during the period when stage I zoeae were in the water column of Auke Bay; and, that these taxa may be important to survival of first-feeding red king crab. Nakanishi (1987) reports use of *Artemia* nauplii, rotifers and planktonic diatoms (including *Thalassiosira*) to culture king crab zoeae. Cultures of *Thalassiosira* were used as a standard food source for stage I king crab zoeae in 1988 at the Akeshi station of the Japan Fish Culture Association (Otto, personal observation). Goering and Iverson (1981) state that "*Thalassiosira* and *Chaetoceros* dominate stage I Bering Sea phytoplankton" and that the "major genera" include *Thalassiosira* and *Chaetoceros* during stage II which persists through mid- to late-May. The first two stages of the spring phytoplankton bloom in the eastern Bering sea are hence generally completed before June and are characterized by the prevalence of *Thalassiosira* and *Chaetoceros*. Larvae hatched in or after June may suffer poor survival if they are dependent on the above diatoms. Late spawning in the early 1960s may have contributed to low abundance indicated by survey and fishery data in the late 1960s and early 1970s (Otto, 1981). More research on the survival of king crab larvae relative to food availability is needed.

At the early end of the breeding season, Hsu (1987) uses data from winter NMFS trawl surveys in 1983 and 1985 to show that primiparous female extrusion was largely completed by February 20 and 13 of those two years, respectively. Females with new, purple embryos were found during the last week of January in 1985. In 1983 molting and extrusion spanned the period February-June, while in 1985 it began by late January and had essentially been completed prior to June (Fig. 3). February data did not indicate that hatching had started, since over 90 percent of females with eyed eggs carried full clutches in both years. In February 1983, however, about 3 percent of the females with eyed eggs revealed a well developed new shell when a dactyl was broken, indicating that the beginning of the hatching-molting-mating period was imminent. Hatching may occur as early as March and certainly occurs in April (Fishery Agency of Japan, 1964).

In Bristol Bay embryogenesis resulting from primiparous spawning likely exceeds 12 months as no hatching activity was observed contemporaneously with primiparous spawning. Embryogenesis resulting from multiparous spawning may last less than 12 months but certainly exceeded 12 months in years where substantial numbers of eyed embryos were found in June following years when virtually none were. The

duration of embryogenesis is known to be influenced by rearing temperature (Nakanishi, 1987) and is difficult to determine from our data. For example, the occurrence of many females with eyed eggs in one June followed by few in the next June would imply embryogenesis in less than 12 months only if we assume survival of late spawning females.

In Norton Sound, fall NMFS survey data provided fewer clues to the timing of the reproductive season. In every year, all gravid females carried embryos of the same year class. The extent to which embryos are eyed presents some information on the timing of reproduction. Stevens and MacIntosh (1986) found 39 percent of clutches collected in September, 1985 had at least some eye pigment present. In this study, 26 percent of August 1982 clutches had some pigment present. Under varying conditions of rearing, other investigators have found that eye pigment appears 100 (Marukawa, 1933) to 201 (Nakanishi, 1987) days after fertilization. Back calculating by 100-201 days from the times of the 1982 and 1985 collections provides very rough fertilization dates of January to May (1982) and February to June (1985). These ranges overlap that of Powell et al. (1983) who concluded that mating occurred in Norton Sound in April to June.

Embryo Clutch Size Distribution

Clutch sizes for Bristol Bay and Norton Sound are shown in Table 4. In Bristol Bay, the percentage of ovigerous females with full clutches varied from 49 percent in 1976 to 97 percent in 1983. The unweighted average clutch size distribution for the 15 year period is: Full - 81 percent, 3/4 Full - 11 percent, 1/2 Full - 5 percent, 1/4 Full - 1 percent, and Trace to 1/8 Full - 1 percent. A high percentage of partial clutches can be caused by several factors, one of which is an artifact of the timing of collection relative to embryo extrusion and the other is method of capture. In 1976, for example, prevalence of partial clutches was probably caused by inclusion of females that were captured before complete extrusion had taken place or had carapaces so soft that embryos were dislodged during capture. One station, in fact, was removed from the 1976 Bristol Bay data because 58 percent of the females with uneyed embryos were soft shelled. In the fall 1982 and winter 1983 samples, the percentage of full clutches was 96 percent and 91 percent respectively. In Norton Sound, the percentage of females with full clutches varied from a high of 100 percent in 1985 to a low of 51 percent in 1976. The unweighted average clutch size distribution for the 5 survey years is: Full - 83 percent, 3/4 Full - 7 percent, 1/2 Full - 5 percent, 1/4 Full - 3 percent, Trace to 1/8 Full - 1 percent.

The ability of field personnel to consistently allocate observed red king crab clutches into categories such as those above has recently been questioned. Johnson et al. (Unpubl. manuscr.) found that when three clutch size categories of 0-29 percent, 30-59 percent, and 60-100 percent were used, categorization by multiple observers showed 86 percent agreement among pairs of observers and 59 percent among all eight observers. When more and narrower clutch size categories were used, agreement among observers dropped significantly. To approximate the categories used by Johnson et al., NMFS categories were combined as: Full plus 3/4 Full (100-62.5%); 1/2 Full (62.4-37.5%); and 1/4 Full plus Trace - 1/8 Full (37.4-0%). Using this arrangement, 89 percent of clutches were in the fullest clutch size category in 13 of the 15 Bristol Bay survey years, and 4 of the 5 Norton Sound survey years. Using either system of categorization, the 1984 Bristol Bay and 1976 Norton Sound samples have an unusually high percentage of partial clutches. No explanation for this fact is apparent.

The proportion of females with full clutches varies by size. Figure 4 (sample sizes

<10 were excluded) shows that in both Bristol Bay and Norton Sound populations, the smallest mature females tend to have a lower proportion of full clutches. The largest Bristol Bay females also may tend to have fewer full clutches while Norton Sound females do not. Matsuura and Takeshita (1985) hypothesized that the poorer physical fit of the flatter abdominal segments to the thoracic sternites in primiparous females might result in higher egg loss at extrusion or later during incubation. This might account for the lower incidence of full clutches observed among the smallest females in both areas. The prevalence of primiparous females in the smallest size groups would also lead to smaller clutch sizes if they carry fewer embryos than multiparous females (see below under fecundity).

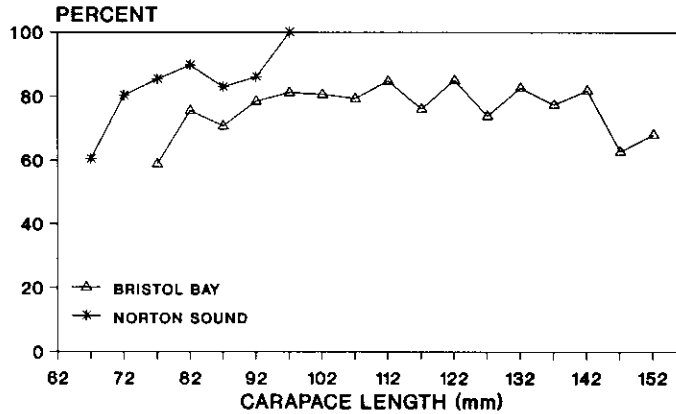

Figure 4. Percent of ovigerous female red king crab from 1975-1989 NMFS trawl surveys with a "full" clutch of uneyed (Bristol Bay) or eyed plus uneyed (Norton Sound) embryos. Unweighted data for each year combined and grouped by 5 mm increment of carapace length. Sample sizes less than 10 not shown.

Embryo Size and Profile Area

Geometric mean embryo size increased over time in Bristol Bay (Table 5). The mean embryo sizes (millimeters) for the Bristol Bay samples were June - 0.968, 0.936, 0.938; July - 0.939; September - 1.004; and February - 1.031. The single Norton Sound September sample had a mean size of 0.972. The rate of embryo development and thus embryo size is linked to cumulative degree days (Nakanishi, 1987). Several uncontrolled variables limit the value of comparisons of embryo size between our Norton Sound and Bristol Bay samples. Annual temperature regimes were not known for the collection years, nor were precise egg extrusion periods. Although each sample was ascribed to a certain month, the collection dates within the month varied (Table 1). The proportion of the crab in each sample that were primiparous, and therefore extruded earlier in the season, is also unknown. Despite limitations, Norton Sound embryos appear to be smaller than Bristol Bay embryos. While Bristol Bay embryo size exceeded that of Norton Sound in September, mean profile area (Table 5) was considerably smaller for Bristol Bay (5.2%, SD 1.4) than for Norton Sound (21.7%, SD 8.8). This indirectly points to a larger size at hatching for Bristol Bay embryos. Alternatively and extrapolating linearly, a Bristol Bay embryo with 22.7 percent profile area would be about 4 percent larger than a Norton Sound embryo.

Table 5. Size and profile area of red king crab embryos in Bristol Bay and Norton Sound.

Collection	Mean Len.[1]	SD	Mean Wid.[2]	SD	Mean Size[3]	SD	Profile Area	SD
Bristol B.								
BB-6-82	1.02	0.033	0.95	0.031	0.968	0.023	-	-
BB-6-83	1.01	0.050	0.90	0.039	0.936	0.033	-	-
BB-6-85	1.01	0.043	0.91	0.032	0.938	0.027	-	-
BB-7-85	1.03	0.050	0.90	0.033	0.939	0.029	-	-
BB-9-82	1.10	0.042	0.96	0.037	1.004	0.029	5.2	1.4
BB-2-83	1.14	0.049	0.98	0.039	1.031	0.034	63.7	5.4
Norton S.								
NS-9-85	1.09	0.065	0.92	0.053	0.972	0.051	21.7	8.8

[1] The longest axis of the embryo in millimeters.

[2] Perpendicular to the longest axis of the embryo in millimeters.

[3] Geometric mean size of embryo (millimeters).

Clutch Symbionts

We examined 243 clutches from Bristol Bay and 23 clutches from Norton Sound for symbionts (Table 6). No clutches showed signs of embryo loss subsequent to attachment, however, if partial clutches had been collected, a different picture of the symbiont community and egg loss might have emerged.

In addition to amphopods and turbellarians, three other organisms were found. The bivalve *Modiolus modiolus* was found in a single clutch from collection BB-2-83, and single polychaete worms were found in one clutch each from collections BB-2-83 and NS-9-85. Three clutches from BB-9-82 contained single worms that resembled *Carcinonemertes regicides* but positive identification was not possible (A. Kuris, Dept. of Biol. Sci., UC Santa Barbara, Santa Barbara, CA 93106, pers. commun., February, 1989).

Kuris et al. (In press) found no nemertians in 67 clutches collected 1984-1985 from Bristol Bay and single worms in 2 of 77 clutches collected 1983-1985 from Norton Sound. The only certain occurrence of *Carcinonemertes* in Bristol Bay red king crab was one on a male crab examined in 1987 by the NMFS, Alaska Fisheries Science Center pathology group (Frank Morado, NMFS, 2725 Sand Point Way N.E., Seattle, WA 98115, pers. commun., November, 1989). Kuris et al. (1990) linked *Carcinonemertes* to partial or total loss of embryos in red king crab populations from Southeast Alaska to Dutch Harbor, Alaska. Nemertian infestations generally show low intensity early in the brood period when most of our Bristol Bay collections were made. Nevertheless, there is no evidence that nemertians have ever occurred in Bristol Bay or Norton Sound populations in densities associated with high embryo mortality elsewhere in Alaska.

Table 6. Prevalence of amphipods and Turbellarian flatworm adults and eggs in the embryo clutches of Bristol Bay and Norton Sound red king crab.

Collection	Clutches Examined	With Amphipod	With Turbellarian: With Adult	With Egg	With Adult & Egg	With Adult &/or Egg
Bristol Bay						
BB-6-82	28	0	3	5	3	5
BB-6-83	48	1	6	0	0	6
BB-6-85	34	1	1	2	1	2
BB-7-85	41	1	24	6	6	24
BB-9-82	82	6	50	43	34	59
BB-2-83	10	3	5	0	0	5
Total	243	12	89	56	44	101
% of Total		5%	37%	23%	18%	42%
Norton Sound						
NS-9-85	23	1	0	0	0	0
% of Total		4%	0%	0%	0%	0%

An amphipod (*Ischyrocerous* sp.) was found in 12 Bristol Bay clutches and one Norton Sound clutch. Kuris et al. (1990) found frayed funiculi in the guts of *Ischyrocerous* sp. taken from red king crab clutches and concluded that they do consume live embryos. The amphipod *Ischyrocerus anguipes* was not considered to be an embryo predator by Enequist (1949).

The most prevalent symbionts were one or more species of turbellarian flatworm. At least one species, *Ectocotyla hirudo*, was present in our samples. Turbellarians, with a mean length of about 1.3 mm, were present in 89 (37%) of the 243 Bristol Bay clutches (Table 6). All Bristol Bay collections contained some clutches with turbellarians. We have no data on mean intensity of turbellarians but numbers found ranged from one to hundreds, and were seldom more than tens. Turbellarian eggs (single, stalked spheres about 0.3 mm in diameter) were present in some clutches. Adults and/or eggs were found in 101 (42%) of the Bristol Bay clutches. We found no turbellarians or eggs in 23 Norton Sound clutches. Kuris et al. (1990) report 79 percent prevalence with mean intensity of 33 (±33, sd) per pleopod for 19 Bristol Bay clutches in 1984; 10 percent prevalence with mean intensity of 11 (±12) per pleopod for 28 Bristol Bay clutches in 1985; and one of 30 clutches with 11 worms per pleopod from Norton Sound in 1984. Kuris et al. (1990) found no correlation between the intensity of turbellarians and egg mortality in red king crab from Uganik Bay, Kodiak Island, Alaska and did not associate their presence with embryo mortality in other areas. The turbellarian *Peraclistus oofagus* has been found on *Chionoecetes opilio* and *Hyas araneus* from the east coast of Canada, but was termed an ectocommensal by Fleming and Burt (1978). Apparent turbellarian embryo predation has been observed, however, in the Tanner crab, *Chionoecetes bairdi* from the Gulf of Alaska (G. Mueller, Dept. of Botany, Univ. of Washington, Seattle, WA 98115, pers. commun., November, 1989).

Available evidence suggests that symbionts cause little embryo mortality in Bristol Bay and Norton Sound. Because of our selection of full clutches, lack of data on symbiont intensity, and infrequent sampling late in the brood period, however, we cannot draw definite conclusions. Occasional unexplained reductions in clutch size in both Bristol Bay and Norton Sound red king crab populations have occurred, and possible causes, including egg predators, warrant a closer monitoring.

Fecundity

We have presented the relationship between the number of embryos per clutch and carapace length in both arithmetic and logarithmic terms (Table 7) in order to facilitate comparison with other studies. We chose to use logarithmic transformations of the data as a standard for comparison of populations and collections (Fig. 5). This was done both to facilitate ANCOVA and because the relationship between ovary size, hence eggs produced, and carapace length is likely to be allometric (Teissier, 1960; Hines, 1982). The equations in Table 7 and Fig. 5 were fitted to the data without assuming common slopes. Common slopes and intercepts are given below.

Table 7. Red king crab fecundity regression equation parameters both linear and log transformed.

	Log Transformed			Linear		
Collection	A	B	r^2	A	B	r^2
Bristol Bay						
all June[1]	-4.835	3.54	.836	-242387.64	3435.73	.844
BB-7-85	-6.449	3.90	.928	-321874.02	4364.33	.845
BB-9-82	-4.690	3.46	.789	-194985.16	2800.52	.810
BB-2-83	-4.499	3.42	.756	-193422.74	2778.78	.750
Norton Sound						
all fall[2]	-4.590	3.53	.779	-154708.53	2643.22	.809

[1] June collections are BB-6-82, BB-6-83, and BB-6-85.

[2] NS-9-82 and NS-9-85.

Analysis of the relationship between natural logarithms of embryos per clutch and carapace length showed differences between Norton Sound and Bristol Bay as well as between collections within populations. ANCOVA showed that slopes could be considered identical in the following sets of collections: within Bristol Bay collections ($F = .092$, $df = 5, 294$, $P = 0.47$); within Bristol Bay samples grouped by month of collection ($F = 0.89$, $df = 3, 298$, $p = .045$); and within September collections in Bristol Bay and Norton Sound ($F = 0.33$, $df = 2, 182$, $p = 0.72$). If June and July data are combined as a separate set, however, the hypothesis of equal slopes is rejected ($F = 2.10$, $df = 3, 142$, $p = 0.103$). Some differences between summer collections probably result from tallying June and July collections over several years in order to achieve a near constant cumulative sample size in each 5 mm carapace length group. This resulted in uneven sampling of the length distribution in most collections. In what follows we sometimes group data although they are not entirely homogeneous.

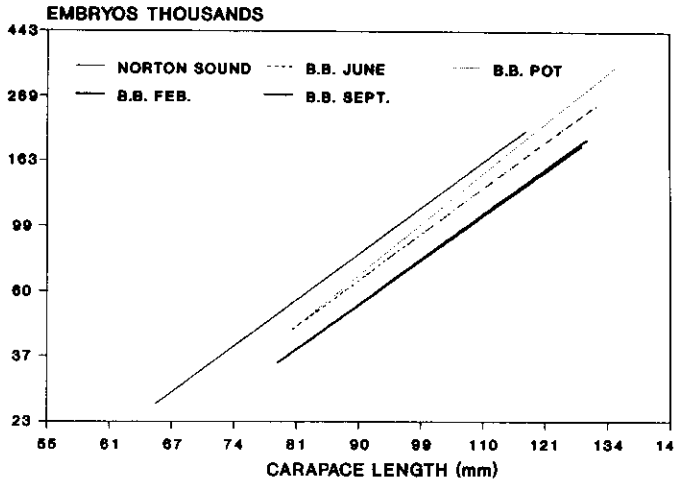

Figure 5. Linear regressions of embryos per clutch on carapace length. Both variables were transformed to natural logarithms. Norton Sound data were pooled from two years September trawl collections, Bristol Bay June data were pooled from three years trawl collections and the pot collection was taken in July (see Table 7).

Comparison of adjusted means showed differences between collections within each of the above analyses. Statistical significance of differences between adjusted means (hence intercepts) was judged at 5 percent and 1 percent levels using Bonnferoni critical values (Milliken and Johnson, 1984). Since slopes were considered identical, differences in embryo numbers between collections are proportional for any carapace length. The proportional difference in fecundity is approximated by taking the ratio of antilog intercepts determined from the common slope and adjusted mean computed within the ANCOVA.

One problem with comparing fecundities between areas or collections is that primiparous females may carry fewer embryos than multiparous females. Primiparous females cannot be identified within our collections and our regression lines tend to be parallel. A high proportion of primiparous females in a collection might decrease the intercept and hence fecundity relative to another collection. Somerton and Meyers (1983) found that regression equations representing the fecundity of primiparous and multiparous Tanner crab (*C. bairdi*) had parallel slopes for log-transformed data and that primiparous females carried about 30 percent fewer embryos than multiparous females. The primiparous molt of female Tanner crabs is a terminal molt. The lesser fecundity of primiparous females might be explained by energy being applied to both somatic and ovarian growth in primiparous females but only to ovarian growth in multiparous females. It's also possible that ovary size is simply proportional to pre-molt rather than post-molt body size.

King crabs do not have a terminal molt at maturity but mature females have smaller growth increment per molt than immature females (Weber, 1967, 1974) and a tendency for growth per molt to decrease with increasing size (Gray, 1963; Powell, 1967; McCaughran and Powell, 1977). Observations of primiparous molting near Amak Island indicated that incremental growth was 8-9 mm during January of 1985

(MacIntosh, personal observation). While Weber's (1974) data indicate an increment of about 5 mm for mature females, Gray (1963) and Powell (1967) showed that incremental growth averaged only 2-3 mm for the largest females found near Kodiak Island. Mature females are also wider for a given length than immature females (Wallace et al., 1949; Weber, 1967). If ovary size is conditioned on premolt size or shape, primiparous female red king crab may carry fewer eggs than multiparous females at a given size.

Comparison of fecundities in Bristol Bay shows differences between collections in different months as well as within the June collections (Table 8). Females

Table 8. Comparison of Bristol Bay collections assuming common slope for the regression of ln (eggs per clutch) on ln (carapace length). See text.

A. Calculation of intercepts.

Collection	Sample Size	Mean	Adjusted Mean	Intercept	Slope
BB-6-82	28	11.13	11.41	-4.814	3.512
BB-6-83	48	11.56	11.51	-4.716	3.512
BB-6-85	34	11.47	11.58	-4.647	3.512
BB-7-85	40	11.89	11.62	-4.608	3.512
BB-9-82	82	11.25	11.31	-4.912	3.512
BB-2-83	74	11.35	11.30	-4.925	3.512

B. Computation of Bonferroni critical values for 15 pairs, 299 degrees freedom and standard error of 0.209 with T (0.05, 15, 299) as 2.94 and T (0.01, 15, 299) as 3.40.

Comparison		Difference	p = 0.05	p = 0.01
BB-6-82	BB-6-83	0.098	0.146	0.169
	BB-6-85	0.167	0.157	0.182
	BB-7-85	0.207	0.152	0.175
	BB-9-82	0.097	0.135	0.156
	BB-2-83	0.111	0.137	0.158
BB-6-83	BB-6-85	0.069	0.138	0.160
	BB-7-85	0.108	0.132	0.152
	BB-9-82	0.196	0.112	0.129
	BB-2-83	0.209	0.114	0.132
BB-6-85	BB-7-85	0.039	0.144	0.166
	BB-9-82	0.265	0.126	0.145
	BB-2-83	0.278	0.127	0.147
BB-7-85	BB-9-82	0.304	0.119	0.137
	BB-2-83	0.317	0.121	0.140
BB-9-82	BB-2-83	0.013	0.099	0.114

C. Percent increase or decrease in fecundity at any size. Significance determined from above (*, p = 0.05; **, p = 0.01; NS = not significantly different).

Collection	Antilog Intercept	With respect to: BB-6-82	BB-6-83	BB-6-85	BB-7-85	BB-9-82
BB-6-82	0.00811	0.0				
BB-6-83	0.00895	10.3NS	0.0			
BB-6-85	0.00959	18.2*	7.1NS	0.0		
BB-7-85	0.00997	23.0**	11.4NS	4.0NS	0.0	
BB-9-82	0.00736	-9.3NS	-17.8**	-23.3**	-26.2**	0.0
BB-2-83	0.00726	-10.5NS	-18.9**	-24.3**	-27.2**	-1.3NS

collected in July 1985 (BB-7-85) carried about 23 percent more embryos than those collected in June 1982 (BB-6-82). Among the June collections, 1982 showed the lowest fecundity, perhaps because multiparous females were not available for sampling (See Fig. 3). The July 1985 collection showed the highest fecundity. The July 1985 females were taken in pots while all other were taken in trawls. The method of collection, however, does not appear to be related to the number of embryos per female since the July and June 1985 samples do not differ significantly. Rather, it appears that fecundity increased in the June samples with the 1982 level less than the 1983 level which in turn is less than the 1985 level. Within 1982 collections fecundities were smaller in September than June but not significantly so. Also the September 1982 collection did not differ from the February 1983 collection (eyed eggs), perhaps indicating that whatever egg loss that occurs during embryogenesis tends to occur during the summer months. Matsuura and Takeshita (1985) observed that most embryo loss occurred during the first 136 days of incubation. ANCOVA showed that slopes were parallel for pooled monthly samples, and the common exponent of carapace length in the power curve was 3.541. The proportional differences in fecundity can be computed from values of the antilog intercepts: 0.0078 for June, 0.0087 for July, and 0.0061 for September and February. If the June data are pooled and compared with September and February data, the apparent rate of loss during incubation is 17 to 19 percent which compares favorably with Matsuura and Takeshita's (1985) observation of 13 to 24 percent loss for three multiparous females maintained in a laboratory.

We compared our pooled June fecundity data to those of Rodin (1985) and Takeuchi (1967) by computing power curves from their published data. Rodin's data were given as mean counts per 5 mm width groups. We converted midpoints of the width groups to length using Weber's (1967) length-width equation before fitting the power curve. Neither author describes how clutches were selected, however, a plot of Takeuchi's data indicated that he had probably not used partial clutches of "new eggs". Comparison of computed values (Table 9) shows that our results differ considerably from Rodin's but are very similar to Takeuchi's. It is possible that Rodin's data included partial clutches, as for example, did Haynes's (1968) data in which partial clutches appear more prevalent at larger sizes. The use of conversion factors and unweighted means in our fit of Rodin's data also may have contributed to the differences observed. Takeuchi's data were collected in the

Table 9. Comparison of calculated numbers of uneyed embryos at length for Bristol Bay red king crab; calculated values are a proportion (A) of carapace length raised to a power (B). Data from Rodin (1970 and 1985, A = 0.720, B = 2,603), Takeuchi (1967, A = 0.005, B = 3,623) and this paper (A = 0.008, B = 3.541, pooled June data), see text.

Carapace Length	Present Paper	Rodin	Difference %	Takeuchi	Difference %
80	42736	64683	51.4	39148	-8.4
90	64850	87889	35.5	59986	-7.5
100	94171	115620	22.8	87870	-6.7
110	131969	148174	12.3	124113	-6.0
120	179583	185835	3.5	170112	-5.3
130	238421	228880	-4.0	227346	-4.6
140	309954	277575	-10.4	297373	-4.1
150	395717	332177	-16.1	381828	-3.5
160	497306	392938	-21.0	482418	-3.0

springs of 1955 and 1956 and hence represent a pooled sample. Differences between Takeuchi's data and our own are well within the range of differences found among our June samples (Table 8).

Comparing fecundities between Bristol Bay and Norton Sound September collections indicates that Bristol Bay females carry significantly fewer embryos (Table 10). If ovary size were about constant for a given carapace length, then the smaller mean size of Norton Sound embryos could account for perhaps 3 to 4 percent of the difference. This is small relative to the 28 to 38 percent difference observed. The fact that Norton Sound embryos were more developed than Bristol Bay embryos indicates that differences between populations could be more extreme than indicated in Table 10. Unfortunately there are no data available to compare morphometry between the two populations. Our results show that Norton Sound females carry

Table 10. Comparison of the September Bristol Bay collections with Norton Sound collections assuming common slope for the regression of ln (eggs per clutch) on ln (carapace length). See text.

A. Calculation of intercepts.

Collection	Sample Size	Mean	Adjusted Mean	Intercept	Slope
NS-9-82	70	10.90	11.20	-4.45	3.484
NS-9-85	36	11.08	11.35	-4.30	3.484
BB-9-82	82	11.25	10.87	-4.78	3.484

B. Computation of Bonferroni critical values for 3 pairs, 184 degrees freedom and standard error of 0.224 with T (0.05, 15, 299) as 2.39 and T (0.01, 15, 299) as 2.94.

Comparison		Difference	p = 0.05	p = 0.01
NS-9-82	NS-9-85	0.142	0.110	0.135
	BB-9-82	0.0336	0.087	0.107
NS-9-85	BB-9-82	0.478	0.107	0.131

C. Percent increase or decrease in fecundity at any size. Significance determined from above (**, p =0.01).

Collection	Antilog Intercept	With respect to: NS-9-82	NS-9-85
NS-9-82	0.01171	0.00	
NS-9-85	0.01350	15.31**	0.00
BB-9-82	0.00837	-28.53**	-38.02**

more and smaller embryos than those from Bristol Bay but more research will be necessary in order to understand why this might be so.

It is tempting to use the relationship between embryos per clutch and carapace length, in combination with annual data on relative clutch size and population numbers, in order to construct an overall index of reproductive potential. In fact, one reason for using only full clutches in the fecundity analyses is to facilitate the creation of such an index. Hsu (1987), for example, presents estimates of annual egg production using Haynes's (1968) equation, logistic curves relating percent ovigerous to carapace length, and relative clutch sizes. We believe that more research should be conducted before trying to apply our data in the context of indices of egg production in stock-recruitment or similar relationships. We hence recommend further research in the following areas:

1) the fate of late spawning females relative to survival and subsequent spawning or resorption of unspawned eggs,
2) the extent of egg loss during embryogenesis,
3) differences in initial fecundity as well as egg loss between primiparous and multiparous females, and,
4) further characterization of interannual differences in fecundity within populations.

SUMMARY

1. Estimated size at 50 percent maturity (SM50) for females is smallest in Norton Sound (71.4 mm CL), intermediate in Bristol Bay (88.8 mm CL) and largest in the Pribilof Islands (102.1 mm CL).

2. Variations in estimated SM50 within populations are small relative to differences between populations and may be caused by biological factors or sampling bias; preferably, several years of collections and sampling methods should be used in characterizing SM50.

3. Timing of molting and mating in Bristol Bay is variable, occurring as early as the last week in January among primiparous females and extending through the last week of June among multiparous females; hatching may occur as early as March but certainly extends from April through June with peak activity in May or June but possibly as early as April in some years.

4. Embryogenesis resulting from primiparous spawning in Bristol Bay exceeds 12 months as does that resulting from multiparous spawning in at least some years; shorter durations may occur in the case of multiparous spawning but cannot be determined from our data.

5. Reproductive activity in Norton Sound apparently occurs in the spring and may extend into June.

6. Over the 15 year data series, an average of 93 percent of newly spawned Bristol Bay females were carrying clutches judged to be 3/4 full or full. For five triennial surveys from Norton Sound the corresponding average is 90 percent. There was one year with an unexplained prevalence of partial clutches in each population.

7. Norton Sound embryos were smaller than Bristol Bay embryos despite more advanced embryo development in the Norton Sound sample, at a comparable state of development; Bristol Bay embryos would be about 4 percent larger than Norton

Sound embryos.

8. While potential egg predators were found in Bristol Bay and Norton Sound embryos, there is no evidence that they have contributed significantly to embryo mortality in either population.

9. Fecundity varies between collections within populations and these differences are generally proportional at any size. Bristol Bay females were 28 to 38 percent less fecund at any size than Norton Sound females.

10. Fecundity is a proportion (A) of carapace length raised to a power (B) and ANCOVA showed that slopes in regression equations could be considered parallel. Common slopes (exponent B) were: 3.51 for Bristol Bay collections taken singly, 3.54 for Bristol Bay data grouped by months, and 3.48 for Norton Sound and Bristol Bay September data. Intercepts were not identical and representative antilogs (proportion A) were: 0.0078 for pooled Bristol Bay June data (new eggs); 0.0064 for Bristol Bay in February (eyed, pre-hatch); and .0117 to .0135 for Norton Sound in August-September.

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Disorders of the Reproductive Cycle in Crab Females of the Genus *Paralithodes*

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ABSTRACT

Two types of disorders are observed in the reproductive cycle of females: "nonbreeding" and "pseudo-nonbreeding." In pseudo-breeding there are no eggs on the pleopods after spawning, but the gonads grow normally. In nonbreeding females the eggs are lost and a resorption of oocytes in gonads takes place. "Nonbreeding" is abnormal and affects the reproduction of the population. The existence of "pseudo-nonbreeding" females is normal and doesn't cause a fluctuation in stock abundance.

Scientific methods of commercial crab stock management require more investigations of fluctuations in the abundance of natural populations. Thus, studies of the factors regulating crab abundance have practical applications. Studies of the limiting factors in the reproductive system will permit a more exact evaluation of the influence of the fisheries and natural factors on reproduction by these populations.

The regulation of stock abundance occurs under the influence of limiting factors at each stage of the reproductive process. Fedoseev and Rodin (1986) listed the following stages: gametogenesis, embryonic development of eggs, postembryonic development of larvae, growth of immature individuals and the formation of spatial structure of a population.

Initial stock abundance is formed at the stage of gametogenesis. Following gametogenesis there will be some reductions caused by regulatory mechanisms at each specific stage of the reproductive process. At the initial stages of the reproductive process reductions of the developing population result from

environmental influences on the parent stocks; i.e., the ripening of gametes, the spawning stage and embryonic development are related to influences on the whole population and are a function of the adaptation of the population to these various influences. Environmental influences on the progeny occur at later stages, beginning with the development of larvae.

Under normal conditions, the main stock reductions result from predation and are determined by the quantity of predators. So the negative actions of the fishery and natural factors reduce crab population at the early stages of the reproductive cycle. Thus the investigation of these factors has a great importance. From the analysis of spawning in 1987 on the Kamchatka shelf we have proposed that unsuccessful spawning by female *Paralithodes camtschatica* occurred due to an absence of males ready for spawning. This situation is likely to occur in commercial fisheries taking mostly mature males during spawning. The external eggs were lost by the females and the remains were easily removed from the pleopod rami. At the same time, there were normal oocytes in the gonads of these females. This phenomenon had been referred to earlier as "nonbreeding."

The percentage index of "nonbreeding" females in the mature population has served as one of the main criteria for estimation of the biological condition of the population. As revealed above, females with a disruption of the reproductive cycle would not produce any progeny the next year. However, because they produce normal oocytes, these females will undoubtedly spawn under favorable conditions, i.e., their reproductive cycle will recover. This hypothesis is verified by the existence of large-sized females in prespawning condition without empty shells on pleopods, indicative of a prolonged period without the storage of developing eggs. Apparently, "nonbreeding" females appear as described above in the year following the spawning disorder.

We were forced to revise our opinion on "nonbreeding" by events occurring in 1988. We found nonmolted blue crab females (*P. platypus*) in the initial stage of oocyte resorption on the Western Kamchatka shelf and Ayan-Shantarsky shelf of the Okhotsk Sea. These females had not formed pods and were further out to sea than the main stocks of post-spawning females. Although there were no special data on the abundance of these females, they may add up to as much as 10%. All the females in the initial stages of oocyte resorption had empty egg shells on pleopods, verifying the favorable outcome of spawning during previous years. The simultaneous initiation of the resorption process in such a considerable number of "nonbreeding" females indicates the influence of abnormal conditions. Resorption of oocytes is thought to be caused by a disorder of the larval spawning process. For unknown reasons, females have temporarily lost the capability of molting. This prevents the females from releasing the eggs onto the pleopods. Oocytes in these females overripen and begin resorption. Resorption of the oocytes blocks the development of the sex cell, thus reducing the normal function of genital systems during several subsequent years. Resorption was also found in king crab females but in much lower amounts.

Thus, two types of disorders of the reproductive cycle of females are revealed based on previous investigations. The first type of disorder is of short duration and is the result of a lack of males to copulate with the available females. There are no pathological changes in the genital systems and females may function normally. Such a cycle is named "pseudo-nonbreeding." The second type of disorder of the reproductive cycle is accompanied by pathological changes in the genital system causing a loss of the reproductive function of the females for a long period and is named "nonbreeding."

These two types of disorders of the reproductive cycle cause different damage to the reproduction of the population. "Pseudo-nonbreeding" females are removed from reproduction for only one year and decrease the abundance of a single-year class. "Nonbreeding" females can't take part in reproduction for several years until oocyte resorption in the gonads is complete. A large number of these females in the population causes a prolonged population depression. The loss of reproduction by the females is, consequently, the main problem in the investigation of reproductive processes of the crab populations. Some disorders of the female reproductive cycle may play a definite role in population regulation and be a normal part of the reproductive strategy of the species. However, there must be a positive aspect to the negative character of the influence, which may be absent in the case of "nonbreeding." "Nonbreeding" is evidence of a physiological disorder in the females and, in our opinion, doesn't have a positive influence at the population level. Thus, the phenomenon is abnormal and it disturbs reproduction in the population. As for "pseudo-nonbreeding" females, a small quantity in the population seems to be normal and doesn't cause fluctuations in stock abundance. Currently, these phenomena are being investigated with the help of electron-microscopic, histological, biochemical and physiological techniques.

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The Size at the Onset of Maturity in Male *Chionoecetes bairdi* (Decapoda, Majidae)

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ABSTRACT

The vas deferens of male tanner crab, *Chionoecetes bairdi*, were examined for the presence of spermatophores and mating experiments were done to see if males that were just beginning to produce spermatophores could fertilize primiparous mates. Sixty-four percent of the males with carapace widths of 51-60 mm were producing spermatophores and 53% of them fertilized primiparous mates. In the 61-70 mm carapace width class 70% were producing spermatophores and a similar percent were successful breeders. All males over 80 mm were producing spermatophores and fertilized their primiparous mates. Small males that were producing spermatophores did breed, so examining males for spermatophore production histologically appears to be one way to determine the size at the onset of maturity for this brachyuran species.

INTRODUCTION

The subject of reproduction is of critical importance to understanding the effect of male removal from the population in species like the tanner (*Chionoecetes* spp.) crab that are harvested intensively. The fishery is regulated by restricting both the number and size of males harvested. The management goal is to ensure that enough breeding males remain in the population so that all females are fertilized annually. A minimum legal size limit on males is one management strategy used to keep viable males in the population.

There are two morphological states for egg producing female tanner crabs. Primiparous crab are those that have just undergone their final molt to maturity, and are bred in the soft shell state. During their second and subsequent annual

breedings they are in the hard shelled multiparous state (Paul, 1984). Multiparous crab can fertilize the eggs using sperm stored from previous matings or remate to acquire fresh sperm (Paul, 1984). Some previous information is available on the size of male *Chionoecetes bairdi* (Rathbun) that can mate with primiparous females (Adams and Paul, 1983; Adams, 1985). However, these studies poorly described the size at the onset of male sexual maturity.

A histological examination of the vas deferens was done to determine the size of males which produce spermatophores. Nonmotile sperm is produced in the testes and then packaged inside spermatophores for transfer to the spermathecae of a mate. The spermatophores for *C. opilio* have previously been described (Beninger *et al.*, 1988). The round spermatophores of *C. bairdi* appear to be identical to those of *C. opilio*. The absence of spermatophores in the reproductive tract indicates immaturity or sterility, while their presence indicates the maturation process has started. Previously spermatophore formation had not been used to determine size at maturity in brachyuran crabs. In recent literature on *C. opilio* (Conan and Comeau, 1986) the term functionally mature has been used to describe males that actually breed. It is suggested that these males are identifiable through analyses of allometric relationships between chela size and carapace width. This same report also uses the term morphometric maturity to describe these males. Conan and Comeau (1986) also state that there exist physiologically mature males, identified by relatively small chela widths, which produce spermatophores but do not breed. The authors however do not state why these small males cannot use their sperm to fertilize mates. Hartnoll (1965) emphasized that the presence of fully formed spermatophores in the sperm ducts of small males is only circumstantial evidence of maturity and laboratory mating experiments are required to demonstrate maturity. The objective of this study was to see if small male *C. bairdi*, just starting to produce spermatophores, could breed with primiparous mates.

Previously it was generally stated that male *Chionoecetes* molt throughout their lives (See Donaldson and Johnson 1988 for a review). More recently Conan and Comeau (1986) reported that male *Chionoecetes opilio* undergo a terminal molt only after which are they capable of breeding. During the latter stages of this study observations on molting by successful male parents were noted to help address the now controversial question of molting in mature male *Chionoecetes*.

MATERIALS AND METHODS

Male *Chionoecetes bairdi*, 21 to 90 mm carapace width, were captured in Resurrection Bay, north Gulf of Alaska. The size at the onset of maturity was determined by histological examination of the vas deferens. The vas deferens were first fixed in Bouin's solution. Standard paraffin embedding techniques were used to mount the tissue and sections were cut 10 to 12 microns thick. The standard Ehrlich's hematoxylin and eosin yellow staining sequence (Clarke, 1973) was used to enhance morphological identification of spermatophores. The number of specimens examined, and their carapace widths occur in the results.

In the laboratory males of selected sizes were placed with pubescent females from Resurrection Bay just after their maturity molt. This is the period when they normally breed (Paul and Adams, 1984). The seawater was 5.0°C (±0.5) and salinity 31-32 ppt. Each pair was watched for copulatory behavior. The size of the holding tanks was 0.6 x 1.2 m. Small tanks were adequate for these experiments since newly molted primiparous crab are unable to walk and can not exhibit an escape response to the male embrace. If the female extruded eggs, they were examined at egg age one week for division which indicates successful fertilization. One hundred eggs randomly selected throughout the egg clutch were examined with the aid of a microscope to determine the mean percentage of eggs undergoing division.

Twenty-one males that successfully fertilized their primiparous mates were held captive for 6 months to see if they would molt. These males were between 51 and 75 mm carapace width. The water temperature during the holding period ranged from 6° to 9°C.

RESULTS

The histological examinations of vas deferens (Table 1) suggested that crab of 41 to 60 mm carapace width are just maturing and starting to produce spermatophores. Sixty to 64% of these groups had spermatophores. Spermatophores were being produced by 70% of the 61 to 70 mm group, and 83% of the 71 to 80 mm males. Based on the presence of spermatophores, it appears that the size at the onset of maturity varies with each individual and generally can occur between 40 and 70 mm carapace width. Above 80 mm most males are producing spermatophores.

The mating experiments with primiparous females supported the histological estimates of size of maturity. Fifty-three percent of the 51 to 60 mm males that were involved in mating experiments were successful in fertilizing their mates (Table 2). Normal clutches with dividing eggs were produced by 77% of the females mated to males 61 to 70 mm carapace width. All males over 71 mm were successful in breeding primiparous mates. Figure 1 provides information on relative carapace widths of pairs successful and unsuccessful at breeding.

As male size increased from 50-59 mm to over 70 mm, the percent of the eggs in clutches that had initiated division increased from an average of 82% to 99%, respectively (Table 2). Qualitatively all clutches appeared to be of normal size compared to literature values (Adams and Paul, 1983). In cases where a nonviable clutch was produced (Table 2, column 6), sperm was present in only two spermathecae. In all but one of the cases where no eggs were extruded (Table 2, column 7), copulatory behavior was noted, but no sperm was deposited in the spermathecae. The only male that did not attempt copulation had carapace width of 50 mm. Eighty percent of those males who failed to fertilize primiparous females they were held with did not have spermatophores in their vas deferens. Primiparous carapace widths averaged 90 mm (SD = 5 for all 56 females) and

Table 1. Spermatophore presence relative to carapace width for male *Chionoecetes bairdi.*

Carapace width	Percent with spermatophores	Number of crab
21 - 30	0	28
31 - 40	0	14
41 - 50	60	30
51 - 60	64	99
61 - 70	70	101
71 - 80	83	100
81 - 90	100	14

Table 2. Egg production by primiparous *Chionoecetes bairdi* mated to males of different carapace widths.

Male width (mm)	Female width (mm)	Number of pairs	% Normal ovulation	% eggs dividing Mean (SD)	% all nonviable eggs*	% No eggs +
51-60	79- 89	19	53	82 (38)	37	10
61-70	79- 101	22	77	88 (31)	14	9
71-80	85- 94	4	100	99 (1)	0	0
81-90	90- 100	10	100	99 (1)	0	0

*The clutches of females in this group contained only nondividing eggs.
+These females did not extruded any eggs.

the mean size of the 14 females in unsuccessful matings was also 90 mm (SD = 4), with a range of 67 to 94 mm.

In the group of 21 successful male parents held for six months 71% molted. Their carapace widths and chela heights occur in Table 3.

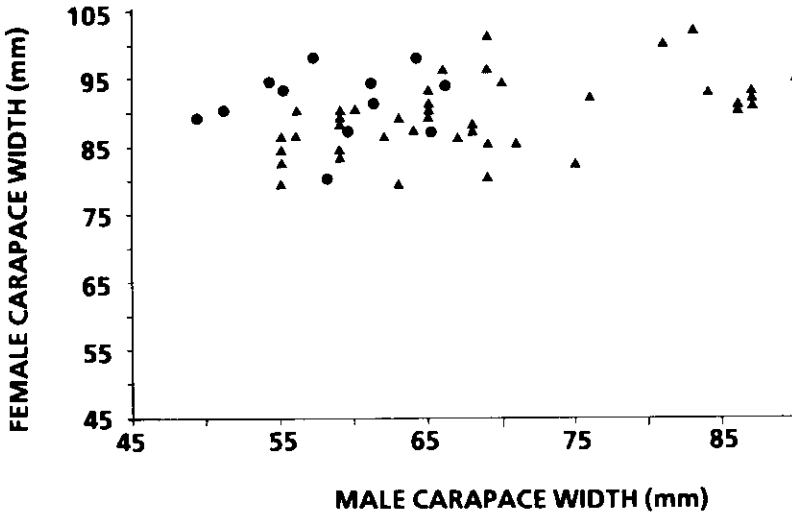

Figure 1. Carapace widths (mm) of pairs of *Chionoecetes bairdi* that produced fertilized egg clutches (+) and unsuccessful pairs (.).

DISCUSSION

Only one previous breeding experiment provides information on the success of very small male tanner crab mating with primiparous females. Adams (1985) mated 14 males 55 to 59 mm carapace width with soft-shell mates. Seventy percent of those females produced eggs that initiated division but estimates of percent fertilization and clutch size were not made. Nor was information on whether the males unsuccessful at fertilizing females were producing spermatophores. The same report provides the observations on the percent of males producing spermatophores. Adams' (1985) data is provided in Table 4.

Both the current study and that of Adams (1985) show that some males 41 to 50 mm are maturing. However, the present results do not agree with those of Adams on the size class at which 100% of the males are producing spermatophores (Table 1). In Adams' sample all crabs over 51 mm had spermatophores. In contrast only 64% of the 51-60 mm males in the current collection had spermatophores (Table 1). In this study even within the 71 - 80 mm size group examined histologically, 17% of the crabs were not producing spermatophores. Since the specimens were collected in the same area, the differences in the two reports are probably due to larger sample sizes in this study, or perhaps the molt stage. Many of the specimens in this study were recently molted crabs. In the closely related, but smaller, *C. opilio* spermatophores are generally present in males larger than 60 mm (Conan and Comeau, 1986).

Table 3. Premolt carapace widths and chela heights of male *Chionoecetes bairdi* that molted after successfully fertilizing primiparous mates.

Carapace Width (mm)	Chela Height (mm)	Carapace Width (mm)	Chela Height (mm)
54	7	64	9
55	7	65	8
57	7	70	9
59	7	73	10
59	8	75	11
59	9		
59	9		
60	9		
61	9		
62	9		

Table 4. Male size and spermatophore presence data from Adams (1985).

Carapace width (mm)	Sample size	Spermatophore walls present (% of sample)
21-25	13	0
26-30	6	0
30-35	6	0
41-45	3	33
46-50	5	80
51-55	5	100
56-60	9	100

The histological survey and the mating experiments estimated that males had to be at least 71-80 mm carapace width before consistent breeding success in primiparous mating was observed. It was previously demonstrated that successful breeding males, regardless of size, generally provide primiparous females with a surplus of sperm over their needs for fertilization of the first egg clutch (Adams and Paul, 1983).

Based on reproductive tract weights and chela morphometry it has previously been suggested that only 50% of 109-117 mm male *C. bairdi* are sexually mature

(Brown and Powell, 1972; Somerton, 1981). The results of this study indicate that these estimates of size of maturity based on morphometry may be too large since most crabs over 70 mm are capable of fertilizing the eggs of primiparous mates. Likewise, in *Macrobrachium rosenbergii* measurement of claw growth has been demonstrated to be inappropriate for determining male size of maturity (Kuris et al., 1987). The results of this study and Kuris *et al.*, (1987) suggest that morphometric estimates of size of maturity should be used with caution.

These breeding studies with tanner crab were done in a laboratory where males were isolated from other male competitors. This technique was adopted since the objective of the study was to determine the smallest size at which males could consistently breed primiparous females. There may be some behavioral aspects of the reproductive process that may preclude some small mature males from mating even though they are capable of the act. SCUBA diver observations indicate that the size range for males grasping pubescent females *C. bairdi*, prior to their maturity molt, is 79 - 163 mm, with a mean value of 112 mm carapace width (Brown and Powell, 1972; Paul *et al.*, 1983). In all of these diver observations of grasping pairs the male was larger than the female. Previous observations suggest that large *C. bairdi* males out compete small mature males for mates (Paul *et al.*, 1983; Donaldson and Adams, 1983).

This study was restricted to primiparous females and similar work with multiparous females is needed. Limited laboratory work suggests males must be larger than multiparous females to overcome their resistance to the mating embrace and copulate with them (Adams, 1982; Donaldson and Adams, 1989). Thus small males that can mate with soft-shell primiparous females might not be able to breed multiparous mates.

This report provides information on the size of onset of maturity for male *C. bairdi*. Most males over 71 mm carapace width are producing spermatophores and can fertilize primiparous females in the laboratory. The study also demonstrated that small mature males molt. This is in contrast to some observations for *C. opilio* in which mature males are thought not to molt (Conan and Comeau, 1986). All of the molting males in this study would have to molt twice (W. A. Donaldson, Alaska Department of Fish and Game, personal communication) before reaching the allometric size of maturity as defined by morphometry (Brown and Powell, 1972; Somerton, 1981).

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Size at Maturity of Female Red King Crabs (*Paralithodes camtschatica*) in the Adak Management Area, Alaska

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ABSTRACT

Alaska Department of Fish and Game shellfish biologists studied female red king crabs (Paralithodes camtschatica) caught in pots on commercial and research vessels fishing red king crabs from 1969 to 1977 and in 1979 in the Adak Management Area, Alaska. Carapace lengths, shell-ages, and external reproductive data were recorded, summed, and analyzed to obtain the size at maturity of female crabs from this area. There were 12,448 exuviant females captured that had both carapace length and either embryo presence or absence status noted. A logistic curve was fit using female crabs in the size range of 75-115 mm carapace length. In this size range there were 10,113 females; 8% did not have embryos (only silky pleopodal setae) and 92% had embryos (or only matted pleopodal setae composed of embryo membranes and funiculi remnants). The 50% size at maturity for female red king crabs in the Adak Management Area was estimated at 89 mm carapace length (SD = 2.6 mm). Possible reasons for differences in female red king crab sizes at maturity and the methodologies for deriving size at maturity are contrasted between broad geographic areas.

INTRODUCTION

Size at maturity estimates of crabs are used to establish retention size limits in commercially exploited crab populations, a crab management tool commonly used to reduce chances of overexploitation. Commercial harvest of red king crabs (Paralithodes camtschatica) began in Alaska in 1920 (Alaska Department of Fisheries 1954) and continues today. Eleven of the 12 management units, as delineated by the Alaska Department of Fish and Game (ADF&G 1988), have supported this males only fishery at one time or another.

The 50% size at maturity (SM50) for both male and female red king crabs has been determined only in the Bristol Bay Management Area (Wallace et al. 1949; Weber 1967; MacIntosh et al. 1979; Somerton 1980; Otto et al. 1980 and Hsu 1987).

Within the Adak Management Area, neither chelae height nor reproductive tracks have been collected or examined to determine SM50 for male red king crabs. There are some female size at maturity data for this area, but no SM50 was established (McMullen and Yoshihara 1970, 1971). In this paper, additional female red king crab data is examined and the SM50 for the Adak Management Area is described.

The Adak Management Area (hereafter referred to as Adak) lies between 171° W longitude and the U.S.-Russian Convention line of 1867 (ADF&G 1988). The area encompasses the westernmost three quarters of the Aleutian Islands (Figure 1).

Adak's geographical position makes it an interesting location to compare female red king crab size at maturity with adjacent areas. Adak is not only the westernmost area but also extends furthest east and south of any of Alaska's other red king crab management areas. It is also the closest area in Alaska to adjacent populations of red king crabs in the Soviet Union and Japan.

Commercial harvests of red king crab have produced 91 thousand tonnes (200 million pounds) of red king crabs in the 28 fishing seasons from 1960/61 to 1988/89 (ADF&G 1989). The area ranks fourth behind Bristol Bay, Kodiak and Dutch Harbor Management Areas in historical red king crab production in Alaska (Blau 1985).

METHODS AND MATERIALS

Alaska Department of Fish and Game (ADF&G) shellfish biologists gathered female red king crab data on 20 different vessels during 25 different trips conducted in Adak from 1969 to 1977 and in 1979. On 18 of these trips biologists served as observers on private vessels (one per vessel) which were commercially fishing for red king crabs. On the remaining seven trips, biologists were part of the biological crew on ADF&G's RV/Resolution or on vessels chartered by ADF&G. Biologists conducted the following types of research on Adak red king crabs: population assessment surveys, male tagging, and test fishing. All fishing efforts occurred in the waters around Seguam Island on the east, to Petrel Bank on the west, with most of the effort occurring in the Andreanof Islands primarily north and south of Atka and Amlia Islands (Figure 1).

Red king crabs were captured with steel frame pots. Most pots measured either 198x198x86 cm or 203x203x86 cm (6x6x 2.8 ft or 7x7x2.8 ft) weighing 273 kg or 295 kg (600 lb or 650 lb) respectively. These pots were covered with tarred nylon webbing with stretch mesh sizes ranging from 9-28 cm (3.5-11 in). The smallest pot meshes were used on most ADF&G surveys to increase the retention of smaller crabs. Pots were baited primarily with chopped herring in perfor-

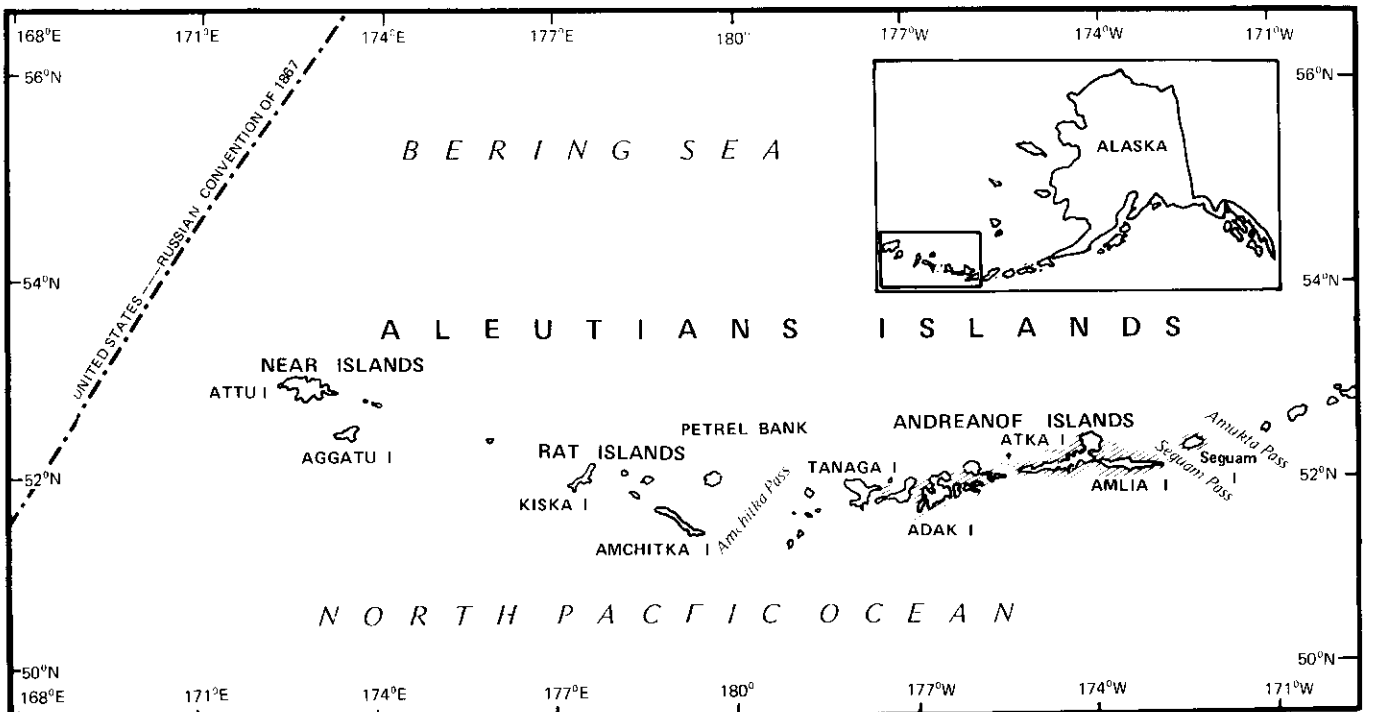

Figure 1. The Adak Management Area is located between 171° W longitude and the U.S. - Russian Convention Line of 1967 and between 51° N and 55°30' N latitudes. Shaded areas indicate where female red king crab data were collected from 1969 to 1977 and in 1979.

ated containers and soaked on the bottom generally between 15-48 hr. Most of this fishing effort occurred from 73-183 m (240-600 ft) although pots were fished from 16-393 m (54-1,290 ft). Data were gathered by ADF&G observers on commercial vessels from November to March, the months encompassing the commercial seasons. Data on ADF&G surveys were gathered from January through March and from June through October.

The carapace length (CL) of each female red king crab was measured from the posterior margin of the right eye orbit to the midpoint of the posterior margin of the carapace, to the nearest millimeter using Vernier calipers (Wallace et al. 1949). Exoskeletons were recorded as either exuviant (new-shell) or anexuviant (old-shell). The external reproductive condition of each female was examined for the presence or absence of embryos on the pleopods. Exuviant barren females were recorded as having either "silky" pleopodal setae, lacking any empty embryo membranes or funiculi, or "matted" setae where embryo cases and funiculi remained. Maturity was defined as the presence of embryos or matted setae on exuviant females. Anexuviant females (about 200) were excluded from the data analysis. Pleopods on anexuviants were not checked because all were barren. The previous presence or absence of embryos on exuviant crabs was indeterminable on anexuviants because pleopodal setae may become fouled with marine animals and embryo membranes and funiculi wear off over time. Also excluded from the analysis was one barren female which had the externae of the castrating rhizocephalan barnacle Briarosaccus callosus (Overstreet 1983) attached to its abdomen.

Carapace length frequencies of female red king crabs were summed from all data collected by ADF&G biologists for each of the 25 trips in Adak. These frequencies were spit into two groups; 1) those females with embryos, regardless of clutch size, including barren females which had matted setae, and 2) females without embryos, having only silky setae. Only raw data were used. Embryos can be present only on exuviant red king crabs, and if so hatch in about a year's time (Marukawa 1933; Powell and Nickerson 1965a: and Haynes 1968). No adjustments were made to the number or condition of females for: subsampling, varying soak times, differing pots or pot web sizes used.

The percent mature by 1-mm carapace length intervals were plotted for each of the four largest samples gained from the 25 fishing trips (sample sizes = 2,207, 2,108, 1,741, and 1,068). These samples were collected in 1970 and 1975-77 in the months of June through October from the Andreanof Islands. The four samples represented 57% of the total crabs measured and they ranged in size from 54-159 mm CL. From these graphs it was determined that the distributions of percent mature in each of these samples were similar throughout the female size ranges. The female data for all 25 trips was then combined and fit to a logistic function using nonlinear least squares BMDP 3R (Dixon 1977).

RESULTS

There were 12,448 exuviant females measured, of which 1,462 (12%) did not have any embryos, and 10,986 (88%) that had embryos or embryo remnants (Table 1). Sixty-eight percent of the samples were taken from June through March; 60% of these measurements were gathered in June and July. The remaining 32% of the total measurements were taken by ADF&G observers while aboard vessels commercially fishing red king crabs during the months of November through March. Ninety percent of all measurements were taken in the Andreanof Islands, primarily from the north and south sides of Atka and Amlia Islands (Figure 1). The remaining 10% of the female measurements came from Petrel Bank.

Female sizes ranged from 54 to 166 mm CL, and the smallest females with embryos were 75 mm CL (Table 1). Females ≥101 mm CL were ≥95% mature, except at 144 mm CL where one out of seven females were barren. The SM50 of the female red king crabs considered was 89 mm CL (SD = 2.6 mm). The logistic curve was fit using data from 75-115 mm CL (Figure 2). This size range was composed of 10,113 females, of which 92% had embryos and 8% did not.

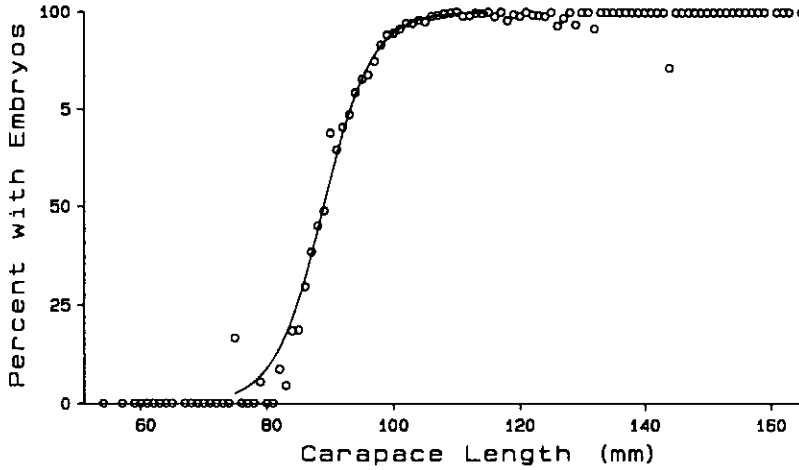

Figure 2. SM50 for female red king crabs in the Adak Management Area, Alaska is 89 mm CL. The logistic curve was fit using females from 75 to 115 mm CL.

DISCUSSION

Adak female red king crabs SM50 of 89 mm CL was generally closer to the SM50 figures generated by other investigators for the southeastern Bering Sea than it was to other areas where the SM50 has been calculated (Table 2). This similarity is not surprising since these two areas are the

Table 1. Length frequencies and percent maturity of all exuviant female red king crabs measured by Alaska Department of Fish and Game biologists from 1969 to 1977 and in 1979 in the Adak Management Area, Alaska.

Carapace Lengths (mm)	Number of Females: Without Embryos[a]	With Embryos[b]	Total Females	Percent Mature	Carapace Lengths (mm)	Number of Females: Without Embryos[a]	With Embryos[b]	Total Females	Percent Mature	Carapace Length (mm)	Number of Females: Without Embryos[a]	With Embryos[b]	Total Females	Percent Mature
54	1	0	1	0.0	94	73	279	352	79.3	129	1	30	31	96.8
57	1	0	1	0.0	95	73	351	424	83.8	130	0	40	40	100.0
59	3	0	3	0.0	96	59	304	363	83.7	131	0	33	33	100.0
60	1	0	1	0.0	97	43	296	339	87.3	132	2	46	48	95.8
61	2	0	2	0.0	98	39	415	454	91.4	133	0	20	20	100.0
62	3	0	3	0.0	99	17	266	283	94.0	134	0	23	23	100.0
63	3	0	3	0.0	100	23	397	420	94.5	135	0	20	20	100.0
64	1	0	1	0.0	101	14	299	313	95.5	136	0	27	27	100.0
65	3	0	3	0.0	102	11	360	371	97.0	137	0	17	17	100.0
67	2	0	2	0.0	103	13	426	439	97.0	138	0	15	15	100.0
68	2	0	2	0.0	104	7	317	324	97.8	139	0	19	19	100.0
69	2	0	2	0.0	105	12	451	463	97.4	140	0	17	17	100.0
70	4	0	4	0.0	106	4	376	380	98.9	141	0	11	11	100.0
71	8	0	8	0.0	107	3	348	351	99.1	142	0	14	14	100.0
72	3	0	3	0.0	108	2	402	404	99.5	143	0	5	5	100.0
73	4	0	4	0.0	109	1	344	345	99.7	144	1	6	7	85.7
74	7	0	7	0.0	110	0	417	417	100.0	145	0	10	10	100.0
75	10	2	12	16.7	111	4	348	352	98.9	146	0	8	8	100.0
76	9	0	9	0.0	112	3	324	327	99.1	147	0	9	9	100.0
77	12	0	12	0.0	113	1	372	373	99.7	148	0	5	5	100.0
78	26	0	26	0.0	114	1	251	252	99.6	149	0	11	11	100.0
79	17	1	18	5.6	115	0	338	338	100.0	150	0	6	6	100.0
80	33	0	33	0.0	116	3	252	255	98.8	151	0	9	9	100.0
81	25	0	25	0.0	117	0	245	245	100.0	152	0	8	8	100.0
82	31	3	34	8.8	118	6	254	260	97.7	153	0	7	7	100.0
83	42	2	44	4.5	119	1	160	161	99.4	154	0	3	3	100.0
84	57	13	70	18.6	120	2	176	178	98.9	155	0	5	5	100.0
85	69	16	85	18.8	121	0	130	130	100.0	156	0	1	1	100.0
86	59	25	84	29.8	122	1	123	124	99.2	157	0	1	1	100.0
87	69	43	112	38.4	123	1	118	119	99.2	158	0	4	4	100.0
88	101	83	184	45.1	124	1	88	89	98.9	159	0	3	3	100.0
89	88	84	172	48.8	125	0	100	100	100.0	161	0	3	3	100.0
90	83	183	266	68.8	126	2	54	56	96.4	162	0	1	1	100.0
91	94	171	265	64.5	127	1	64	64	98.5	163	0	1	1	100.0
92	84	199	283	70.3	128	0	59	59	100.0	165	0	1	1	100.0
93	78	217	295	73.6						166	0	1	1	100.0
									Grand Totals:		1,462	10,986	12,448	87.9

[a]Females with silky pleopodal setae and no embryos. [b]Females with embryos or embryo membrane remnants or funiculi.

Table 2. Parameters contributing to the derivation of the 50% size at maturity figures (SM50) for female red king crabs from various areas.

Areas	Latitudes	Years Data Collected	No. Females Sampled: No Embryos	No. Females Sampled: With Embryos	No. Females Sampled: Total	Anexuviants Included	Size Range mm CL	Smallest Mature mm CL	Size Groups: 1 mm	Size Groups: 2 mm	Size Groups: 3 mm	Size Groups: 5 mm	Percent Mature: Unweighted	Percent Mature: Weighted[a]	Logistic Curve	5 Yr Av. SM50	SM50	Sources
Norton Sound	64°N	1981	398	1,535	1,933	NA	43-121	60	+				+				68	Powell et al. (1972)
Norton Sound	"	1985	104	47[b]	151[b]	Yes	16-103	67[b]			+			+			75[c]	Stevens and MacIntosh (1986)
S.E. Bering Sea	55°-57°N	1940-41	88	104	192	?	71-139[d]	71[d]		+			+				97	Wallace et al. (1949)
S.E. Bering Sea	"	1956-58	1,133	6,401	7,534	?	<70->145	75-79			+		+				91-98[e]	Weber (1967)
S.E. Bering Sea	"	1975-79	4,082[f]	9,996[f]	14,078	Yes	16-192[b]	70			+			+		+	86-90	MacIntosh et al. (1979)
S.E. Bering Sea	"	1975-79	4,082[f]	9,996[f]	14,078	Yes	16-192[b]	70			+			+		+	86-90	Otto et al. (1980)
S.E. Bering Sea	"	1940-41	NA	NA	80[g]	NA	78-150[g]	98[g]		+			+				102[h]	Somerton (1980)
S.E. Bering Sea	"	1972-85	?	?	?	Yes	?	66-80			+			+	+		87-97	Hsu (1987)
Adak	52°-53°N	1969-77,79	1,462	10,986	12,449	No	54-166	75	+						+		89	Blau, this paper
W. Kamchatka Pen.	54°-58°N	1967	354[i]	2,095[i]	2,449	No	66-112[j]	77[j]			+				+		82[j]	Matsuura et al. (1972)
Pacific Ocean	?	1940-41	149	357	506	?	71-139[d]	71[d]		+			+				106	Wallace et al. (1949)

[a]Number of females at each NMFS trawl station were weighted by a sampling fraction.

[b]Data not in cited reference source, but made available by R. MacIntosh, NMFS, Northwest and Alaska Fisheries Center, Kodiak, Alaska, 11/89.

[c]SM50 taken from Figure 7 in Stevens and MacIntosh (1986).

[d]Since data was reported in 3 mm size classes in Wallace et al. (1949) these are estimates of the correct size.

[e]These figures are estimates by the author taken from Weber (1967) Table 3 and Figure 6.

[f]The numbers under the no embryo and embryo columns are the number of measured crabs ≤ 90 mm CL or > 90 mm CL, and not numbers of immature and mature crabs, R. MacIntosh, NMSF, pers. comm. 11/89.

[g]Numbers given are estimated from Figure 6 in Somerton (1980).

[h]SM50 is based on chela height vs. carapace length.

[i]Matsuura et al. (1972) classified females as having either: 1) no mature ovarian eggs or eggs attached to the pleopods (placed under the no embryos column) or 2) having either or both mature ovarian eggs or eggs attached to the pleopods (placed under the females with embryos column).

[j]Figures converted from carapace width after Matsurra and Takeshita (1976).

closest to each other. Additional information from the literature on female red king sizes near maturity is presented in Table 3 for studies in which a SM50 was not calculated, like the Kodiak Archipelago and Nemuro, Japan areas. Additional information for the west coast of the Kamchatka Peninsula is also presented in Table 3 which corroborates the SM50 reported for this area by Matsurra et al. 1972 (Table 2).

Table 3. Approximate female red king crab sizes at maturity for three areas.

Area	Latitudes	Comments and Sources
Kodiak Archipelago	(56°-59°N)	"At sexual maturity females range in size from 95-113 mm length" (Gray 1963).
Kodiak Archipelago	"	"...a practical average for the biological minimum length for both sexes to be approximately 100 mm" (Powell and Nickerson 1965a).
W Kamchatka Peninsula	(51°-58°N)	Females and males reach biominimum size from 79-82 mm CL (Marukawa 1933).[a]
W Kamchatka Pen.	"	Females mature at 75-81 mm CL (Vinogradov 1945).[a]
W Kamchatka Pen.	"	Primiparous females had a mean of 85 mm CL (Takeuchi 1967).[a]
Nemuro, Japan	(44°N)	Females and males reach biological minimum sizes from 90-93 mm CL (Marukawa 1933).[a]

[a]Converted from carapace width after Wallace et al. 1949.

Why size at maturity for female red king crabs varies from area to area is not known, although environmental conditions, particularly ocean bottom temperatures, are suspected factors (Marukawa 1933; MacIntosh et al. 1979; and Somerton 1980). Size at maturity does not always increase with decreasing latitude. Some southern areas have the same or smaller sizes at maturity than more northernly areas (Tables 2 and 3). A comparative study of the bottom temperature regimes from these areas may reveal that temperature has a better correlative role in determining size at maturity than does latitude.

SM50 point estimates will vary somewhat within any region both spatially and temporally. Multi-year estimates of the SM50 for Norton Sound and southeastern Bering Sea both reveal ranges in the SM50 for their areas (Table 2). From 1972 to 1985 a 10 mm CL range in the SM50 was calculated for the southeastern Bering Sea population of female red king crabs (Hsu 1987). In addition, within-year analyses of the SM50 for seven strata in this area revealed 4-23 mm CL range differences in the SM50 for female crabs between strata (Hsu 1987).

The size-maturity composition of the samples collected for an area may skew the resultant calculation of the SM50. For example, the data used in the derivation of Adak's SM50 is not evenly distributed around 89 mm CL (Table 1). If it were, the SM50 would decrease. This data was composed predominately of mature female crabs; attributable primarily to the depths fished and to a lesser degree by the type of pots used. Most fishing occurred in waters deeper than 73 m (240 ft); depths at which one would expect to undersample juveniles. Juvenile red king crabs live in shallower waters on a year round basis than do the adults (Marukawa 1933; Powell and Nickerson 1965b; Weber, 1967; and Hsu, 1987). Therefore it should be noted that the validity of SM50 estimates lies in part on representative sampling for both immature and mature adult females (Weber 1967). Red king crabs have displayed irregular recruitment patterns with great fluctuations in abundances of juvenile females (Blau 1985 and 1986). For these reasons female size-maturity samples may also be skewed.

The methodologies used to calculate the SM50 reported in Table 2 varied substantially. The definition of maturity in these studies included both the presence of embryos on the pleopods and, in one case, included females with ovarian eggs (Matsuura et al. 1972). Another study based SM50 on the change in chela height (Somerton 1980). Some studies included both exuviants and anexuviants. Other parameters used in the calculation of SM50 varied greatly like: sample sizes (80 to 14,078); carapace length size groups (1 to 5 mm); and sampling periods (1-, 5-, 10-years). Figures used to estimate SM50 were derived using either empirical or weighted percentages, or logistic curves. Even when the same data set was used, different methods produced different SM50 estimates. The SM50 derived by Wallace et al. (1949) and Somerton (1980) using females from the same data set differ by 5 mm because different criteria were used to define maturity (Table 2).

ADF&G has collected at least 10 years of female red king crab data from annual surveys and other sources in the Dutch Harbor, Alaska Peninsula, Kodiak, Cook Inlet and Southeastern Management Areas. The SM50 values for each of these areas could be calculated using methods similar to those presented for the Adak Management Area. Female red king crab SM50 data can be used in conjunction with male growth and other data used in defining male sexual maturity to re-evaluate minimum size limits currently established for each management area.

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Life History

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The Utility of Artificial Substrate Collection Devices To Determine Time and Location of Red King Crab (*Paralithodes camtschatica*) Glaucothoe Settling in Auke Bay, Alaska

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ABSTRACT

Several types of artificial substrate collection devices were used to sample for glaucothoe and first benthic stages of red king crab (*Paralithodes camtschatica*) in Auke Bay, Alaska during 1988 and 1989. Catch rates were greatest with a design using plastic aquarium plants in a wire mesh basket as settling habitat for crab. These early benthic stages were not evenly distributed among sites where the collectors were deployed. In 1989, 84% of crab were collected at two of the six collector sites. As many as 33 crabs/m^2 of collector surface area were captured during the experiment. Glaucothoe were first found on the collectors during late May, peaked in number during the middle of June, and were last found in August.

INTRODUCTION

King crab (*Paralithodes* spp.) exhibit four planktonic zoeal stages followed by the glaucothoe stage (Marukawa, 1933), which has the ability to swim. Glaucothoe settle to the bottom where they molt into the first (C1) benthic stage resembling the adult crab. The adult and planktonic larval life history stages of the red king crab (*P. camtschatica*) are relatively easy to sample, and consequently, much is known about the biology of these stages. Less is known about juvenile red king crab, who until about two years of age live a solitary existence among the benthos, taking refuge among cobble, gravel, and debris in the littoral zone (Powell and Nickerson, 1965; Sundberg and Clausen, 1979; Jewett and Powell, 1981).

Armstrong et al. (1981) and Armstrong (1983) have hypothesized that year-class strength of king crab is highly dependent on larval settlement in nearshore "refuge" habitats. Early benthic stages are almost entirely restricted to areas that afford adequate cover (substrate crevices) and food (epifaunal invertebrates such as hydroids, bryozoans, and polychaetes) (Sundberg and Clausen, 1979). Young-of-the-year red king crab preferred bryozoan/hydroid assemblages when given a choice of five habitat types in a laboratory experiment (Babcock et al., 1988). Young-of-the-year blue king crab (*P. platypus*) are consistently associated with gravel, cobble, and especially shellhash (Armstrong et al., 1985; Palacios et al., 1985).

Yearly (1980-1988) collection records, by Auke Bay Laboratory staff, indicate that young-of-the-year red king crab in the intertidal zone of the Auke Bay, Alaska area are generally restricted to habitat similar to that described above. These young crab are not evenly spaced throughout this habitat type; they exhibit an extremely patchy distribution.

Artificial substrate collectors have not been used for sampling settling stages of king crab, however, they have been used for other decapod crustaceans, including *Cancer irroratus* (Beninger et al., 1986), *Panulirus interruptus* (Serfling and Ford, 1975), *Panulirus argus* (Witham et al., 1968) and *Panulirus cygnus* (Phillips, 1972; Morgan, 1980; Morgan et al., 1982). The objectives of our study were to determine if newly-settled red king crab could be effectively sampled with artificial substrate collection devices; and, if so, to gain some insight into the time of settlement and densities of these early life history stages.

METHODS

In 1988 artificial substrate larvae collectors were deployed at the northeast (Site A) and northwest (Site B) corners of Auke Bay, Alaska (Fig. 1). Scuba divers installed collectors at depths of 2.3 and 8.3 m below mean lower low water (MLLW) at Site A and 3.8 m below MLLW at Site B. These sites were chosen primarily because numerous young-of-the-year crab were collected from there during January-April 1988 (Auke Bay Laboratory collection records) and we surmised that early benthic stage king crab do not migrate far from the initial point of settlement. Also, the natural substrate at both sites afforded abundant cover in the form of numerous small interstices. Interstices at Site A were formed by overlapping plates of downward sloping, broken shale, whereas interstices at Site B were formed by more rounded gravel, pebble and cobble. Abundant shellhash was present at both sites.

Five different collectors were deployed at each site and depth, for a total of 15 collectors. Collectors were attached to concrete block anchors and set in a line parallel to shore. They were buoyed 0.8 m above the bottom by plastic floats attached to 5-mm polypropylene line fitted with snap links (Fig. 2). Collector designs were of two general types: Box- or plate-type. Box-type collectors were constructed of 6-mm galvanized hardware cloth and measured 45 x 45 x 7 cm.

They were filled with either Tuffie[1] pot scouring pads (design 1), Penn Plax Aqua Plant plastic aquarium plants (design 2), or American Air Filter Amer-glas furnace filters (design 3). Plate-type collectors were constructed of 6-mm PVC sheeting covered with either indoor-outdoor carpet or fine-mesh plastic screening and measured 45 x 45 cm. Screened plate collectors had Penn Plax Baby Hide Out plastic aquarium plants fastened to them (design 4) and carpeted plate collectors had Fritz Breeding Grass fastened to them (design 5). All collectors were "aged" in fiberglass aquaria supplied with flowing unfiltered seawater for 3 weeks prior to deployment.

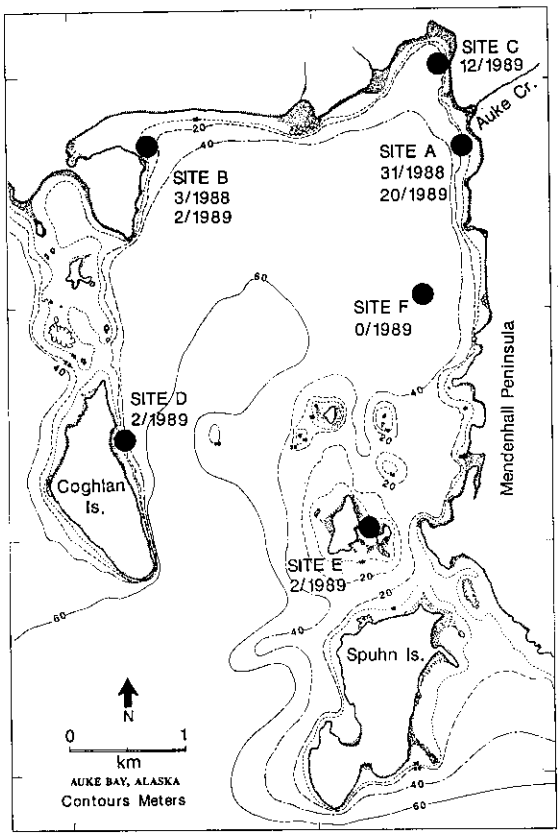

Figure 1.--Locations of artificial substrate collectors, and numbers of newly-settled red king crab found on collectors/year.

[1]Use of brand names does not imply endorsement by the National Marine Fisheries Service

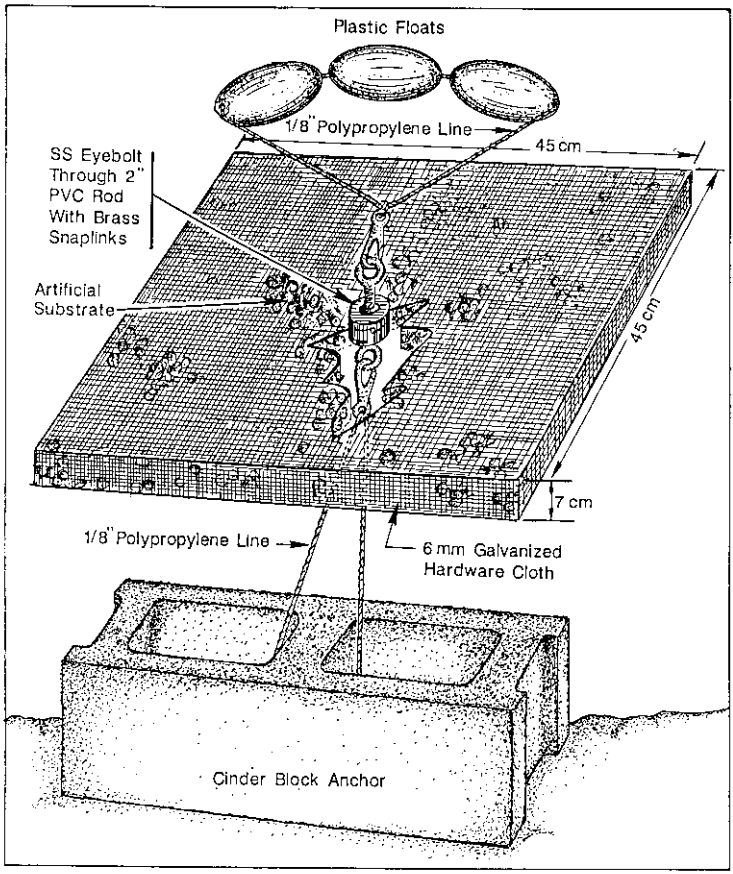

Figure 2.--Diagram of box-type artificial substrate collecting device used to collect settling red king crab.

Based on 1988 results, only box-type collectors filled with plastic aquarium plants were utilized in 1989. Second Nature Plantastics Ambulia and Cabomba plastic plants were substituted for the Fritz products used in 1988 because they more closely resembled bryozoans, a preferred habitat type for young-of-the-year crab (Babcock et al., 1988). They were deployed in sets of three at six locations (Sites A-F; Fig. 1) for a total of 18 collectors. Sites A and B were the same as in 1988. The substrates at Sites A and C were similar, as were the substrates at Sites B and D. Site E substrate was mostly silt. All collectors except those at Site F were set off the bottom at a depth of approximately 8 m below MLLW in 1989. Water depth at Site F (located several hundred meters offshore) was approximately 50 m; collectors were deployed from a surface buoy so that they hung approximately 8 m below the surface. Site F was included to determine if

glaucothoe would settle at a mid-water location not adjacent to shore if suitable habitat was available.

In 1988 divers installed collectors on 18 May (Site A) and 19 May (Site B). In 1989, collectors were installed on 22 May (Site A), 23 May (Sites B and C), 25 May (Sites D and E), and 19 June (Site F). Collectors were retrieved and processed approximately once per week. Divers unfastened collectors from the anchors, placed them in bags constructed of nylon netting, and brought them to the boat. Collectors were rinsed in large plastic tubs with an on-deck washdown pump; the bags were rinsed in a similar manner. All material in the tubs was filtered through nylon netting, and flora and fauna retained by the filters was transferred to small plastic containers filled with seawater.

Samples were examined in the laboratory within 3 hours of collection. All glaucothoe and early benthic stages were separated from other material and preserved in seawater-buffered 10% Formalin. Carapace length was measured (Weber, 1967) under a dissecting microscope (6x magnification).

RESULTS

1988 Results. All collectors floated horizontally during the experiment. Collectors were colonized by a variety of algae, and invertebrate and fish larvae soon after placement. A small amount of fine sediment also settled on the collectors. Most of the flora, fauna, and sediment were removed from the collectors when they were rinsed during weekly processing, with the exception of the box-type furnace filter collectors; this type was extremely difficult to clean, and became progressively matted and compacted during the study. The other collectors remained relatively clean and free of debris.

A total of 34 red king crab settled on the collectors in 1988, including glaucothoe, C1 (first instar) and C2 (second instar) stages, and a glaucothoe exoskeleton. Collector designs 2 and 4 (see Methods) were most successful, with 10 individuals found on each type (59% of total). Seven individuals were found on design 1 (21% of total); the remaining seven individuals were found on designs 3 and 5.

Most crab settled on the deepest collectors. Ninety-one percent (31 individuals) were collected at Site A (Fig. 1). Twenty-six (84%) of these were found on the 8.3-m deep collectors; five individuals (16%) were found on the 2.3-m deep collectors. Three individuals (9% of the total) were collected at Site B.

Crab were found on the collectors from 27 May to 8 August (Fig. 3). Collectors at Sites A and B were initially checked on 27 and 26 May, respectively. One glaucothoe was collected at Site A at 8.3 m, however no glaucothoe were collected at Sites A or B at the 2.3-m depth. Collectors at Sites A and B were checked at a second time on 3 June and 2 June, respectively; at that time a single glaucothoe molt was found at Site B. Twenty-two newly-settled crab, representing 65% of the total collected during the experiment, were found on the collectors from 9 to 30 June. No crab were found on the

collectors at Site B after 10 June. Crab continued to be collected at Site A until 8 August. Collectors at Site B were removed on 10 August; those at Site A were removed on 6 September.

Maximum numbers of glaucothoe were collected during 9-23 June. All specimens collected on or before 23 June were glaucothoe. Except for one molting individual, no glaucothoe were found on the collectors after 23 June. C1 instars were first noted during the third week of June and comprised 76% of total specimens collected from 23 June to 21 July. No C2 instars were collected prior to 28 July; three were found from 28 July to 8 August.

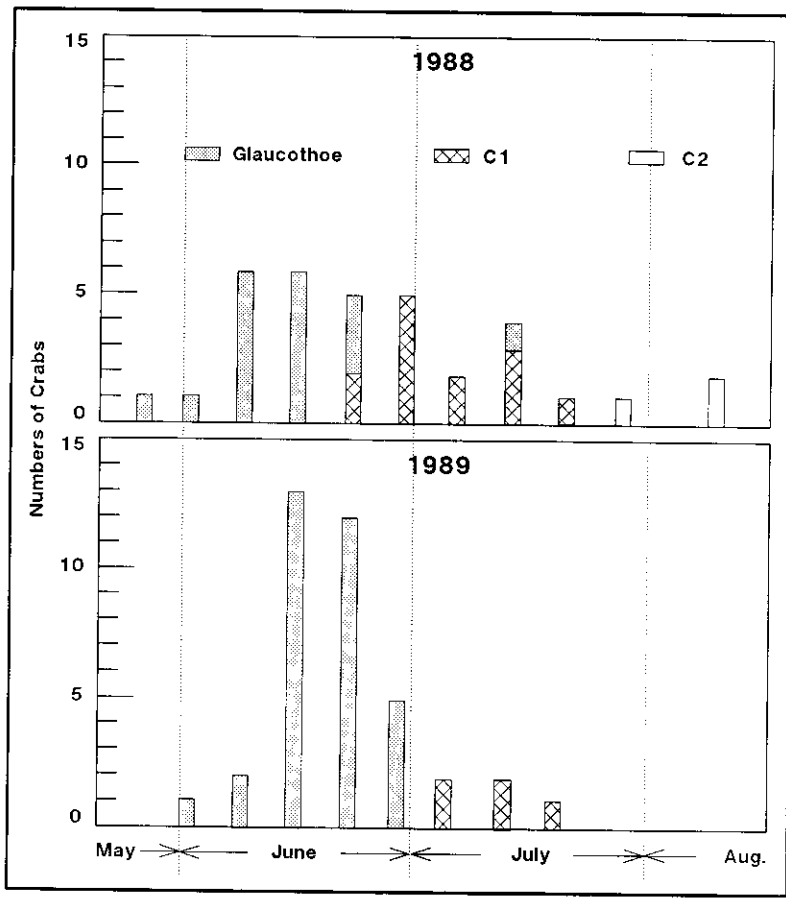

Figure 3.--Numbers of newly-settled red king crab on artificial substrate collectors in Auke Bay, Alaska, 1988 and 1989.

Of the 34 specimens collected, 18 (53%) were at the glaucothoe stage of development; 13 (38%) were first benthic stage (C1) juveniles and three (9%) were second benthic stage (C2) juveniles. Carapace lengths for each developmental stage were fairly discrete and ranged from 1.57 to 2.04 mm ($\bar{x}$ = 1.77 mm) for glaucothoe, 2.04 to 2.36 mm ($\bar{x}$ = 2.20 mm) for C1 stage, and 2.67 to 2.83 mm ($\bar{x}$ = 2.72 mm) for C2 stage.

1989 Results. A total of 38 glaucothoe and C1s were collected in 1989. Fifty-three percent (20 individuals) were collected at Site A (Fig. 1). Thirty-two percent (12) were found on the collectors at Site C. Sites B, D, and E each accounted for 5% (2) of the total. No crab were found on the off-shore collectors at Site F.

Early benthic stage crab were found on the collectors from 1 June through 20 July (Fig. 3). Thirty individuals, representing 79% of the total collected, were found on 15 and 29 June. All specimens collected on or before 29 June were glaucothoe. An additional five specimens (all C1s) were found during 5 through 20 July. No C2 instars were collected during 1989. All collectors were removed on 8 August.

DISCUSSION

Artificial substrate collection devices can be effectively used to sample for post-larval king crab. Although the numbers of crab that we found were relatively small, so, too, were the number and size of the collectors. Total areas sampled at each of the sites were only 1.00 m^2 in 1988 and 0.60 m^2 in 1989. Total numbers of crab collected were 20.0 m^{-2} and 33.0 m^{-2} at Site A in 1988 and 1989, respectively. Shirley and Shirley (1989) sampled plankton during the king crab larval period in Auke Bay weekly from 1985 to 1989. If glaucothoe collected during their studies are summed over the season, and are assumed to settle uniformly in depths of less than 20 m, the calculated high and low densities would be 2.4 m^{-2} and 0.83 m^{-2} for 1987 and 1986, respectively (T. Shirley, Univ. of Alaska Southeast, Juneau, personal communication). Their calculated values and our measured values are within an order of magnitude, and differences may reflect selective settlement of glaucothoe on substrates which provide cover (e.g., artificial substrate collectors). Sundberg and Clausen (1979) surveyed post-larval king crab in nearshore waters of Kachemak Bay, Alaska with a suction dredge and calculated a mean density of 1.3 m^{-2} individuals.

Crab were found on all collector types, but most were found on designs 2 and 4 (see Methods). The efficiency of design 3 (box-type furnace filter) was reduced due to difficulty in removing accumulated silt and debris, and subsequent compaction of the filter material. The presence of C1 and C2 stages in four of the five collector types suggests that not all glaucothoe were removed from the collectors during prior weekly rinsing; and that actual numbers of glaucothoe (as opposed to C1 and C2 stages) on the collectors were greater than the results indicate. It is unlikely that C1 and C2 crab climbed onto the collectors from the surrounding natural substrate because to do so they would have had to negotiate smooth brass and stainless steel fittings.

Collector designs 1 and 3, especially, provided abundant cover in the form of thousands of small interstices, but also made it virtually impossible to remove all newly-settled crab during each rinsing. Ease of collector assembly, and efficient removal of specimens, were the primary reasons why collector design 2 (box-type with plastic aquarium plants) was used exclusively in 1989. Use of this design may also explain why fewer post-glaucothoe specimens were collected in 1989; most C1 and C2 individuals collected in 1988 were probably recent molts that had not been rinsed from the collectors during prior weekly sampling.

Research (Powell and Nickerson, 1965; Weber, 1967; Sundberg and Clausen, 1979; Jewett and Powell, 1981) indicates that young-of-the-year crab inhabit shallow inshore waters. However, exact depth preferences of red king crab glaucothoe have not been established. McMurray et al. (1984) found young-of-the-year king crab at depths of 20-50 m in Bristol Bay, Alaska, but others report finding young-of-the-year in both shallower and deeper water. Powell and Nickerson (1965) found post-larval king crab from the littoral zone to a depth of 106 m in the vicinity of Kodiak Island, Alaska. Vinogradov (1969) captured young juveniles at depths of 5-15 m in the Sea of Okhotsk, whereas Sundberg and Clausen (1979) failed to find any in depths greater than 27 m in Kachemak Bay, Alaska, though they were common in shallower inshore waters. Young juveniles (C1 and C2) are also found in Auke Bay in areas of shellhash and arborescent ectoprocts (T. Shirley, personal communication).

All researchers found young juvenile crab in areas characterized by coarse substrate and abundant epifaunal cover, regardless of depth. Tsalkina (1969) points out that larval king crab are widespread along the western Kamchatka Shelf, but only settle and metamorphose to C1 stage at depths of 1.5 to 20 m in a relatively small discrete area, the only section of the shelf with a stony bottom and abundant epifauna. Thus, substrate composition is probably a more important determinant of vertical distribution than depth *per se*.

During 1988, post-larval king crab in Auke Bay showed a strong preference for the deeper (8.3 m) collectors at Site A, although the deep and shallow collectors were installed over areas of similar substrate, and horizontal distance between the two sets of collectors was only 25 m. Auke Creek enters Auke Bay in the immediate vicinity of Site A so reduced salinity of surface waters could explain the lack of glaucothoe on the shallow collectors. Red king crab zoeae are known to exhibit decreased euryhalinity with ontogeny (Shirley and Shirley, in press).

The lack of king crab on the collectors at Site B (1988 and 1989) and at Sites D-F (1989) highlights the patchy distribution of these crab, as well as our lack of knowledge regarding factors responsible for their distribution. Numerous juvenile crab from the previous year's (1987) hatch were collected at Site B during January-April 1988, so evidently there is also interannual variation with regard to location of larval settling. Prevailing water currents in large gyre systems have been proposed as a transport mechan-

ism for planktonic larvae (Hebard, 1959; Haynes, 1974; Armstrong et al., 1983). It is not known how larvae are transported out of the gyre systems to nearshore settling areas, although along-shore currents and selective swimming behavior have both been proposed (Sundberg and Clausen, 1979). Recent work by Shirley and Shirley (1988a) confirms that larval king crab can regulate their distribution by swimming in response to environmental variables. A determination of factors responsible for transport of larvae to areas of settlement in Auke Bay was beyond the scope of our study, but it is interesting to note that in 1988, 91% of crab were captured at Site A, and in 1989, 84% of crab were captured at Site A and nearby at Site C.

All glaucothoe were captured during June in both years. This agrees closely with the findings of Shirley and Shirley (1989). They found that maximum densities of king crab glaucothoe in the water column occurred during the first 3 weeks of June; maximum densities were collected in 1988 on 7 June (1.0 ± 0.2 crab/$100m^3$) and in 1989 on 23 May ($0.4 \pm 0.1/100m^3$). The development of both eggs (Nakanishi, 1985; Shirley and Shirley, 1988b) and larvae (Kurata, 1960; Kurata, 1961; Nakanishi, 1985) is dependent on seawater temperature, so some degree of interannual variability with regard to glaucothoe density maxima is not unexpected.

In summary, artificial substrate collection devices can be used to sample for glaucothoe and early benthic stages of king crab. This technique may eventually prove useful for identifying important habitat for these early life-history stages, and for predicting later recruitment of adult crabs to the fishery, based on relative abundances of first benthic stages (Morgan et al., 1982). However, it is important to point out that the abundances of newly-settled king crab on artificial substrates may not accurately reflect abundances in surrounding natural substrates (Yoshimura and Yamakawa, 1988). In the future we plan to compare abundance of crabs settling on artificial versus natural substrates, and to determine which environmental variables affect the distribution of newly-settled king crab.

ACKNOWLEDGEMENTS

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Proc. Int. Symp. King & Tanner Crabs
Nov. 1989, Anchorage, Alaska

Behavioral Ecology of Podding Red King Crab, *Paralithodes camtschatica*

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ABSTRACT

Diel activity cycles and foraging dynamics for two pods of approximately 500-800 juvenile red king crab, *Paralithodes camtschatica*, were monitored for 196 days (Nov 87-June 88) and 148 days (Oct 88-Feb 89) in Womans Bay, Kodiak, Alaska, using SCUBA. Nocturnal foraging and homing behavior of podding red king crab were documented for the first time. Variation in time of pod dispersal into a nightly foraging aggregation was explained ($R^2 = 0.72$) by changes in water temperature, crab weight, and time of sunset. A trend of increased foraging time and movement to deeper, cooler water was apparent after mid-April, as water temperatures reached 4°C and began a sustained summer increase. Molting was observed to occur only at night, and seasonal variations in molting rate were estimated using molting probability models based on length-frequency distributions. Average direction of pod movement was counter to the direction of strongest water currents, and homing behavior suggested some affinity for a low-light environment characterized by abundant man-made niches. Items most frequently observed being eaten were sea stars (*Evasterias troschelii*) and macrophytes (*Laminaria* sp. and *Ulva* sp.). I discuss the inception of podding as a discontinuity in behavior, perhaps reflecting a break in the fractal continuum of niche availability within red king crab habitat.

This paper is in press, Canadian Journal of Fisheries and Aquatic Sciences 47(9), September 1990.

Proc. Int. Symp. King & Tanner Crabs
Nov. 1989, Anchorage, Alaska

Population Biology of the King Crab *Paralithodes camtschatica* Tilesius in the North Pacific Ocean

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ABSTRACT

A comparison is presented of the biology of all red king crab populations within the limits of their distribution. The ecological variability, variations in the distribution and functional structure of the populations and numerical abundance are examined. Based on three populations (Bristol Bay, Ayano-Shantarskiy and West Kamchatka), the basic factors determining the production of all developmental stages are presented.

The king crab has been studied for a long time and its general biology is fairly well understood. Data accumulating in recent years has allowed a more precise determination of its distribution and especially its ecology and the distributional and functional structure of the populations. The northern limits of its range in the Asiatic coast of the Bering Sea occurs at Karaginskiy Island, where adult specimens are sporadically seen. The northern limit on the American coast is approximately 59° N. The northern limit of juvenile specimens in the Okhotsk Sea is Gizhiginskiy Bay, but adult specimens occur near Okhotsk and in Tauyskiy Bay.

The southern limits of the range of this species is considered to be the [Kraboe Peninsula?] in Pos'yet Bay, Sea of Japan, and Cape Erimo, Hokkaido. The southern limit on the American coast is British Columbia (Vinogradov, 1947).

There are two large populations of crab in the Okhotsk Sea: the West Kamchatka (superpopulation, Vinogradov, 1970) and the Ayano-Shantarskiy population, whose ecology is the most specialized among the crab populations (Rodin and Myasoyedov, 1982). There is also the large Bristol Bay population in the Bering Sea and the Alaskan population in the Gulf of Alaska. In addition to these there are comparatively small populations: northern and southern

Primor'ye, Western Sakhalin, Aniva Bay, Terpeniya Bay, southern Kuriles, Hokkaido and East Kamchatka populations. Based on the three reproductively independent and most productive populations (West Kamchatka, Bristol Bay and Ayano-Shantarskiy), one can establish the basic factors in the complex of bio-geo-cenosic and oceanographic features of the habitat of these crabs:

1. The conditions and period of massive hatching of larvae in the coastal zone must be combined with the subsequent transport of the larvae to favorable habitats for survival of the young and the formation of harvestable stocks. The larval crabs, developing in the pelagic environment pass through four larval stages in about two months. They are passive and can be transported by currents for considerable distances (for example, for 100 to 150 miles along the coast of West Kamchatka).

2. A well-developed sessile community (dense concentration and large areas of hydroids, bryozoans and sponges) and a food base is necessary where the massive settlement of larvae occur. The settlement area must have favorable feeding conditions and refuges from predation.

3. A broad continental shelf is necessary with a rich food base for the adult crab.

4. A shelf region is necessary on which the reproductive populations on the one hand and the juveniles on the other are not separated by deep trenches, silty sediments and other barriers, hindering the movement of subadults to spawning regions. In the reproductive cycle of the highly productive crab populations, clear differences in the direction of the movement of the life stages occur: the larvae are transported in one direction, the juveniles go in the opposite direction. The most important, judging from everything, is the presence of favorable habitat conditions for the post-larval stages.

The interrelationships and degree of independence of the smaller crab populations is as yet insufficiently studied, particularly with respect to the dispersion of larvae and return of juveniles to the migrating portion of the populations.

There may be exchange of larvae between the West Sakhalin and Primor'ye populations, between the Southern Kuriles and Aniva Bay populations and also a portion of the adult specimens may migrate between the Alaskan and Bristol Bay populations and the West Kamchatka and Northern Kurile populations.

The Ayano-Shantarskiy population, which lives in an almost subarctic habitat, occupies a special place among the crab populations. The severe temperature conditions in the northwestern Okhotsk Sea are the reason for the slow growth of the crab. Nevertheless, the principles affecting the distributional character of the

populations are basically the same as with the West Kamchatka crab. The major flow of the North-Okhotsk current transports the larval crab from the parent habitat in the Ayanskiy region (136-140°E.) toward the Shantarskiy Islands, where an epifaunal community of sponges, bryozoans and hydroids, having biomass in excess of 1,000 g/m2 develops on the shallow rock bottom. Between these two regions there is no barrier for the migration of subadults back to the parent populations. As the crab grow and develop, there is a gradual migration to the north along the western coast of the Okhotsk Sea. In this direction there is a gradual decrease in the number of females, subadults and adult males and in the Okhotka region, at the northern end of the range of this population, only adult specimens of maximum size occur (males of 20-21 cm carapace width). An analogous pattern of crab distribution is observed within the range of the West Kamchatka population, but in this case the juveniles are found to the north and the older individuals occur to the south (Galkin, 1960, Vinogradov, 1969).

With respect to the Ayano-Shantarskiy population, even in the most severe of temperature regimes, with no obstacles to the migration of the various age classes to reproduction and foraging habitats, a fairly large reproductively independent population is produced. With respect to total production (biomass of 120,000 tons), this population is exceeded only by the most productive West Kamchatka population (biomass of 360,000 tons) and is similar to the Alaskan and Bristol Bay population, which inhabit an area of fairly high temperatures (Fig. 1).

The king crab ranges during various seasons from depths of 4 to 300 m at temperatures of -1.7 to +11°C and salinities of 28-30 ppt and higher.

The West Kamchatka crab population overwinters on the continental slope in the zone where the warm Pacific Ocean water mixes with the colder waters of the shallow shelf. The migration period from the overwintering area to shallow water depends on warming of the bottom water, as well as the physiological condition of the crab preparing for spawning and molting. The rate at which the shelf water heats from year to year is not constant, especially in the northern and central portions of the West Kamchatka shelf (Vinokurova, 1972). The crab must enter the zone of remnant cold winter waters having subzero temperatures. The geographic extent of this zone and the absolute value of the negative temperatures influence the migration rate of the crab toward shore and the period at which they emerge into the zone of positive temperatures. The females begin the migration from the overwintering area at the same time as the males. However, they lag behind the males. When the larvae are released the position of the male and female crab coincide.

The distribution of the crab along the West Kamchatka shelf is uneven. The crabs are most abundant in the northern part of the range and decrease in a southerly direction (Rodin, 1967, 1969). In the southern regions of the West Kamchatka shelf during the first half of May, adult males often have new carapaces and the females new eggs, which indicates that the larvae were released and the crab spawned at depths of 100-135 m. An advance of these processes

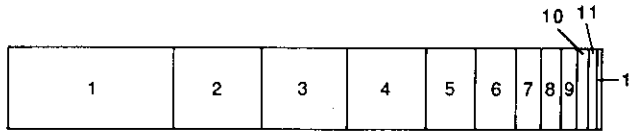

Figure 1. Relative biomass (%) of the red king crab populations (excluding juveniles): 1. West Kamchatka, 2. Bristol Bay, 3. Alaskan, 4. Ayano-Shantarskiy, 5. northern Primor'ye, 6. southern Primor'ye, 7. Western Sakhalin, 8. Terpeniya Bay, 9. Aniva Bay, 10. Southern Kuriles, 11. Hokkaido, 12. East Kamchatka population.

to early periods of the year at this location results from the persistent influence of warm Pacific Ocean water. Spawning of the crabs migrating to the coast occurs later in the central shelf, at the end of May. Here the number of molted males increases from the shore to the open ocean.

The crab on the northern shelf at the end of May are often distributed at a depth of 50 m. The highest density of males and females are observed at 10-15 m in waters with bottom temperatures of 2.1°C. During this period, old shell crab often predominate among the males. A portion of such crab molt later than in the central and southern region of the shelf, and a portion will molt the following year. In general one can say that the main pods of females and juveniles gravitate to the northern region of the West Kamchatka shelf.

During summer the main mass of the population is distributed in the coastal zone at depths to 50 m. At this time they forage and migrate along the coast to the south. The female crab are less motile and are distributed in the shallows where temperatures vary from 2 to 5°C.

In the fall, autumn-winter migration pods form. The crab concentration in deep water increases with respect to the summer distributions and the adult males migrate to deep water first. Crab distribution in years of cold weather differs from that described above. A portion of the juvenile and adult crab are unable to withstand the zone of negative temperatures during the shoreward migration and they remain for some time at depths of 100-150 m. These crab come together in the coastal zone at a later period, and in the later half of the summer the distribution becomes typical. However, the fall migration of crab to deep water in cold years occurs later and the major portions of the population are still in shallow water in October (Fig. 2).

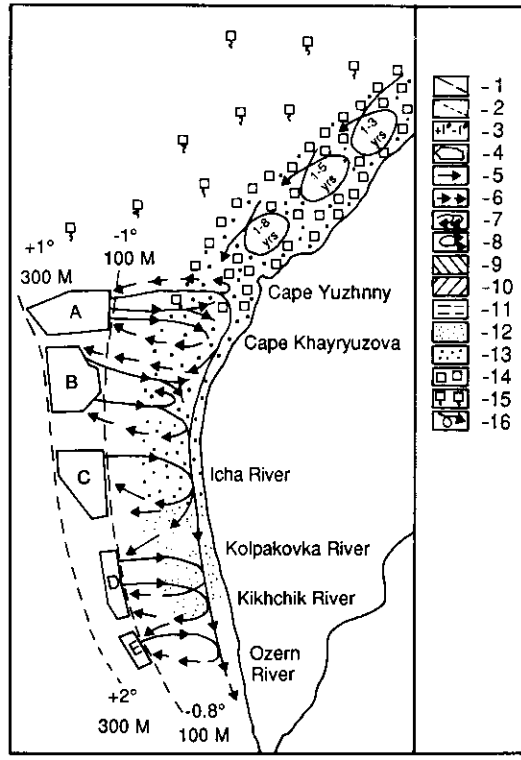

Figure 2. Diagram of the distributional structure of the West Kamchatka red king crab population. 1. isobaths, 2. currents, 3. bottom water temperature in the overwintering area, 4. overwintering area of subpopulations: A and B - Khayryuzovskiy independent; C - Ichinskiy semi-independent; D - Kolpakovskiy and Kikhchiskiy dependent; E - Ozernovskiy pseudopopulation; 5. spring spawning migration, 6. fall migration to the winter habitat, 7. migrational links between subpopulations, 8. individual pods of adult males, 9. summer distribution of adult males (frequency of 1-23 individuals per catch), 10. egg bearing females, 11. undersize males, 12. pelagic larvae rarely seen, 13. concentrations of zoea stages I and II, 14. drift and concentrations of zoea III and IV, 15. larval settlement zone, 16. migration of juveniles of age 1-8.

During winter the Bristol Bay crab populations concentrate in the southern regions of Bristol Bay at depths of 80-90 m where water temperatures are about 3-4°C. Adult males often occupy different habitats from females and juveniles during this period. In April, as in West Kamchatka, depending on the extent of the cold intermediate layer, the crab begin their spring migration to the shallow areas of Bristol Bay. However, in contrast to the adult crab of the West Kamchatka population, a portion of the males molt during winter, remain in the overwintering region and forage.

During May when the females are migrating to the shallow regions of Bristol Bay, the larvae are released, and some individuals have already molted at this time and carry new eggs under the abdomen. The juvenile crabs of this population are widely distributed over the whole bay. During June they inhabit areas with bottom water temperatures of 2-4°C, and 3-7°C in August (Rodin, 1970). During the summer in Bristol Bay there is a gradual decrease in the abundance of females and juvenile males from the open areas of the bay to the shore. Beginning in September and early October, decreasing water temperatures lead to redistribution and migration of the crab to their overwintering habitat (Fig. 3).

In the western Okhotsk Sea, where observations were made only in August through November, the king crab are distributed in a relatively narrow zone having a mix of cold (-0.9°C) and warm (12.4°C) water at depths of 16-19 m. The number of adult and undersized males decreases from Ayano-Shantarskiy to the Okhotsk and Tauyskiy regions (42.5, 6.2 and 2.0 million individuals respectively). Female crab are not seen in the catches from the latter two regions. With increasing distance from the center of reproduction (i.e., Ayano-Shantarskiy region) the size of the individuals increases. Male crab in the northern limit of their range reach their greatest size. In August the adult females extrude new eggs, which is an indication that by this time they have released all their larvae, molted and copulated. During September egg-carrying females inhabit shallow water (15-20 m depth) where the water is fairly warm (10-11°C). They move to depths of 40-50 m in October. During this period adult males are distributed at depths of 60-70 m at temperatures of 1.4-10.5°C (i.e., the thermal and depth range of the males is greater than that of the females). In general the seasonal migration of the crab is apparently not great and is determined by the distribution of the bottom water having minimal positive temperatures in the fall-winter period along the west coast of the Okhotsk Sea (Fig. 4).

Reproduction of the crab and hatching of the larvae can occur at almost all areas of the West Kamchatka shelf. However, the main reproductive region is the area between 57° 40' and 55° N. In the temperate regions the main hatching event is in May, in the colder regions in June. The hatched-out larvae in various regions of the West Kamchatka shelf are subject to transport from the south to the north and into Penzhinskiy Bay.

During development the number of larvae markedly decreases, especially during the first larval stage. During cold years the release of larvae by females which were unable to penetrate through the cold water layer (-1 to -1.7°C) into the coast-

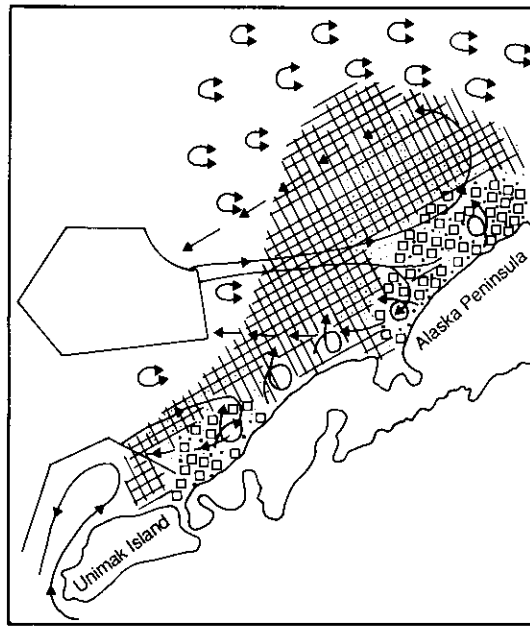

Figure 3. Diagram of the distributional structure of the Bristol Bay red king crab population. Symbols same as in Figure 2.

al zone, occurs at depths of 80-120 m. In such cases, due to the severe conditions and because the larvae are transported to unfavorable areas for settlement (beyond the edge of the northern West Kamchatka shelf, for example), larval mortality is apparently higher than during temperate and warm years. Therefore, the year class of crab hatched out in cold years is much smaller (Rodin and Lavrent'yev, 1974).

Analysis of the dynamics of the size composition of males in the West Kamchatka shelf population indicates that during 1958 through 1983 relatively high-year classes occurred with a periodicity of 5 to 7 years. These cohorts were detected in the Khayryuzovskiy region, when having reached 8-10 cm, they first occurred in the catches of the research vessel. This was observed in 1958, 1963, 1970, 1975, and 1980. It is interesting that the five-year periodicity in populations relative to water temperature at the spawning grounds was also observed in females of the West Kamchatka yellow fin sole population (Tikhonov, 1981).

As an example we will examine in more detail the last of the above cohorts in the migrating crab populations, i.e., 1980. During the year there was a marked increase in 8-9 and 9-10 cm crab by 6 and 7 million individuals respectively, in the harvestable cohorts in the Khayryuzovskiy region. Note that the actual number of

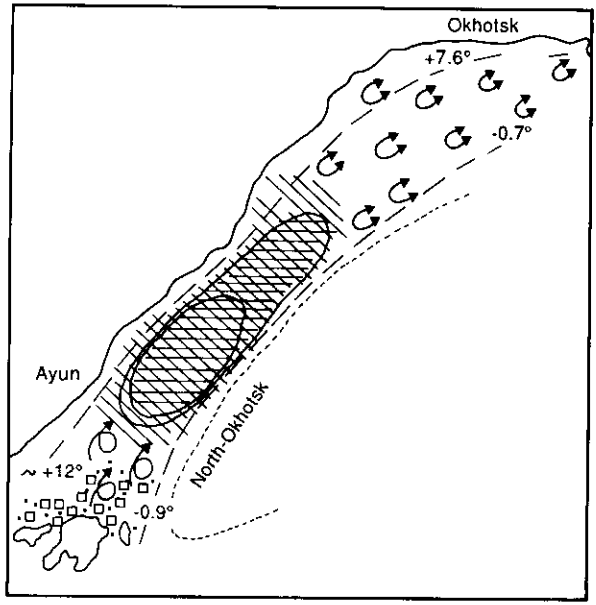

Figure 4. Diagram of the distributional structure of the Ayano-Shantarskiy red king crab population. Symbols same as in Figure 2.

individuals in the 8-10 cm size class in the Khayryuzovskiy region was 2 to 3 times the above figures; bottom conditions did not permit a count of the crab over their entire habitat.

During the following year, 1981, a portion of the harvestable cohorts moved to the neighboring Ichinskiy region. A distinct mode of 10-11 cm crab occurred in the size composition of the population from this region and the amount of crab in this modal group increased by 16 million individuals. In 1982 a portion of the individuals of the above cohort moved from the Ichinskiy region to the neighboring Kolpakovskiy and Kikhchiskiy regions, where they reached sizes of 13-14 and 14-15 cm and increased by 5 and 4 million individuals, respectively. An analogous "pulsed" migration of crab from one subpopulation to the neighboring population, moving from north to south along the West Kamchatka coast, was observed during the previous periods of harvestable cohorts.

In eastern Bristol Bay, where the majority of migrators are females, the major larval hatching event is observed in April and May. The larvae drift from the west to the east, and concentrations of larvae are observed in the area of confluence of gyres, created by water flow along the Alaska Peninsula. There are two main

regions of larval habitat: the area near Port Moller and near Unimak Island. High concentrations of oxygen (6.6-8.2 ml/l in the 0-50 m layer) and nutrients (12-14 mg/m3) [probably phosphate], moderate temperatures (0 in winter, 5°C in summer) and a rich epifauna produces favorable conditions for larvae and newly settled juveniles.

Later, the juveniles from this region enter the migrating portion of the population and begin seasonal migrations along with the adults. As they grow, the juvenile crab undergo longer migrations toward the open areas of the bay.

Therefore, the generalized distributional features of the larvae from the above populations are similar. Larval concentrations are found in certain regions, the centers of reproductive activity. These regions are characterized by unique hydrodynamics and the presence of epifauna where the settling crab encounter favorable conditions to feed and hide from predators.

According to some authors (Marukawa, 1933; Vinogradov, 1945, 1969; Cleaver, 1963; Weber, 1962, 1967), the Bristol Bay crab have a higher growth rate than the West Kamchatka crab, especially the Khayryuzovskiy subpopulation which inhabits an area of low water temperatures. In the more temperate oceanic regimes the production is higher. The average fecundity (the number of new eggs beneath the abdomen of the females) of the West Kamchatka population increases from the north to the south: in the Khayryuzovskiy region 60,000 eggs, Ichinskiy 78,000 eggs, Kolpakovskiy 118,000 eggs, Kikhchikskiy 150,000 eggs, and Ozernovskiy 220,000 eggs.

The fecundity of crab from the southeast Bering Sea is substantially higher than from Kamchatka. Adult females of 94-171 mm carry 72,000 to 445,000 eggs, averaging 206,000. In the Khayryuzovskiy reproductive region of the West Kamchatka populations 86-115 mm females have an average of 61,000 eggs.

There are two main types of annual cycles in the Okhotsk and Bering Sea red king crab populations. The first type is characteristic of individuals from the most northern part of the West Kamchatka shelf. At lower temperature conditions the crabs undergo a marked spring spawning migration to shallow water. Adult males in the late (stage III and IV) intermolt period predominate and there is an absence of significant molting in the winter. Hatching of larvae occurs when the main body of crab reach the coastal zone.

The second type of cycle is characteristic of crab from the central West Kamchatka shelf, where early spring molting of males is observed. During spring the males and females are more widely and evenly distributed from shore to a depth of 100-120 m. Hatching occurs everywhere where pods of females crab occur. A similar cycle occurs in crab from the southern West Kamchatka shelf and the southeast Bering Sea shelf. Winter molting of males is characteristic. Molted males do not participate in the spawning migrations of the females to the coastal zone.

Due to the length of the West Kamchatka shelf from north to south (540 miles) and the variability in conditions, there is a propensity for formation of geographically complex structures in the crab populations. The distributional features of the various size and sex groups, differences in the larval release period, molting and mating, and the number and sex ratio in various areas of the West Kamchatka shelf provide a basis for distinguishing individual migrating groups or subpopulations. The subpopulations are named by geographical region along the Kamchatka Peninsula from north to south: Khayryuzovskiy, Ichinskiy, Kolpakovskiy, Kikhchikskiy and Ozernovskiy (Vinogradov, 1970). Within each subpopulation there is a seasonal migration from the overwintering region to the shore, reproduction, summer foraging and return to winter habitat.

In the winter, fall and early spring the subpopulations have the most varied distribution. In summer, when they are near shore, the crab gradually intermix from north to south along the Kamchatka coast. During the summer migrations, portions of the pods move into the neighboring region, and in the central and southern West Kamchatka shelf an intermixing of subpopulations is sometimes observed. The replenishment of juvenile individuals to all the subpopulations occurs from only the most northern part of the West Kamchatka shelf (56°- 60° N.), the main reproductive center of the West Kamchatka population.

According to the terminology of V. N. Beklemishev (1960), the northern Khayryuzovskiy group is an independent subpopulation. The Ichinskiy is semi-independent (apparently, without replenishment of juveniles from the north these populations will not reach high numbers). The Kolpakovskiy and Kikhchikskiy are dependent (due to the low number of females and substantial transport of larvae to the north, reproduction is insignificant). The Ozernovskiy is a "pseudo-population" with the lowest numbers and replenished exclusively from the northern regions. Each of the subpopulations on the West Kamchatka shelf are significantly different by size and sex composition. The number of females and juvenile males gradually decreases from north to south, i.e., the sex ratio is a function of the distance from the main reproductive region. The crab population in the southeast Bering Sea has a simple biological structure, due to its localized habitat. This population is represented by a single generalized group in which the males, females and various size classes intermix, i.e., it has all the features of an independent crab population similar to the Khayryuzovskiy subpopulation on the west coast of Kamchatka. Although the various age and sex groups of the Bristol Bay population overwinter in more or less distinct locations, the overwintering areas are not far from one another, whereas on the West Kamchatka shelf each subpopulation has a distinct overwintering location.

The complex structure of the crab populations must be considered during commercial exploitation of the resource. The most important consideration is the distribution of the commercial take with respect to the individual intrapopulation groups, their numbers and significance to the reproductive population.

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Proc. Int. Symp. King & Tanner Crabs
Nov. 1989, Anchorage, Alaska

The Effect of Shell Condition on Male Snow Crab, *Chionoecetes opilio*, Weight-Width Relationships

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ABSTRACT

From August to October 1989, 710 legal-sized male snow crab, Chionoecetes opilio, from the east coast of Newfoundland were sampled in order to determine what effect shell condition had on live weight and by inference, yield. Results demonstrate that in undamaged, live individuals shell condition has little effect on weight. The implications of this information to the processing and harvesting sectors of the industry in Newfoundland are discussed.

INTRODUCTION

The snow crab, Chionoecetes opilio fishery began on the northeast coast of Newfoundland in 1968. The processing sector of the industry produces frozen or canned product, with little if any emphasis on producing cooked sections. While as many as 17 processing licensees have been active at any one time, the industry is largely dependent on 10 processing operations situated along the northeast coast.

As in any operation relying on labour-intensive processing methodologies, profitability is dependent on price, productivity, and yield from the raw product.

In most areas of Newfoundland the snow crab fishery is prosecuted from mid-April until either area quotas have been caught, or until the end of November when the fishing season ends. During July, August and September most commercial fishing areas along the coast experience a high incidence of newly-molted soft-shelled snow crab in commercial catches. Until 1986, this constituted a serious nuisance effect but a strictly enforced regulation prohibiting the landing of soft-shelled crabs, effectively prevented the problem from developing into a major concern to the processing sector.

In 1986 the regulation that had effectively prevented the landing of soft-shelled crab was struck down due to the fact that the definition of soft-shelled crab was considered as being too subjective to withstand scrutiny in a court of law. Although an attempt to devise a tool that will provide an objective means of distinguishing between hard and soft-shelled has had promising results, (Foyle et al., 1989) there is at present no regulatory means of preventing the landing of this low-yield poor-quality product.

Processors who ultimately must bear the responsibility and indeed the cost of harvesting soft-shelled crab, have long maintained that it was in the fishermen's interest to return soft-shelled crab to the water. It was reasoned that fishermen would enjoy increased benefits by harvesting these animals after they had recovered to a hard-shelled condition and the round weight per individual increased as the water absorbed following ecdysis was replaced by muscle, a period of from 2-3 months duration (Taylor et al., in press).

The dropping of this regulation prohibiting the landing of soft-shelled crab coincided with a sharp decline in resource availability (Taylor and O'Keefe, 1987). This scarcity of resource combined with high prices resulted in large quantities of soft-shelled crab being landed and accepted by processors at many Newfoundland ports (Taylor and O'Keefe, 1988). This study was undertaken in order to determine what effect if any, the harvesting of soft-shelled crab has on the whole weight of fishermen's landings.

MATERIALS AND METHODS

During August, September and October of 1989, commercial-sized (>=95mm carapace width (CW)) male snow crab were sampled from commercial catches held at several processing plants along the northeast coast of Newfoundland and from catches obtained during a research cruise in Bonavista Bay.

During plant sampling, crabs were measured from randomly selected tote boxes that had been iced and stored in the facility's holding shed. The CW and degree of shell hardness (Taylor et al., in press) were determined for all sampled animals, while animals with all limbs intact were weighed to the nearest 0.1 gm on a Sartorius Model U3600 balance equipped with the MP 8-4 data input option designed to enhance accuracy in weighing live specimens.

At-sea sampling was directed exclusively at soft-shelled individuals. Specimens were obtained by means of baited traps fished during the annual time-series research cruise conducted in Bonavista Bay. Soft-shelled crabs were carefully placed in tote boxes, covered with a tarpaulin and transported to the crab processing plant in nearby Bonavista for detailed sampling and weighing.

RESULTS

710 legal-sized male snow crab were sampled during the course of this study. Crabs were separated into groups based on shell condition and weight plotted against CW by group (Fig. 1). Widths ranged from 95 to 129 mm, while weights ranged from 275 to 1078.4 gms (Table 1).

Table 1. Summary of snow crab, Chionoecetes opilio, width-weight-shell condition data collected from the northeast coast of Newfoundland, August-October, 1989.

Shell Condition	No.	Width (mm)			Weight (gms)		
		Min	Mean	Max	Min	Mean	Max
Soft-shell	183	95.0	106.8	127.0	289.4	498.5	840.8
New-hard	457	95.0	104.3	129.0	275.0	476.9	1078.4
Old-hard	70	95.0	105.1	121.0	340.1	496.1	810.5

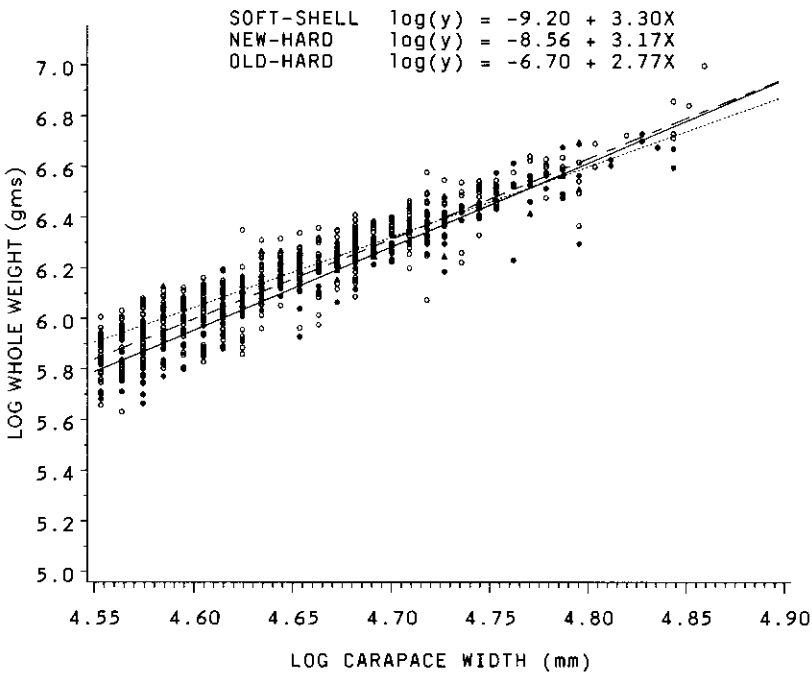

Fig. 1. Plot of snow crab, Chionoecetes opilio, whole weight (gm $\log_e$) versus carapace width (mm $\log_e$). Solid circles (solid line) - soft-shelled; open circles (dashed line) - new/hard; solid triangles (dotted lines) - old/hard.

Let x_{ij} and y_{ij} denote, respectively, the CW and the weight of the jth crab of the ith category, the categories being 1 - soft-shell, 2 - new/hard and 3 - old/hard. Of the models relating weight to CW the two leading competitors appear to be

$$y_{ij} = a_i + b_i x_{ij} + e_{ij} \qquad \text{Model 1}$$

and

$$\log(y_{ij}) = \log(a_i) + b_i \log(x_{ij}) + e_{ij} \qquad \text{Model 2}$$

where $\log(h_{ij}) = e_{ij}$ and the e_{ij} are assumed to be independent random variables with zero mean and constant variance. These will be referred to as Model 1 and Model 2, respectively. It is sometimes convenient to think of h_{ij} as equal to $1+e_{ij}$ with the e_{ij} small, so that $\log(h_{ij}) \sim e_{ij}$.

We are interested in testing the hypothesis that weight - carapace-width relationship is independent of the category, i.e. that $a_1=a_2=a_3$ and $b_1=b_2=b_3$. We begin by fitting, by conventional least-squares methods, separate lines for each category under each of the above models. (For convenience, in fitting model 1, the weights (in grams) have been divided by 1000). The residual sums of squares, on 704 degrees of freedom (d.f.), are then

Model 1: 107.4499; Model 2: 4.5141.

These residual sums of squares contain two components which are commonly referred to as the "pure error" and the "lack of fit". To explain these note that, for any given value of CW, there is a range of weights. Regressing weight on carapace width cannot do anything to reduce the variation between individual weights at a given width. This is the "pure error". The best tracking of the dependent variable that can be made from a single independent, or predictor, variable (including transformations) would pass through the mean values of the dependent variable at each of the values of the independent variable. The departure of the fitted line from these means defines the "lack of fit". If the fit is good, the measure of the lack of fit should be comparable to the pure error. A lack of fit substantially less than the pure error is suggestive of a fit that is "too good to be true". For example, the lack of fit can be made zero by use of a sufficiently high-order polynomial in the independent variable, but such would almost certainly be meaningless. In this study multiple observations of weight are available at most carapace widths; various authors have, however, developed methods for the construction of pure error in the absence of multiple observations. For the data of the study we find

Model 1

Source	D.F.	Sum of Squares	Mean Square
Lack of fit	80	19.2108	0.2401
Pure error	624	88.2391	0.1414

Model 2

Source	D.F.	Sum of Squares	Mean Square
Lack of fit	80	0.4825	0.0060
Pure error	624	4.0316	0.0065

Thus, for Model 1, a test for lack of fit is given by F = 0.2401/0.1414 = 1.70, and by F = 0.0060/0.065 = 0.93 for Model 2, both on 80 and 624 d.f. Although under Model 1 the lack of fit is clearly not large, it is formally significant at the 1% level, primarily because of the large number of degrees of freedom available. On the other hand, under Model 2, there is no indication a lack of fit. Accordingly, in what follows we focus on Model 2.

If we fit a single line, i.e. assume $a_1=a_2=a_3$ and $b_1=b_2=b_3$, we obtain a residual sum of squares of 4.8136 on 708 d.f. The difference between this and the separate-line model is 4.8136-4.5141 = 0.2995 on 4 d.f. For testing the hypothesis, it is inconsequential whether we use the pure error mean square of 0.0065 on 624 d.f. of the residual mean square of 4.5141/704 = 0.0064 on 704 d.f. With the latter, the test statistic is F = 0.2995/(4 x 0.0064) = 11.7. Clearly the single-line hypothesis should be rejected.

The step from separate lines to a single line can be broken into meaningful components. Firstly we may test whether the lines are parallel, i.e. $b_1=b_2=b_3$ and then, given that they are parallel, the hypothesis that they are coincident i.e. $a_1=a_2=a_3$ given $b_1=b_2=b_3$. Note that the second subhypothesis becomes meaningful only if the first subhypothesis can be accepted. The residual sum of squares from the distinct parallel-line model (the first subhypothesis) is 4.5731 on 706 d.f. A test of the subhypothesis is, therefore, given by F = (4.5731-4.5141)/(2x0.0064) = 4.61. This value is formally significant at close to the 1% level; thus the hypothesis of parallel lines is not acceptable, and it would be inappropriate to proceed to the second subhypothesis.

The estimates of the three separate lines are:

Category 1: log(y) = -9.2030 + 3.2949x
Category 2: log(y) = -8.5610 + 3.1649x
Category 3: log(y) = -6.7029 + 2.7711x

This suggests the possibility that the lines for Categories 1 and 2 might be parallel, or even coincident. Accordingly, we may test the hypothesis $b_1=b_2$ but with b_3 possibly distinct. This leads to a residual sum of squares of 4.5254 on 705 d.f. and a test statistic F = (4.5254-4.5141)/0.0064 = 1.77, which is clearly not significant at conventional levels. Some caution must be exercised here, however, since the hypothesis being tested has been suggested by the data. If we now add the hypothesis $a_1=a_2$ (meaningful since $b_1=b_2$ has been accepted) we obtain a residual sum of squares of 4.6928 on 706 d.f. The test statistic would be F = (4.6928-4.5254)/(4.5254/705) = 26.1; clearly the hypothesis must be rejected.

The most parsimonious acceptable fit is that of parallel but distinct lines for Categories 1 and 2 with a separate line, of shallower slope, but greater intercept, for Category 3.

Interestingly, essentially the same conclusion is reached if Model 1 is used. The residual sum of squares for the single-line model is 112.7102 on 708 d.f., leading to a test statistic of F = (112.7102-107.4499)/(4 x 0.1526) = 8.62; the single-line model is, thus, rejected. (Note that the use of Model 1 implies the tacit ignoring of the lack of fit and hence the use of the residual mean square for subsequent hypothesis tests).

Under the distinct parallel-line model the residual sum of squares is 108.3963 on 706 d.f., leading to a test statistic of

$$F = (108.3963-107.4499)/(2 \times 0.1526) = 3.10.$$

Because of the large number of d.f. of the denominator, this value is formally significant at the 5% level.

The residual sum of squares under the subhypothesis $b_1=b_2$ is 107.4622 on 705 d.f., leading to a test statistic F = (107.4622-107.4499)/0.1526 = 0.08, but under the additional hypothesis, $a_1=a_2$ the residual sum of squares is 110.9351 on 706. d.f., leading to a test statistic

$$F = (110.9351-107.4622)/(107.4622/705) = 22.8$$

and the rejection of the latter.

The fact that the most parsimonious acceptable model still has three distinct lines in a somewhat natural ordering would appear to have more an academic than practical value. Relative to the range of the data, the three lines are remarkably close. In particular, it can be readily seen that there would be a high frequency of misclassification if the weight for a given carapace width were used to classify individuals as to shell type.

DISCUSSION

Miller and Watson (1976) present a weight-width regression for C. opilio from the Western Gulf of St. Lawrence but do not specify whether it is based on animals of various shell conditions, or whether only undamaged complete crabs were used. Similarly, Phinney (1977) fails to report either the shell condition or degree of leg loss of the crabs sampled in deriving the regression equation he used to determine the weight-width relationship for C. bairdi from Alaska. It must be recognized however, that at the time these two studies were conducted, the landing of soft-shelled crab was not a problem in their study areas.

The implications of these results to the crab fishing industry are quite clear. Processors who purchase soft-shelled crabs are paying virtually the same price for these animals as they would for more-desirable hard-shelled individuals. In Newfoundland, fisherman are paid for the landed weight of their catches prior to butchering. Therefore the difference in yield is not evident until after processing of the catch has been completed. In purchasing soft-shelled crabs and basing payment on landed rather than butchered weight all incentive for the crab fishermen to return soft-shelled crabs to the fishing grounds is removed. It is hoped that the results of this study will encourage processors to refuse to accept these crabs on the basis of sound economics which is, as they themselves so frequently say, the bottom line.

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Proc. Int. Symp. King & Tanner Crabs
Nov. 1989, Anchorage, Alaska

Life History Characteristics of *Chionoecetes tanneri* off British Columbia

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ABSTRACT

Chionoecetes tanneri occurs in modest commercial quantities off the west coast of British Columbia on the continental slope. During much of the year, males were found at 580-670 m depth, with females concentrated at 670-720 m, although some were trapped as shallow as 460 m. In late March and April, vertical distribution appeared to change; ovigerous females with eyed eggs and males with relatively fouled carapaces predominated between 580-670 m and clean carapace males (recent moults) and nonovigerous females predominated below 720 m. Juveniles were mostly caught at 720-1100 m throughout the year. Data suggested that C. tanneri were interacting with sablefish (Anoplopoma fimbria) since there were few sablefish caught in the depth range inhabitated by C. tanneri.

Analysis of morphometric proportions suggested that chelae length versus carapace length gave the best criteria for distinguishing between potentially preterminal and terminal moult male crabs. Equations distinguishing the two morphs are proposed, but because few potentially preterminal moult crabs were present in commercial catches, regressions could be refined as additional data become available.

INTRODUCTION

In early 1988, a fishery for male tanner crab, Chionoecetes tanneri, was initiated off the upper west coast of Vancouver Island, British Columbia (Fig. 1). Currently, there is no restrictive regulation as to what quantity and size of crab should be exploited to both conserve the resource and achieve maximum yield per recruit (Jamieson, 1990). The present report provides initial results of an ongoing study to provide data for rational management of this newly discovered resource.

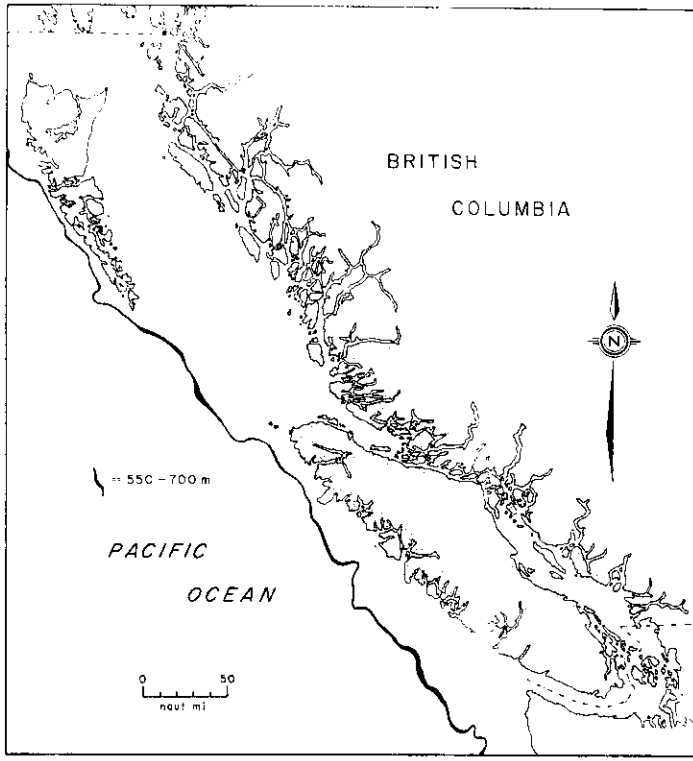

Fig. 1. Geographical location (dark line) off the west coast of British Columbia where C. tanneri generally occurs. Exploratory commercial fishing for C. tanneri has occurred off the middle third of Vancouver Island (the largest island in the figure).

Based on views arising from a recent workshop on the biology of C. opilio in the Gulf of St. Lawrence (Jamieson and McKone, 1988), we assumed that a terminal moult might occur in C. tanneri in British Columbia and that biological management advice should be developed to reflect this the implications of a terminal moult in males. The concept of a terminal moult for male Chionoecetes is not currently accepted in the management of Chionoecetes in Alaska (Donaldson, 1988).

The present paper describes data on experimental commercial fishing to date, the biology and distribution of C. tanneri in British Columbia, and analytical results in trying to identify preterminal and terminal moults in male crabs.

METHODS

Data on distribution and relative abundance of crabs were obtained from interviews with fishermen actively involved in the fishery. Morphometric measurements were obtained in 1988 from 976 crabs

collected off the west coast of Vancouver Island by the W. E. RICKER and the TRANSPACIFIC #1. During the three TRANSPACIFIC #1 trips sampled between February-April, 1988, three types of tanner crab traps were used: modified blackcod traps; 116 cm square, stackable traps with removable bottoms; and conical traps of 135, 142, or 229 cm diameter. The 229 cm conical traps had a 12.7 cm escape ring. All traps were baited with frozen hake and were fished at depths ranging from 325 to 770 m. In late April and May, 1988, tanner crabs were collected with the W. E. RICKER using square, 116 cm tanner crab traps baited with fresh herring. Depths fished ranged from 325 to 770 m. Soak times ranged from 1-7 d.

Each tanner crab caught was sexed and weighed and a number of morphometric measurements were taken. These measurements were the same as those collected by Conan and Comeau (1986) for C. opilio in the Gulf of St. Lawrence, and included chela length, width, and height (Fig. 2) and both minima and maxima carapace length (CL) and width (CW). Maximum CL was defined as the length from the tip of the

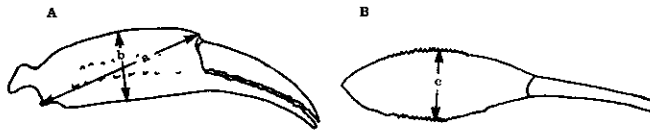

Fig. 2. Tanner crab chelae measurements. A. Lateral view: a. chela length; b. chela height. B. Dorsal view: c. chela width.

rostrum to the posterior edge of the carapace, while minimum CL was measured from the inside notch of the bifid rostrum to the posterior edge of the carapace. Maximum CW was defined as the widest section of the carapace, including the spines; minimum CW excluded the spines. Only data collected from male tanner crabs with intact non-regenerating right claws were used in data analyses.

A principal components analysis (PCA) was used to detect clustering within the population, as described by Conan and Comeau (1986). To identify variables which best distinguished between preterminal and terminal moult clusters, pairs of variables were plotted and visually examined, using natural logarithmic transformations of measurements in order to linearize the data. Two pairs of measurements were found to be most useful in identifying elliptical clusters of observations, and these pairs were further analyzed. Linear discriminant functions separating terminal and preterminal moult individuals were derived in the following manner. First, the major and minor axes of the ellipse containing the data were determined using the pooled covariance matrix. An initial boundary, parallel to the major axis of the ellipse, was then constructed between the two classes. The degree of separation was then calculated by determining the spread of each class along the minor axis of the ellipse. The slope and intercept of the initial boundary were then adjusted to minimize the spread of the data along a line perpendicular to the new boundary, taking into account the number of samples in each class. Statistical procedures and analyses were preformed using SAS (Statistical Analysis System).

RESULTS

A. Biological and Fishery Observations

Off B.C., commercial concentrations of male C. tanneri occur primarily between the 580-670 m depth isopleths on the continental slope. The species ranged from about 420 -1100 m depth, with adult females primarily from 670-720 m and juveniles from about 720-1100 m depth. In addition to vertical stratification within C. tanneri by sex and size, there appeared to be vertical stratification among species. Lithodes aequispina occurred from 400-550 m depth, L. couesi from 500-580 m, C. tanneri from 580-720 m, and C. angulatus below 720 m. This basically agrees with the general depth ranges reported by Hart (1982). Fishermen also noted that blackcod (Anoplopoma fimbria) overlaped little in vertical distribution with C. tanneri, being most abundant just above C. tanneri. Overall, the order of greatest abundance was C. tanneri, L. couesi and L. aequispina.

Exploratory work was also conducted in 1989 on sea mounts off the B.C. coast, with most effort directed towards Union Sea Mount (330 km WSW of the northern end of Vancouver Island). L. aequispina was the most abundant of the 4 species. Species distribution seemed to be affected by substrate type as well as depth, with L. couesi preferring a rockier bottom. Union Sea Mount has a surface area of about 100 km^2 above 800 m depth, with a lesser slope and a softer substrate on the western side than on the eastern side. L. aequispina seemed to be most abundant on top, with C. tanneri dominating on the western side and L. couesi on the eastern side.

The general vertical distribution by sex described above for C. tanneri on the continental slope apparently breaks down in late March and April. Ovigerous females with eyed eggs move upwards into the 580-660 m depth stratum and traps which previously caught just males now became saturated with females. Catch rates of over 100 females per trap, and only a few males, become common and fishing for males became uneconomical. Males caught with ovigerous females were reported by fishermen to have relatively fouled carapaces, with cleaner carapace males and nonovigerous females predominating below 720 m. These latter crabs may represent annual recruitment to the terminal moult cohort. This phenomenon basically terminates the fishery until fall, as fishermen then become engaged in fishing other species. Soft-shell males are seldom caught, both because of the relatively shallow depth range currently fished and a lack of fishing in the spring and summer, the time of year when most crab would be recently moulted.

From a fishery perspective, market demand (in order of preference) is currently greatest for L. aequispina, L. couesi and C. tanneri, opposite to that of their relative abundance. C. tanneri may have a lower meat yield than does C. opilio, the species it is currently competing with on international markets, but initial processing techniques in British Columbia may not have been optimal and greater yields may be possible. Current fishing activity is influenced by the timing of other regional fisheries, notably blackcod, and fishermen currently involved in the fishery are only prepared to participate from about August to March. The price for C. tanneri has recently dropped from about $CDN 0.45 to 0.18 kg^{-1}, apparently because of a surplus of crab on international markets, making any fishing for tanner crab uneconomical in the latter part of 1989. In general, bigger traps yield more crab but trap size has to be balanced with the handling difficulties associated with large gear in rough seas.

Fishing trips are generally 3-4 d each (6 d maximum). Some problems were encountered maintaining crab quality and survival when surface water temperatures exceeded 10°C., which is usually from June to October. Survival seemed best when crab were sprayed with refrigerated water rather then holding them submerged in water. High water temperature is a greater seasonal problem on the sea mounts because being further offshore, they are in the path of subtropical water which typically moves northward across the Pacific during the summer months. In 1989, temperatures above 18°C. were observed in August on Union Sea Mount.

B. Analytical Studies

In the PCA, component 1 explained 90% of the variance, and while component 2 only explained 6.0% of the variance, this was about three

Measurement	Eigenvector	
	Component 1	Component 2
Minimum carapce width	0.448	-0.522
Minimum carapace length	0.449	-0.505
Claw length	0.457	0.144
Claw height	0.449	0.301
Claw width	0.433	0.600

Table 1. Loading factors for the major principal components (N=976).

times as much as component 3. Loading factors are given in Table 1. The morphometric measurements (Fig. 2) which best showed a clustering of the data visually were chela length : minimum CW and chela length : minimum CL. These measurements were different from those found best for C. opilio in the Gulf of St. Lawrence by Conan and Comeau (1986), namely chela height : CW.

The regressions relating chela length to carapace size were:

chela length (y) : minimum CL (log to log)

$$y = 1.65CL - 4.01$$

chela length (y) : minimum CW (log to log)

$$y = 1.45CW - 3.16$$

The estimated linear discriminant functions are:

log(chela length) = 1.41 log(minimum CW) - 2.92

and

log(chela length) = 1.47 log(minimum CL) - 3.11

These equations can be rearranged to provide a maturity code (MC) which can be easily determined in the field. The MC presented in this paper is constructed to be positive for preterminal moult crabs and negative for terminal molt crabs. The MC for the two sets of variables considered are:

$$MC = \log(\text{chela length}) - 1.41 \log(\text{minimum CW}) + 2.92$$

and

$$MC = \log(\text{chela length}) - 1.47 \log(\text{minimum CL}) + 3.11$$

The effectiveness by which the data were separated is shown for each pair of observations (Figs. 3 and 4, respectively).

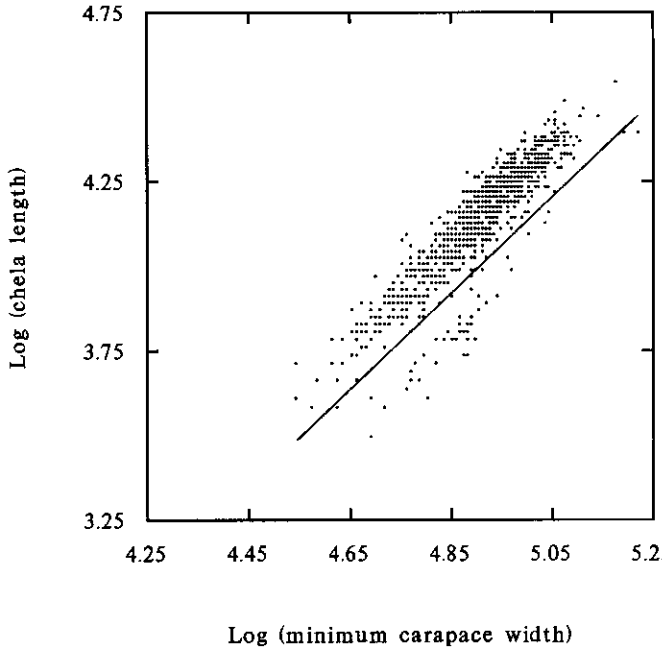

Fig. 3. Morphometric relationships between tanner crab chelae length and carapace width. The line is the linear discriminant function separating hypothesized preterminal and terminal moult crabs.

DISCUSSION

A recent review of Chionoecetes biology and life history (Jamieson and McKone, 1988) accepted that for C. opilio in the Gulf of St. Lawrence, and probably for all Chionoecetes species, both males and females have a terminal moult. For males, the carapace size at which a terminal moult may occur can be quite variable. From a management perspective, this means that a size limit based on male gonadal maturity, even if it allowed males to survive and theoretically moult at least once more after they reached a size where they had mature sperm, may not always result in the achievement of optimal yield per recruit from the resource. Evidence suggests that male Chionoecetes must be morphometrically mature, i.e., have reached their terminal moult, before they can effectively mate, even though they may have been producing apparently functional sperm for a number of years as earlier instars before their final moult (Jamieson and McKone, 1988). The

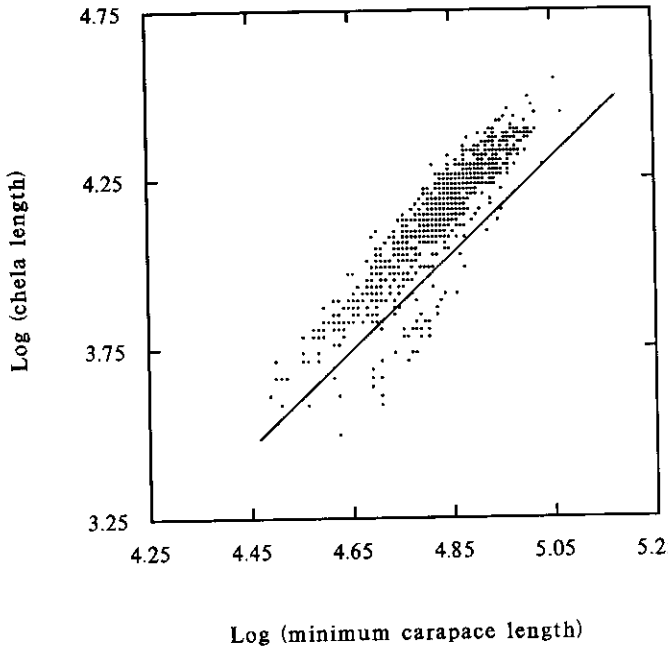

Fig. 4. Morphometric relationships between tanner crab chelae length and carapace length. The line is the linear discriminant function separating hypothesized preterminal and terminal moult crabs.

size at which males stop moulting, i.e., reach terminal moult, may be influenced by the relative size frequencies of terminal moult individuals in the population, although it is not currently clear how this might be effected biologically. It has been suggested (Conan and Comeau, 1986) that in the early stages of a fishery, large, older male crabs will predominate. If their exploitation rate is too high and their relative abundance decreases substantially, future recruitment to the terminal moult cohort may occur at progressively smaller sizes until ultimately, most terminal moult males may be in the instar immediately after gonadal maturity is reached. It is thus important to characterize the size frequency structure of preterminal and terminal moult individuals at the beginning of a fishery, i.e., in the virgin population. This should allow an optimal size limit or catch quota to be estimated, based on the above unique biological features, and allow future fishery-induced changes in population age and size structure to be interpreted correctly.

Research described here is preliminary, and effort on identification of terminal moult individuals is continuing. A large number of animals were assessed but to date, there appears to be relatively few preterminal moult animals in the samples obtained. This may be the result of the relative preponderance of terminal moult animals in the population since there is evidence (Conan and Comeau, 1990; Yamasaki and Sinoda, 1990) that male Chionoecetes may live at least 3 y after

their terminal moult. Fishermen may also selectively fish concentrations of the largest animals, hence biasing the data, which is possible because of the apparent spatial separation of juvenile and adult animals of different sizes and/or maturity stages.

To evaluate adequately the existence of a terminal moult stage, we need to obtain more individuals in smaller size ranges. Final estimation of minimum legal size criteria must be delayed until smaller crabs can be obtained, but from the analyses presented here, it should be possible to tentatively identify preterminal and terminal moult individuals in the future in the field, thereby perhaps allowing other visually identifying characteristics to be assessed. A carapace size measurement may not be best to identify individuals which should be retained by a fishery and an alternative may be use of a chelae measurement to identify the harvestable cohort.

Tester and Carey (1986) *did not accept that male C. tanneri have a terminal moult and using the relative length of chelar propodus to* carapace width, suggested that males with a carapace width, notch-to-notch, greater than 118 mm were sexually mature. Our data (Fig. 3) suggests that functional maturity, ie. terminal moult, may occur in animals as small as 95 mm CW. Tester and Carey's (1986) conclusion that adult male C. tanneri moult frequently enough to maintain their carapaces mostly free from epifauna and bacterially-induced lesions was based on this suggestion by Baross et al. (1978). Specimens from this latter study were predominantly female (70%) and from April-June samplings, indicating that they had probably been collected at a time when mating was actively occurring. While only 29% of males had bacterial infections, the male sample size was only 124 and newly-moulted, terminal moult males could easily have been over-represented in proportion. The suggestion that this unequal sex ratio might result from a greater mortality associated with continued moulting in males is not well supported by the data they presented. Baross et al. (1978) noted that female C. tanneri have an exceptionally high incidence (76%) of bacterial infection and while the incidence in males was lower, it was still much greater than the less than 10% reported for other adult crabs, notably king crabs, and other species of crustaceans collected along with the C. tanneri.

The relative spatial separation of juveniles, adult females and adult males by depth observed here is similar to that reported by Pereyra (1966, 1968, 1972) in his study off Oregon. Through much of the year, males were shallowest, with females and juveniles progressively deeper. The depths observed for each group between the two locations were generally similar. However, whereas Pereyra (1966, 1968, 1972) reported a gradual migration of males into the deeper depth range occupied by the females during the winter, it appeared to be females which migrated up into the depth range occupied by the males off British Columbia. This movement of females was also relatively sudden and coincided with the appearance of eyed eggs, indicating imminent hatching. A movement to shallower waters by females at the time of egg hatching and/or mating has been reported for other crustaceans inhabiting deeper waters, e.g., lobsters (Homarus americanus) in inshore areas near Grand Manan, Bay of Fundy (Campbell, 1986), and C. opilio in Bonne Bay, Newfoundland (Hooper, 198; Dufour, 1988). This may favour both survival and dispersal of surface-dwelling larvae. Pereyra (1968) speculated that C. tanneri larvae were surface-dwelling, but this needs to be confirmed before adult distribution by depth, egg-hatching and species dispersal strategies can be more fully evaluated.

Pereyra (1966, 1968) observed most egg hatching between January and March, followed almost immediately by extrusion of a new egg mass, whereas most hatching off British Columbia appeared to occur in March and April. He reported brood incubation to take about one year, which suggests that few mature females should be found without eggs. Our data is presently not extensive enough to confirm this phenomenon.

ACKNOWLEDGEMENTS

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Review of Literature on Life Histories in the Genus *Chionoecetes* in Light of the Recent Findings on Growth and Maturity of *C. opilio* in Eastern Canada

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ABSTRACT

The traditional interpretation of the life history of the genus Chionoecetes was based until recently on general principles accepted for most decapod crustaceans. However, these principles differ from what is accepted for other genera in the majid family. In Canadian fisheries for Chionoecetes opilio, it was assumed that all males were mature and had the opportunity to mate before they reached the minimal harvestable size of 95 mm carapace width (C.W.). It was also thought that females mate only once, shortly after the final molt to maturity; a female would thereafter use spermatophores stored in her spermathecae for fertilizing eggs in successive broods. All male C. opilio were believed to have the potential to grow until they reached an asymptotic size equivalent to the maximum size observed in commercial landings (130-140 mm C.W.).

Recent work in Canada has shown the necessity of a critical re-interpretation of the life history of the C. opilio in the Atlantic. The authors review growth and reproduction of the species in the context of published and unpublished results.

INTRODUCTION

Directed commercial exploitation of snow crab, Chionoecetes opilio (Brachyura, Majidae), off Atlantic Canada began in 1966 and developed into one of the most valuable fisheries in the region (Elner 1982; Elner and Bailey 1986; Mallet et al., 1989 for reviews). Congeners (i.e. C. bairdi, C. japonicus, C. opilio elongatus and C. tanneri) exploited in the North Pacific and in the Japan Sea (Colgate 1982; Sinoda 1982) are absent off Atlantic Canada. The genus Chionoecetes appeared, until recently, unique within the majid family in that males were considered to continue to molt after attaining maturity (Watson 1970; Sochasky 1973). Females, in all majid species, tend to be smaller than males and are accepted to attain terminal molt status at maturity (Sochasky, 1973).

In the early stage of the Atlantic snow crab fishery, there was no size limit but processors voluntarily agreed to only accept crabs over 4 inch (102 mm) carapace width (C.W.). The size was selected prior to understanding of maturity or the reproduction. Since about 1973, a minimum legal size of 95 mm carapace width has been enforced; this size represented the smallest crab that was acceptable to processors, as well as size at maturity and mating observed by Powles (1968) and Watson (1970, 1972). Both the 102 mm and the 95 mm C.W. minimum sizes had similar biological implications; most apparently, the fishery became dependent on male snow crab that were believed to be mature. Females, after undergoing a terminal molt to maturity, achieve maximum sizes of between 47-95 mm C.W. and are effectively barred from commercial exploitation. Watson (1970) concluded that males attain maturity between 51 and 72 mm C.W. and are able to mate in the intervening years before recruiting into the fishery. The lack of barren females and the large numbers of eggs produced by each female (Elner and Gass, 1984; Conan et al.,1989) allayed fears of a reduction in recruitment due to a lack of mature males. Hence, the 95 mm C.W. minimum size limit was widely accepted as having maximized egg production and made the Atlantic snow crab stocks inviolate to recruitment overfishing. Although no biological basis was available to set an appropriate exploitation level (Moriyasu and Conan, 1985), management attempted to maintain a target annual exploitation rate of 50-60% for most stocks on the rationale of promoting stability and avoiding reliance on newly recruited crab (Elner, 1982). However, widely different responses to exploitation between various Atlantic snow crab stocks under the same management regime (Davidson et al. 1985; Bailey and Elner, 1989) caused doubts about management strategy. Similarly, massive collapses in congeneric stocks in the NW Pacific (Colgate, 1982) sensitized managers to the instability of single-sex fisheries for Chionoecetes.

REVIEW OF LITERATURE

Terminal Molt:

With the sole exception of some species of the genus Chionoecetes, all species of majid crabs are believed to share a common life history characteristic only exceptionally found in other crab families. Specifically, both male and female majids molt for the last time when they attain morphometric maturity. This "terminal molt" is followed by "terminal anecdysis", a non-evolutive molt stage defined as C_4T according to Carlisle and Dohrn (1953). The females are able to extrude several batches of eggs after terminal molt. These eggs can be fertilized by sperm which is stored in a pair of well-differentiated, internal spermathecae (Hartnoll, 1968; Beninger et al. 1988; Diesel, 1989). It is not clearly shown in all species whether females mate only once after the terminal molt, or are able to mate again while in terminal anecdysis. Mating in most non-majid crabs takes place between a soft-shelled female and a hard-shelled male (Hartnoll, 1969).

The existence of a terminal molt in majids was first suggested by Teissier (1933) for Macropodia rostrata and by Teissier (1935) for Maia squinado. However, Teissier did not provide experimental evidence showing that a terminal molt was actually reached at the onset of maturity. He described a "puberty molt" characterized by a change in allometric relationships between chela size and C. W. for males. The "puberty molt" for females was characterized by a change in allometric relationships between abdomen size and C.W. and to a lesser extent chela size and C.W. From there on, the concept of "maturity" was assimilated with "puberty molt" both for males and females. In order to avoid confusion between the two concepts inherent to early literature, we shall distinguish "prepuberal" from "post puberal" individuals as a function of whether or not they achieved the puberty (terminal) molt and avoid the wording "maturity" unless the authors have actually tested the reproductive capability.

Carlisle (1957) stated a few experimental results demonstrating terminal molt, but did not provide data. Molt hormone extracts from postpuberal Maia squinado did not induce molting in shrimp, Leander serratus, while extracts from prepuberal Maia were effective in activating molting. Carlisle concluded that the organ producing molting hormones degenerates in postpuberal Maia. Actual degeneration was demonstrated by histology for Acanthonyx lunulatus by Chaix et al. (1976).

Vernet-Cornubert (1958, 1959, 1960) observed that ablation of the eye stalks, believed to contain the organ producing a molt inhibiting hormone, would induce molting of prepuberal Pisa tetraodon, but not of postpuberal individuals. Therefore, she concluded that the molt organ degenerated in postpuberal individuals after the puberty molt. Carlisle (1957) reported that Maia squinado which had entered terminal anecdysis (i.e. postpuberal), were no longer capable of regenerating damaged tissues or limbs. Carlisle concluded that this is an indication that the Y-organ had degenerated. He referred to Echalier (1955) who reported that a crab, in the absence of the Y-organ, cannot regenerate missing limbs, nor form the bud from which such regeneration begins. However, the accurate reference is Echalier (1956) who reported on the absence of limb regeneration for individuals of a non-majid crab, Carcinus maenas, in which the Y-organ had been experimentally ablated. Skinner and Graham (1972) reported that spider crab, Libinia emarginata, with autotomized legs did not show any sign of regeneration over a 10 week period. However, they did not check the maturity or terminal anecdysis status of the crab under observation. We found no reference to any experimental demonstration showing that limbs of postpuberal majids do not regenerate, although there is a tradition among many British and French biologists that this absence of regeneration is a fact. However, Vernet- Cornubert (unpublished data, USTL, Laboratoire de Physiologie des Invertébrés , 34060 Montpellier, France), conducted experiments on Pisa tetraodon supporting the belief on non-regeneration.

Hartnoll (1963) searched for individuals in premolt stages (proecdysis) among postpuberal males and females from three majid species (Hyas coarctatus, Inachus dorsettensis and Macropodia rostrata). One-hundred and seventy-five out of 2494 postpuberal individuals examined were in proecdysis, while none of the 2363 prepuberal specimens showed any indication that they were going to molt. He also kept an equal number ("several dozen") of prepuberal and postpuberal crabs in the laboratory. No postpuberal individuals ever molted while prepuberal ones frequently did so.

Teissier (1934, 1955) reported that Maia squinado goes through three stages of allometric relative growth. Numerous molts during the immature stage are followed by one "prepuberal" molt and later by one "puberal" i.e. terminal molt. In order to avoid confusion, we shall use the terminology immature prior to the prepuberal molt, prepuberal for stages between prepuberal and puberal molts and postpuberal for stages beyond the puberal molt. There is a change of slope, that Conan et al. (1988) later called the "angular point", between the major axes drawn from the swarm of points separated by the "prepuberal" molt. There is a change of elevation but no well marked change of slope between the major axes drawn from the swarm of points separated by the "puberal" molt. Allometric plots of logarithms of chela size vs. logarithms of C. W. fall onto three distinct straight lines. Vernet-Cornubert (1958,1960) also reported immature, prepuberal and post puberal allometric stages for Pisa tetraodon. Hartnoll (1963) showed that the males of 9 species of Manx majids go through these three stages of allometric relative growth. However, he mentioned that no angular point at a prepuberal molt could be found for the females. Teissier (1933) did not find such an angular point marking prepuberty for males or females of Macropodia rostrata. Hartnoll (1963) mentioned that, for some of the species he studied, prepuberal males had gonads with mature spermatozoa. In Hyas coarctatus, Eurynome aspersa, E. spinosa and Inachus dorsettensis the testes were never mature before the puberty molt, but in Pisa gibbsi, Inachus leptochirus, I. phalangium, Macropodia rostrata and M.

longirostris, a proportion of prepuberal males had mature testes. Hartnoll was uncertain whether prepuberal males with mature spermatozoa could mate.

The range of sizes reached after the puberty or terminal molt is very wide in all species described: some 8 to 20 mm carapace length for male and female Macropodia rostrata (Teissier, 1933), 130 to 226 mm carapace length for Maia (Teissier 1935, 1955), and 15 to 35 mm C.W. for Pisa tetraodon according to data from Vernet-Cornubert (1958). Hartnoll (1963) reported even wider ranges of carapace lengths among mature animals: 12.5 to 40.5 mm for male Hyas coarctatus, 10.6 to 34.5 mm for the females, 12.5 to 30.5 mm for male Inachus dorsettensis, 13.5 to 23.5 mm for the females. Chaix (1977) reported C.W. varying from 5 to 14 mm for mature males Acanthonyx lunulatus and 5 to 10 mm for females.

In the literature, there is evidence that a puberty terminal molt exists for all species of majid crab except, until 1986, for Chionoecetes spp. A terminal molt for female C. opilio, although never experimentally demonstrated, is generally well accepted. Yoshida (1941) appears to have been the originator for this opinion; however, he merely suggested this as a possibility after noticing 1) the wide size difference between males and females (he believed "mature" males did not stop growing); 2) mating of males with females in a hard-shelled condition; and 3) females do not molt between hatching of the old batch of eggs and spawning of the new batch, and, intuitively, do not molt while they are carrying eggs. Nevertheless, Ito and Kobayashi (1967) reported the capture of an ovigerous female undergoing ecdysis, and Hooper (1986) collecting at least two exuviae with remnants of hatched eggs on the pleopods. Although these two latter reports challenge the rigidity of the female terminal molt premise, the paucity of such observations suggests that post-maturity molting by female snow crab is an anomaly.

Relative growth of the abdomen vs. the carapace of female Chionoecetes follows the pattern described for all other terminal molt majids. The carapace sizes of prepuberal and post puberal females overlap widely. However, no discernable change in allometry (angular point) at a prepuberal molt is usually reported. Such plots for relative growth can be found in Donaldson et al.(1980) for C. bairdi, and in Ito (1957), Watson (1970), Kanno (1972) and Fujita et al. (1988) for C. opilio. Ito (1957) reported a change in relative growth of the abdomen vs. C.W. for female C. opilio. He distinguished "young" (immature in our notation) females below 30 mm carapace width, "immatures" (prepuberal) between 30 and 70 mm and "mature" (postpuberal) females between 50 and 75 mm. However, as he did not use a logarithmic scale for his plots, the angular point at 30 mm may be explained by the curvature of a single allometric function. There is also a decline of growth in carapace size (defined as the linear relationship between premolt and postmolt size) at the molt to maturity. This is documented by Kon et al. (1968), Miller and Watson (1976), Kon (1980) and Moriyasu et al. (1987) for C. opilio, by Donaldson et al. (1980) for C. bairdi.

Watson (1970) stated that female did not molt after "maturity" (i.e. spawning); however, he did not produce new evidence, rather he referred to Kato et al. (1956), Ito (1963) and to Hartnoll (1969) for majids in general. The former two authors worked on Chionoecetes but did not present experimental evidence for a terminal molt in females. Hartnoll (1969) did not work on Chionoecetes, and did not proffer any specific information on this genus. In references since 1970, and despite the critical review by Sochasky (1973), it seems an established "fact" that female Chionoecetes experience a terminal molt to maturity (Miller and Watson 1976: Kon 1980, Donaldson et al., 1980, 1981; and Somerton 1981).

Let us now consider the information on growth after "maturity" for male Chionoecetes. In all references on growth in Chionoecetes, prior to 1986, it is generally held that males do not experience a terminal molt at onset of "maturity". In the literature on Chionoecetes anterior to 1986, there is a confusion between the concepts of male "maturity" and puberty molt characterized by a morphometric

differentiation of the claw. The authors generally mean post puberal males bearing differentiated claws when they described "mature" males. This is probably because a mature female is easily identified as bearing eggs, while the definition of maturity for a male is the ability to mate successfully and is difficult to identify. Male Chionoecetes are surmised to eventually reach a terminal molt but only several molts after "maturity" (Miller and Watson 1976 for C. opilio, Donaldson et al. 1980 for C. bairdi). Here again, the opinion that "mature" males continue growing can be traced back to Yoshida (1941). Yoshida did not prove this experimentally, he only stated that males are considerably larger than females and that, since they do not carry eggs and are not limited by the requirement of not loosing their brood at molt, they may be able to achieve growth each year. This opinion is also held by Ito (1957, 1970), Ito and Kobayashi (1967), Powles (1968), Sinoda (1968), Watson (1970), Kon (1980) for C. opilio, and Somerton (1981) for C. opilio and C. bairdi. Kato et al. (1956) stated that they guessed that "mature" males continued to molt because there were modes in the adult size classes. Sinoda (1968) constructed a growth curve for "mature" males after conducting a modal analysis of the size frequency distributions of "mature" males.

Male Chionoecetes have a relative growth of the chela vs. carapace which follows the pattern described for all other majids. At the puberty molt, there is a change of allometry with a discontinuity in elevation between prepuberal (morphometrically immature) and postpuberal (morphometrically mature, according to the terminology of Conan and Comeau, 1986), regression lines. Plots for relative growth can be found in the reference already cited for females and in Powles (1968) for C. opilio. The increment in carapace size at molt of "mature" males is reported to be smaller than for "immature" males by Miller and Watson (1976) and by Kon (1980) for C. opilio, and by Donaldson et al. (1980) for C. bairdi.

References in which "mature" male C. opilio are reported to have molted in aquaria are suspect. Miller and Watson (1976) defined "mature" male C. opilio as larger than 57 mm because an earlier work (Watson 1970) had shown, on the basis of vasa deferens weight and presence of spermatophores, that 50% "maturity" occurred at this size. They did not check the morphometric state of each individual prior to molting. They also reported that no crab with old shells greater than 70 mm C.W. molted and that these could have reached a terminal molt stage, but they did not relate this terminal molt to changes in morphometry.

Donaldson et al. (1980) also used a 50% "maturity" size, established on the same basis as above, for defining "maturity" of male C. bairdi, and did not actually report that any individuals molted again after a molt to morphometric maturity. They reported that among males, 90 mm C.W. appears to be the precise size at which the molt to "maturity" occurs and that such individuals would reach "maturity" at 112 mm C.W. The implication is that every male larger than 112 mm C.W. is "mature".

As shown earlier, the wide range of sizes among postpuberal morphometrically mature Chionoecetes in terminal anecdysis is not unusual among majids. This indicates that the terminal molt can be reached by individuals having gone through a range in number of molt instars rather than a precise number (Comeau and Conan, 1989). It is likely that individuals may reach terminal molt over a range of ages. The apparent gap in size between the largest morphometrically mature (postpuberal) males and the largest morphometrically immature (prepuberal or juveniles) males is likely to be due either to a sampling artefact or yearly fluctuations of size at terminal molt. Watson's (1970) data show a gap from 80 to 150 mm CW but Powle's data (1968) only 120 to 150 mm C.W. for the same area, while Coulombe et al. (1985) data (still for the same area) suggest a gap of only 100 to 125 mm. A size increment at molt of 30 mm is well within the range of possibility for a 120 mm male. Miller and Watson's (1976) data suggest average growth increments of 20% or more. Recent observations reported by Comeau and Conan (1989) show that in a stable population very few juveniles make the transition to morphometric maturity; older morphometrically mature individuals must disappear to leave room for the juveniles.

The sole reference dealing with regeneration of limbs that could give a clue about a terminal molt at onset morphometric maturity of C. opilio is Miller and Watson (1976). Unfortunately, the authors, once again, did not identify morphometric maturity status. Nevertheless, they stated that none of the crabs over 70 mm C.W. with encrusted shells regenerated limbs. Their report of individuals with scars molting and reforming scars cannot be used because they did not report at what molt stage the animals lost their limbs. It is frequently stated that limbs casted in a late premolt (D) stage do not regenerate before or immediately after the first molt (Skinner and Graham 1972; Kuris and Mager 1975). What Watson and Miller interpreted as molts of "mature" males are likely to have been, just as for the females, puberty terminal molts to morphometric maturity.

In the past, incidental observations should have led biologists to suspect the existence of a terminal molt for morphometrically mature male snow crab. From survey data on snow crab shell condition from a Newfoundland bay, Miller and O'Keefe (1981) suggested that a relatively large number of males larger than 95 mm C.W. had attained a terminal molt, but they did not relate their observations to morphometrics. In a mark- recapture experiment, using tags that were not retained through ecdysis, proportionally more tagged males with old, as compare to new, hard shells were recovered after a molting period (Bailey, 1978). Thus, Bailey's initial assumption, that crabs with old, shells had been in intermolt for a relatively long time and, thus were more likely to molt than newer-shelled crabs had to be reversed. Similarly, Miller and Watson (1976) observed that only individuals with relatively new shell molted in the laboratory, while individuals with old encrusted shell did not. Kon (1980) also mentioned that the molt cycle of "large" newly molted males is likely longer than 12 months.

Mating:

Although, the fundamental sequence of events in mating for C. bairdi was first reported by Takeshita and Matsuura (1980), and for C. opilio by Watson (1970, 1972), the authors described only mating involving primiparous females, i.e. females having recently achieved their terminal molt to maturity. Watson suggested, on the basis of aquaria observations, that mating (with primiparous females) occurs in early February while the new shell is still soft; i.e. shortly after the female's molt to maturity. Since Watson's (1972) observation that multiparous females seemed incapable of mating, it had been assumed , until 1986, that females mate only once and store spermatophores in their spermathecae to ensure successful fertilization of their ova over several spawnings.

In the Japanese literature, there is little or no mention of mating by multiparous females of C. opilio. Kon (1980) stated that the mating and spawning of C. opilio primiparous females in the Japan Sea occurs during the summer, while the spawning of multiparous females occurs during the spring. The mating period of primiparous females in the Japan Sea was also reported by Ito (1967) as taking place between September and October. No information is available on mating of multiparous females of Chionoecetes spp. in the Japan Sea. Kon (1980) suggested that males averaging 80 mm C.W. mate once with postmolt (primiparous) females in a zone around 250 m depth then move down 275 m - 400 m. Subsequently, they rarely participate in reproduction. The minimum size at maturity of male C. opilio in the Japan Sea is reported by Yoshida (1941) as 66 mm C.W. and by Nishimura (1967) as 80 mm C.W. (In comparison, Watson (1970) reported that the minimum size of maturity for male C. opilio in the Atlantic was 51 mm C.W.). Kon and Nanba (1968) reported that a male at 67.1 mm C.W. had successfully mated with two postmolt (primiparous) females and molted after mating. This is the first published observation on mating of C. opilio involving primiparous females, but detailed observations on mating behavior were not provided. Kon and Honma (1970) observed that almost all males of the 9th molting

group (mean carapace size of 49.2 mm) had spermatophores in their vasa deferentia and speculated that mating capacity of males increases significantly at the subsequent (10th) molting group (mean carapace size of 65.2 mm). Takeshita and Matsuura (1980), and Matsuura (1988) described mating in aquaria between primiparous females and males for C. opilio from the Bering Sea. They reported that mating occurs in spring (February-April) as well as in summer (June-August). However, no information was provided on the existence of two molting seasons for primiparous females or on the morphometric maturity of male partners. Matsuura (1988) also observed that a male of 83.1 mm C.W. mated successfully with six different soft-shell females.

Complete mating behavior involving both primiparous and multiparous females was not described until Adams (1982, 1985) for C. bairdi, and Moriyasu and Conan (1988) for C. opilio. The reproductive behavior of C. bairdi has been reported by numerous authors (Donaldson and Adams, 1989 for review). Adams (1982) reported that small male C. bairdi mated successfully with newly-hardened, primiparous females. Donaldson and Adams (1989) reported that postmolt primiparous females are flaccid, incapable of evasion, can mate with males 25 to 30 mm smaller in C. W. However, old-shelled, multiparous females resisted mating attempts by small males (Adams, 1982). No male under 120 mm C.W. was able to mate successfully with a multiparous female. Adams (1982) mentioned that the female's intergonopore distance vs. the spread of the male's first pleopods may be important in determining mating success for C. bairdi.

Paul et al. (1983) observed that male C. bairdi, 65 to 100 mm C.W. successfully mated with primiparous females, but eleven males 56 to 58 mm C.W. mated without success. For mating involving multiparous females, they found that the minimum male size for successful mating is considerably increased i.e. 110 mm C.W. They also observed that smaller males (under 118 mm C.W.) with new shells did not mate successfully with multiparous females, while a 130 mm C.W. male mated with eight multiparous females. Paul and Adams (1984) reported that the fertile period for primiparous C. bairdi ranged from less than 1 day to 28 days, while multiparous females showed a narrower mating period (4 days after cleaning their pleopods). They suggested that although multiparous female C. bairdi could fertilize eggs with stored sperm from their spermathecae (Paul, 1984), they generally avoid doing so if mature males are present. Somerton (1982), for C. opilio elongatus and C. tanneri, suggested that mating occurs amongst members of two distinct life-history groups, one comprised of primiparous females and recently morphometrically matured males and the other composed of multiparous females and older morphometrically mature males.

RECENT FINDINGS IN CANADA

Terminal Molt:

Conan and Comeau (1986) demonstrated that male and female snow crab reach a terminal molt at onset of morphometric maturity equivalent to the puberty molt of earlier authors. The differentiation of the claw is identified in males by bivariate discriminant analysis of claw size vs. C.W. The differentiation of the claw at onset of morphometric maturity justified behaviourally by the fact that morphometrically mature males "grab" females and hold them in a characteristic way for extensive periods of time. The grasp is so strong that "grasping marks" are formed on the female's pereiopods, and remain permanently visible.

Since Conan and Comeau (1986), we have obtained further information on C. opilio molting in the Gulf of St. Lawrence. Molting of large morphometrically immature males is limited to one well marked period in the spring. During trawl surveys conducted from July to November for three consecutive years (1987,1988 and 1989), we have observed no premolt stages among 38845 mature males and no advanced premolt or early postmolt stages among 22256 immature males examined

(M.Moriyasu, pers. obs.). In the samples taken from October to November, among 2885 morphometrically mature and 3550 immature males, no morphometrically mature males were found in premolt stage, while 3542 immature males were in premolt stages between D_0 and D_1.

Based on aquaria observations of snow crab conducted in three consecutive years, Moriyasu et al. (1987) identified two distinct molting seasons for two different groups of crab: 1) primiparous females ongoing terminal molt in early February; and 2) Non-terminal males and females, and the terminal molt of males, in February to late April. Within the latter period, non-terminal ecdysis of males larger than 45 mm C.W. occurs slightly earlier than for males undergoing the terminal molt.

Moriyasu et al. (1987) and Moriyasu (personal observations) report that one thousand two hundred and fifty six morphometrically immature males survived more than 6 months (from October/November) in aquaria at temperatures simulating their natural habitat. All of these advanced in molt stage during the winter and molted successfully , or died in the process of molting, between the following late March and late April. Ecdysis was never observed outside of this period. Among 768 morphometrically mature males kept in aquaria, none molted or were ever found in the premolt stage. Conan and Comeau (1989) observed a well synchronized spring molt of morphometrically immature males in nature in Bonne Bay Fjord identified in the form of a large amount of recent exuviae collected by diving in early April of 1988.

Cormier (1986) compared the quantity of the molt hormone (ecdysone) in the hemolymph of morphometrically mature and immature males by radioimmunoassay. Among individuals in intermolt C_4, morphometrically mature males have little ecdysone in comparison with immature individuals of similar size. Low levels of ecdysone may be expected if males stop molting after the molt to morphometric maturity. Bailey et al. (1986) compared the structure of the "Y" organ between mature and immature females and concluded that the "Y" organ tends to degenerate in mature females. Similar results were obtained by Bataller et al. (1989) for male crab.

Mating:

Reaching terminal molt has an influence on the mating ability of snow crab. Our observations show that morphometrically mature males carry spermatophores in their vasa deferentia all year round, but the abundance of spermatophores may vary between individuals. In harvested stocks, maturity indices (Watson, 1970) or gonadal weight tend to be negatively correlated with body size. Conan and Comeau (1986) observed that the presence of spermatophores may not necessarily imply that a male is functionally able to mate. The term "gonadal maturity" should be separated from morphometric maturity (differentiation of secondary sexual characters) and from functional maturity (ability to mate successfully). (see also Conan et al., 1988; Elner and Beninger, 1989).

Moriyasu et. al. (1987) and Moriyasu and Conan (1988) observed two types of mating patterns for C. opilio: 1) terminal-molt males with a hard shell, and multiparous females; and 2) males (terminal and non-terminal molt individuals) and soft shell primiparous females. The first type of mating occurs from April to May, and has been observed in nature by Conan and Comeau (1986) in western Newfoundland (Bonne Bay). Conan and Comeau (1986) reported that, in nature, mating between hard shell morphometrically mature males and hard shell females can occur shortly after the females release their previous brood. This agrees with independent observations made by Taylor et al. (1985) and Hooper (1986) although their interpretation of the facts differs. Conan and Comeau (1986) suggested that multiparous females usually mate every year and the storage of spermatophores is a safeguard mechanism against unsuccessful mating. Conan and Comeau (1986) observed in the field in Bonne Bay

that only morphometrically mature males larger than 95 mm C.W. mated efficiently with multiparous females.

The second type of mating involving primiparous females has never been observed in the wild in eastern Canada, and may be difficult to observe due to the presence of a thick cover of breaking sea ice early in the season. Moriyasu et al.(1987) suggested, on the basis of aquaria experiments, that mating with primiparous females occurs in early February while the females are still soft after the molt. Egg extrusion occurs shortly after molting and mating. In aquaria, both morphometrically mature and non terminal molt males mate with soft shell females (Moriyasu and Conan, 1988). The smallest non terminal molt and morphometrically mature males which successfully mated with post-molt females were 47 and 60 mm C.W. respectively. According to Comeau (1987), 50% of males reach gonadal maturity of males is at about 34 mm C.W. at which size the allometric relationship between C.W. and claw height changes slightly but significantly. This is equivalent to the prepuberal molt described by early authors for other majids.

In the first type of mating, the pre-copulatory embrace lasts several days and the copulatory behavior of males is highly competitive. In the second type of mating, the embrace is very short and non competitive among males, it involves a soft shelled female and a hard shelled male. The prerequisite that the male must have a larger C.W. than the female for successful mating appeared to be less of a deterrent in the second type of mating. The importance of matings of the second type in the reproductive potential of the stocks remains unknown since it has never been observed in the wild.

Ennis et al. (1988-b.) reported that the mean C.W. of males in sexual pairs during the annual spring breeding in Bonne Bay, Newfoundland, decreased significantly in 1987 compared to previous years due to an increase in males smaller than 95 mm C.W. (smallest size at 62 mm C.W.) participating in mating. Comeau et al. (1989) identified this occurrence of small males and females as pertaining to a cohort reaching the terminal molt for the first year and noticed that small males mated almost exclusively with females from the same cohort. Based on aquaria observations and on spermathecae of females paired with males, Ennis et al. (1988-a) concluded (but see Elner and Beninger 1989) that in the Canadian snow crab fishery, reproductive potential is being maintained at a high level. Ennis et al. (1988-b) also reported that not only can morphometrically mature sublegal size males successfully mate with multiparous females but that in the absence of competing larger males, morphometrically immature males can mate with multiparous females, some of which are larger than the males.

Moriyasu and Conan (1988) reported that although they observed that a male of 70 mm C.W. successfully mated with a smaller multiparous female, mating success increases in relation to male C.W., with 50% success at 80-84 mm C.W. without competition, and 90-94 mm C.W. under competitive conditions. Although there was no correlation between the size of the male and the size of the female in successful matings (G. Y. Conan, unpublished data), males almost exclusively mate with multiparous females which are smaller than themselves. Conan, Moriyasu and Comeau have observed in nature that, due to the timing of the molt and of the reproduction, males that have not achieved the terminal molt one year earlier during the previous molting season are still soft during the mating season of multiparous females (shortly after hatching of their previous brood) and cannot normally mate with these multiparous females.

DISCUSSION

Essentially, all of the material we have utilized in this review was readily available from biological sampling or published papers. Until a workshop in Montreal in 1987 (Jamieson and McKone, eds. 1988), the arguments concerning growth and

maturity appear never to have been rigorously debated; remarkably fisheries biologists uncritically reiterated the summaries of earlier authors and wove their own findings into the framework of unsupported assumptions. We trust that the present review may lead to a reappraisal of existing paradigms and, ultimately, a better understanding of Chionoecetes growth and reproductive biology.

In accepting the male terminal molt concept for Chionoecetes spp., the conclusions of many previous studies become suspect. For example, studies analyzing male size-frequency profiles to determine growth (Ito, 1970; Somerton, 1981) and mortality (Bailey, 1978) have the underlying assumption that morphometrically mature males continue molting. Similarity, extrapolation of mark-recapture and growth data to the population level would produce biased production estimates if males are assumed to continue growth after morphometric maturity (Sinoda, 1982). Some studies have been based on the implicit assumption that all males above a given size are "mature" and will continue to grow. For example, Miller and Watson (1976) assumed that all males above 57 mm C.W. were mature and estimated the growth rate of "mature" crab on this basis. Davidson et al.(1985) used a similar assumption in comparing snow crab morphometrics from four areas in eastern Canada. Distinct morphological differentiation between crab was argued to indicate "phenotypic" stocks; however, artifacts may have been created in the database if samples contained differing ratios of morphometrically mature/immature individuals.

Post 1986 literature suggests that Chionoecetes spp. grow and mature as all other majids. Females reach maturity (ability to mate and spawn fecundated eggs) at onset of a terminal molt accompanied by morphometric differentiation of the abdomen for carrying eggs, and to a lesser extent, of the claw. Males reach a first morphometric differentiation of the claw (the prepuberal molt of earlier authors) roughly at the time at which their gonads mature and may start producing spermatophores. They reach a second morphometric differentiation of the claw at onset of the terminal molt. They become able to efficiently mate in nature with hard shelled multiparous females (females having spawned at least once) only after the terminal molt. Although mating or at least pairing of a non terminal molt male with a multiparous female may have been observed in aquarium, in nature the timing of molting of non terminal molt males shortly before the mating season of multiparous females seems to prohibit this behaviour. The mating of non terminal molt males with primiparous females has been observed in aquarium but never in the wild, its contribution to natural reproduction remains unknown.

In evolutionary terms, it is challenging to consider whether the terminal molt is an archaic trait or a new discovery? We favor the latter interpretation, terminal molt appears to have been "discovered" independently by several families of crab (R.G. Hartnoll, pers. comm. Department of Marine Biology, University of Liverpool, Port Erin, Isle of Man, United Kingdom). Intuitively, a terminal molt to maturity is advantageous for both sexes in that molt-related mortality factors such as fish predation (Robichaud, 1985) are avoided and most of the metabolism can be diverted into reproduction. However, on the negative side, a crab in terminal molt cannot regenerate lost limbs becomes prone to shell disease.

The selective pressure for maximizing number of offspring may provide a competitive advantage to large males in securing multiparous females but is counterbalanced by the unproductive time and risk involved in growing to a large size. Conversely, the disadvantages of small males during the vigorous competition for multiparous females is offset by their relatively longer time-at-large and, thus, increased, albeit low-probability, opportunities for mating. Also, in primiparous matings, the smaller mature males may be less disadvantaged, as compared to the multiparous situation. The duality of mating patterns observed in aquaria is analogous to the existence of dominant large chelae males vs "sneaker" males in Macrobrachyon shrimps (Ra'anan and Sagi, 1985).

Our reviews re-interpreting the life history of Chionoecetes opilio has direct implications for resource management. In the Gulf of St Lawrence, processors rely on hard shell morphometrically mature males that have molted one year of more prior to the fishing season. At an early state of exploitation, most individuals captured in the southern Gulf of St. Lawrence were morphometrically mature (terminal molt) ones which had been accumulated over many years. As the fishery developed, old mature males were fished out and the proportion of newly molted individuals increased in the commercial catch. The current harvest, being based almost entirely on annual recruitment (newly molted morphometrically mature individuals), became extremely sensitive to annual fluctuations of recruitment. This situation has also created processing-related quality problems due to the growing amount of recently molted males in the catch. The life history of C. opilio in terms of timing of molt and reproduction (newly molted males have no chance to mate before completely hardening the carapace) needs to be considered in designing strategies for the fishery to avoid harvesting recent molters. Also, both yield per recruit and quality consideration would be optimized if the fishery harvested only morphometrically mature males that had molted at least 12 months previously (Conan et al., 1988; Mohn and Elner, 1988). This could be achieved either by using traps that select against morphometrically immature males on the basis of behavior (Moriyasu et al., 1989), or introducing a gauge to select for morphometrically mature males on the basis of claw size. In order to rebuild the stock and to stabilize commercial landings, both the protection of annual recruitment (morphometrically immature crab and recent postmolt crab) and catch limitation on hard shell terminal molt crab are necessary. A major unresolved research issue is what determines whether a juvenile (non terminal molt) C. opilio will opt to molt to terminal molt status or continue to molt; again, the answer could have major implications for management, since many crabs reach a terminal molt at a size smaller than the legal limit.

We believe some of the documented problems with interpreting the life history of C. opilio resulted from of the ambiguous definition of technical terms concerning maturity and, further, that there is continuing confusion in this aspect (Elner and Beninger, 1989). As suggested by Conan et al. (1988), we prefer to avoid the term "prepuberal" molt since it erroneously refers to both gonadal and morphometric maturity (Hartnoll, pers. comm. Department of Marine Biology, University of Liverpool, Port Erin, Isle of Man, United Kingdom). Rather, we propose for male the use of "juvenile" molt to define the angular point in the allometric relationship between chela size and carapace size, which corresponds to 50% gonadal maturity (Comeau, 1987). Similarly, we refer to the "molt of morphometric maturity" to identify the change in elevation in the same allometric relationship. We have shown for both male and female C. opilio that the molt of morphometric maturity is the "terminal molt". We refer to individuals as "immature" before the "juvenile molt" ("prepuberal" molt of early authors), "juvenile" between the juvenile molt and the molt of morphometric maturity ("puberal" molt of early authors), and "morphometrically mature" after the morphometric maturity molt. Comeau (1987) and Conan et al. (1988) have shown that, in contrast to immature males, both morphometrically mature and a major part of juvenile males have fully formed spermatophores in their vasa deferentia. For female, gonad maturity is achieved slightly prior to the terminal molt (Kon, 1980). Female functional maturity, is reached at the same time as morphometric maturity (differentiation of the abdomen to hold the brood) at onset of the terminal molt. We refer to females as "immature" before the terminal molt, "mature" after the terminal molt.

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Longevity of Red King Crab, *Paralithodes camtschatica*, Revealed by Long-Term Rearing Study

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ABSTRACT

Long-term laboratory rearing study was made for 2 male and 3 female red king crabs captured in the west Kamchatka waters, from 1972 to 1985.
Rearing data showed that molting of males 85 mm to 136 mm in length occurred annually. One male had been reared successfully during 13 years, and grown from 118 mm to 173 mm in carapace length. The successive rearing data for this male showed that biennial molt occurred two times since 136 mm in length and the crab reached 160 mm in length. The final molt occurred 4 years after the second biennial molt and the crab reached 173 mm in length. The crab died 4 years and 6 months after the final molt. This crab was alive approximately for 21 years, since age of the crab at the start of rearing was estimated to be 8 years old. It is notable that the crab successfully mated over the rearing years.
The rearing data are compatible with the past findings for the longevity of male red king crab. As to females, the rearing records showed that the crabs died within 4 years after attaining sexual maturity, and the average life span of males might be rather longer than that of females.

INTRODUCTION

To obtain biological information on molting and growth of king crab, long-term laboratory rearing study have been made with 2 males and 3 females from Kamchatka field, during the period from 1972 to 1985. In the earlier papers, we have described the growth observations from the 1972-79 rearing studies (Matsuura and Takeshita, 1976 and 1979). The purpose of this study is to present further growth

information from the study in the 1980-85 period, and also to discuss growth trend and longevity of crabs based on the comprehensive rearing data since 1972.

MATERIALS AND METHODS

Crabs for laboratory study were captured with tangle nets in the waters off the west coast of Kamchatka at about 57°15'N-155°50'E on July 17, 1972 and transferred by sea to Hakodate, and then by air to the Fishery Research Laboratory of Kyushu University, Fukuoka.
Long-term rearing was made for one immature female and one immature male, two mature females and one mature male.
During this study each of the crabs was held in a laboratory aquarium (45-75 cm in width, 90 cm in length and 40 cm in height) which received fresh sea water continuously at a rate of 100-150 liters per hour. Water temperature for aquarium was generally maintained between 3 °C and 5 °C, being comparable to the summer environmental temperature range of below 0 °C to 9 °C in the Kamchatka fields at depths of 50 m to 120 m.
The crabs were fed mollusks, crustaceans and fishes. The major food items were scallops, short-necked clam, decapod crustaceans, salmons and sardines. Food intake per day, based on the 1975 rearing data, was about 13 g in wet weight for a mature male and about 8 g for a mature female (Table 1). General maintenance procedures were as described in our previous reports.

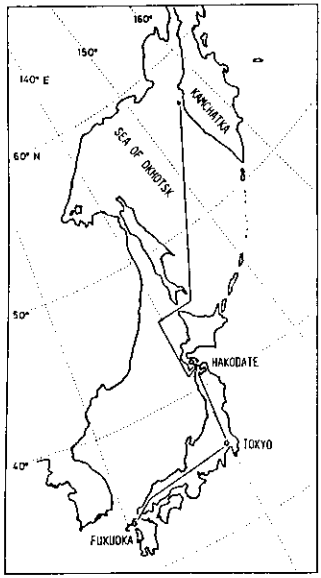

Figure 1. Map showing the route tranferring red king crabs.

Table 1. Summary of food intake per day for a mature red king crab, based on the 1975 rearing data. Daily data are combined semimonthly (Matsuura and Takeshita, 1976)

	Food intake per day (Wet weight, g)			
	Male*1		Female*2	
Month	Former half	Latter half	Former half	Latter half
Jan.	0*3	12.0	6.8	5.7
Feb.	13.3	18.8	4.1	0*3
Mar.	20.0	23.5	7.2	11.0
Apr.	16.5	12.0	13.5	13.8
May	17.9	16.4	17.1	10.2
Jun.	15.9	16.4	7.3	11.6
Jul.	16.3	13.0	7.4	6.9
Aug.	15.1	15.0	7.0	7.2
Sep.	12.7	12.2	9.2	7.4
Oct.	12.8	11.3	6.8	8.2
Nov.	8.9	8.4	9.8	8.4
Dec.	6.4	5.7	5.3	2.0
Average (Jan.-Dec.)	12.9		7.8	

*1 Carapace length, 124.3 mm.
*2 Carapace length, 101.1 mm.
*3 Molting period.

RESULTS AND DISCUSSION

Molting Period

Successive molting records for the reared crabs were shown in Table 2. The virgin female (76.4 mm in carapace length at the start of rearing) molted at the beginning of December just prior to the first mating. The second molt for mating occurred in February, 14 months after the first mating. The third molt as well as the fourth occurred in February. Consequently, from the second molt on , the time interval between molting was nearly 12 months. The adult females with fostering eggs (88.9 mm and 96.5 mm in carapace length at the start of rearing) molted annually, during the months from March to April, just prior to mating.
The small male (85.4 mm in carapace length at the start of rearing) first molted in November after 4 months of rearing. The second, the third and the fourth molts occurred annually, in February, January and again January of successive years.

Table 2. Successive molting records for the reared red king crab*1

No.	Date	Carapace length (mm)*2		Growth increment (mm)	growth rate (%)
		Pre-molt	Post-molt		
Female					
(1)	12/ 4/72	76.4	88.1	11.7	15.3
	2/21/74	88.1	97.1	9.0	10.2
	2/24/75	97.1	101.1	4.0	4.1
	2/ 9/76	101.1	104.6	3.5	3.5
(2)	3/27/73	88.9	96.9	8.0	9.0
	3/ 2/74	96.9	103.9	7.0	7.2
(3)	4/11/73	96.5	103.3	6.8	7.0
	3/27/74	103.3	108.6	5.3	5.1
Male					
(1)	2/ 1/73	117.7	133.2	15.5	13.1
	12/23/74	133.2	145.8	12.6	9.4
	1/23/77	145.8	160.2	14.4	9.8
	1/ 8/81	160.2	173.1	12.9	8.1
(2)	11/29/72	85.4	99.0	13.6	15.9
	2/11/74	99.0	110.7	11.7	11.8
	1/24/75	110.7	124.3	13.6	12.3
	1/14/76	124.3	136.3	12.0	9.7

*1 The rearing was commenced on July 23, 1972.
*2 Carapace length is defined as the distance from the posterior median edge of the carapace to the extreme concavity of the right eye orbit.

The large male (117.7 mm in carapace length at the start of rearing) molted for the first time in February, after 6 months of rearing and the second molt occurred 22 months after the first molt. This male molted for the third time, 25 months after the second molt. The fourth molt occurred 48 months after the third molt. Thus, the second and the third molt of this male were biennial and the fourth molt was quadrennial.
The present rearing records on the molting period correspond well to past findings that adult females molt annually in the spring months just before mating and that adult males molt in the winter months, with increase of time-interval between molts according to age of crab. Regarding molting of the adult virgin female, it is notable that molting for the first mating occurred at an earlier time than the following annual molts, and that the development of the fertilized eggs was successful during the 14 months incubation. The ability of male to mate even in the winter is also notable.

GROWTH PER MOLT

This study provides annual , biennial and quadrennial molting measurements through successive molting season and thus some indications of growth of west Kamchatka king crab, at least under laboratory conditions.
For the virgin female of length at 76 mm, length increment per molt was 12 mm, while in the mature females, it ranged from 5 mm to 9 mm.
For one male, an annual molter, length increment per molt ranged from 12 mm to 14 mm while growing from 85 mm to 136 mm. Another male, as a biennial molter, attained 13 to 14 mm increase per molt while growing from 133 mm to 160 mm in length, and as a quadrennial molter, attained 13 mm increase per molt at 160 mm in length. These growth data for Kamchatka males suggest that length increment per molt remains similar between annual and biennial or even quadrennial molter, and also the data are compatible with the past findings.

GROWTH TRENDS AND LONGEVITY

These growth measurements thus obtained for each sex were combined progressively to enable tracing an annual growth trend. The trend of growth is presented graphically in Figure 2 for males from 85 mm to 173 mm in length extending over 12 years, and for females from 76 mm to 109 mm in length extending over 5 years.
Matsuura et al. (1972) reported that Kamchatka females become ovigerous at lengths ranging from 77 mm to 94 mm, and 50 % maturity is shown at a length of 82 mm. Matsuura and Takeshita (1976) also reported that females in the size group at lengths between 77 mm and 82 mm with an average of 79.5 mm are presumed to be 5-year-olds and those in the size group between 83 mm and 94 mm to be 6-year-olds, based on accumulation of the past findings (Weber, 1967; Powell, 1967; Kurata, 1961). There is agreement in published

reports that the growth of juveniles of both sexes is similar before attaining sexual maturity. The size of 5-year-old males, therefore, is considered to be very close to that of 5-year-old females.

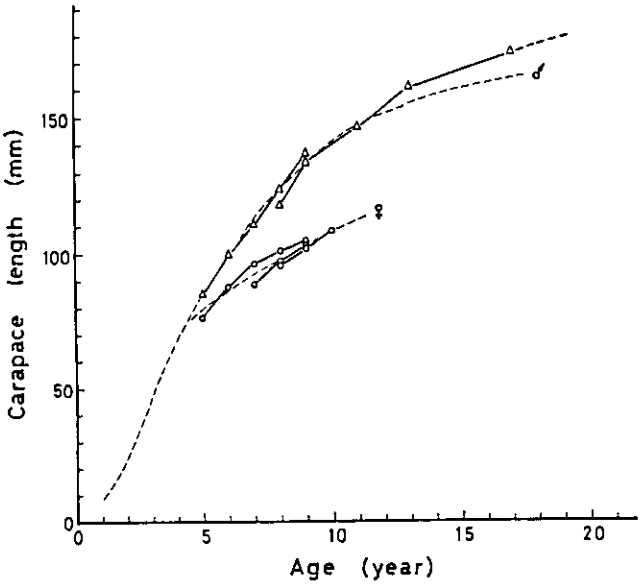

Figure 2. Growth of the laboratory reared Kamchatka red king crabs. Curve for male is calculated using the growth model by Weber and Miyahara (1962). Curve for immature is derived from Kurata (1961). Curve for female is derived from Matsuura et al. (1972). Carapace length and corresponding ages are shown in Table 4.

Table 3. Average length by age of young red king crabs from published results

Age (year)	Weber (1967) Southeastern Bering Sea	Powell (1967) Pacific Ocean on Alaska	Kurata (1961) Hokkaido Waters
1	11	12	8.2
2	35	35	24.0
3	60	61	50.3
4	78	84	71.6
5	90	100	85.2
6	98		101.0

Table 4. Carapace length in mm corresponding to age for adult red king crab in the Kamchatka waters

Age (year)	5	6	7	8	9	10	11	12	13	14	15
Male*1	85.0	98.6	111.6	123.6	133.4	140.8	146.4	150.8	154.3	157.1	159.5
Female*2	79.5	86.6	92.5	97.8	102.8	107.4	111.8	119.3			

*1 Calculated by the growth model of Weber and Miyahara (1962).
*2 Derived from Matsuura et al.(1972).

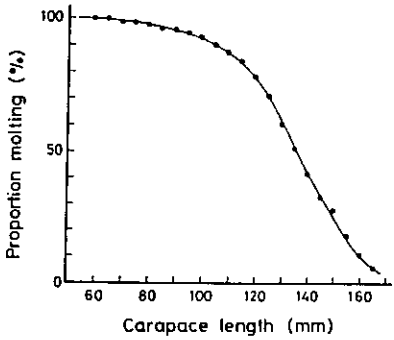

Figure 3. Proportion molting in the Kamchatka male red king crabs by length groups. Trawl and tangle net survey data in the Kamchatka waters, 1963-1966.

The above estimations for Kamchatka females are compatible with Kurata's estimates at five years of age, and size of Kamchatka males at five years of age is presumed to be 85 mm in length. Thus, the male 85.4 mm in length and the female 76.4 mm in length at the start of rearing are considered to be 5 years old at that time. Considering their growth trend, the male 117.7 mm in length and the female 96.5 mm in length at the start of rearing are also considered to be 8 years old at that time.

In Figure 2, growth curve was also shown for each sex. The curve for immature is derived from Kurata's estimate (Kurata, 1961) and the curve for mature males was calculated by the Weber and Miyahara's growth model, based on the field data on proportion molting by crab sizes and the laboratory observations on length increment per molt, 14 mm (Figure 3, Tables 3, 4 and 5). The curve for mature females was derived from Matsuura et al. (1972). The trend of growth in the reared crabs was compatible with the growth curve for males thus calculated as well as with that for females presented by Matsuura et al. (1972).

Successive rearing data for the male 117.7 mm at the start of rearing showed that biennial molt occurred two times since the crab attained 133 mm in length. The final molt occurred 4 years after the second biennial molt, with increase of length from 160 mm to 173 mm. The crab died 4 years and 6 months after the final molt, being alive approximately for 21 years, because age of this crab at the start of rearing was considered to be 8 years old.

The rearing data for this crab are compatible with the past indications for the longevity of male red king crab by Marukawa (1933) and Hoopes and Karinen (1972). It was notable that this crab had successfully mated over the rearing years. As to the females, the rearing data showed that the crabs died within 4 years after attaining sexual

maturity. Average life-span of males might be rather longer than that of females.

Table 5. Growth of adult male red king crabs in the Kamchatka waters*1

Age (year)	No. of crabs	Carapace length*2 (mm)	Proportion molting*3	No. of crabs in the following year by length groups (mm)								Average carapace length (mm)
				85	99	113	127	141	155	169	183	
n	10,000	85	0.97	300	9,700							
Total				300	9,700							98.6
$n+1$	300	85	0.97	9	291							
	9,700	99	0.93		679	9,021						
Total				9	970	9,021						111.6
$n+2$	9	85	0.97		9							
	970	99	0.93		68	902						
	9,021	113	0.85			1,353	7,668					
Total					77	2,255	7,668					123.6
$n+3$	77	99	0.93		5	72						
	2,255	113	0.85			338	1,917					
	7,668	127	0.65				2,684	4,984				
Total					5	410	4,601	4,984				133.4
.	.	.	.				.	.				.
.	.	.	.				.	.				.
.	.	.	.				.	.				.
$n+7$	1	113	0.85				1					
	269	127	0.65				94	175				
	3,503	141	0.39					2,137	1,366			
	5,206	155	0.17						4,321	885		
	1,003	169	0.05							953	50	
	18	183	0.02								18	
Total							95	2,312	5,687	1,838	68	154.3

*1 Calculated by the growth model of Weber and Miyahara (1962).
*2 Length increment per molt is 14 mm (Matsuura and Takeshita, 1979).
*3 Field survey data in the Kamchatka waters, 1963-66 (Kawasaki et al., unpublished, see Figure 3).

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Seasonal Migration of Primiparous and Multiparous Female Red King Crabs (*Paralithodes camtschatica*)

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EXPANDED ABSTRACT

The timing of major reproductive events differs between female red king crabs (*Paralithodes camtschatica*) reproducing for the first time (primiparous) and those that have brooded eggs previously (multiparous). Primiparous females have been observed to be courted by males a month earlier (Powell et al. 1973), their larvae in laboratory tests have hatched earlier, and they have subsequently molted and extruded eggs earlier than multiparous crabs. This temporal shift of life events continues at least through the start of movement to deeper water after reproduction. We studied red king crabs in Auke Bay, Alaska, May 1988-1989, to determine whether seasonal movement patterns of primiparous and multiparous crabs differed, and if so, to relate the movement patterns to differences in reproductive timing and water temperature. We present preliminary findings here.

We attached ultrasonic tags to 20 females: ten primiparous [carapace length (CL) 93.6-108 mm], and ten multiparous (CL 124.5-167.1 mm). Crabs were released close to their capture sites. We were able to follow the movements of seven primiparous and five multiparous crabs through one complete reproductive cycle. Unless otherwise stated, one-way analysis of variance (ANOVA) was used to test for differences between means of variables. The Kruskal-Wallis test was used when data failed to meet the assumptions of the ANOVA.

All crabs in our study followed a general pattern of seasonal movement that can be divided into three phases: 1) gradual movement from shallow to deeper water after reproduction, and residence there through early November; 2) abrupt, synchronous movement back to shallow water in November, and res-

idence there through late February or early March; 3) gradual synchronous movement to intermediate depths followed by movement onto the spawning grounds from late March through May.

Tagged crabs generally remained in close association with one another, especially during winter. Winter observations by divers revealed dense aggregations consisting of both primiparous and multiparous crabs. These aggregations usually remained intact when crabs changed depth strata. The abrupt, synchronous movement of crabs in November and March was coincident with thermohaline mixing of the water column in Auke Bay; these coincident events require further study to postulate a functional relationship.

Although general movement patterns were similar, differences between primiparous and multiparous crabs were observed when movements were examined in detail. The maximum distance crabs moved from point of release differed significantly ($P < 0.01$) between the two groups. Primiparous crabs ranged 4.5-8.6 km from point of release, and half of them gradually moved to areas outside Auke Bay. In contrast, all multiparous crabs remained within Auke Bay during the entire study, and none migrated further than 3.7 km from point of release. The annual range (the area within which each crab moved during the year as estimated by the minimum-convex polygon method) of primiparous crabs ($\bar{x}$ = 11.9 km^2) also exceeded ($P < 0.025$) that of multiparous crabs ($\bar{x}$ = 3.6 km^2).

The distance between site of release and site of ecdysis a year later tended to be less in multiparous crabs than in primiparous crabs ($P < 0.001$). Primiparous crabs molted 2.3-5.6 km from the release site, whereas multiparous crabs molted 0.1-1.9 km from their release site. The depths at which primiparous crabs molted (7.3-61.6 m) did not differ significantly from those at which multiparous crabs molted (11.6-24.1 m).

Primiparous crabs showed seasonal differences in activity rate (calculated as distance moved in meters divided by time in days between successive observations), whereas multiparous crabs did not. Primiparous crabs were less active in winter ($P < 0.05$, Kruskal-Wallis test) than during other time periods. Primiparous crabs were significantly ($P < 0.05$) more active than multiparous crabs, particularly during the summer/fall period ($P < 0.01$).

Primiparous crabs were found at greater depths ($\bar{x}$ = 60.5 m) than multiparous crabs ($\bar{x}$ = 42.2 m) in the summer/fall period ($P < 0.001$), and thus experienced lower mean water temperatures, 6.12°C and 6.51°C respectively. Differences in mean annual water temperatures to which primiparous and multiparous crabs were exposed, (5.41°C and 5.51°C respectively), probably were not great enough to cause differential rates of embryonic development.

Our study indicates that general seasonal movement was similar for primiparous and multiparous crabs in Auke Bay. However, the movements of multiparous crabs tended to be more conservative than those of primiparous crabs. Primiparous crabs tended to be more active, move further from the area

where they molted and mated, and cover a greater area and (in summer/fall) greater depth range than multiparous crabs.

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Oriented Movements of Tagged Male Snow Crabs (*Chionoecetes opilio* O. Fabr.) off the North Shore of the Gulf of St. Lawrence

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ABSTRACT

Tagging experiments on male snow crabs (Chionoecetes opilio) have been conducted off the north shore of the Gulf of St.Lawrence during the summers 1981 and 1982, when 3167 and 1937 individuals, respectively, have been released. Crabs were identified with "T" tags, inserted between the cephalothorax and the abdomen, and "Spaghetti" tags, tied around the carapace. Crabs were released at the surface above depths varying from 50 to 170 m. Recaptures were provided by commercial fishermen during the seasons 1981 to 1983. The recapture rate for "Spaghettis" was 34% and 30%, respectively for the two years of tagging, and 5% and 6% respectively for the "T" tags. Informations on date, depth and area of recapture have been provided. The area is a square with 10' sides. The location was then estimated from the shortest distance between the point of tagging to the known depth in the given area. This approximation seems realistic, considering the bathymetry of the region and the errors due to other causes. Trends in the orientation of movements have been verified using circular statistics.

Recapture rate appears to be highly correlated to the distribution of fishing effort, which explains 36% of the variation of this rate among areas. The maximum observed travelled distance is 34 km after three years of freedom.

Over a short term period (tagging and recapture during summer 1982), the smallest individuals (carapace width < 90mm) show slower movements than the largest ones (CW > 109 mm), 160 m/d and 370 m/d respectively. Crabs released above 90 m depth shows a strong significant southward displacement, directed towards deeper areas. Orientation of crabs released above the deepest levels (> 130 m) is not as

well defined. The average speed of displacement is also relative to the depth, 220 m/d and 130 m/d for depths < 90 m and > 130 m, respectively. These observations support the hypothesis of a recruitment "by platoons" on the deeper fishing grounds from the upper bathymetric levels. Between two successive seasons (1981-1982) differences between small and large crabs are no more observed. The general southward trend remains, with some variations following the period of recapture for individuals released deeper than 130 m. At the beginning of the fishing season (April-May), these individuals show an upward movement towards shallower waters, trend that disappears during the summer. This result is in agreement with other observations on seasonal movements of snow crabs.

The general pattern of the snow crabs movements indicates possible exchanges between fishing areas. Density regulation mechanisms are proposed to explain these exchanges.

INTRODUCTION

Present management policies for the snow crab (Chionoecetes opilio) stocks in the Eastern Canada devide the exploitation in coastal and off-shore fisheries, division which comes from the assumption that few interactions may exist between the two areas (Brêthes and Coulombe, 1987). This assumption is certainly violated during the pelagic larval stages, due to their duration that creates a certain phaenotypic and genotypic plasticity within the present management units (Davidson et al., 1985). Tagging experiments of adult males of C. opilio conducted by Watson (1970a) and Watson and Wells (1972), on the fishing grounds, led to the conclusion of small amplitude movements, generally less than 20 km, even if few displacements larger than 50 km have been observed over a 3 year period. These observations suggested few exchanges between fishing areas. Following this conclusion and on the basis of the emergence of regional industries (Elner, 1982), the regulation implemented the first coastal fishing zones in 1977. Socio-economical pressures still lead to the definition of new such areas, along with the concession of new fishing licences. In this context, a good knowledge of movements patterns becomes a important issue in order of verifying the rationale of management principles and regulations.

Long term displacements have been considered through direct or indirect studies. In the Canadian Atlantic, after the tagging experiments of Watson (1970a) and Watson and Wells (1972), Taylor et al. (1985) and Hooper (1986) have demonstrated the evidence of a breeding migration in Spring towards shallower depths, in Bonne Bay (Newfoundland). In the North Pacific, McBride (1982) observed large scale movements covering an average distance of 78 km. Indirect informations on the movements of the species may be deducted from the study of the size frequency distributions. Coulombe et al. (1985) suggested that crabs should move to deeper waters following physiological maturity associated with increasing

size and Bouchard et al. (1986) made the assumption that the recruitment to the fished stock follows a "platoon type" (Ricker, 1975), individuals moving towards the deep fishing grounds from the upper bathymetrical levels through a migratory process, depending on the size of the individuals involved. This assumption is supported by the fishing surveys of Coulombe (MS 1984) who observed concentrations of commercial sized crabs on areas submitted to low exploitation rates. These areas have been qualified as "buffer zones", able to compensate the decreasing abundance of snow crabs on fishing grounds through a mechanism of density regulation.

Following the current assumptions, crabs being located on shallow grounds should present an oriented movement, towards deeper bottoms, which should not be observed for the individuals located deeper. The largest individuals should demonstrate a clearer orientation than the smallest ones. Another question is the possibility of exchange between neighbouring fishing grounds, despite apparent geographical barriers. The present work, while presenting results of tagging experiments off the north shore of the Gulf of St.Lawrence, intends to bring some answers to those questions.

MATERIAL - METHODS

Tagging and Recaptures of Snow Crabs

Three tagging cruises have been undertaken in June 1981, June and July 1982, along the north shore of the Gulf of St. Lawrence (Fig. 1) between the rivers Sheldrake and Saint-Jean (50°15' - 50°10'N, 64°10' - 65°00 W). Crabs were captured in baited conical traps, with entrance at the top and covered with a 45mm netting. Traps with 76mm netting were also used in 1981. Fishing depths varied from 50 to 170m. Crabs have been identified with two types of tags : "T" tags, inserted in the muscles between cephalothorax and abdomen (Fujita and Takeshita, 1979), and "Spaghetti" tags tied around the carapace. Male crabs, which are only concerned with exploitation, were tagged as soon as possible after having been fished. The maximal carapace width (CW) was measured, to the nearest mm. Claw height was used as an index of physiological maturity (Watson, 1970b, Conan and Comeau, 1986) ; according to the criteria used by Coulombe et al. (1985), all the released animals were physiologically mature. The liberation of crabs was done at the surface, close to the location of capture. In 1982, crabs were kept in tanks alimented with running sea water and covered by a cloth and tagging was done solely early in the morning, in order to limit the mortality due to the manipulations. For each crab, the delay between the capture and the liberation never exceeded one hour. The tags were returned by commercial fishermen who were asked to provide the date, the depth and the location of the recapture. Location was indicated by statistical squares, as used on this area for general statistical purposes, i.e. squares of 10' on each side (Fig. 1).

Data Analysis

In order to face the relative lack of precision in the provided data, the point of recapture is estimated in plotting on a map the smallest distance between the point of releasing and the known depth in the statistical square provided. The travelled distance and the displacement orientation must be then considered as estimates ; they seem, however realistic representations of the actual movements, considering

the bathymetry of the whole area and the errors due to others causes (liberation at the surface for instance). As the released individuals have been transported by currents before reaching the bottom, any calculated displacement < 1 km is considered as no displacement. To assess the influence of the distribution of the fishing activity on the recapture rate, the fishing effort, in number of fishing trips by month and statistical square is provided.

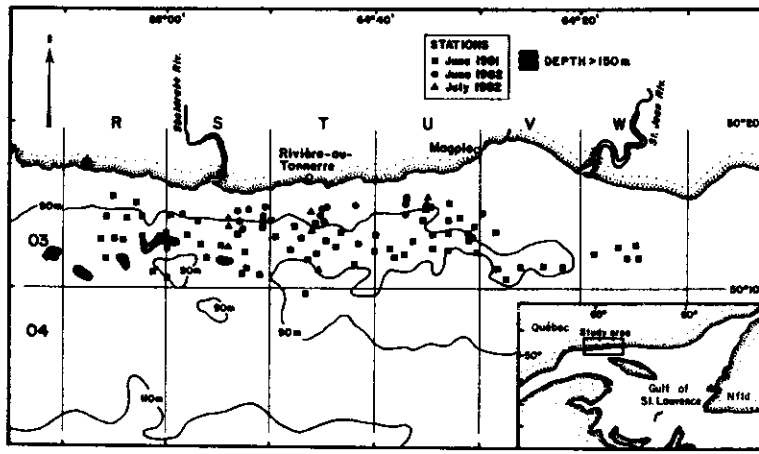

Fig. 1 - Location of study area and position of tagging stations.
Squares indicate statistical areas designated by letters (on top) and numbers (on the right side). Uncomplete representation of bathymetry.

Recaptures obtained during the fishing season of 1981, that corresponded to the first tagging operation, did not provide useful informations (no or incomplete data were given along with the tags). Only the results of the recaptures from 1982 and 1983 are considered, in term of displacements. To analyze the data, three classes of CW are considered (CW < 90 mm, 90-109 mm and CW ≥ 110 mm), which correspond to a certain size distribution pattern in recaptures, and three classes of releasing depth (D < 90 m, 90-129 m and D > 130 m), on an arbitrary basis.
Movements of crabs tagged in 1982 and recovered the same season (1982-1982) are analyzed following (1) individual size, (2) releasing depth and (3) the month of recapture ; distances are then expressed in m/d, in order to limit the bias caused by the differences in time of freedom between individuals, which appears to become important over a short period of time. Trends in displacements observed between 1981 and 1982 (1981-1982) are also analyzed considering the releasing depth, for the whole fishing seasons ; total travelled distance (km) is then considered. In order to assess the possible seasonal migrations, displacements of crabs released deeper than 130 m in 1981 and recovered in 1982 are considered, following the month of recapture : these animals are the most likely able to show an upward movement to shallower waters.

Displacements are described as vectors of orientation defined by their lengths and angles relative to the geographical north. For a group of displacements, the length, r, of the mean vector is calculated as (in Zar, 1984) :

$$r = \sqrt{[(\Sigma \sin a_i)/n]^2 + [(\Sigma \cos a_i)/n]^2} \quad (1)$$

where a_i is the observed angle, relative to the north, of a given displacement and n is the number of observations.

The mean angle, a, is defined through the relation :

$$\cos a = (\Sigma \cos a_i)/n \quad \text{and} \quad \sin a = (\Sigma \sin a_i)/n \quad (2)$$

If r = 0, it means that the mean angle, a, is undefined and that there is no mean direction. Following that, the significance of the mean angle is tested by the non-parametric Rayleigh test (in Zar, 1984), with H_0 meaning that the population angles are randomly distributed, i.e. no trends in displacements. The "Rayleigh-z" has been calculated as :

$$z = n \cdot r^2 \quad (3)$$

RESULTS

General results (Table 1) show a very low recapture rate for the "T" tags, less than 6%, while almost one third of the "Spaghetti" tags have been recovered. Distribution of fishing effort presents a strong effect on the distribution of the recaptures among the various areas. A linear correlation calculated between fishing effort (expressed in number of trips/month) and the number of recaptures for 1982 appears to be highly significant ($r = 0.61$; $DF = 36$; $p < 0.01$). It means that a third of the variation in the distribution of recaptures may be due to the variation in the distribution of the effort.

Table 1 - Summary of tagging and recapture experiments conducted along the north shore of the Gulf of St.Lawrence in 1981 and 1982.
D = depth of releasing (m) ; N = Numbers ; S = "Spaghetti-tags"; T = "T-tags.

	Tagging				Recapture			
Year	D	N	Tag	N/Tag	1981	1982	1983	%
1981			S	962	105	209	16	34
			T	2205	52	63	5	5
	<90	232						
	90-130	1147						
	>130	1788						
1982			S	1000	--	251	44	30
			T	937	--	47	6	6
	<90	1207						
	90-130	369						
	>130	361						

Displacements Within a Season

Displacements within a single season have been studied from the crabs tagged in June 1982 and recovered during the same summer. Travelled distances (Fig. 2) can reach 24 km. These distances depend on the releasing depth. Above 90 m, 42% of the individuals have travelled 3 to 5 km. Between 90 and 130 m, the mode is observed at 1-2 km (26%). A large proportion (32%) of the crabs released below 130 m did not move. These differences are also found in the orientations of the movements (Fig. 3). A clear southern orientation is observed (Fig. 4) in every areas as verified by the Rayleigh z-test ($P_z < 0.01$). That trend is however less evident for the individuals released below 130 m. When the distance is considered (Table 2), the difference coming from depths of releasing becomes clearer. The observed residual speed of the movement of crabs released above 130m is twice the speed of the crabs released deeper. The pattern remains when the actual speeds are considered. It seems then, that the deeper crabs move less and show less trend in the orientation than the shallower ones.

Orientation and speed can be influenced by the size of the individuals involved. The effect of the size is considered with the crabs made free above 90 m depth, as they appear to move the most. The main difference is observed for the travelled distances, as they increase significantly with the size of individuals (Table 2). The Rayleigh-z test calculated on the orientation indicates a significant trend ($P_z < 0.001$), roughly southward, wich correspond to a movement towards deeper bathymetric levels (Fig. 5).

Table 2 - Average distance travelled by tagged crabs within the season 1982 following depth of tagging and CW, and residual vectors of displacement. One -way variance analysis is used to compare actual gross displacements.

			residual vector	
Depth (m)	N of recaptures	Average distance (km . d^{-1})	vector length (km . d^{-1})	mean angle
< 90	131	0.23±0.05	0.19	192
90-130	57	0.30±0.14	0.17	239
> 130	108	0.13±0.04	0.08	255
ANOVA	F = 5.87 ; DF = 2 , 294 ; $P_F < 0.01$ (significant)			
CW (mm)				
< 90	41	0.16±0.07	0.13	171
90-109	72	0.24±0.06	0.19	198
> 109	18	0.37±0.13	0.34	192
ANOVA	F = 4.37 ; DF = 2 ; 128 ; $P_F < 0.025$ (significant)			

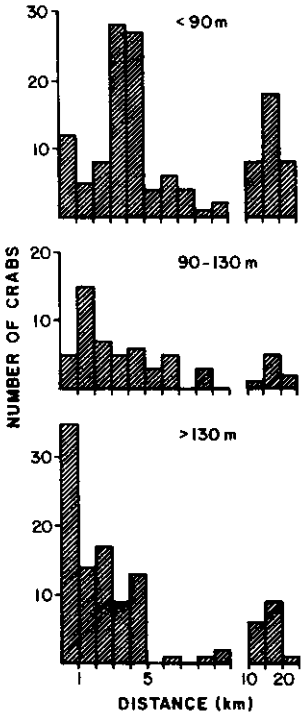

Fig 2 - Distribution of distances travelled before recapture following depth of releasing (tagging and recapture during season 1982)

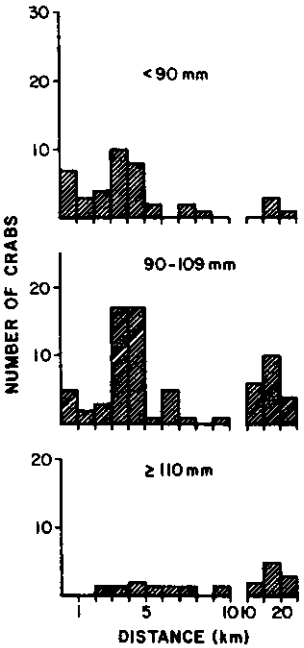

Fig . 3 - Distribution of distances travelled before recapture following size of crabs (tagging and recapture during season 1982, depth < 90 m).

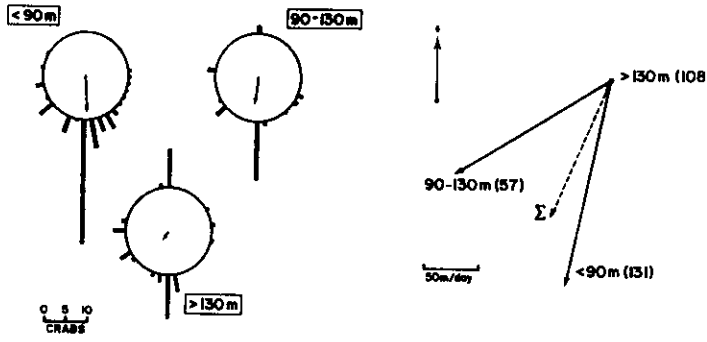

Fig. 4 - Orientations of displacements and residual vector, for crabs tagged in 1982 and recaptured the same season, following depth of releasing. On the left : only orientations are considered ; on the right, residual vectors calculated from orientation and speed.

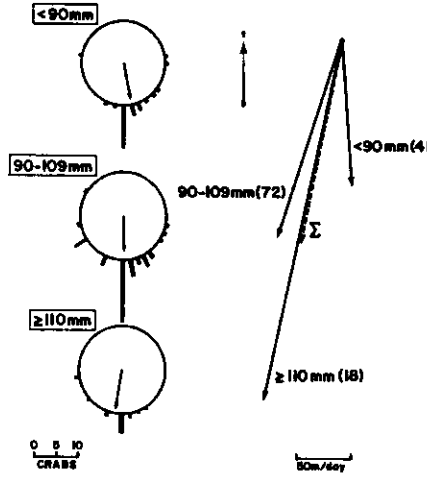

Fig 5 - Orientations and residual vectors of displacements for crabs tagged and recaptured the same season, following size of individuals (depth of releasing < 90 m). Same presentation as Fig. 4.

Displacements Between Seasons

Crabs tagged in 1981 and recaptured in 1982 are considered in this study. Maximal travelled distance is 34 km. The variations in distances following depth observed for the season 1982 are also found here (Fig. 6). No trends are observed if the size of individuals is considered (ANOVA : $F=0.33$, $DF=265, 2$, $P_F>0.5$, non significant). The general orientation of movements is towards south-west (245°).

In 1983, recaptures were low, 59 tagged individuals having been reported. The average distance was 16±2 km (maximum : 34 km). The general orientation was directed south-southwest (218°). Fifty one crabs were found deeper than 130m while 36 were coming from depth < 90 m.

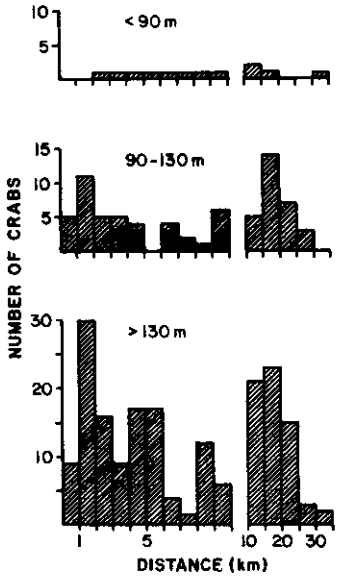

Fig. 6 - Distribution of distances travelled before recapture. Tagging in 1981 and recapture in 1982.

Displacements are studied following the period of recapture, knowing the published observations on seasonal movements. The crabs released above the deepest areas (> 130 m) only are considered here, as they are expected to show the clearest trends. In Apri-May and June, the orientation is north-west (Fig 7), the Rayleigh-z test, however, indicates that this trend is not significant. A significant southern orientation ($P_Z < 0.002$) is observed in July and August-October.

Another information is provided by the differences between the depth of releasing and the depth of recapture (Table 3). Results indicate a general upward movement toward shallower bottoms, with a difference of -30 m observed in April-May and June. This movement becomes less evident from July to August-October, which would mean a return to deeper bottoms during the summer.

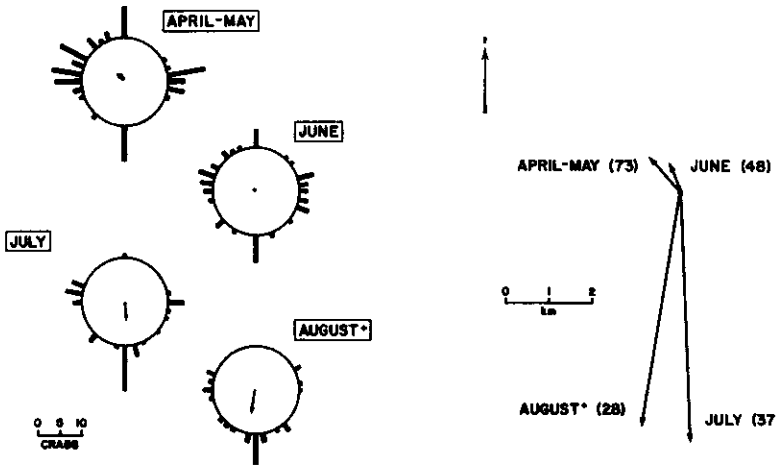

Fig. 7 - Distribution of orientations and residual vectors of crabs' movements between 1981 and 1982, considering the period of recapture (August+, correspond to the period August-October). Crabs released at depth > 130 m.

Table 3 - Differences in depth (m) between tagging and recapture for C. opilio tagged in 1981, at depth > 130 m, and recaptured in 1982, following the period of fishing.
Paired t-test compared to null hypothesis (no variation). NS = non-significant.

Period of recapture	N	Average difference	Standard deviation	t	P_t
April-May	75	- 29.2	27.92	9.1	< 0.001
June	47	- 33.8	35.50	6.5	< 0.001
July	37	- 14.0	21.00	4.1	< 0.001
August-October	29	- 9.0	26.57	1.8	> 0.05 NS

DISCUSSION

Two types of tags have been used and have shown different recapture rates. The "T-tag" did not provide good results as few recaptures have been reported. The high level of recapture rates for the "Spaghetti-tags" indicates an important fishing pressure exerced on the local stocks of snow-crabs.

The results presented on movements present several obvious biases. Positions of recapture are just estimates, and actual distances may differ from few kilometers from the calculated ones. As very common in such experiments, releasing has been done at the surface, and the crabs may have been dispersed quite extensively before reaching the bottom. Both biases induce an uncertainty on the validity of the results, wich will have to be interpreted only in term on trends.

The number of recaptures per sector is highly dependent on the activity of the fishing fleet. Therefore, the picture of the displacements as drafted out from the results can be either an actual picture of the movements or a picture of the displacement of the fishing effort. This bias tied to the fishing activity seems to be common to most of the tagging programs involving the commercial fishermen. However, according to Campbell and Stasko (1985), this bias does not affect the general conclusions of this type of study. Following these authors, the variance only is affected and less the mean trend, would become not as general as expected. The inference to the entire population become hazardous as the statistical significance of a result may be due to an artefact (Diamond and Hankin, 1985). Displacements themselves, however, are actual facts that can be interpreted.

The observed displacements are generally shorter than 20 km, which corresponds to the previous observations of Watson (1970a) and Watson and Wells (1972) in the south-western Gulf of St.Lawrence. According to the criteria defined by Harden-Jones (1984), Chionoecetes opilio is a kind of sedentary species, showing movements essentially on a local scale. These results seem to be quite common for crabs. Diamond and Hankin (1985) observed that 63% out of 643 tagged females of Cancer magister moved less than 5 km after 3 years of freedom off the Californian coast. A more littoral species as Scylla serrata (Portunidae), in Australia, show average movements of 4 km (Hyland et al., 1984). Chionoecetes bairdi, off Alaska, showed an average distance of 24 km over a six year period (Colgate, 1982). For C. opilio, however, McBride (1982) reports average displacements of 75 km off Alaska. The general morphology of the grounds, in the Gulf, provide a serial of deep holes or channels, relatively isolated, where the crabs appear to be trapped, to some extends, and may limit the extension of the movements of C. opilio.

Watson and Wells (1972) concluded the snow crabs move randomly in the south-western Gulf. Recent observations seem to modify these conclusions that may not be general for every geographical areas.

The present results indicate a seasonal movement towards shallower waters observed in spring. This type of migration was assumed by Somerton (1982) for C. opilio, and observed by Pereyra (1966) for C. bairdi along Oregon coast. For snow crab, Hooper (1986) has demonstrated the evidence seasonal breeding migrations off the west coast of Newfoundland.

Along the north shore of the Gulf of St.Lawrence, random-like displacements are only observed for the deeper areas, below 130 m depth. On upper bathymetrical levels, movements are clearly oriented southward, which actually corresponds to a movement towards deeper bottoms, considering the general morphology of the area (geographical orientation does not appear to be really meaningful). This movement seems also to be faster for large individuals than for the smallest ones. These observations may confirm the hypothesis of Coulombe et al. (1985) and of Bouchard et al. (1986), for the southwestern Gulf : deeper fishing bottoms being fed by movements from the upper ones, differences in speed between small and large crabs justifying the pattern of recruitment by "platoons" (Ricker, 1975) on the deep grounds. Greendale and Bailey (1982) have already assumed that the snow crabs fished on the grounds located the further away from the coast may come from the littoral zone. The present observations would confirm these assumptions.

According to a definition of F.A.O. (1973), displacements of snow crabs correspond to two types of movements. A migration, i.e. a round trip, would drive individuals to shallower waters in spring for reproduction. Depth of departure and arrival may be related to the age of crabs, as proposed by Somerton (1982). A general movement towards deep grounds, related to the size of individuals, may not be considered as a true migration. It may correspond to a general ontogenic movement, common to benthic species. Some of these displacements may also correspond to a density regulation mechanism driving animals towards low density places. It is possible to make the hypothesis that some exchanges between fishing areas "compensate" the effect of differential fishing mortalities among fishing grounds. The influence of heavy fishing activities on the movements of snow crabs should be further investigated.

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Feeding and Growth

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Nov. 1989, Anchorage, Alaska

Effects of Cohort Density and Habitat on Survival and Growth of Juvenile Red King Crab, *Paralithodes camtschatica*

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ABSTRACT

The effects of cohort densities and available cover on survival and growth of 1-yr-old and 2-yr-old juvenile red king crabs, *Paralithodes camtschatica*, were studied in the laboratory over a 4½-month period. Survival of 1-yr-old crabs was related to cohort density and cover, whereas survival of 2-yr-old crabs was not. Growth in both age classes was not significantly ($P \leq .05$) related to cover or cohort density. Mortality rates in 1-yr-old crabs were highest at high cohort densities (11 crabs) in habitats that afforded no cover (sand). Mortality at low cohort densities (3 crabs) showed no relation to available cover. At high cohort densities, total mortality was greater in 1-yr-old crabs than in 2-yr-old crabs, irrespective of available cover. Cannibalism was the major cause of mortality for both age groups. Mortality due to cannibalism was significantly greater in 1-yr-old crabs only at high densities with no available cover. Mortality associated with ecdysis (excepting cannibalism) was similar for both age groups. That survival of 1-yr-old crabs at naturally occurring densities is favored by complex habitats, indicates the importance of natural habitats that provide ample cover to this age class.

INTRODUCTION

One-year-old red king crabs, *Paralithodes camtschatica*, are found in habitats that provide more cover and at lower cohort densities than 2-yr-old crabs. The younger juveniles are found on intertidal cobble beaches (Bright et al., 1960; Karinen, 1985) and in subtidal epifaunal associations (Tsalkina, 1969; Sundberg and Clausen, 1979; McMurray et al., 1984). McMurray et al. (1984) stress the importance of this

epifaunal habitat in providing food and protection from predators. At this age crabs are solitary; Sundberg and Clausen (1979) estimate densities of 1.3 ± 1.5 crabs/m^2 in the epifaunal habitat.

Dependence on the epifaunal community apparently decreases as crabs grow older (Jewett and Onuf, 1988); crabs become less vulnerable to predation with increased body size and reduced frequency of molting. Tsalkina (1969) found 2-yr-old crabs in this habitat, but the density of the epifauna was considerably lower than in areas where younger crabs were found. Communal groups (pods) of up to 500,000 individual 2-yr-old crabs have been observed in littoral and subtidal zones (Powell and Nickerson, 1965), predominantly on substrates affording little cover (Bright et al., 1960).

In tests conducted at Auke Bay Laboratory, the two age classes showed differences in habitat preference. One-yr-old crabs selected habitats that provided cover at 53-63% of the observations; they chose the bryozoan/hydroid assemblage significantly more often than shell, cobble, or shale, and least preferred bare sand. Two-yr-old crabs selected habitats that provided cover at 2-27% of the observations; for this older age class, there was no significant difference in frequency of choice of the bryozoan/hydroid assemblage over cobble, the two most preferred habitats (Rice et al., 1988).

Although habitat and cohort density preferences for juvenile king crabs have been described, survival and growth in relation to these factors have not been studied. Our study tested these hypotheses: 1) that survival and growth of 1-yr-old and 2-yr-old crabs is related to cohort density or habitat cover, and 2) that survival and growth of 2-yr-old crabs is less affected by cohort density and available cover than survival and growth of 1-yr-old crabs.

METHODS

Juvenile red king crabs representing two age classes, 1-yr-old and 2-yr-old, were collected in April and May 1987 in the Auke Bay, Alaska vicinity. The younger crabs (carapace length 5.9-14.0 mm) were collected from intertidal areas at tides below -.7m and from subtidal bryozoan/hydroid communities at 15-20 m depths. We considered these crabs to be 1-yr-old individuals that hatched the previous spring and settled out of the water column in June or July (Freese and Babcock, proceedings this symposium). Two-yr-old crabs (carapace length 23.6-38.3 mm) were collected from one subtidal pod by Auke Bay Laboratory divers.

The 1-yr-old crabs were held individually in divided incubators (Arasmith et al., in Press) and the older crabs were held outdoors in fiberglass tanks; both holding systems were supplied with seawater at 6-7°C and 29°/$_{oo}$. Waterflow and temperature were monitored daily. Crabs were checked daily for molts and deaths, and fed, ad libitum, a rotating diet of squid, shrimp, fish, and clams twice a week. Uneaten food from the previous feeding was removed at each feeding.

Crabs were tagged for individual identification. One-yr-old crabs were tagged with colored beads and 2-yr-old crabs with numbered plastic tags; tags were attached with cyanoacrylic gel glue. Initial length (from the posterior margin of the right ocular orbit to the midpoint of the posterior margin of the carapace) and blotted wet weights were recorded for each crab.

Crabs were tested in 208 x 55 cm outdoor fiberglass tanks covered with translucent fiberglass covers and illuminated with natural light. Tanks were supplied with running (50-80 mL/s) filtered seawater, at 5-9°C with salinity at 29 $^{\circ}/_{\circ\circ}$, to a depth of 25 cm. Water flow was adequate to keep temperature relatively constant despite lower air temperatures in the latter days of the test.

Each of the four tanks used for tests on 1-yr-old crabs was divided with screens into three sections. One of three habitats--sand, cobble, or plastic plants (simulated bryozoan/hydroid assemblage)--was placed in each of the 12 tank sections. Habitats were arranged to eliminate tank effects. Sand was obtained locally, then washed, graded (0.06-2.36 mm dia), and layered to 3 cm deep in tank bottoms. Sand also served as a base for the cobble and plant habitats. Cobble (4-6 cm dia) was collected from local intertidal areas, then washed and placed over 50% of the sand base. Plastic aquarium plants were used because we felt that live bryozoan/hydroid assemblages would greatly deteriorate during this 4- to 5-month study. Use of plastic plants also eliminated natural food sources associated with the epifauna that would not be available to crabs in other test habitats. Preliminary tests indicated that crabs used plastic plant assemblages and epifaunal assemblages similarly for cover. Plastic plants were soaked in running seawater overnight before placement in tanks.

Crabs were randomly placed in each tank section at two densities--3 or 11 crabs. All test conditions were duplicated. A 2-way ANOVA considering degree of cover and cohort density found no significant differences among the 12 groups with respect to initial mean lengths, weights, or sex composition. We started this 139-day test on 20 July 1987 and ended it 6 December 1987; this time period encompassed two intermolt periods for 67% of the crabs and three intermolt periods for 23% of the crabs.

Tests for the 2-yr-old crabs were run in eight tanks, each divided by screens into two sections. Each section contained one of two habitats--sand or cobble. Sand was prepared as in the 1-yr-old tests; cobble used for the older crabs was larger (10-17 cm dia). A "plant" habitat was not used for the 2-yr-old crabs because earlier tests showed no significant difference in preference between the epifaunal assemblages and cobble habitats (Rice et al., 1988).

Crabs were randomly placed in the 16 tank sections at three cohort densities--3, 7, or 11 crabs. Test conditions were replicated two or three times. The 16 groups did not differ significantly with respect to initial mean lengths, weights, or sex composition. Test duration for this age class was

also 139 days, spanning one intermolt period for 91% of the crabs and two intermolt periods for 9% of the crabs.

Deaths were classified by cause (cannibalism, no apparent cause, or ecdysis-related) and by temporal relationship to an individual's molt (molt or intermolt). Ecdysis-related deaths occurred at or within 4 days of ecdysis. Missing crabs were considered eaten because they disappeared at molt, when they were most vulnerable to cannibalism.

Two to four days after ecdysis, length, blotted weight, and comments regarding missing and regenerating limbs were recorded and tags were replaced.

For each age class, relative length and weight increases at each ecdysis (transformed with arcsine transformation) and length of intermolt periods were tested for homogeneity of variances with Bartlett's test, then analyzed by 2-way ANOVA with respect to habitat and cohort density. We used chi-square contingency tests to analyze differences among groups' mortality in each age class and to compare mortality in the two age classes. The level of significance for all tests was $P \leq .05$.

RESULTS

Survival in 1-yr-old Crabs

In the 1-yr-old age class, total mortality was 45%. In high density tanks (11 cohorts) total mortality was significantly related to degree of cover; total mortality was higher in sand tanks and lower in cobble and "plant" tanks (Fig. 1). In low density tanks (three cohorts) mortality was not significantly related to degree of cover.

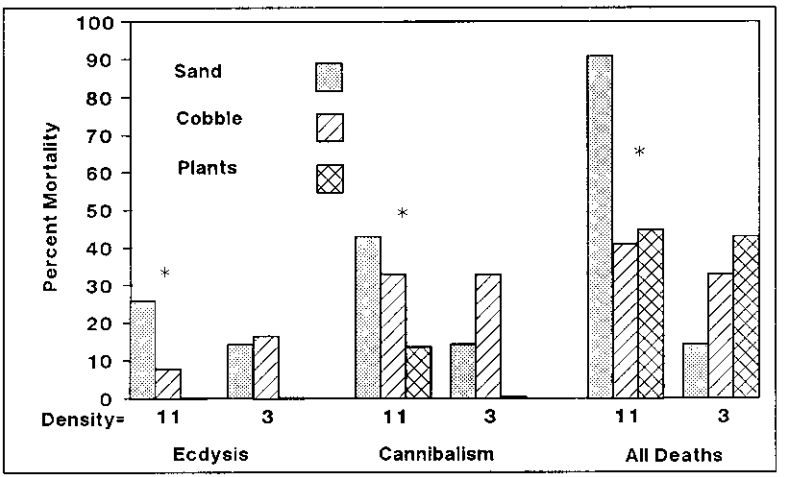

Figure 1.--Mortality in 1-yr-old crabs held at two cohort densities in three habitats. * = significant differences in % mortality among groups of crabs.

Cannibalism accounted for 50% of the total mortalities. Cannibalism occurred within 4 days of a victim's molting with four exceptions. In high density tanks, mortality related to cannibalism was inversely related to cover--highest in sand tanks, moderate in cobble tanks, and lowest in "plant" tanks (Fig. 1). Cover was not significantly related to mortality in low density tanks. Carapace length of cannibalised crabs was smaller than the mean length of surviving tankmates. All victims of intermolt cannibalism were the smallest crabs in their tank at their time of death.

Twenty-three percent of the crabs lost one or more limbs. Whether these limbs were actively removed by tank mates or lost during ecdysis, they were consumed. The proportion of animals that lost limbs in high density tanks was significantly higher in plant tanks. Injured crabs may have been better able to avoid further limb loss and death in the higher cover tanks than in tanks that provided less cover.

Most (90%) of the deaths that were not related to cannibalism occurred during intermolt periods and seemed to be disease related (Brodersen et al., proceedings this symposium). Bodies commonly appeared rigid with swollen abdomens several days before death. Intermolt deaths were most common in high density tanks with no cover. Ecdysis-related deaths accounted for 30% of the total mortality. Degree of cover was again important to survival in high cohort density tanks, but not in low density tanks (Fig. 1).

Although mortality from all causes in low density tanks was generally lower than in high density tanks of like habitat, differences were significant only in sand.

Survival in 2-yr-old Crabs

In the 2-yr-old age class tests, total mortality was 20%. Neither cohort density nor habitat showed any significant relationship to mortality (total mortality, cannibalism, or ecdysis-related mortality).

Cannibalism accounted for 79% of the total deaths and always occurred at the victim's ecdysis. As in the 1-yr-old age class, victims were generally smaller than tank mates. Sixteen per cent of 2-yr-old crabs lost limbs. Deaths not related to cannibalism occurred only at cohort densities of 7 and 11, with equal frequency at ecdysis and intermolt periods. We saw no deaths associated with a swollen abdomen, common in the 1-yr-old crabs.

Comparison of Survival Between the Two Age Groups

When the two age classes held at like cohort densities (3 or 11 crabs) and like habitats (sand or cobble) were compared, total mortality at high densities was greater in 1-yr-old crabs in both habitats (Fig. 2). Cannibalism was significantly greater in 1-yr-old crabs only at high densities in sand tanks. Low density tanks were similar in proportions of total mortality and in proportions of cannibalism. Age was not significantly related to ecdysis-related deaths at either density or in either habitat.

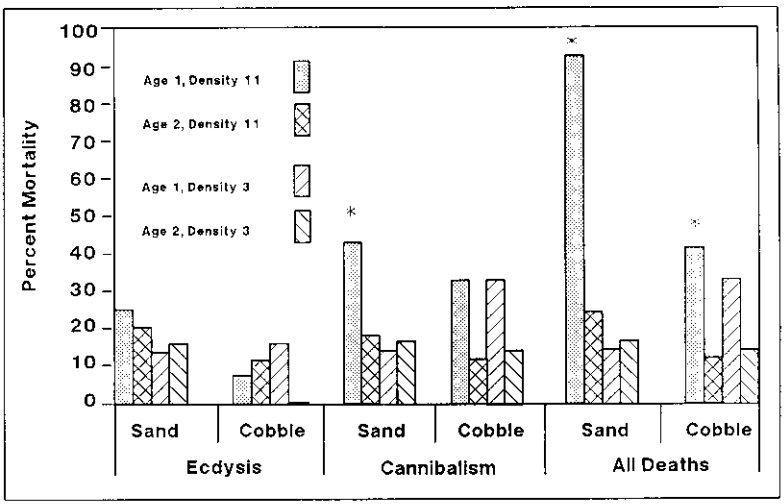

Figure 2.--Mortality in 1-yr-old and 2-yr-old crabs held at two cohort densities in two habitats. * = significant differences in % mortality between the two age classes.

Growth in 1-yr-old and 2-yr-old Crabs

In both age classes there were no significant differences among the six treatment groups in mean relative length and weight increases at each molt or overall. Similarly, mean molt dates, intermolt periods, and number of successful molts per crab did not differ.

DISCUSSION

That survival in 1-yr-old crabs is directly related to availability of cover indicates that natural habitat providing cover (i. e., epifaunal associations or cobble) is important to this age class. Although cover in our study was not significantly related to survival at low cohort densities, it must be remembered that test crabs were subject only to intraspecific predation. Predation on juvenile lobsters, *Homarus americanus,* by other species is reduced by complex habitats affording cover (Johns and Mann, 1987; Wahle, 1988). Food sources associated with epifaunal associations increase the importance of this habitat to 1-yr-old crabs (Tsalkina, 1969; Armstrong et al., 1981).

Consistent occurrences of cannibalism across both densities and habitats in the 2-yr-old test groups (compared to the more variable incidence in 1-yr-old groups) implies that cannibalism in the older crabs is less related to these factors. That the rate of cannibalism at high cohort densities in habitats providing no cover is significantly higher

in 1-yr-old crabs than in 2-yr-old crabs and that this is not so in habitats with available cover indicates the higher importance of cover to the younger crabs.

The smaller size of victims cannibalized relative to cohorts may indicate a social hierarchy in both age classes. Sastry and Ehringer (1980) found that when a dominant (usually larger) juvenile lobster molted, cohorts were agonistic towards each other, but not towards the dominant. If a less dominant juvenile molted, he was often injured or killed. Such hierarchy could be expected in the usually communal 2-yr-old crabs. During our study, the older crabs frequently grouped in pods on screens separating tank sections and often were in contact with a complementary pod on the other side of the screen. Aggregations of 1-yr-old crabs occurred occasionally on tank substrates only in the latter days of the study. Test conditions may have promoted such behavior in the younger crabs, or the 1-yr-old juveniles may have been approaching "podding" age.

In addition to the effects of habitat cover and cohort density on cannibalism, the effects of diet must be considered. Brodersen et al. (1988) found that maintenance of both age classes on single item diets greatly affected rates of cannibalism. First year crabs that were fed only shrimp, and raised on bare sand at densities similar to our high density tanks (11 crabs), had rates of cannibalism similar to our crabs at high densities on bare sand. Crabs that were fed only mussels (with shell) had significantly lower rates of cannibalism. Our crabs (on a mixed diet) in the high-cover habitat had rates of cannibalism between the two extremes, suggesting that the effects of diet on cannibalism may be moderated by habitat cover.

Our findings that neither available cover nor cohort density are related to growth are consistent with studies of other decapods. Juvenile lobsters reared at the same densities showed different survival rates on four substrates, but no difference in growth over 6 months (Van Olst, 1975).

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Food and Feeding Habits of Red King Crab from Northwestern Norton Sound, Alaska

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ABSTRACT

Six data sets of food from red king crabs (*Paralithodes camtschatica*) in Norton Sound are presented. Four were collected through the ice by pots from nearshore locations near the city of Nome, Alaska, in March 1986-89. Two additional data sets were collected by trawls from offshore locations during September 1976 and 1985.

The food group that consistently dominated crab prey nearshore were unidentified fishes; sea urchins, hydroids, polychaete worms, bivalves, sand dollars, brittle stars and sea stars followed in importance. Crabs from 1986 had significantly ($P<0.05$) more stomach contents than crabs from 1987, 1988, and 1989. The prey weight in crabs from 1987-1989 was statistically similar. No significant difference was detected in weight of prey among crabs from different nearshore sites.

Food groups most important among crabs taken offshore were bivalve and gastropod molluscs, brittle stars, crabs, and unidentified crustaceans. The weight of stomach contents among offshore crab samples was significantly ($P<0.05$) greater in 1976 than in 1985. Furthermore, the weight of stomach contents from the 1976 offshore crabs was significantly ($P<0.05$) greater than the stomach weights in all nearshore crabs (1986-1989) and the prey weight of 1985 offshore crabs was significantly ($P<0.05$) less than any of the nearshore samples.

INTRODUCTION

Red king crab (*Paralithodes camtschatica*) of Norton Sound in the northeastern Bering Sea represents the northern-most commercial fishery for this species in the world. This small fishery is centered in the northwestern part of the Sound, south and east of Sledge Island (Wolotira *et al.*, 1977; Powell *et al.*, 1983). The harvest quota has dwindled from 204,120 kg in 1985 to 90,720 kg in 1989. Approximately 79,000 crabs were harvested in three days in August 1989 for a $739,460 yield to fishermen (Merkouris, 1989).

The population is generally confined to waters less than 30 m. A northerly migration of adult and subadult males into coastal waters occurs in late fall or early winter (Powell *et al.*, 1983). Small, sporadic commercial and subsistence fisheries also exist for this species in winter through the ice adjacent to coastal villages (Powell *et al.*, 1983).

A major prerequisite for management of the Norton Sound king crab fishery is knowledge of crab distribution, abundance and behavior. Information on distribution, abundance and condition of the stock is compiled through periodic trawling surveys by the National Marine Fisheries Service (e.g., Stevens and MacIntosh, 1986). This paper presents the only available feeding data on red king crab from Norton Sound.

MATERIALS AND METHODS

King crabs were collected for stomach analysis within 2 km of shore during March 1986, 1987, 1988, and 1989 as part of an environmental monitoring study (Jewett *et al.*, 1990). A total of 348 nearshore crabs were collected by baited commercial pots in approximately 6 to 14 m of water (Figure 1). All crabs were taken from pots within 4 to 24 hours of setting to minimize crab digestion time since capture. Bait was changed approximately every 48 hours. All crabs were measured (carapace length), weighed (blotted-dry wet weight), and sexed immediately after capture. Exoskeletal condition was noted as individuals that molted during the past year (termed new-shell) and those that failed to molt during the last year (old-shell). Observations on reproductive stage of the females were also noted. Stomachs were removed in the field, preserved in 10% buffered formalin, and shipped to the Institute of Marine Science at the University of Alaska Fairbanks for processing.

In addition to the samples collected nearshore, two crab stomach data sets were obtained from sites 15 to 50 km offshore and at depths 16 to 31 m. These samples were processed for comparison with nearshore samples. A total of 46 male crabs were collected from four locations (Figure 1) in September/October 1976 during a demersal trawling survey (Feder and Jewett, unpubl.). These crabs were measured and exoskeletal and reproductive stages noted. Stomachs were removed, preserved and archived until processing in 1985. The second offshore collection was made during a National Marine Fisheries Service crab trawling survey in September 1985 (Stevens and MacIntosh, 1986). A total of 32 crabs (21 males and 11 females) were randomly collected from four locations (Figure 1), frozen whole and shipped to Fairbanks for processing. The 1985 crabs were similar to the 1976 samples in terms of method, month, depth, and general location of collection.

The 1976 and 1985 data sets were presented in Rusanowski *et al.* (1986). Data sets for 1986, 1987, 1988, and 1989 were respectively presented in Rusanowski *et al.* (1987, 1988) and Jewett *et al.* (1989, 1990).

Stomach contents were sorted in the laboratory and identified to the lowest practical taxon. Crab prey from nearshore crabs was presented as percent frequency of occurrence and percent blotted-dry wet weight. The percent frequency of occurrence is the percentage of stomachs containing various food items relative to the total number of stomachs examined. An Index of Relative Importance (IRI) of various food items was calculated using frequency of occurrence and weight parameters (modified after Pinkas *et al.*, 1971). This index was calculated as follows: IRI = % frequency of occurrence x % weight x 100. Prey from offshore crabs was only presented as percent frequency of occurrence, although the blotted-dry wet weight of the total stomach contents of each crab was obtained. Comparisons of weight of stomach contents were

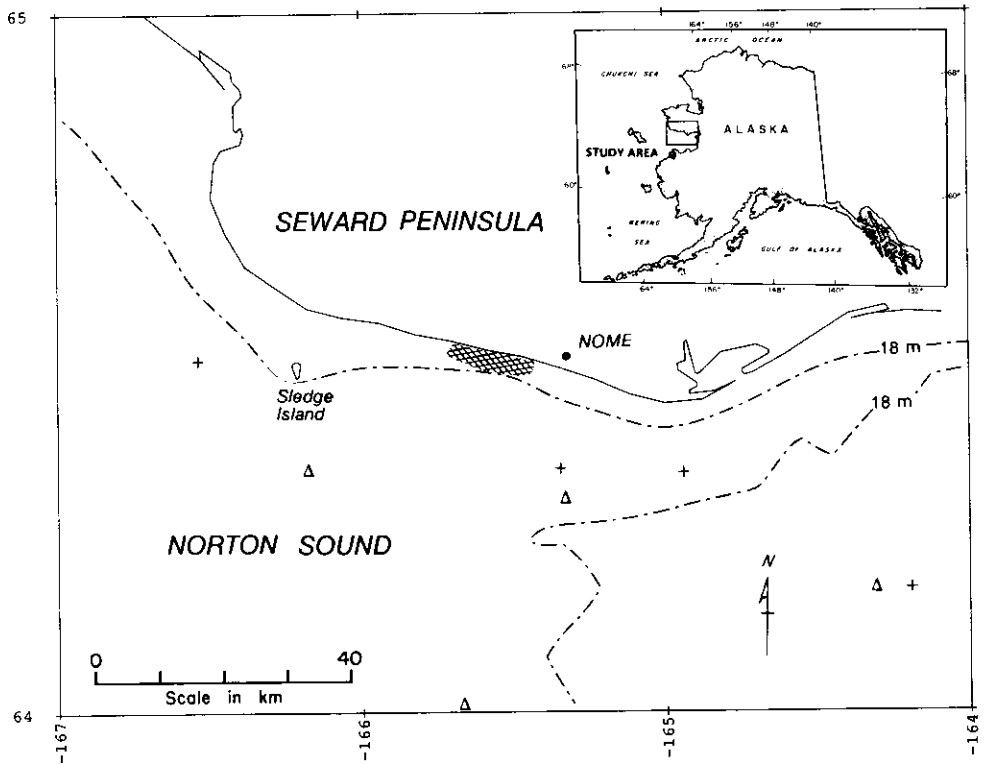

Figure 1. Locations where red King crabs, *Paralithodes camtschatica*, were collected for stomach analyses nearshore 1986-89 (cross -hatch) and offshore 1976(Δ) and 1985 (+).

made between sexes, stations, years, and nearshore versus offshore stations using the Mann-Whitney Test and the Kruskal-Wallis Test (Zar, 1974).

RESULTS AND DISCUSSION

Nearshore Crabs

Crabs sampled nearshore from 1986 through 1989 were composed of 313 males and 35 females with 49 males and 21 females in 1986, 86 males and 5 females in 1987, 107 males and 3 females in 1988, and 71 males and 6 females in 1989.

The average size (± 1 standard deviation) of all crabs from 1986, 1987, 1988, and 1989 was 94 ± 20.1 m, 99 ± 13.4 mm, 106 + 12.9 mm, and 103 ± 16.5 mm, respectively (Table 1).

All but 16 of the 313 males were of adult size, approximately 80 mm CL or larger (see Powell *et al.*, 1983 for maturity criteria). The average size of males from 1986, 1987, 1988, and 1989 was 104 ± 16.3 mm (values ranged from 67-128 mm), 100 ± 12.3 mm (range = 72-124 mm), 107 ± 12.1 mm (range = 75-133 mm), and 105 ± 14.8 mm (range = 75-142 mm), respectively. No significant difference ($P>0.05$; Kruskal-Wallis Test) was detected between size of males from 1986, 1988 and 1989, however, males from 1987 were significantly ($P<0.05$) smaller than males from 1988 and 1989.

The condition of the exoskeleton of the males from 1986-89 was mostly new-shells (Table 1), i.e., crabs that molted within the past year and had few or no abrasions and little or no attached epifauna. Few males were one to two years since molting (old-shells), as indicated by exoskeletal abrasions and larger attached epifauna, such as barnacles.

Among the 35 females examined from 1986-89, 26 were juveniles and 9 were adults. Their respective average sizes were 72 ± 5.1 mm and 78 ± 7.2 mm. The paucity of females may, in part, be explained by their molting/mating activity. Four of the adults were carrying purple, uneyed eggs, indicative of recently spawning; four adults were carrying brown, eyed eggs, indicative of eggs near hatching; and one adult had no eggs, apparently due to a disease. Since feeding is somewhat curtailed during the molting/mating period, fewer females would enter a baited pot.

The average weights of stomach contents for the four years were 0.41 ± 0.24 g in 1986, 0.42 ± 0.60 g in 1987, 0.38 ± 0.44 g in 1988, and 0.33 ± 0.35 g in 1989 (Table 1). These averages are similar to the average values observed among similarly sized red king crabs off the west coast of the Kamchatka Peninsula (Takeuchi, 1967).

Since 1986 crabs consisted of a high proportion of females (30%), the weight of stomach contents were compared between sexes using the Mann-Whitney Test. The test revealed no significant difference ($P = 0.599$) in amount of food between males and females, therefore, the sexes were combined in all subsequent analyses.

The weight of stomach contents (sexes combined) was statistically similar ($P>0.05$; Kruskal-Wallis Test) between 1987, 1988, and 1989 (Figure 2). It would appear that since the 1988 crabs consisted of 20 empty stomachs, 1988 crabs would have significantly less food than crabs in other years. However, the amount of food in the remaining stomachs was so great that the test revealed no difference ($P>0.05$) between the three years. Crabs in 1986 had significantly ($P<0.05$) more food in their stomachs than the other three years.

Table 1. Summary of stomach analysis from red king crabs collected off Nome in March 1986-1989.

Sampling dates	22-30 March 1986		20-31 March 1987		22-29 March 1988		23-29 March 1989	
Sampling depths:	11-14 m (36-46 ft)		7-14 m (22-46 ft)		6-13 m (21-44 ft)		8-11 m (26-35 ft)	
Sampling method:	Commercial pots		Commercial pots		Commercial pots		Commercial pots	
Number stomachs examined:	70		91		110		77	
$\bar{X} \pm 1$ SD crab size:	94 ± 20.1 mm carapace length		99 ± 13.4 mm carapace length		106 ± 12.9 mm carapace length		103 ± 16.5 mm carapace length	
$\bar{X} \pm 1$ SD crab weight:	709 ± 436 g		796 ± 315 g		979 ± 341 g		901 ± 403 g	
Crab composition:	49% new-shell males >80 mm 30% juvenile females 14% old-shell males > 80mm 6% new-shell males < 80mm		59% new-shell males >80 mm 31% old-shell males >80 mm 4% new-shell males <80 mm 3% juvenile females 2% adult females		77% new-shell males >80 mm 17% old-shell males >80 mm 3% new-shell males <80 mm 1% juvenile females 2% adult females		77% new-shell males >80 mm 14% old-shell males >80 mm 1% new-shell males <80 mm 1% juvenile females 7% adult females	
Empty stomachs:	4 (5.7%)		7 (7.7%)		20 (18.2%)		4 (5.2%)	
$\bar{X} \pm 1$ SD weight of contents from all crabs:	0.41 ± 0.24 g		0.42 ± 0.60 g		0.38 ± 0.44 g		0.33 ± 0.35 g	
Dominant Prey: Index of Relative Importance*	Fishes	20.94	Fishes	6.15	Fishes	20.68	Fishes	6.13
	Polychaetes	3.65	Sea urchins	2.41	Sea urchins	1.03	Sea urchins	2.18
	Brittle stars	1.44	Sand dollars	2.16	Eelgrass	0.50	Sea stars	0.61
	Bivalves	1.32	Sea stars	0.15	Bivalves	0.12	Unid. crustaceans	0.42
	Sea urchins	0.86	Bivalves	0.04	Hydroids	0.10	Amphipods	0.08
	Sand dollars	0.86	Hydroids	0.04	Sand dollars	0.04	Hydroids	0.07
	Hydroids	0.01	Polychaetes	0.03	Polychaetes	<0.01	Hermit crabs	0.02

*Index of Relative Importance (IRI) = % frequency x % weight x 100.

YEAR		86	87	88	89
Y	86		>	>	>
E	87			=	=
A	88				=
R	89				

Figure 2. Statistical comparisons of weight of king crab stomach contents from nearshore sites by sampling year (Kruskal-Wallis test at $\alpha = 0.05$)

NEARSHORE YEAR		76	85	86	87	88	89
OFFSHORE YEAR	76		>	=	>	>	>
	85			<	<	<	<

Figure 3. Statistical comparisons of weight of king crab stomach contents from nearshore and offshore sites by sampling year (Kruskal-Wallis test at $\alpha = 0.05$)

No significant difference ($P>0.05$) was detected in weight of prey among crabs from different nearshore locations. Similar results were obtained among nearshore crabs in the vicinity of Kodiak Island (Jewett and Feder, 1982).

Dominant Foods. Dominant foods, in terms of IRI, in nearshore crabs from 1986-89 were fishes and sea urchins (*Strongylocentrotus droebachiensis*), although hydroids, polychaetes worms, bivalves, sand dollars (*Echinarachnius parma*), brittle stars and sea stars were also dominant in some of the other years (Table 1). Two food groups that dominated in crabs from 1986-88, bivalves and sand dollars, were not important in 1989 crabs. Furthermore, sand dollars were completely absent from the stomachs in 1989. Polychaete worms were only important prey in 1986. The frequency of occurrence of prey groups and prey taxa from all nearshore, as well as offshore, data sets is presented in Tables 2 and 3.

Fishes remained the single most dominant king crab prey group in 1986-89 as (Tables 2 and 3). In 1989 fishes occurred in 29.9% of the crabs examined, somewhat lower than than the 1986-89 average of 41.1%. The fish remains were typically in the form of bone fragments, tissue and eggs. Due to the poor condition of the digested fish remains and the absence of scales or otoliths, the identity of the fishes consumed off Nome was not determined. Bone and cartilage fragments suggest that a wide range of fish sizes were taken.

Fishes are a common prey group in king crabs elsewhere, but not as prevalent as in crabs near Nome. The percent frequency of occurrence of fishes within southeastern Bering Sea king crabs ranged from 4% (Pearson *et al.*, 1984) to 13% (Cunningham, 1969). Feniuk (1945) found fishes in 2% of the king crabs off the west Kamchatka shelf. Kulichkova (1955) reported that 10% of the volume of crab food from the west coast of South Sakalin was herring, and speculated that the fish were not alive when taken from the sea floor. Jewett and Feder (1982) found fishes in 17% of the king crabs at various locations nearshore and offshore adjacent to Kodiak Island. In Izhut Bay on Afognak Island (June and July), fishes occurred in 65% of the 40 adult crabs and accounted for 80% of the food weight (Jewett and Feder, 1982). Evidence suggested that some of the fishes, i.e., capelin (*Mallotus villosus*) and Pacific sand lance (*Ammodytes hexapterus*), preyed upon by near-surface-feeding birds and sea lions, fell to the bottom after injury or regurgitation by these predators. These fishes were presumably taken by the scavenging crabs.

Remote Operated Vehicle (ROV) video filming made in nearshore northwestern Norton Sound in March 1988, when king crab were being caught, covered nearly 1,200 linear meters of transects. During this filming 23 fishes were seen, including 12 sculpins, seven flatfishes, two pricklebacks, and two unidentified dead fishes.

Nearshore benthic sampling as part of an environmental monitoring program over the last few years has yielded only twelve fishes comprising four species with sandlance and sculpins dominating (Jewett *et al.*, 1990). Since fish easily avoid the benthic sampling equipment used for invertebrate assessments, they are probably significantly underrepresented in the benthic data. Furthermore, their infrequent occurrence may also be an artifact of their seasonal movements. Fishes, in particular spawning fishes, are likely to be more abundant in shallow waters off Nome during ice-covered months when salinities approximate 30 ppt than during ice-free months when salinities range between 20-27 ppt.

Table 2. Comparison of prey groups from stomach contents of red king crabs collected from northwestern Norton Sound, September 1976 and 1985 and March 1986, 1987, 1988 and 1989. Prey are presented in percent frequency of occurrence from all crabs examined; frequency of occurrence is shown in parentheses.

	Offshore	
Prey Groups	1976 20-26 m (n=46)	1985 16-31 m (n=32)
Foraminiferins	4.3 (2)	9.4 (3)
Hydroids	6.5 (3)	18.8 (6)
Segmented worms	13.0 (6)	3.1 (1)
Clams/cockles/mussels	67.4 (31)	18.8 (6)
Snails	19.6 (9)	28.1 (9)
Barnacles	13.0 (6)	3.1 (1)
Crabs	10.9 (5)	46.9 (15)
Other crustaceans	21.7 (10)	46.9 (15)
Sand dollars	0.0 (0)	3.1 (1)
Sea urchins	0.0 (0)	0.0 (0)
Brittle stars	47.8 (22)	50.0 (16)
Fishes	1.7 (1)	3.1 (1)
Sediment	40.0 (18)	28.1 (9)

	Nearshore			
Prey Groups	1986 11-14 m (n=70)	1987 7-14 m (n=91)	1988 6-13 m (n=110)	1989 8-11 m (n=77)
Foraminiferins	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
Hydroids	15.7 (11)	16.5 (15)	30.0 (33)	24.7 (19)
Segmented worms	52.9 (37)	13.2 (12)	5.5 (6)	2.6 (2)
Clam/cockles/mussels	41.4 (29)	7.7 (7)	12.7 (14)	5.2 (4)
Snails	14.3 (10)	7.7 (7)	1.8 (2)	0.0 (0)
Barnacles	0.0 (0)	1.1 (1)	1.8 (2)	0.0 (0)
Crabs	0.0 (0)	0.0 (0)	0.0 (0)	1.5 (1)
Other crustaceans	4.3 (3)	12.1 (11)	7.3 (8)	19.5 (15)
Sand dollars	18.6 (13)	19.8 (18)	3.6 (4)	0.0 (0)
Sea urchins	12.8 (9)	16.5 (15)	9.1 (10)	19.5 (15)
Brittle stars	20.0 (14)	3.3 (3)	0.0 (0)	0.0 (0)
Fishes	61.4 (43)	26.4 (24)	48.2 (53)	29.9 (23)
Sediment	32.9 (23)	15.4 (14)	10.0 (11)	5.2 (4)

Table 3. Comparison of prey taxa from stomachs of red king crabs collected from northwestern Norton Sound, September 1976 and 1985 and March 1986, 1987, 1988, and 1989. Prey taxa, identified to the lowest practical level, are presented as percent frequency of occurrence from all crabs examined.

Collection Date:	9/76	9/85	3/86	3/87	3/88	3/89
Depth (m):	20-26	16-31	11-14	7-14	6-13	8-11
Stomachs Examined:	46	32	70	91	110	77
Location:	Offshore	Offshore	Nearshore	Nearshore	Nearshore	Nearshore
	Percent Frequency of Occurrence					
Foraminiferida	4.3	9.4	-	-	-	-
Bryozoa	-	9.4	-	-	-	-
Hydrozoa	6.5	18.8	15.7	16.5	30.0	24.7
Porifera	-	3.1	-	-	-	-
Annelida (segmented worms)						
Unid. polychaeta	-	-	38.6	4.4	-	1.3
Lumbrineridae	-	-	1.4	-	-	-
Polynoidae	4.3	-	-	-	3.6	1.3
Pectinariidae	4.3	-	11.4	8.8	1.8	-
Oweniidae	4.3	3.1	-	-	-	-
Sabellidae	-	3.1	-	-	-	-
Travisia sp.	-	-	1.4	-	-	-
Sternaspis scutata	2.2	-	-	-	-	-
Mollusca (bivalves & snails)						
Unid. Bivalvia (clams, cockles, mussels)	32.6	6.2	23.4	3.3	5.4	3.9
Nuculidae	2.2	-	-	-	-	-
Nuculanidae	-	3.1	-	-	0.9	-
Yoldia sp.	21.7	-	-	1.1	-	-
Lyonsia sp.	19.6	9.4	-	-	-	-
Crenella decussata	6.5	-	-	-	-	-
Mytilidae	-	-	1.4	-	-	-
Musculus sp.	6.5	-	5.7	-	-	-
Cardiidae	-	-	10.0	2.2	6.4	1.3
Cardiomya sp.	-	3.1	-	-	-	-
Cyclocardia crebricostata	2.2	-	-	-	-	-
Clinocardium sp.	4.3	-	-	-	-	-
Serripes groenlandicus	43.5	-	-	1.1	-	-
Liocyma fluctuosa	6.5	-	-	-	-	-
Macoma sp.	2.2	-	-	-	-	-
Mya sp.	2.2	-	-	-	-	-
Pandora sp.	2.2	-	-	-	-	-
Unid. gastropoda	2.2	18.8	11.4	5.5	0.9	-
Trochidae	6.5	3.1	2.9	1.1	0.9	-
Solariella sp.	-	3.1	-	-	-	-
Margarites sp.	-	6.3	-	-	-	-
Naticidae	5.2	-	-	-	-	-
Cylichna alba	-	-	-	1.1	-	-

Table 3 (cont'd)

Collection Date:	9/76	9/85	3/86	3/87	3/88	3/89
Depth (m):	20-26	16-31	11-14	7-14	6-13	8-11
Stomachs Examined:	46	32	70	91	110	77
Location:	Offshore	Offshore	Nearshore	Nearshore	Nearshore	Nearshore
	Percent Frequency of Occurrence					
Arthropoda (crustaceans)						
Unid. crustacea	-	-	7.1	5.5	2.7	9.1
Balanus spp. (barnacles)	13.0	3.1	-	1.1	1.8	-
Cumacea	15.2	-	1.4	-	-	-
Isopoda (pill bugs)	6.5	3.1	-	-	-	-
Amphipoda (sand flea)	4.3	28.1	2.9	5.5	3.6	7.8
Photis spaskii (sand flea)	-	3.1	-	-	-	-
Calanoidea (copepods)	-	6.3	-	-	-	-
Ostracoda (mussel shrimps)	-	3.1	-	-	-	-
Halacaridae (sea mites)	-	3.1	-	-	-	-
Decapoda (crabs and shrimps)	-	34.4	-	-	2.7	-
Paguridae (hermit crabs)	6.5	6.3	-	-	-	1.3
Majidae (spider crabs)	6.5	6.3	-	-	-	-
Echiurida (unsegmented worms)						
Echiurus echiurus	6.5	-	-	-	0.9	-
Echinodermata						
Unid. echinodermata	-	-	1.4	1.1	-	1.3
Unid. echinoidea (sand dollars/urchins)	-	-	4.3	-	-	-
Echinarachnius parma (sand dollars)	-	3.1	18.6	19.8	3.6	-
Strongylocentrotus droebachiensis (urchin)	-	-	12.9	16.5	9.1	19.5
Ophiuroidea (brittle stars)	47.8	50.0	20.0	3.3	-	-
Asteroidea (sea stars)	-	-	-	3.3	2.7	1.3
Other						
Bryozoa	-	-	-	-	5.4	2.6
Fishes	1.7	3.1	61.4	26.4	48.2	29.9
Unid. animal material	41.3	34.4	15.7	11.0	63.6	71.4
Plant material	5.0	-	4.3	12.1	29.1	7.8
Sediment	40.0	28.1	32.9	15.4	10.1	5.2
Empty	15.2	-	5.7	7.7	18.2	5.2

Potential forage fishes/eggs in king crab are the saffron cod (*Eleginus gracilis*), sculpins (Cottidae) and Pacific sand lance. A trawl survey in Norton Sound in the fall of 1976 determined that saffron cod and six species of sculpins were among the 20 most abundant fish taxa collected (Wolotira *et al.*, 1977). An estimated 760 million saffron cod with an associated biomass of about 16,600 mt was found in Norton Sound in that 1976 survey. A review of the biological data (mainly Soviet sources) on saffron cod (Wolotira, 1985) revealed that adults generally move inshore in winter and offshore in summer. Demersal spawning occurs in winter under coastal sea ice in very shallow areas (2-10 m) on sandy-pebbly substrate and where highly saline waters are under strong tidal influence. Saffron cod in western Alaska waters have a high rate of natural mortality; approximately 60-80% of the population dies annually and less than 1% of the stock survives past the age of 5 years. The physiological demands of winter spawning could result in spawning stress mortality, but this was not stated in the reviewed literature (Wolotira, 1985).

As for the sculpins, the most abundant sculpins found in the 1976 survey (*Myoxocephalus joak*; *M. scorpius groenlandicus*; *M. quadricornis*; *Gymnocanthus tricuspis*; *Enophrys diceras*, and *Megalocottus platycephalus*) (Wolotira *et al.*, 1977), and other less common species, presumably inhabit the coastal waters near Nome in winter. Most sculpins spawn during the ice-covered months of winter and early spring depositing large (2-3 mm) eggs in clusters among rocks (Andriyashev, 1954; Hart, 1973; Eschmeyer *et al.*, 1983).

Sand lance apparently spawn in intertidal and shallow subtidal regions, burrowing into coarse sand substrates (1-4 mm) or fine gravel (5-15 mm) (Dick and Warner, 1982). Sediments of similar sizes occur in the nearshore Nome vicinity (Jewett *et al.*, 1990). Sand lance have been reported to be the most abundant fish species in Golovin Bay, 130 km east of Nome (Barton, 1978). Therefore, it appears that sand lance, in addition to saffron cod and sculpins, are the likely fishes taken by king crabs near Nome.

Offshore Crabs

The 46 king crabs collected offshore in 1976 were all large males ($\bar{X} = 117 \pm 14.1$ mm; range = 78-157 mm). Approximately 66% were new-shell and 35% were old-shell individuals. A total of 39 (85%) contained food. The average weight of the stomach contents was 0.65 ± 0.68 g for all 46 crabs.

The size of the 21 males and 11 females collected offshore in 1985 averaged 100 ± 17.7 mm (range = 36-117 mm) and 54 ± 5.6 mm (range = 43-62 mm), respectively. All but one (36 mm) of the males were adults, based on the maturity information presented in Powell *et al.* (1983). All females were juveniles. All males, with the exception of the smallest one, had exoskeletons that were near or at least one year old. All of these old-shell crabs had large (4-15 mm base width) barnacles attached to the exoskeletons. New exoskeletons were developing beneath the old ones, indicating the approaching molting phase. Wallace *et al.* (1949) noted that most crabs in this condition had completely molted by one month later. Exoskeletons on three of the males were judged as skipmolts or very-old-shells, i.e., individuals that may not have molted for two years. Conversely, all females had new exoskeletons, indicating that molting had probably occurred within the last six months. The exoskeleton condition of these 32 crabs was representative of the condition of the king crab stock in Norton Sound during September (Stevens and MacIntosh, 1986) and August (Stevens, 1989).

Although all crab stomachs from 1985 contained food (Table 3), most of the males contained very little (<25% full; $\bar{X}=0.22 \pm 0.21$ g), presumably reflecting a reduction of food intake near the time of molting. This contrasted to female stomachs in which most were 75 to 100% full ($\bar{X}=0.32 \pm 0.13$ g). Also, the feeding intensity of these males was much less than males observed in September/October 1976. The quantity of stomach contents among 1985 males was significantly less ($P<0.05$) than 1985 females and 1976 males.

Dominant Foods. The most frequent prey among 1976 crabs were brittle stars and bivalve mollusks (Tables 2 and 3). Although the brittle stars could not be identified, it probably was *Diamphiodia craterodmeta*, the dominant brittle star encountered in benthic samples in this region in a 1973 study (Feder and Mueller, 1974). Important bivalves taken were the Greenland cockle *Serripes groenlandicus*, *Yoldia* sp., and *Lyonsia* sp. (Table 3).

The most common prey in both crab sexes from 1985 were brittle stars, miscellaneous crabs, amphipods, snails and bivalve mollusks, in decreasing percent frequency of occurrence (Tables 2 and 3).

One of the differences between the food of offshore crabs from 1976 and 1985 was the high frequency of occurrence of the Greenland cockle in 1976 samples and its absence in 1985. While previous benthic sampling in Norton Sound (e.g., Feder and Jewett, 1978; Stoker, 1978) showed that large individuals of this cockle were once abundant, a 1985 survey found the numbers to be greatly reduced (Fukuyama and Oliver, 1985). In 1976 this cockle was also a dominant food of starry flounder (*Platichthys stellatus*) (Jewett and Feder, 1980) and four species of sea stars (Feder and Jewett, 1981). Reduced numbers of this cockle are presumably attributed to the recent elevated populations of Pacific walrus and bearded seal which prey intensively on large, mature cockles (Fukuyama and Oliver, 1985). Since red king crab are extremely opportunistic predators/scavengers (Jewett and Feder, 1982), the absence of a specific prey like the Greenland cockle from their diet is not likely to severely impact the crab population. Presumably other prey will replace the one(s) reduced or removed.

Nearshore-Offshore Comparisons

All previous studies that address food of red king crab conclude that at least one food group and/or species is dominant and that prey composition is usually area-specific. Some of the differences in the quality and quantity of prey between nearshore and offshore crabs are presumably attributed to the time of year the samples were collected, i.e., nearshore-March and offshore-September. Migratory behavior driven by molting/mating activities subject the crabs to different foods for variable food needs. Red king crab feeding studies in the Kodiak Island vicinity have shown that, in general, crabs from spring-early summer (May-July) contained significantly more food than crabs from late summer-fall-winter months (August, November, and February) (Jewett and Feder, 1982).

When the quantity of stomach contents was compared between male crabs offshore (1976 and 1985) and combined sexes nearshore (1986-89), 1976 offshore crabs had significantly ($P<0.05$) more contents than nearshore crabs, except for ones in 1986. Conversely, 1985 offshore crabs had significantly less contents than all nearshore crabs (Figure 3).

Some of the major prey groups consumed by crabs offshore differed from prey taken nearshore. The most notable difference was the preponderance of fish in nearshore crabs. Other food groups that dominated in nearshore crabs and not among those taken offshore were sea urchins and sand dollars.

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Diel Feeding Periodicity of Larvae of the Red King Crab, *Paralithodes camtschatica*

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ABSTRACT

Larval red king crabs (Paralithodes camtschatica) collected from 5, 10, 15, 20 and 30m at 4hr intervals for 24hr were examined for evidence of feeding periodicity. Percent of larvae with food in the gut (%WF), gut fullness (GFI) and position of food along the digestive tract (PF) were measured. Time of day and depth significantly affected %WF, GFI and PF (ANOVA, $P<0.05$). Larval stage was a significant determinant of %WF and GFI. Feeding patterns were consistent with the reverse diel vertical migration of king crab larvae; larvae fed at 5 to 10m during the day and fed at reduced rates or did not feed at night. An interruption in feeding was also observed at 1200hr coincident with a descent of larvae from 5 to 10m. Phytoplankton and copepod nauplii, potential food sources for larval king crabs, were concentrated at 8 and 5m, respectively, during the day when larvae occupied the upper 15m of the water column. Feeding periodicity was directly related to the vertical migration pattern of larval red king crabs.

INTRODUCTION

Larval feeding of red king crabs (Paralithodes camtschatica) has been investigated in laboratory studies relating to culture of the species (Sato, 1958; Kurata, 1959, 1960; Nakanishi and Naryu, 1981). Many diets have been proven successful to support growth and survival of larvae in the laboratory. Red king crab larvae are polyphagic, but their diet in the laboratory and the field generally consists of a combination of diatoms and crustacean nauplii with additional small contributions of other items (Sato, 1958; Kurata, 1959, 1960; Nakanishi and Naryu, 1981; Bright, 1967). The importance of initial feeding and starvation has been determined as well as the minimum ration for successful survival, molting and growth of first stage zoeae (Paul and Paul, 1980; Paul et al., in press).

Few studies have focused on in situ larval feeding. The temporal relationship between hatching and potential food sources has been examined with respect to larval survival (Shirley and Shirley, 1989, in press-b), but little is known of feeding periodicities or preferred feeding depths. Kurata (1960) reported that larvae in the laboratory fed more at night than during the day. His results appear contradictory to vertical migration patterns of king crab larvae observed in southeastern Alaska. Larvae were at 30m depth at night, an area of low food concentration, and at 5 and 10m during the day (Shirley and Shirley, in press-a).

The objectives of this study were to examine king crab larvae collected from discrete depths over a 24hr period for evidence of feeding patterns with depth and time. Percentage of larvae with food in the digestive tract, gut fullness and position of food in the gut were measured at 4hr intervals at five depths to determine when and where feeding occurred. Relationships between feeding and food abundance were investigated as was feeding of the different larval stages of red king crabs.

MATERIALS AND METHODS

Red king crab (Paralithodes camtschatica) larvae were collected on 22 and 23 May 1987, along a single cruise track located near the center of Auke Bay about 20 km north of Juneau, Alaska (58°22'N, 134°40'W) (Figure 1). Three replicate horizontal tows of an opening and closing 1.0 m^2 Tucker trawl equipped with 0.505 mm^2 mesh were made at 4hr intervals for 24hr beginning at 0800hr. The net was towed at approximately 2 to 3 $km \cdot hr^{-1}$ at the surface (neuston), and sequentially at depths of 5, 10, 15, 20 and 30m. A second vessel tracked the net hydroacoustically during deployment trials to verify sampling depth. The average depth along the cruise track was 50m, however, the maximum depth that could be sampled without encountering bottom obstructions or irregularities was 30m. The net was opened at each depth for 3 min. The volume of water filtered was measured with a General Oceanics digital flowmeter located within the mouth of the net. A drogue having the same resistance as the net was opened only when the net was closed to compensate for the difference in drag coefficients between an open and closed net.

Samples were fixed in 5% formalin on board the ship immediately after collection and returned to the laboratory for sorting and enumeration. King crab larvae were identified to larval stage using the criteria of Marukawa (1933) and Sato and Tanaka (1949).

Intact king crab larvae from one replicate (30 samples) were examined microscopically for determination of feeding periodicity by examining the presence of food material in the gut. Because king crab larvae are transparent, examination of digestive contents was possible without special staining techniques or dissection.

Three aspects of feeding were analyzed: percent of larvae with food in the gut, gut fullness and position of food within the digestive tract. The percentage of larvae with food in the digestive tract (%WF) was calculated from a binary determination of presence or absence of any ingested material in the larval guts. Position of food within the tract and gut fullness index were determined by subdividing the length of the digestive tract into four segments

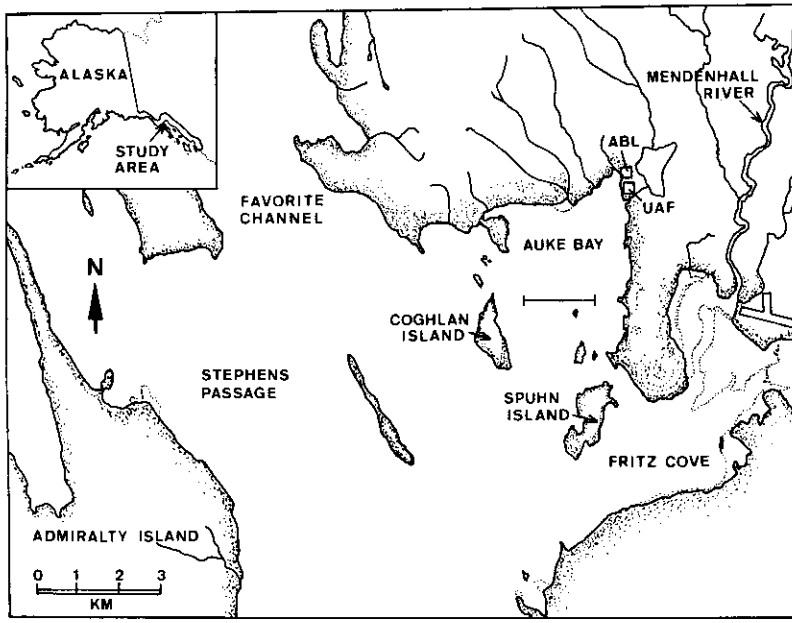

Figure 1. Location of study area in Auke Bay, Alaska. The sampling cruise track is indicated by the horizontal bar within Auke Bay and the University of Alaska Fairbanks Juneau Center for Fisheries and Ocean Sciences is labeled UAF.

numbered 1-4 from anterior to posterior. Position of food (PF) was scored as the location where food was first encountered along the gut progressing from the larval mouth to the anus. A score near 1 indicated food close to the mouth while a score near 4 indicated food close to the anus. The gut fullness index (GFI) was calculated as a measure of the percentage of the total length of the digestive tract that contained food. For example, if digestive tract segments 2 and 3 and the anterior half of segment 4 contained food, 62.5% of the length of the digestive tract contained food ((1+1+0.5)x25%=62.5%); the GFI value would be 62.5% and the PF value would be 2. A larvae with food in all 4 digestive tract segments would have a GFI of 100% and an PF of 1. The GFI was not used as a quantitative measure of food volume nor type of food ingested, but as a qualitative estimate of consumption, which, with %WF and PF, was used to determine feeding patterns of king crab larvae.

Feeding activity of king crab larvae (%WF, GFI and PF) was examined in two ways. Data were analyzed by time of day with all depths and larval stages combined for general trends in larval feeding. Data were also analyzed by time of day and depth to examine relationships between the diurnal vertical migration of king crab larvae and other stimuli. Gut fullness index and %WF were weighted to reflect number of larvae present at each depth by multiplying GFI or %WF by the percentage of total larvae for that time of day at a particular depth. Differences in feeding activity between larval stages were noted where appropriate.

All data are presented as mean ± one standard error of the mean. Multiple analysis of variance and multiple comparison t-tests were used to test for variation in %WF, GFI and PF among and between sampling times, larval stages and depths (SAS, 1985).

RESULTS

Sampling dates were selected to coincide with the limited time (approximately one week) that all larval stages of Paralithodes camtschatica were present in the water column of Auke Bay (Shirley and Shirley, 1989, in press-b). During this time, densities of stage 1 zoeae (ZI) and glaucothoe were low compared to densities of zoeal stages 2, 3 and 4 (ZII, ZIII and ZIV). A total of 776 red king crab larvae were examined for evidence of feeding activity: 31 ZI's, 220 ZII's, 304 ZIII's, 211 ZIV's and 10 glaucothoe.

Percent with food in the gut

Percent of larvae with food in the digestive tract varied significantly (ANOVA, $P<0.01$) with time of day, but over 80% of the larvae had food in their guts at any time of the day. More larvae had food present at 0400 (95.9 ± 0.2%) and 0800hr (95.2 ± 0.0%) than at other times (Figure 2). The lowest %WF was in larvae collected at 2400hr (80.6 ± 0.1%). The percentage of larvae with food present decreased significantly ($P<0.05$) with each consecutive sampling period from 0800 to 1600hr. A significant increase in %WF occurred from 2400 to 0400hr.

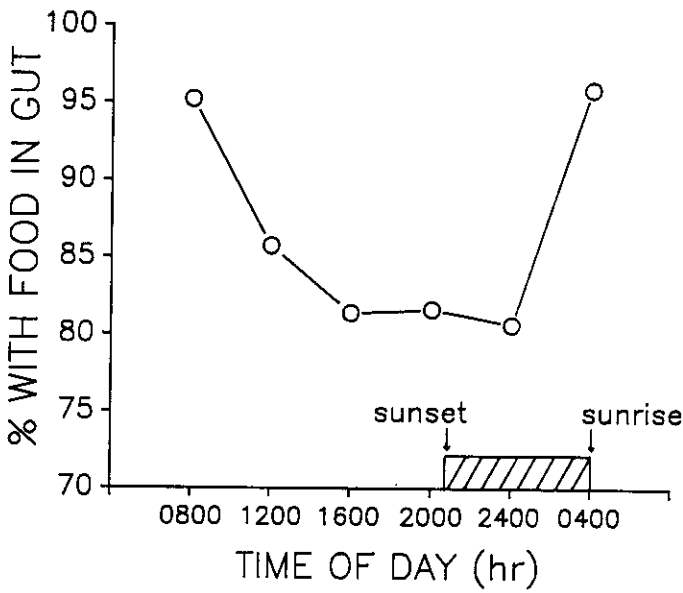

Figure 2. Percentage of king crab larvae with food in the digestive tract (all sampling depths and larval stages combined) over 24hr on 22-23 May 1987 in Auke Bay, Alaska.

Percent with food in the gut was also significantly related to depth and larval stage (ANOVA, P<0.01), and to interactions between time and depth, time and stage and depth and stage. At 2000 and 2400hr, the nocturnal samples, the weighted %WF was highest at depths of 15m and below (Figure 3). At 2000hr, the weighted %WF was highest at 15m, while at 2400hr the highest weighted %WF was at 30m. High %WF values were obtained from 10 to 20m at 0400hr with the maximum at 15m. A similar depth range of weighted %WF values was obtained at 0800hr with the maximum values at 5m.

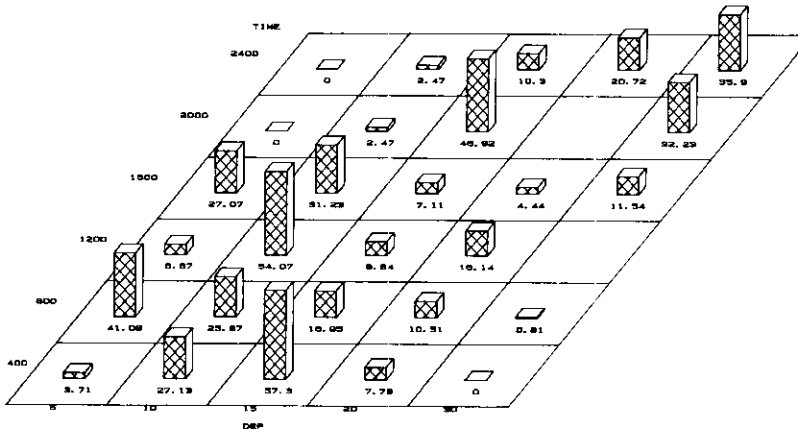

Figure 3. Percentage of king crab larvae with food in the digestive tract (all larval stages combined) by time and depth. Percentage values are weighted to reflect number of larvae collected at each time/depth (dep) combination.

Larval stages ZII, III and IV had food in their guts at 5 to 20m from 0400 to 1200hr. Only ZIII's and ZIV's had food present at 30m at 2000 and 2400hr; ZIV's also contained food at 15 and 20m at 2400hr. Too few ZI's and glaucothoe were collected at any time and depth to determine if %WF was different from the other larval stages.

Gut Fullness Index

Significant changes in GFI occurred between all consecutive sample periods except 0400 and 0800hr (P<0.05). Two periods of low GFI in king crab larvae were evident over a 24hr period. Gut fullness decreased significantly from a high of 58.5 ± 2.9% at 0800hr to 19.9 ± 1.3% at 1200hr (Figure 4). Gut fullness increased significantly at 1600hr and decreased again at 2400hr to 19.8 ± 3.7%.

The amount of food in the digestive tracts of king crab zoeae was related to time (P<0.01), depth (P<0.05) and stage (P<0.05) and

interactions between time and depth (P<0.01) and time and stage (P<0.05, ANOVA). The depth pattern of weighted GFI values was similar to that of weighted %WF except in the 2000 and 2400hr samples (Figure 5). Although weighted %WF was high at 15 to 30m (Figure 3), weighted GFI was low except at 15m at 2000hr (Figure 5). Mean gut fullness of ZI's and ZII's, averaged over all times and depths, was significantly lower than ZIII's and ZIV's.

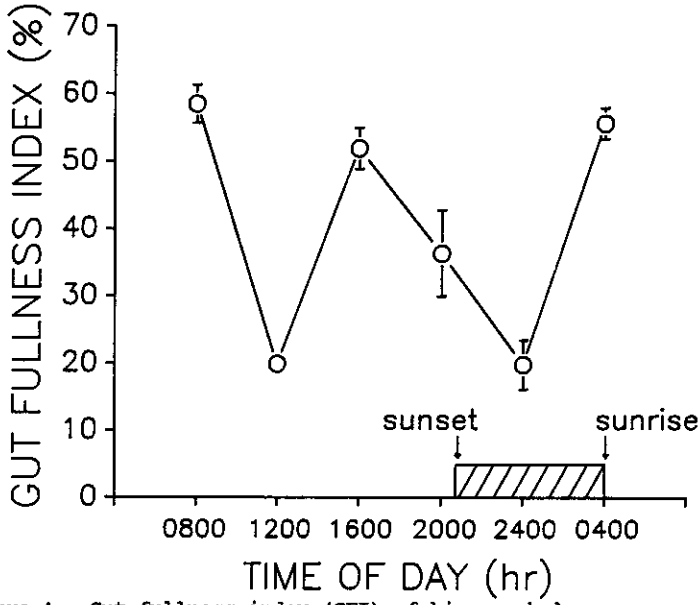

Figure 4. Gut fullness index (GFI) of king crab larvae over 24hr (all sampling depths and larval stages combined). Values are means ± one standard error. Where not visible, error bars are within the dimensions of the symbol.

Food Position

Position of food in the guts of king crab larvae did not change significantly over time except at 1200hr (Figure 6). Food position ranged from 1.6 ± 0.1 at 0400hr to 2.5 ± 0.1 at 1200hr. Depth and larval stage were not significantly related to food position (ANOVA).

DISCUSSION

The importance of using more than one index of larval feeding in the field was evident from our data. The %WF measurements suggested that king crab larvae were feeding at all depths and times because the percent of larvae with food in the digestive tract was always greater than 80%. The PF values indicated that active feeding may have occurred at all times except 1200hr because food was always present near the mouth. However, %WF and PF in conjunction with GFI indicate that larvae were feeding in shallower depths during the day and most larvae did not feed or fed at a reduced rate at night at depth. In contrast, Kurata (1960) reported in laboratory studies stage one zoeae of red king crabs fed more on *Artemia* nauplii at night than during the day.

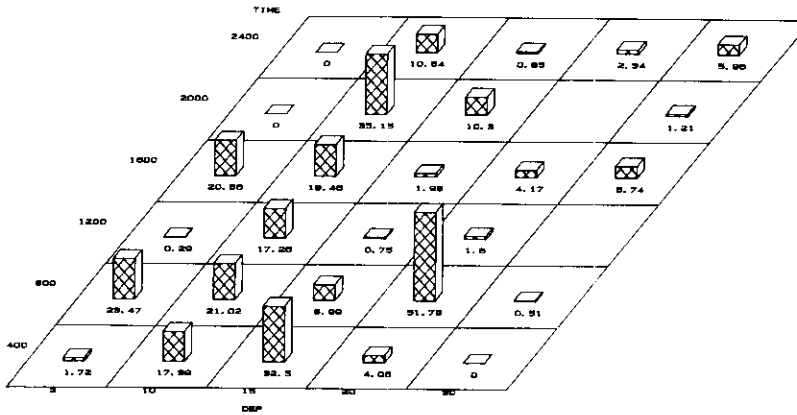

Figure 5. Gut fullness index (GFI) for king crab larvae over 24hr. Values are weighted to reflect number of larvae collected at each time/depth (dep) combination.

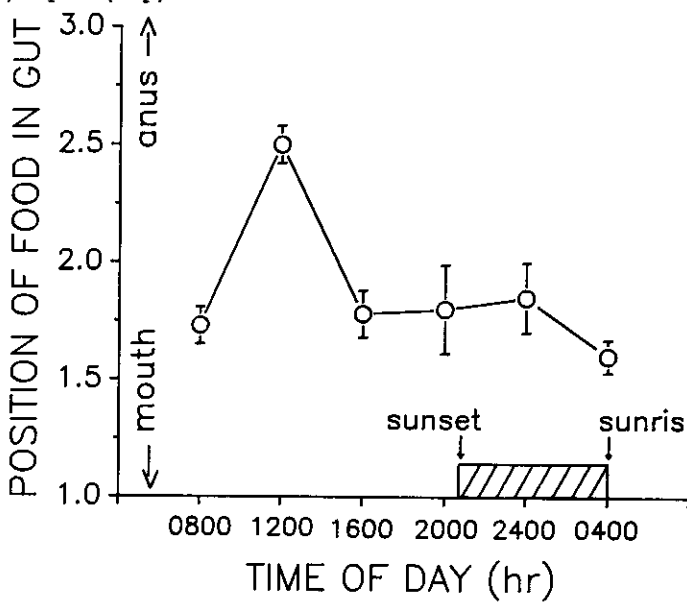

Figure 6. Position of food (PF) in the digestive tract of king crab larvae over 24hr (all sampling depths and larval stages combined). A PF near 1 indicates food near the mouth; a value near 3 indicates food in the lower digestive tract near the anus. Values are mean ± one standard error.

Gut fullness was greater during the day than at night and provided the best estimate of feeding activity in the field by king crab larvae. Because of the possibility of induced defecation with formalin fixation (Gauld, 1953), GFI values should be considered underestimates of actual gut fullness, even though ingested material was frequently observed in the posterior digestive tracts of many preserved larval king crabs.

Feeding by king crab larvae coincided with periods when larvae were at depths shallower than 20m. Feeding periodicity appeared to be directly related to the diurnal vertical migration. Red king crab larvae exhibit a pattern of reverse diel vertical migration (Shirley and Shirley, in press-a). Larvae are shallow during the day and at depth at night. In laboratory behavior studies, red king crab larvae displayed positive phototaxic responses to bright light and negative phototaxic responses to dim light. The photoresponses were consistent with the reverse diel migration pattern measured in the field (Shirley and Shirley, 1988).

Both feeding and vertical migration patterns coincided with the depth distribution of the predominant food sources for larvae in Auke Bay. Similar relationships between diurnal migrations and feeding in areas of food concentration have been established in the literature for other planktonic crustaceans (Gauld, 1953; Mackas and Bohrer, 1976; Arashkevich, 1977; Harris, 1988). Hatching of king crab larvae is temporally synchronized with the spring phytoplankton bloom in Auke Bay (Shirley and Shirley, 1989, in press-b). On 21 May 1987, the majority of the phytoplankton was between 4 and 15m with the maximum chlorophyll-a concentration at 8m (Figure 7, Ziemann et al., 1988). Below 15m, chlorophyll concentrations were an order of magnitude less than the maximum concentration. Copepod nauplii (100 to 350 µm in length), another potential food source for king crab larvae (Paul and Paul, 1980), were most concentrated at 5m during the day (Paul and Coyle, 1988) (Figure 7). Gut fullness was dependent on food concentration; larvae at 10m had high GFI values regardless of the time of day (Figure 5).

Feeding activity decreased not only at night when larvae migrated to depths with low food concentration, but also at noon when larvae were in the upper 20m of the water column. Food position was significantly more distal in the digestive tract of king crab larvae at 1200hr indicating an interruption of feeding (Figure 6). A midday descent from 5 to 10m was observed in the vertical migration of king crab larvae (Shirley and Shirley, in press-a). Low food availability does not explain the interrupted feeding at noon, as phytoplankton and naupliar concentrations were still high at 10m (Figure 7). As light-adapted larvae descend at noon through the phytoplankton layer they experience an 88% attenuation of light by the phytoplankton, similar to the 92% decrease in light (at 5m) from 1600 to 2000hr (Ziemann et al., 1988). A change in light level without a change in food availability could elicit an altered feeding response, but controlled laboratory studies are necessary to determine if this is the case for king crab larvae.

The reduction in feeding activity of red king crab larvae at night may be a result of several factors. Many zooplankters decrease ingestion rate and gut clearance time at low food concentrations (Boyd et al., 1980; Dagg and Grill, 1980; Dagg and Walser, 1987, 1988). Food concentrations were much lower at depths occupied by

king crab larvae at night than at depths occupied during the day. Also, reduced temperatures at depth may slow ingestion, metabolic and digestion rates (McLaren, 1963). Temperatures varied in Auke Bay on 21 May 1987 from 6.0°C at 5m to 4.7°C at 30m (Ziemann et al., 1988). Ingestion rates of the copepod Corycaeus anglicus, a visual

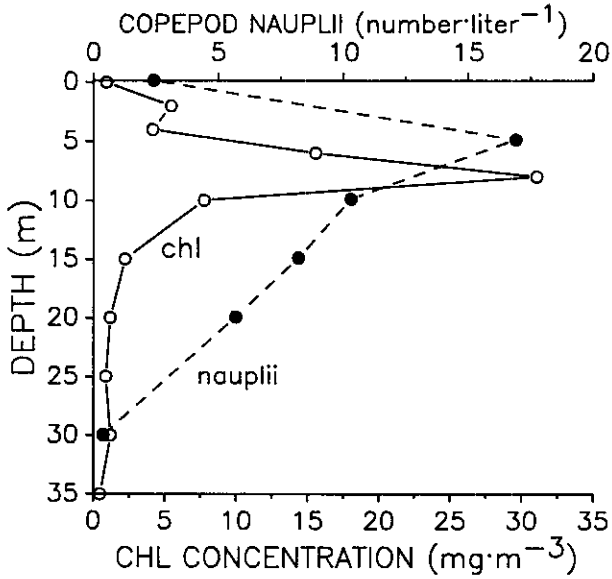

Figure 7. Vertical profile of chlorophyll-a concentration (chl, from Ziemann et al., 1988) and copepod naupliar concentration (from Paul and Coyle, 1988) on 21 May 1987 in Auke Bay, Alaska.

planktonic feeder, during daylight hours exceeded ingestion rates in the dark by an order of magnitude (Gophen and Harris, 1981). The use of visual cues for feeding by red king crab larvae has not been established but seems possible considering their large compound eyes and demonstrated photosensitivity. However, little evidence exists in the literature for dependence on light for feeding by crab larvae (Strathmann, 1987).

Reduced digestion rates may explain the high percentage of larvae with food in the digestive tract at night when feeding activity was low. Food located near the mouth (Figure 6) at night was either recently ingested, or because of slow metabolic rates, was not being digested. Some species retain ingested food for additional weight and reduced buoyancy while occupying depths, and defecate only immediately before vertically migrating upward (Arashkevich, 1977).

Field feeding studies like ours do not have the laboratory-associated problems of availability and proper concentrations and types of foods, lack of interactions between predators and prey, volume restrictions and artificial light and depth constraints. The simplistic methods used provide information on diurnal feeding of king crab larvae in relation to their vertical migration patterns and

food sources. Laboratory techniques for studying gut fullness and gut clearance rates such as gut fluorescence and tracer methodology, would provide complementary information concerning larval feeding biology of red king crab. Continued study of larval king crab feeding both in the laboratory and in the field, coupled with an understanding of environmental variation, may provide the basis for predicting king crab larval survival in relation to timing and availability of food in the field.

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Proc. Int. Symp. King & Tanner Crabs
Nov. 1989, Anchorage, Alaska

Growth of Adult Male Blue Crab (*Paralithodes platypus*)

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ABSTRACT

The National Marine Fisheries Service began tagging blue king crab (*Paralithodes platypus*) in the Pribilof Islands in 1978 and continued tagging through 1982. A total of 11,316 crab were tagged and 924 (8.2%) recovered in the Pribilof area, but no tagged crab were recaptured more than three years after release. Tagging in the St. Matthew area occurred in 1982 and 1983 and a total of 6,608 tagged crab were released. Tagged crab were recovered as long as six years after release in the St. Matthew area among 1,107 (15.4%) total recoveries. Standard isthmus (spaghetti) tags that had long been used for red king crab (*P. camtschaticus*) were used in both areas, but return rates varied considerably both between and within areas. Average single-molt growth increments were 14.3 (S.E. = 0.3) mm carapace length in the Pribilof Islands area and 14.4 (S.E. = 0.6) mm for St. Matthew Island. While growth increments did not differ appreciably between the two areas, St. Matthew crab are more likely to skip molting opportunities at a smaller size than Pribilof Island crab. Consequently, production and average size are higher in the Pribilof Islands.

INTRODUCTION

The blue king crab (*Paralithodes platypus*) is a large lithodid anomuran that occurs discontinuously around the north Pacific rim from Hokkaido to southeastern Alaska and as far north as outer Kotzebue Sound (Somerton, 1985). The species is not known from the Aleutian Islands. In the eastern Bering Sea (EBS), the largest populations occur in association with offshore islands (Otto, 1981) while small populations are known from Herendeen Bay, Nunivak Island, Seward Peninsula-King Island. Populations found near the Pribilof Islands and St. Matthew Island support commercial fisheries on an annual basis. Catches from other areas have been sporadic, incidental to other commercial crab fisheries or limited to small subsistence fisheries. The distribution of blue king crab between the Pribilof Islands

and St. Matthew Island is discontinuous and the two populations are regarded as discrete stocks for regulatory purposes (Alaska Department of Fish and Game (ADF&G), 1989). Interchange of larvae may occur between these two populations but has not been demonstrated. Pribilof and St. Matthew Island blue king crab differ with respect to size at maturity (Somerton and MacIntosh, 1985) and maximum size but do not differ in their weight at a given size (Somerton and MacIntosh, 1983).

Fisheries for blue king crab occur in North American and Asian waters but are much less important than fisheries for red king crab (*P. camtschaticus*). In the EBS and the Aleutian Islands, landings of blue king crab were about 13% of total king crab landings for the years 1979 through 1988. Due to drastic declines in red king crab abundance, however, blue king crab landings have been more important than usual in recent years. Fishing methods for the two species are identical and management measures have been similar through the history of both fisheries (Otto, 1981; Otto, 1986). The two species are not generally distinguished in commercial markets.

The National Marine Fisheries Service has conducted standard trawl surveys (Otto, 1986) of blue king crab in the Pribilofs since 1974 and in the St. Matthew Islands area since 1978. Size frequency data from trawl surveys, however, have not been amenable for growth studies because of overlapping modes, a paucity of small crabs, and generally small sample sizes. Tagging studies were initiated in 1978 and recovery data have been collected through 1989. This paper summarizes available information on growth, movements and mortality derived from blue king crab tagged near the Pribilof Islands (1978-82) and in the St. Matthew Island area (1982-83). Analyses of the tag return data and modeling efforts are still underway, so results given below should be regarded as preliminary.

METHODS

Crab were captured using king crab pots and immediately transferred to running sea water in an on-deck holding tank. Only males were retained for tagging. Crab were usually tagged on the day of capture but sometimes it was necessary to hold them overnight. Crab were checked for injuries and general condition. Only those crab which were vigorous and uninjured were tagged and released. The tagging process requires less than two minutes and is usually completed in about one minute.

Crab were tagged with isthmus loop tags that are sometimes referred to as "spaghetti" tags. These are composed of polyvinylchloride tubing and are approximately 2.0 mm outside diameter and 35 cm long. Each tag was printed with the legend "NMFS Kodiak" followed by a unique code consisting of a letter followed by four digits. Tags were conspicuously colored (florescent orange, red or pink). Tagging needles were made of stainless steel, approximately 1.5 mm diameter by 12.5 cm length and bent into a half circle. The blunt tapered end of the needle was inserted into the tubing and the opposite, sharpened end used to insert the tags. Tags were inserted through the isthmus of tissue that connects the median posterior portion of the carapace with the first segment of the abdomen. After threading tags through the isthmus they were tied with an overhand knot to form a loop.

The isthmus loop tagging procedure has a long history in studies of red king crab (*P. camtschaticus*) in Alaska (Alaska Fisheries Board and Alaska Department of

Fisheries, 1955; Weber and Miyahara, 1962; Hayes and Montgomery, 1963; Grey, 1964; Powell, 1965; Simpson and Shippen, 1968; Hoopes and Karinen, 1972). Development of the method was credited to Mr. E. J. Huizer of the Alaska Department of Fisheries by Hayes and Montgomery (1963) and Grey (1964). Takeshita et al. (1973) reported on the use of this method in the Bering Sea and the Sea of Okhotsk. Grey (1964) reported on a holding experiment in which 300 tagged female red king crab were held for 5-7 days. Grey found that one tag was lost among 261 crab which molted and no tags were lost among crab which did not molt. Grey (1964) reviewed other holding studies of tagged red king crab and attributed higher rates of tag loss to snagging in wire holding pens or to the stiffness of early versions of the tag's tubing. Takeshita et al. (1973) reported no tag-induced mortality in red king crab held for 55 to 65 days and judged that initial tagging mortality was less than 2%. Takeshita et al. also reported a tag loss rate of 2 in 120 for unmolted crab in the same experiment. Powell (1965) reported on recapturing a male red king crab after six years at large. Hoopes and Karinen (1972) reported tagged red king crab that were at large for up to 11 years. The isthmus loop tag was chosen in the present study because blue king crab and red king crab are of similar sizes and nearly identical with respect to relevant anatomical features. We also felt that use of this procedure would facilitate comparison with studies of red king crab. There was, however, no attempt to quantify tag-induced mortality or tag loss in blue king crab.

Data recorded for each tagged crab included carapace length (CL), carapace width, shell condition, date and release position (latitude and longitude to the nearest minute). Carapace measurements were taken to the nearest millimeter according to the method of Wallace et al. (1949). Both length and width were measured because the length-width relationship is useful in identifying potential measurement errors, however, such analyses have not yet been completed. All tag returns occurred during fishing operations. Tags were returned by fishermen and processing personnel. Tag rewards have been $1.00 for a tag returned with no information and $10.00 for tags returned with information as complete as possible. A lottery system on returned tags and bonus tags was also employed. Tag return data was collected by the Alaska Department of Fish and Game (ADF&G) in 1978 and 1979, by NMFS personnel stationed in Dutch Harbor in 1980, 1981 and 1982, and through a post card system supervised by the ADF&G thereafter. Rates of return may have been influenced by collection method, rewards, and fishery related factors, but those possibilities will require further analysis. Return data are frequently not complete and may, for example, consist only of a returned tag, which leads to differing sample sizes with respect to items discussed below.

RESULTS

Total Returns by Year

A total of 17,924 male blue king crab were tagged and 1,941 (10.5%) were recovered with legible tags. An additional 35 illegible tags were recovered but excluded from the analysis below. In the Pribilof Islands, 11,316 tags were released between 1978 and 1982 and 924 (8.2%) were recovered through 1989 (Table 1). In the St. Matthew Island area, 6608 tags were released in 1982 and 1983 while 1,017 (15.4%) were recovered (Table 2). Overall recovery rates were significantly higher in the St. Matthew Island area (Chi-square = 201.1, $p < 0.005$, 1 df). Pribilof Islands crab were not recaptured more than three years after release while one crab tagged in the St. Matthew Island area during June of 1983 was recovered in September of 1989 or 6 years and 3 months after release. Although returned over

Table 1. Release and recovery data for blue king crab tagged in the Pribilof Islands, all recoveries are from the fall fishery which begins September 25.

Release Year (Dates)	Tagged Crab Released	Size Range (CL mm)		Recovery Data				Totals
1978	312	143-187	Yr.	78	79	80	81	
(8/14-8/21)			N	15	7	3	0	25
			%	4.8	2.2	1.0	0.0	8.0
1979	1784	136-191	Yr.	79	80	81	82	
(6/15-6/29)			N	109	102	30	7	248
			%	6.1	5.7	1.7	0.4	13.9
1980	5385	72-190	Yr.	80	81	82	83	
(5/15-6/23)			N	348	162	47	6	563
			%	6.5	3.0	0.9	0.1	10.5
1981	297	79-184	Yr.	81	82	83	84	
(6/16-6/18)			N	30	5	2	0	37
			%	10.1	1.7	0.7	0.0	12.5
1982	3538	74-196	Yr.	82	83	84	85	
(6/25-7/11)			N	34	15	1	1	51
			%	1.0	0.4	0.0	0.0	1.4
Totals	11316		N	536	291	83	14	924
			%	4.7	2.6	0.7	0.1	8.2

Table 2. Release and recovery data for blue king crab tagged in the St. Matthew Island area, all recoveries are from the fall fishery which begins September 1.

Release Year (Dates)	Tagged Crab Released	Size Range (CL mm)		Recovery Data				Totals
1982	2140	77-161	Yr.	82	83	84	85	
(6/15-6/22)			N	122	10	6	0	138
			%	5.7	0.5	0.3	0.0	6.4
1983	4468	78-170	Yr.	83	84	85	86-89	
(6/23-7/03)			N	822	30	24	3	879
			%	18.4	0.7	0.5	0.1	19.7
Totals	6608		N	944	40	30	3	1017
			%	14.3	0.6	0.5	0.0	15.4

a longer period of time, a greater portion of St. Matthew Island returns (93%) occurred during the fishing season immediately following tagging than was true for the Pribilof Islands (58%). By consequence, return data for St. Matthew Island were very sparse and provided less information on incremental growth per molt and the probability of molting (see below). Additionally, total return rates were not homogenous with respect to year of release in the Pribilof Islands (Chi-square = 309, $p < 0.005$, 4 df) or in the St. Matthew Island area (Chi-square = 164.4, $p < 0.005$, 1 df) .

Migration

Information on the geographic position where crab were recaptured was available for 317 returns from the Pribilof Islands and 253 returns from the St. Matthew

Island area. Distances between point of release and point of recapture averaged 52.4 km (S.E. 1.9) and ranged from less than 1.0 km to 178.0 km in the Pribilof Islands. In the St. Matthew Island area such distances averaged 28.1 km (S.E. 1.2) and ranged from less than 1.0 km to 120.0 km. There was no instance where a crab tagged in one of the the above two areas was recaptured in the other. Tag return data hence support the notion that adult blue king crab do not migrate between the Pribilof Islands and the St. Matthew Island area.

Growth Per Molt

In the Pribilof Islands area there were 650 tags returned with carapace length measurements, or 70% of the 924 returns. Measurements from crab returned within the first 6 months provided a preliminary estimate of measurement bias since blue king crab would not normally molt during the summer tagging period and the September fishery. Examination of these data showed however that 18 crab of 376 returned within 6 months had apparent increments of growth greater than 3.0 mm but that none of the deviations between CL at release and recovery were less than -2.0 mm. We simply assigned all crab that showed apparent growth of 3.0 mm or less to measurement error. Using this interval, measurement error between returned CL and released CL averaged 0.3 mm (variance 0.9 mm) for crab at large for less than 6 months. Corresponding average error for the entire Pribilof Islands data set was -0.2 mm (variance 1.0 mm).

In the St. Matthew Islands area 519 of 1,017 (51%) returned tags were accompanied by CL measurements. There were 18 crab for which the deviation between returned and released CL exceeded 3.0 mm in less than 6 months at large and no deviations less than -2.0 mm. For crab at large less than 6 months with deviations of 3.0 mm or less, the mean deviation was -0.3 mm (variance 0.9 mm). Corresponding average error for the entire St. Matthew Island data set was -0.3 mm (variance 0.9 mm).

Since differences between the St. Matthew and Pribilof Islands data sets were small, they were combined and measurement error averaged -0.2 mm (variance 1.0 mm). Both data sets showed deviations that could not readily be assigned to molting or bias (Fig. 1). In the Pribilof Island data set these have a mode at 5.0 mm which could easily arise by misreading a caliper by one major graduation although it is not clear why a corresponding error of -5.0 mm is absent. We consider the interval of 4.0 to 7.0 mm as an indeterminant interval and simply ignored values within it for purposes of characterizing error or apparent growth. This resulted in discarding data for 17 returns from the Pribilof Islands and 10 returns from the St. Matthew Islands area.

Inspection of both data sets showed a mode of apparent growth at 15.0 mm (Fig. 1). We characterized average growth per molt by partitioning the data symmetrically about this mode and computing averages for the interval 8.0 to 22.0 mm of apparent growth. For the Pribilof Islands, the average increment was in this interval was 14.3 mm (variance 10.6 mm). The corresponding average for the St. Matthew Islands area was 14.4 mm (variance 11.0 mm). Since differences between areas were negligible, the data sets were combined and the average for this interval was 14.3 mm (variance 10.6 mm, n = 144). Assuming that error was additive we corrected this mean deviation by subtracting 0.2 mm and its variance by subtracting 1.0 mm. The mean increment of growth per molt for both populations was, therefore, considered as 14.1 mm with a variance of 9.6 mm. We modeled a single growth increment at molting using the normal distribution (Fig. 2) and used this distribution in modeling cohort growth for both areas.

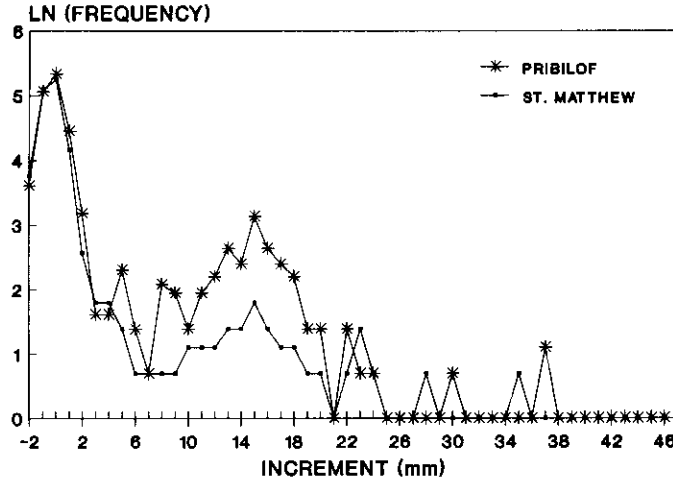

Figure 1. Deviations between carapace length at recovery and length at release for tagged blue king crab released in the Pribilof Islands and the St. Matthew Island area. Frequencies are expressed as natural logarithims for scaling.

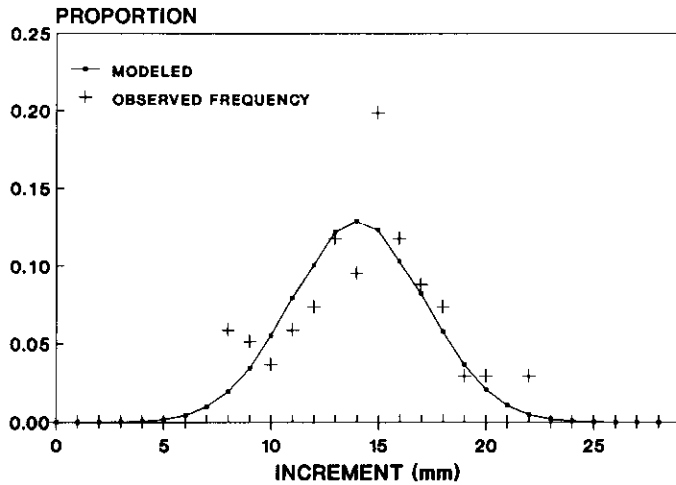

Figure 2. Observed and modeled carapace length increments per molt for combined tagging data from the Pribilof Islands and the St. Matthew Island area.

Probability of Molting

The annual probability of molting was characterized by considering measured crab that were returned between 12 and 18 months of release. These data were further partitioned by 5.0 mm carapace length groups and the proportion molting was computed for each group. Deviations between release and recovery CL that

exceeded 7.0 mm were considered to represent crab that had molted. For the Pribilof Islands area, computed proportions molting tended to decline with increasing size (Fig. 3). There were only 27 returns with measured CL for the St. Matthew Island area that occurred 12 to 18 months after release and data were too

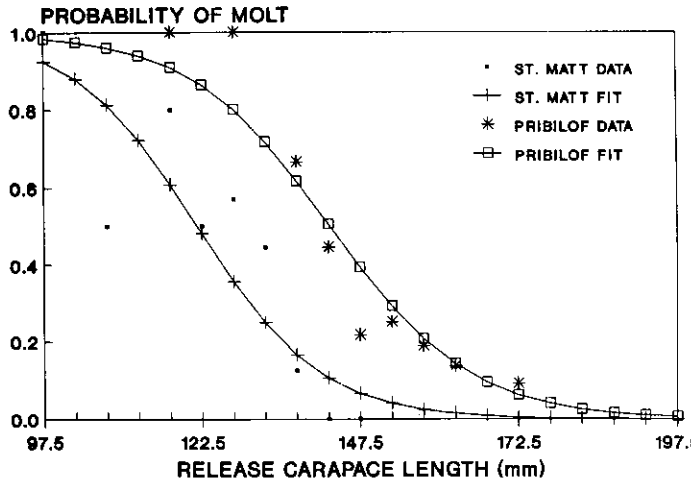

Figure 3. Fits of logistic curves (asymtotes equal to 1.0) to the observed proportion of tagged blue king crab which molted in 12 to 18 months for the Pribilof Islands and for periods greater than 12 months in the St. Matthew Island area, taken by 5.0 mm carapace length group.

sparse to calculate molting probabilities. As a first approximation all return data for times at large exceeding 12 months were used in the St. Matthew area. Data for both areas were modeled by fitting a logistic curve to the proportion molting (Fig. 3). This model assumes that the annual probability of molting is 1.0 at small, unsampled sizes. Parameters were estimated through linear transformation of the logistic curve and unweighted least squares linear regression. The equation for the relationship between the probability of molting (P) and CL at the mid-point of the i'th 5.0 mm interval (x) was:

$$P_i = 1.0/(1.0 + a\, e^{bx}).$$

Parameters were $a = 2 \times 10^5$, $b = 0.091$ and r-square = 0.84 for the Pribilof Islands and Parameters were $a = 3 \times 10^5$, $b = 0.103$, and r-square = 0.64 for the St. Matthew Island area. Despite the crude methods used, the resultant models seem to provide a reasonable summary of available data (Fig. 3). We plan to refine modeling the relationship of molting probabilities to CL but accepted these models as adequate for preliminary characterization of cohort growth.

Mortality

Blue king crab fisheries occur over a short period of time each fall and natural mortality can be conveniently ignored during the fishing season. During the period

from 1978 through 1985 almost all landings of Pribilof Islands blue king crab occurred over a period of time which was less than 6 weeks long. In the St. Matthew Islands area fishing periods between 1983 and 1989 have not exceeded 3 weeks. Total mortalities for each 5.0 mm group were computed by regressing the natural logarithm of the number returned against the number of years at large. There were too few data points (almost always less than 3 years) to test significant of such regressions and resultant slopes or instantaneous total mortality rates were simply accepted as the best determinations available. Survival rates were computed by converting total instantaneous mortality to a proportion and subtracting the rate of utilization in each fishery. The annual expectation of natural death (n) can be computed from the relation $A = m + n - mn$ where total mortality (A) and the expectation of death by fishing or exploitation rate (m) are known. Rates of exploitation were taken as the ratio of crab captured (ADF&G, 1989) to the NMFS trawl survey estimates of legal-size crab abundance (Stevens and MacIntosh, 1989) and averaged over the years that tagged crab were at large in each area. Small crab for which data were lacking were assumed to have a survival rate of 0.9. Calculations are shown in Tables 3 and 4. Resultant survival rates were smoothed by a moving 3-point average and fit to a logistic equation with an asymptote of 0.9 rather than 1.0 (numerator in equation above). Smoothed data points and fitted equations (Fig. 4) represent a first approximation to survival against the force of natural mortality for each size group. Parameters for the Pribilof Islands were $a = 5 \times 10^6$ and $b = 0.077$; and for St. Matthew Islands area they were $a = 5 \times 10^6$ and $b = 0.095$. No statistical analysis of the relationship of natural mortality to size has yet been attempted.

Table 3. Calculated values of survival by 5 mm carapace length (CL) groups for Pribilof Islands blue king crab[1] in comparison to fitted logistic curve.

Size Range (CL mm)	Computed Total Surv.	Smoothed Total Surv.	Annual Probability of Death			Natural Surv.	Curve
			Total	Fishing[2]	Natural[3]		
0-129	0.90	0.90	0.10	0.00	0.10	0.90	---
130-134	0.90	0.90	0.10	0.00	0.10	0.90	0.79
135-139	0.90	0.77	0.23	0.04	0.19	0.81	0.74
140-144	0.52	0.60	0.40	0.15	0.29	0.71	0.69
145-149	0.39	0.40	0.60	0.18	0.52	0.48	0.62
150-154	0.28	0.31	0.69	0.29	0.56	0.44	0.54
155-159	0.27	0.27	0.73	0.24	0.64	0.36	0.45
160-164	0.27	0.27	0.73	0.37	0.58	0.42	0.37
165-169	0.26	0.27	0.73	0.30	0.61	0.39	0.29
170-174	0.29						0.22
175-179							0.16
180-184							0.12

[1] Survival for crab smaller than 139 mm CL are assumed to be the same as those for red king crab (see Balsiger, 1974). Smoothed by three point average.

[2] This is the average rate of utilization for the years 1978 to 1983 determined from length-frequency and total catch provided by the Alaska Department of Fish and Game as compared to National Marine Fisheries Service trawl survey estimates of abundance.

[3] Determined from A=m+n-mn, where A is total mortality, m is the rate of exploitation and n is the conditional rate of natural mortality.

Table 4. Calculated values of survival by 5 mm carapace length (CL) groups for St. Matthew Island area blue king crab[1] in comparison to fitted logistic curve.

Size Range (CL mm)	Computed Total Surv.	Smoothed Total Surv.	Annual Probability of Death			Natural Surv.	Curve
			Total	Fishing[2]	Natural[3]		
0- 99	0.90	0.90	0.10	0.00	0.10	0.90	---
100-104	0.90	0.83	0.17	0.00	0.17	0.83	0.82
105-109	0.68	0.83	0.18	0.00	0.18	0.83	0.78
110-114	0.89	0.71	0.29	0.00	0.29	0.71	0.72
115-119	0.55	0.59	0.41	0.04	0.39	0.61	0.55
120-124	0.32	0.38	0.62	0.17	0.54	0.46	0.45
125-129	0.29	0.27	0.73	0.35	0.59	0.41	0.34
130-134	0.20	0.20	0.80	0.49	0.62	0.38	0.25
135-139	0.10	0.07	0.93	0.44	0.87	0.13	0.17
140-144	0.00						0.12

[1] Survival for crab smaller than 104 mm CL are assumed to be the same as those for red king crab (see Balsiger, 1974). Smoothed by three point average.

[2] This is the average rate of utilization for the years 1982 to 1983 determined from length-frequency and total catch provided by the Alaska Department of Fish and Game as compared to National Marine Fisheries Service trawl survey estimates of abundance.

[3] Determined from A=m+n-mn, where A is total mortality, m is the rate of exploitation and n is the conditional rate of natural mortality.

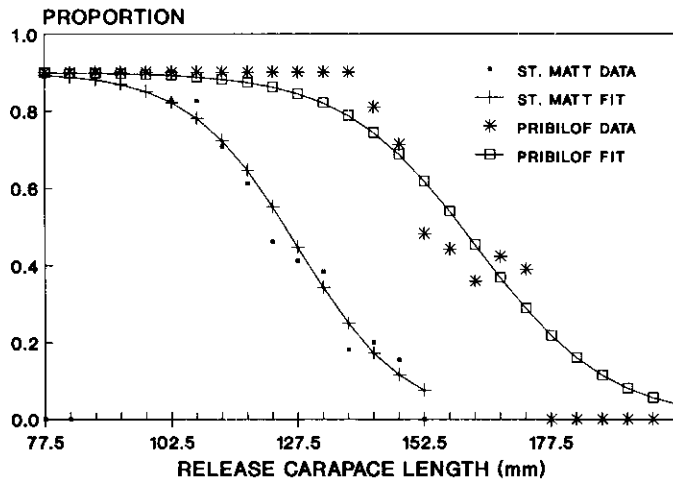

Figure 4. Fits of logistic curves (asymtotes equal to 0.9) to smoothed probabilities of survival in the absence of fishing by 5.0 mm carapace length groups for Pribilof Islands and St. Matthew Island area blue king crab.

Cohort Growth

Incremental growth, the probability of molting and survival were combined to compute the growth and decay of a hypothetical cohort. Calculations are essentially

the same as those given in Otto (1986) except that they were performed recursively. A cohort consisting of 10 million crab between 80.0 and 84.0 mm was used as a starting point and size frequencies of surviving crab were computed in annual steps. Weights were computed from the length-weight relationships given by Somerton and MacIntosh (1985) as applied to midpoints of 5.0 mm groups (as above). Computed cohort numbers and biomass (Fig. 5) show that maximum biomass would be reached at 4 model years for the Pribilof Islands and 2 model years in the St. Matthew Island area. The mean size of a male blue king crab at the time of maximum cohort biomass was 125.0 mm CL for the Pribilof Islands and 102.0 mm CL for the St. Matthew Island area. Legal carapace width for the two areas are 165.0 mm for the Pribilof Islands and 140.0 mm for the St. Matthew Island area. These convert to approximately 135.0 mm CL and 120.0 mm respectively. Apparently maximum cohort biomass is reached at average sizes that are 8 to 15% smaller than legal size.

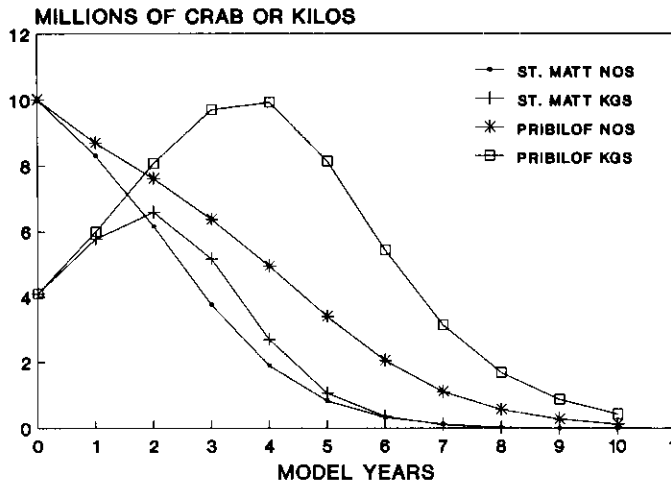

Figure 5. Growth and decay of hypothethical cohorts in Pribilof Islands and St. Matthew Island area blue king crab, 10 million crab averaging 82.5 mm carapacelength are entered at year zero.

DISCUSSION

The models used in this report are in the process of being revised and the above represents a first approximation to the growth and decay of cohorts. Our intent here is simply to provide preliminary results from models presently at hand. One problem that will be difficult to surmount is that the rate of tag return given recapture is not known for any year and may not have been constant over the course of time that tags were returned. As a result, we see few ways of statistically treating estimates of mortality. We will likely be choosing a range of plausible rates in future modeling efforts.

Incremental growth data are somewhat more tractable than mortality data and perhaps amenable to more rigorous statistical treatment. For example, examination of the carapace length-width relationship may allow us to remove some erroneous measurements. The apparent occurrence of molting between the time of release in

June or July and the subsequent fall fisheries which start in September was surprising since we did not observe molting actively during tagging. Crab which molt in late summer may differ in growth characteristics from those molting in late spring or summer, and would tend to be over-represented in the data due to the high proportion of crab returned from the first fishing season following release. If, for example, a disproportionate number of such late-molting crab had small increments in growth per molt, it could prove impossible to assign a reasonable number of moltings to an observed increment of growth. If this appears to be the case we will simply attempt to relate increments of CL between release and recapture to time at large using an empirical probability model.

Data available for estimating the annual probability of molting are sparse, particularly for the St. Matthew Island area. This problem is severe because the probability of molting appears to decline with increasing size and hence would contribute heavily to the relationship between cohort biomass and time. A discrete growth model may provide an approach to this problem but errors in estimating the probability of zero growth will still have a strong influence on growth curves. There also may be an interaction between the probability of molting and natural mortality. Very few tagged crab were recovered that had skipped molting for two years. We plan to examine growth models where the probability of molting and incremental growth are conditional with respect to molting history in the manner described by McCaughran and Powell (1977).

CONCLUSIONS

1. Adult male blue king crab do not migrate between the Pribilof Islands and the St. Matthew Island areas.

2. Incremental growth in carapace length for a single molt averaged 14.1 mm and did not differ between the Pribilof Islands and the St. Matthew Island area.

3. St. Matthew Island area blue king crab are smaller than those in the Pribilof Islands when:
   a) anecdysis begins to occur,
   b) the expectation of natural death begins to increase, and
   c) maximum cohort biomass is reached.

ACKNOWLEDGEMENTS

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Growth of Immature Southern King Crab, *Lithodes santolla*, in the Beagle Channel

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ABSTRACT

Growth in immature (3-75 mm CL) Lithodes santolla was studied in the Beagle Channel, Argentina (55° South Latitude). Crabs have been kept in bottomless cages and acclimatized tanks from September 1986 to March 1988. Increment per molt is: CLpremolt = 3.59 +1.057 CL postmolt. Growth factor decreases as crab size increases (PI% = 28.696 x $e^{-.0157}$ CL). These relationships were not significantly different for both sexes. Crabs 0+ aged molt 6-7 times a year; 1+ molt 4-5 times a year and in 2+ 3 molts can occur or less often 2. Then crabs begin to skip winter molt. Females 3+ molt once a year while males would molt twice a year. It was found that the weight-CL ratio was significantly different for crabs > and < 55 mm CL. This fact coincides with the beginning of gametogenesis process.

INTRODUCTION

The southern king crab, commonly named "centolla" in Chile and Argentina, is an abundant lithodid of the coastal subantarctic waters of South America. In this area, Lithodes santolla, L.turkayi and L.confundens are the three known species of the genus (Macpherson, 1988). L.santolla and the false king crab, Paralomis granulosa are the only commercially exploited species. Both species inhabit the continental shelves and coasts of South Pacific and South Atlantic Oceans, from Tierra del Fuego to Uruguay or South Brazil.

Managing a fishery requires a deep understanding of life history aspects of the involved species. Although it is very important to know the relationship between size and age during their complete life span, biological information

concerning southern king crab was performed mainly on adult crabs or larvae. There are few works dealing with immature animals.

Growth assessments in adult L.santolla were obtained from capture-recapture studies (Geaghan, 1973; Boschi et al., 1984) or from molt observations of confined crabs (Vinuesa and Lombardo, 1982). Campodónico and López (1987;1988) report growth per molt in juvenile crabs from the Magellan Strait, providing considerable information on length increment for specific premolt lengths on the southern king crabs. It is well known that among different geographical areas - and even within the same locality - growth variations can occur (Weber, 1967; Karinen, 1985). It is also known that in mature crabs mean length increment is sex dependent: male growth per molt is larger than that of females (Geaghan, 1973; Vinuesa and Lombardo, 1982;Boschi et al., 1984).

There is little information on molt frequency in L.santolla. Geaghan (1973) proposes that juvenile crabs would probably molt several times a year; mature crabs molt annually and larger animals may molt biennially. Vinuesa and Lombardo (1982) conclude that oviposition is an annual event that takes place after ecdysis. Regarding mature Lithodes santolla, molt process is very similar to that observed in Paralithodes camtschatica (Weber, 1967; McCaughran and Powell, 1977).

The purpose of this study is to describe growth process in Lithodes santolla juveniles in the Beagle Channel area (55° South Latitude).

MATERIAL AND METHODS

Southern king crabs ranging in size from 8.2-75 mm carapace length (CL) were caught in the Beagle Channel and Ushuaia Bay (figure 1) at 6 to 40 m depth by scuba divers, from August 1986 to March 1988. A 3% of the crabs were caught using tangle nets and special outlined pots.

Larger crabs were kept in submerged bottomless cages (figure 2) of which surfaces are wide enough to hold many crabs ranging in size from 30-75 mm CL. Cages were separated into two compartments and had doors to allow an easy access to divers. In an attempt to maintain the natural conditions, cages were placed at the bottom of a shallow bay that is frequently inhabited by immature crabs.

Marking was made by using a numbered "spaghetti" tag tied to the wrist of the crabs. This type of tagging has proved to be satisfactory in previous aquaria experiments, at least in one molt.

When crabs were too small to be tagged their growth was studied by placing them in 90-liter subdivided tanks. In an acclimatized laboratory, water temperatures were maintained similar to those of the sea and salinity oscillated near to

Figure 1: Geographic location of the area of which crabs were collected.

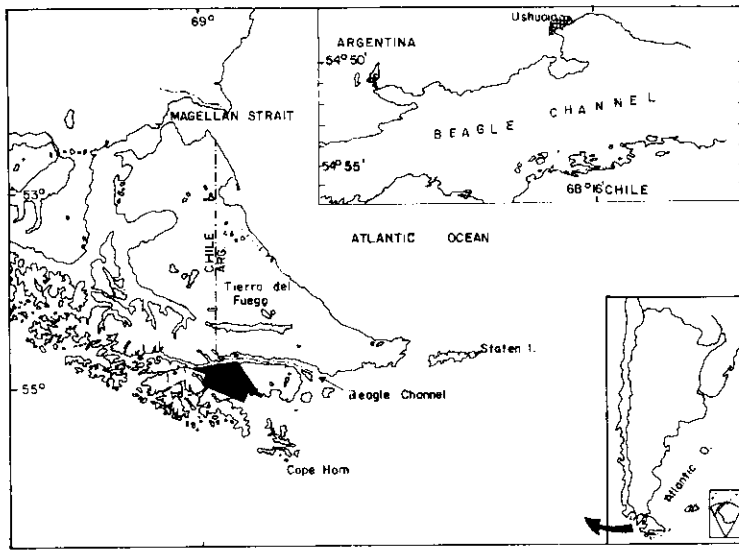
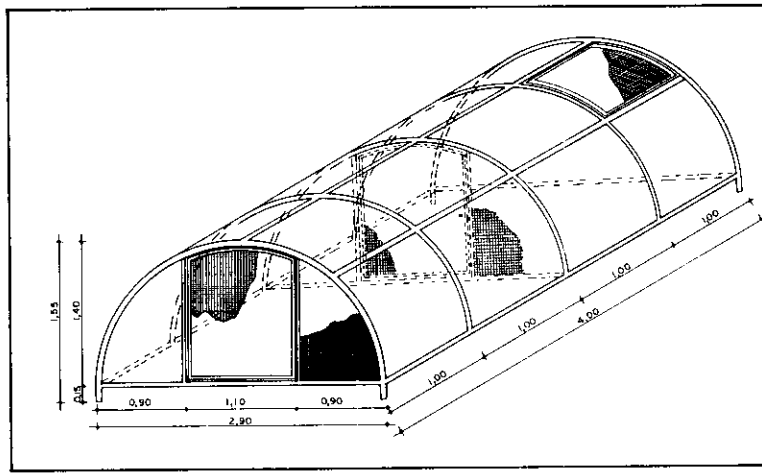


Figure 2: Bottomless cage design.



30 parts per thousand. Tanks were oxygenated by a pump-filter system.

The linear measurements handled are carapace length (CL), right chelae length and second leg merus length. They were measured with a vernier caliper scaled in mm to the nearest one-tenth millimeter. Having casted the old carapace, a brief postmolt expansion period occurs. It finishes when carapace becomes rigid and maximun size is attained. Thus, in this work, early intermolt measurements were considered to be post molt ones. After some minutes of air exposure to remove the excess of water, crabs were weighed to the nearest gram with a portable electronic balance.

Exoskeletal age is the basic parameter to determine molt frequency (Powell, 1967). According to this, color, hardness and abundance of epizoic organisms were taken into account to classify carapace types. These includes four stages: post molt, early and advanced intermolt and premolt.

When the experience begun, crabs had all the appendages and no external parasites. Crabs which had lost chelipeds and/ or legs during molt were not taken into account in the studied data, though they were kept in culture to study regeneration and appendage growth. Molt and mortality events were monthly controlled. Crabs were fed with different species of regional fishes once a fortnight.

Tag and recapture method was not practical to study length increase per molt in juvenile L.santolla, provided that returns are scarce and commercial fishing gear is selective for large crabs only. Modal progression could not be applied as representative monthly samples of juveniles that encompass the whole size ranges were difficult to obtain.

RESULTS AND DISCUSSION

In order to assess size ranges in immature L.santolla, cultured glaucothoe CLs were measured. These ones reflected that CL varies between 1.96 and 2,40 mm, while previous larval studies (Campodónico, 1971) showed that mean glaucothoe CLwas 2.16 mm. Furthermore, the smallest juveniles found in the Beagle Channel were about 4 mm CL. Owing to these data it is possible that the smallest adult form in L.santolla be approximately 3 mm CL.

Sexual maturity varies in relation to regions or depths. This is a very frequent result in the studied lithodids, Paralithodes camtschatica (Marukawa, 1933; Wallace et al., 1949; Weber, 1967); P.platypus (Somerton and MacIntosh, 1983); Lithodes couesi (Somerton, 1981); L.aequispina (Somerton and Otto, 1986) and L.santolla (Geaghan, 1973; Sanhueza, 1976; Campodónico and Hernández, 1983; Vinuesa, 1984;1985). In the studied area, the mean size at sexual maturity was found to be about 75 mm CL. These facts and the purposes of the study, enable us to consider that size ranges in immature southern king crab encompass from 3 mm CL, for the first adult form, to approximately 75mm CL at sexual maturity.

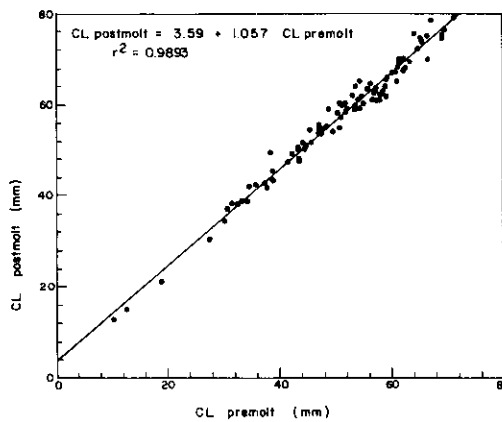
Increment per molt

Lithodes santolla exhibits an indeterminate growth, as it was noted for many crustaceans by Hartnoll (1985). Molt process continues after attaining maturity and until death, with no clear terminal anecdysis.

Some authors pointed out that if crustaceans are kept in cultures for longer than a week, they will present an increment per molt less than that of the recently caught animals that molt in the laboratory (Templeman, 1948; Takeuchi, 1960). To assess the possible effects of confinement on the amount of growth per molt, a comparison of growth per molt in crabs of which molt occur shortly after collecting with the growth per molt of those which molted in captivity two or more months after their capture, was carried out. This comparison of growth percentage increment does not differ significantly between them ($P < 0.001$), suggesting that there is no confinement effect on growth per molt.

The Gray-Newcombe or Hiatt growth diagram of 103 juveniles L.santolla is shown in figure 3. There was no evidence of change in post molt CL with premolt CL for either males or females; i.e. the slopes of the above type of plots did not significantly differ between them, although slope for males (b=1.067) was larger than that for females (b=1.050). So, data from both sexes were assembled. Furthermore, the regression slope for individuals < 55 mm CL did not differ from that for the individuals > 55 mm CL.

Figure 3: Gray Newcombe or Hiatt diagram of 103 immature southern king crab, L.santolla.



Growth factor (percent growth per molt) for both sexes of immature crabs decreases as crab size increases (figure 4). ANOVA for regression showed that the model is significant ($P < 0.01$) and a low but significant ($P < 0.01$) correlation coefficient was observed. This could be due to a high

variability of the individual growth; i.e. for sizes from 36-40 mm CL, percent growth may range from 10 to 30 per cent. The obtained equation was used in order to calculate the number of required molts to reach an expected CL. Starting from 3.0 mm CL and using the obtained post molt CL as the following pre molt CL value, 15 molts were needed to reach a value close to 55 mm cl. Adding 3 other molts an approximately 75 mm CL value was obtained (table 1).

Figure 4: Relationship between the percent increment and carapace length in immature crabs.

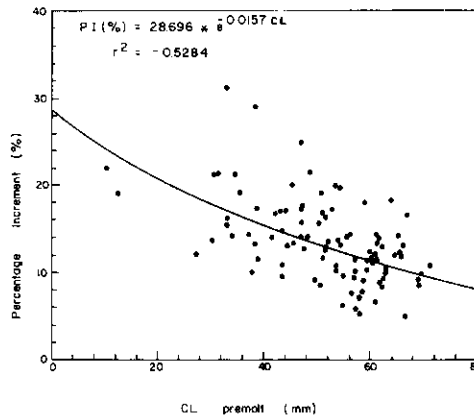


Table 1: Simulated growth process in immature L.santolla according to percent increment here calculated.

Molt event No.	CLpre	PI%	CLpost	Confidence Interval (95%)
1	3.00	27.38	3.82	3.78 - 3.86
2	3.82	27.03	4.85	4.81 - 4.90
3	4.85	26.60	6.14	6.08 - 6.21
4	6.14	26.06	7.75	7.67 - 7.82
5	7.75	25.42	9.71	9.62 - 9.81
6	9.71	24.64	12.11	11.99 - 12.23
7	12.11	23.73	14.98	14.83 - 15.13
8	14.98	22.68	18.38	18.20 - 18.56
9	18.38	21.50	22.33	22.11 - 22.55
10	22.33	20.21	26.84	26.58 - 27.10
11	26.84	18.83	31.90	31.59 - 32.20
12	31.90	17.39	37.44	37.09 - 37.80
13	37.44	15.94	43.41	43.00 - 43.82
14	43.41	14.51	49.71	49.25 - 50.18
15	49.71	13.15	56.25	55.72 - 56.78
16	56.25	11.87	62.92	62.32 - 63.52
17	62.92	10.69	69.65	68.96 - 70.33
18	69.65	9.61	76.34	75.57 - 77.12

Absolute growth per molt increases as size does so (figure 5). Although an analysis of variance for regression showed that the model is significant ($P < 0.01$), the low correlation coefficient (significant; $P < 0.01$), dennotate a high variability of data. The absolute increment may vary from 2.8 to 11.6 mm CL for individuals > 30 mm CL. Means of absolute increments of the studied size ranges are listed in table 2. High variability and mean increment in L. santolla are in accordance with data from the Magellan Strait (Geaghan, 1973; Campodónico and López, 1988).

Figure 5: Relationship between the absolute growth per molt in mm and carapace length in immature L.santolla.

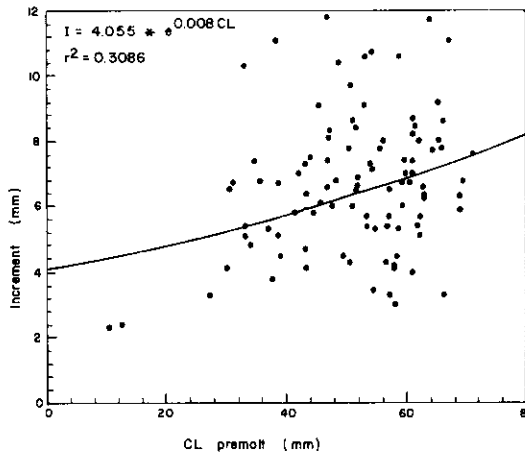


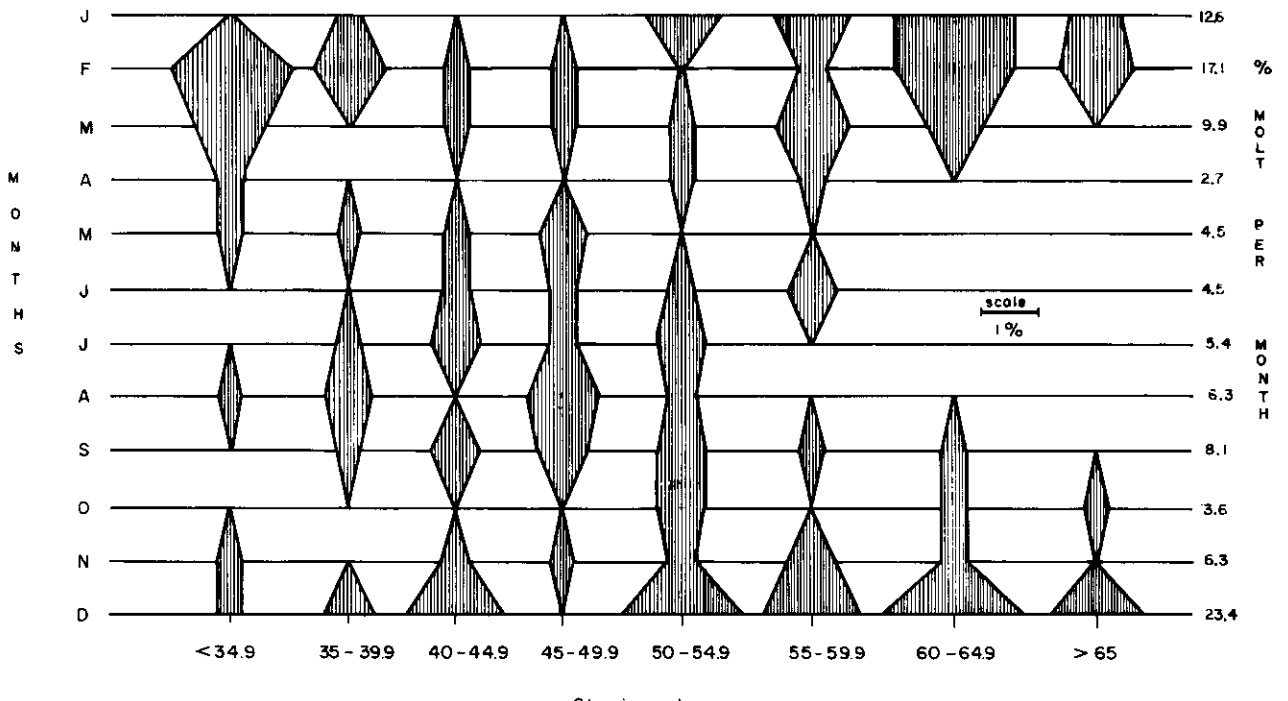
Table 2: Absolute growth per size class in immature southern king crab.

Size range (in mm CL)	Mean Growth(in mm)	S.D.
30 - 34.9	5.21	1.15
35 - 39.9	5.66	1.23
40 - 44.9	6.07	1.10
45 - 49.9	7.36	1.48
50 - 54.9	7.40	1.84
55 - 59.9	5.30	1.53
60 - 64.9	7.09	1.64
65 - 69.9	7.67	2.10

Molt frequency

In cultured crabs, ecdysis occur during all the year. Crabs > 55 mm CL had a major molting incidence between December and March; while crabs < 50 mm CL had it in July and August (figure 6). The lowest molting activity was observed between April and June. These results may be

Figure 6: Molt frequency per size class and per month. Scale bar is 1% of the total of molts observed in culture.



slightly seasonally biased because there are always more cultured crabs during summer. In winter captures are reduced, perhaps due to crab migrations to deeper waters.

Crabs > 55-60 mm CL begin to skip molt in July and August; while crabs < 55 mm CL molt asinchronously and during all the year.

Provided the scarcity of cultured crabs < 30 mm CL, molt frequency for each size class was estimated by applying the relation between the percentage of increment per molt and CL size (figure 4; table 1). This equation was related to some scuba diving samples carried out after 9, 12 and 25 months since November when glaucothoe molt (GM) to the first juvenile instar occurs. In July 1987 (9 months after GM), the capture crabs had an average CL = 8.9 mm. Those caught in December 1987 (13 months from GM) ranged from 10.5 to 12.7 mm CL These data revealed that juveniles from both sexes molt 6-7 times during the first year (table 1).

During the second year, information on molting history was obtained from a sample of 17 crabs from both sexes that were captured in January 1988 (25 months from GM). Mean CL was 35.0 mm, with sizes ranging between 28.7 and 41.8 mm CL. These crabs molted approximately 11 or 12 times. Thus enabling us to expect 4 to 5 molts during the second year.

Crabs captured between March and April 1987 (CL ranging from 43.1 to 48.7 mm) molted from two to three times during the year. One (43.2 mm CL), caught in March in postmolt condition, molted again in July, January and April; another one (43.1 mm CL), captured in April, molted in late April, August and December. Several crabs of similar sizes captured in January molt during that summer, in late winter or early spring and again in the next summer. Two molts were also observed in some captive crabs ranging from 38.7 to 45.3 mm CL. During the third year, three molts can be expected, though less often two molts can occur. At the end of the third year, crab size is approximately 55-60 mm CL.

In the fourth year crabs skip winter molting, but even though, two molts were observed from culture data. Crabs molt in September or October and again in summer or early autumn. Females > 60 mm CL have an annual molt that usually takes place from November to February. In the 77.8% of the captive females > 50.5 mm CL (N=27), ecdysis occured during the latter molting season. These results led us to conclude that male crabs have two molts during the fourth year, but females have an only annual molt.

Males > 65-70 mm CL continue molting twice a year and with larger increments than those of the younger crabs; such as Geaghan (1973) stated, males ranging from 70-74 mm CL begin to molt once a year, and two molts may occur until crabs reach 100-104 mm CL.

Intermolt period reflects a gradual increment from larvae to large adult crabs. Zoeae rearings of L.santolla at

similar temperatures and salinities than those of the Beagle Channel waters showed that the mean duration of the three larval stages was 6, 7 and 10 days respectively (Vinuesa et al., 1985). Cultured glaucothoe remained without molting for longer than 15 days. Juveniles molt several times a year, pubescent females and mature animals molt once a year and large adult male crabs > 105 mm CL begin to skip annual molt (Geaghan, 1973; Boschi et al., 1984; Bertuche et al., 1985).

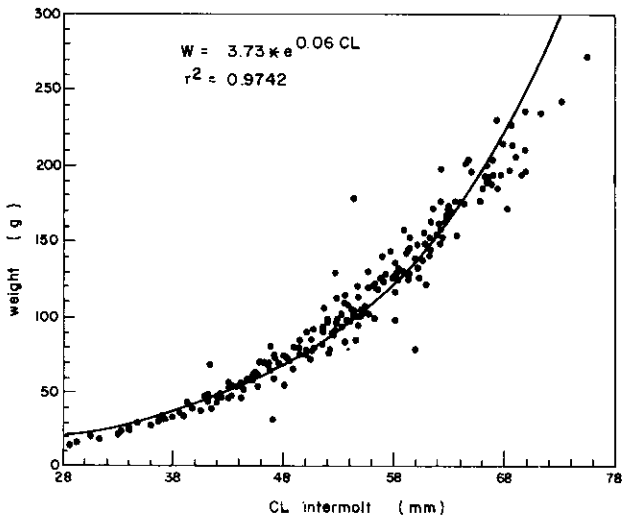
Length - Weight relationship in juvenile crabs

During molting cycle, calculation of length and weight relationship depends, partly, on when weight measurements are taken as weight normally increases after a fast absorption of water. In Lithodes santolla, during intermolt, replacement of heavier body tissues takes place as weight slowly increases. The weight of postmolt crabs may be less than that of premolt individuals of similar lengths such as observed in Paralithodes camtschatica (Weber, 1967) and other crabs (Kurata, 1960).

Figure 7 shows the relationship obtained for 220 crabs during intermolt period. A comparison of regression curves for both sexes, proved to be non-significant. Then all the information for both sexes was assembled.

Weight gain factor (WGF) -calculated as the slope of the exponential function- is 0.070 for animals < 55 mm CL. This value is significantly higher than that for crabs > 55 mm CL (WGF=0.047). It can be observed that a greater part of the data from crabs > 64 mm CL fall under the fitted curve.

figure 7: Relationship between the live intermolt weight and carapace length in immature L.santolla.



Weber (1967) observed in Paralithodes camtschatica an inflexion point in the percent growth per molt at 55-60 mm CL. He stated that at this size range immature king crabs enter into the pre-pubescent phase due to an allometric growth phenomenon. McCaughran and Powell (1967) explained it as a reassignment of energy from growth to reproduction.

In Lithodes santolla it was observed that gametogenesis lasts two year and begins in crabs of which size is approximately 55 mm CL (Vinuesa, MS). In female crabs -close to 60 mm CL- some changes in the allometric growth also occur (Campodónico et al., 1974; Vinuesa, 1984). Though allometric growth among body linear measurements was not found in this study, length and weight ratio for immature crabs, which has an inflexion point at approximately 60 mm CL, could be reflecting the aforementioned fact. Evidently, these changes in the growing process plus a decrease in molting frequency during winter, are due to the beginning of gametogenesis process.

The reassignment of energy in L.santolla females > 55 mm CL would result into a single molt per year, while in males up to approximately 105 mm CL it would be causing two molts per year.

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Nov. 1989, Anchorage, Alaska

Food of Early Benthic Stages of Snow Crab (*Chionoecetes opilio*) in the Southwestern Gulf of St. Lawrence

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INTRODUCTION

The adults of snow crab Chionoecetes opilio are generally considered to live on deep muddy bottoms while the juveniles are found essentially on upper bathymetric levels, on gravelly-muddy bottoms (Coulombe et al., 1985). This change in habitat may induce changes in behavior, and especially in feeding. Brêthes et al. (1984) pointed out the influence of the depth on the diet of adult C. opilio in the southwestern Gulf of St-Lawrence. In the southeastern part of the Bering Sea, the habitat and the feeding of young C. opilio differed from the adults (Tarverdieva, 1976).

This work presents preliminary results on the diet of early benthic stages of C. opilio in the southwestern Gulf of St-Lawrence with special reference to the size of the individuals.

METHODS

The 663 C. opilio of both sexes come from the entrance of the Chaleur Bay, in the southwestern Gulf of St-Lawrence. They were collected with a beam trawl (1,8 m mouth and 12 mm netting), at depths of 70-120 m, on gravelly-muddy and muddy substrates during the summers of 1986 and 1987 at different periods of the day in the entrance of the Chaleur Bay, Southwestern Gulf of St-Lawrence (Fig. 1).

The carapace widths ranged from 5 to 75 mm (Fig. 2). Individuals were preserved in 70% alcohol immediately after the capture. Later, the stomach contents were analyzed and a repletion index (RI) was estimated after a visual examination: a scale from 0 to 10 indicates a stomach empty to full. Daily feeding rhythm of small individuals (CW < 30 mm) was determined after plotting the relative frequencies (%) of RI against time of the day; four classes of RI were considered (0 = empty,

1 to 3 = slightly filled, 4 to 7 = half-full, 8 to 10 = full stomach). In order to know if there is a difference between stomach content between day (from 0500 to 1700) and night (from 2000 to 0500), the distribution of these classes of RI during day and night periods were compared with a Chi-square (X^2) test.

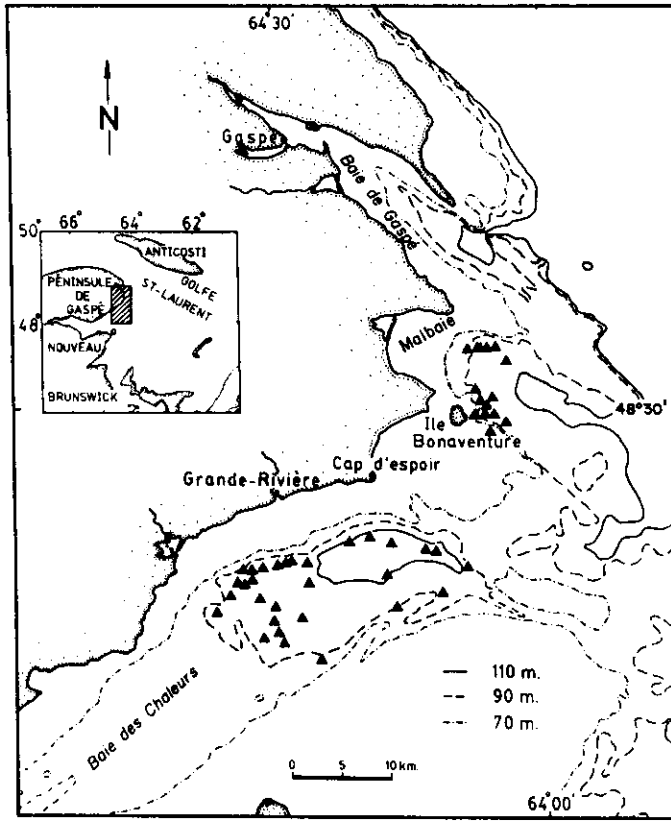

Fig. 1. Location of the study area and position of sampling stations.

The prey were determined at the lowest possible taxon under microscope. Frequency of occurrence was recorded and expressed in terms of the number of stomachs containing one or more individuals of each food category and expressed as a percentage of all stomachs. Numerical presence is the number of individuals in each food category and expressed as a percentage of the total individuals in all food categories (Hyslop, 1980).

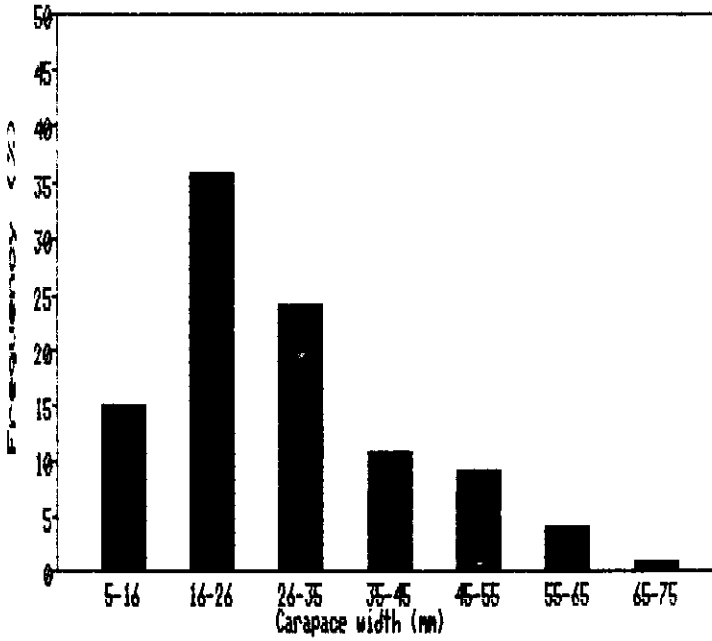

Fig. 2. Size frequency distribution of C. opilio (n=663) used in this study.

In order to verify the hypothesis of a variation in diet with size, individuals were grouped in 4 classes of CW (5-15, 16-26, 26-35 and 35-73 mm). A Chi-square (X^2) test (Scherrer, 1984) was used to check the significance of the association between the main food items and the crab size.

RESULTS

Daily Feeding Rhythm

Within the area studied, the juvenile C. opilio (CW < 30 mm) was feeding chiefly at night (Fig. 3). At 2200 and at 0100, local time, respectively 53% and 50% of stomachs were full. At the beginning of the day, the number of full stomachs declines (55% of stomachs at 0500 to none at 0800) and remains low (< 20% of stomachs) till the end of the afternoon when it increases to 30% at 2000. The variation of the percentage of empty stomachs shows obvious opposite trends. There were more empty stomachs during the day than at night (50% of crabs at midday). The half-full stomachs line shows that there was more food in crabs at night than at day except at 1500.

This variation in the daily feeding rhythm is verified by the Chi-square (X^2) test on the absolute frequencies of repletion index (Table 1). This analysis shows a highly significant difference ($X^2 = 14.08$; df = 3; $P < 0.005$) in the relative proportions of

the distribution of stomach fullness between day and night indicating a larger feeding activity during the night.

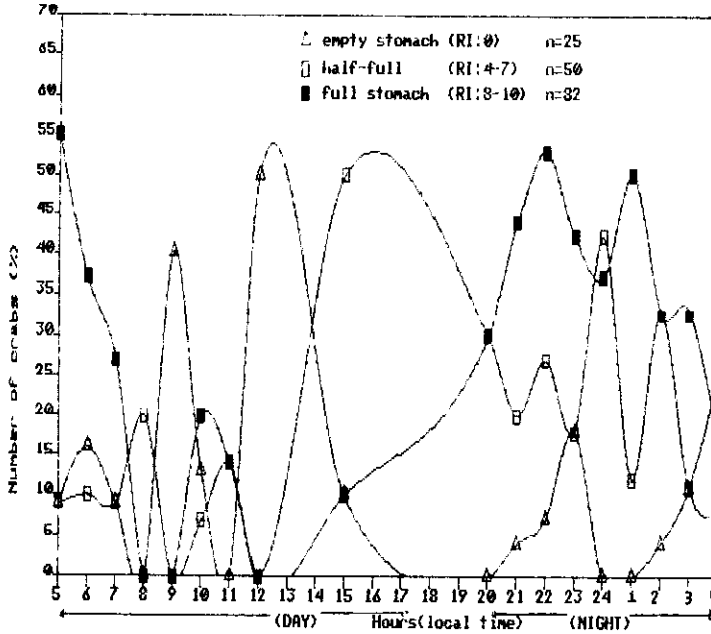

Fig. 3. Daily feeding rhythm of C. opilio (CW < 30 mm).

Table 1. Repletion indices of stomachs of 246 Chionoecetes opilio (CW < 30 mm) collected in the entrance of the Chaleur Bay.

Repletion indices (RI) (scale: 0 to 10)		Number of crabs (%) day (n=87)	night (n=159)
0	(empty stomach)	14	8
1-3	(slightly filled)	48	30
4-7	(half-full)	14	24
8-10	(full stomach)	24	38

Diet of snow crab

Crustacea appear to be the most important food items (Table 2), in terms of frequency of occurrence, as they are found in 83.1% of the stomachs (fig. 4); the greatest part remaining unindentified (30.7%), followed by Euphausiacea (24.9%). Amphipoda, Copepoda and Cumacea occur also frequently.

Table 2. Food items in stomachs of 663 Chionoecetes opilio (CW < 73 mm), collected in the entrance of the Chaleur Bay. (N.p. : Numerical presence; P.f. : frequency of occurrence)

Food items	N.p. %	P.f. %
Polychaeta		
Polynoidae	12,8	46,9
Sigalionidae	8,5	31,2
Nephtydae	7,8	28,6
Phyllodocidae	5,5	20,2
Nereidae	0,1	0,5
Hesionidae	1,2	4,7
Glyceridae	0,3	1,0
Sphaerodoridae	--	0,2
Lumbrineridae	3,9	14,2
Capitellidae	7,0	2,6
Dorvilleidae	0,1	0,3
Spionidae	8,6	31.3
Maldanidae	5,0	18,2
Flabelligeridae	1,7	6,1
Scalibregmidae	0,4	1,5
Trochochetidae	0,2	0,8
Terebellidae	0,4	1,7
Sabellidae	0,7	2,7
Pectinaridae	-	0,2
Serpulidae	0,4	1,5
Ampharetidae	0,2	0,6
Sternaspididae	-	0,2
Tube only	2,0	7,4
Unidentified	6,1	22,3
Total Polychaeta	66,8	**80,9**
Crustacea		
Decapoda	-	0,3
Tanaidacea	0,6	2,3
Cumacea	2,7	10,0
Euphausiacea	6,8	24,9
Amphipoda	4,7	17,0
Copepoda	4,6	16,8
Unidentified	8,5	30,7
Total Crustacea	27,9	**83,1**
Mollusca		
Pelecypoda	1,0	3,8
Gastropoda	2,4	8,8
Unidentified	1,9	6,8
Total Mollusca	5,3	**18,3**
Spicules of sponges		36,2

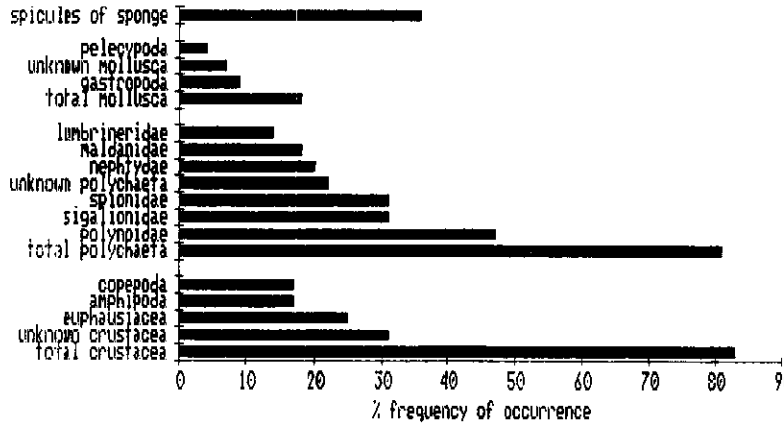

Fig. 4. Relative importance of main food items in stomachs of C. opilio (CW < 73 mm) from Chaleur Bay.

Polychaeta are found almost as frequently as Crustacea in stomachs (80.9%) with the Polynoidae being encountered most often (46.9%), followed by Sigalionidae (31.2%) and Spionidae (31.3%). An importantpart of Polychaeta were unknown (22.3%). Nephtydae, Maldanidae and Lumbrineridae compose the remaining part of the Polychaeta. Mollusca are represented with only 18.3% of frequency of occurrence. Gastropoda (8.8%) were found more often than Pelecypoda (3.8%), although 6.8% of Mollusca remains unidentified. Spicules of sponges were encountered frequently, in 36.2% of stomachs.

In terms of numerical presence, Polychaeta represent 66.8% of the prey compared with Crustacea (27.9%) and Mollusca (5.3%).

When the crabs are grouped in four classes of CW (Table 3 and Fig. 5), frequency of occurrence of Polychaeta increases with size. Mollusca show the same trend. No obvious trend is observed for total Crustacea, although Euphausiacea increase with size. Polychaeta slightly surpass Crustacea in frequency of occurence, except for crabs of 5-15 mm CW where Crustacea are far more frequent in the stomachs.

The X^2 test on the absolute frequencies (Table 3) indicates that the composition of the diet is related to the size of individuals (X^2 = 91,47; df = 21; P < 0,005).

DISCUSSION

The daily feeding rhythm of early benthic stages of Chionocetes opilio corresponds to the observed rhythm for the adults, with a greater activity during the night (Brêthes et al., 1984).

Table 3. Main food items in stomachs of 663 Chionoecetes opilio (CW < 73 mm) grouped in 4 classes of size, collected in the entrance of Chaleur Bay (P.f.: percent frequency of occurrence).

Food items	P.f. (%)			
	Carapace width (mm)			
	5-15 (n=98)	16-26 (n=240)	26-35 (n=158)	35-73 (n=167)
Polychaeta	50	83	89	89
Polynoidae	18	43	54	62
Sigalionidae	19	35	39	26
Spionidae	5	29	44	38
Crustacea	79	82	87	83
Euphausiacea	9	17	22	49
Mollusca	6	21	17	23
Spicules of Sponges	19	43	44	30

The results on feeding are limited since the substratum is not yet taken into account. However, positive tendencies are outlined. Here, only frequency of occurrence will be considered since it was not possible to know exactly how many individuals of each prey were present in a stomach. The opportunistic character of C. opilio from Chaleur Bay is again confirmed except for smallest crabs (CW = 5-15 mm). It seems that these early stages prefer Crustacea in terms of frequency of occurrence and would be more selective, while crabs of CW > 15 mm rely, on most part, on Polychaeta and Crustacea. Tarverdieva (1976) noted this importance of Polychaeta as a food source for crabs with CW of 23-44 mm, in the southeastern part of the Bering Sea: the diet was dominated by Polychaeta (81.7%), then by Mollusca (63.2%) and Crustacea (59.1%, mainly Amphipoda).

The diet of juveniles differ from older stages studied by Brêthes et al. (1984) (Fig. 6). Crustacea are dominant for both stages but Polychaeta are in greater importance for young crabs. The free-moving forms of Polychaeta seem to be easier to catch. The increasing importance of Polychaeta as a food source as the crabs grow does not conform with result of that study on more mature crabs. The use of microscope in this present research has probably made Polychaeta prominent by the identification of the setae. Moreover, setae could remain a long time in the digestive tract before being evacuated. Predominance of Polychaeta has been reported in Newfoundland by Miller and O'Keefe (1981); Polychaeta, followed by Echinodermata and Pelecypoda represented the most frequent prey.

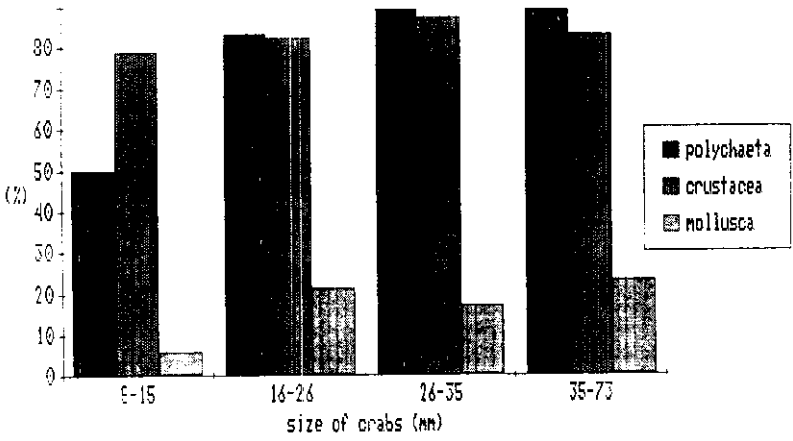

Figure 5. Percent frequency of occurrence of main food items in stomachs of C. opilio from Chaleur Bay.

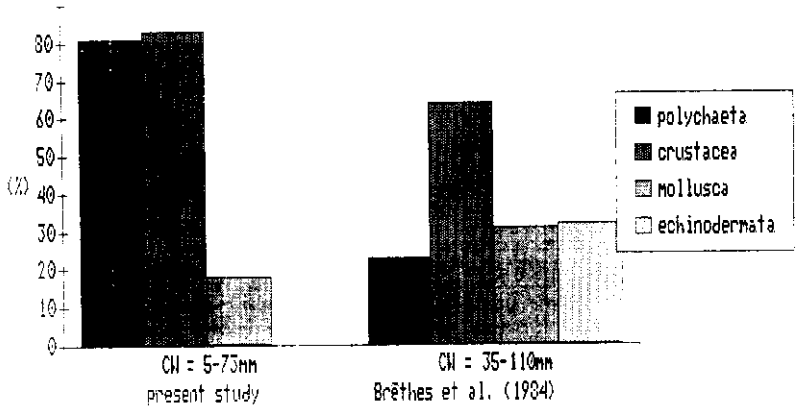

Figure 6. Percent frequency of occurrence of main food items in stomachs of C. opilio from Chaleur Bay.

With the crabs' growth, Mollusca occur more frequently in the stomachs. This occurrence is progressively more common as crabs mature (Brêthes et al., 1984). Mollusca seem to be a more difficult prey for early benthic stages to handle, as may be true of Echinodermata. These are not found in stomach of young crabs. The

above-mentioned studies for older crabs include Echinodermata in their stomachs. It could be a characteristic of juveniles that they are not able to feed on this taxon.

More than 36% of the individuals ingested spicules of sponges which seems to indicate that the early benthic stages of C. opilio ingest a certain amount of sediment while feeding.

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ABSTRACT

Observations with regard to the stomach contents of Chionoecetes opilio (carapace width < 75 mm) were made on specimens found at the entrance of the Chaleur Bay, in the southwestern Gulf of St-Lawrence. Individuals were collected using a beam trawl at depths of 70-120 m, on gravelly-muddy and muddy substrates, during the summers of 1986 and 1987. The contents of 663 stomachs were analyzed. A repletion index (RI) was estimated and the prey were determined to the lowest possible taxon.

The daily feeding rhythm of early benthic stages (CW < 30 mm) was determined while considering four classes of RI on 246 crabs. A significant difference between day and night in the repletion indices was observed, showing a nocturnal feeding activity for these early benthic stages of snow crab, as is the case in the adult stages. The frequency of occurrence of identified prey indicates the importance of Crustacea (83% of the stomachs, mainly Euphausiacea and Amphipoda) and the Polychaeta (81%, mainly Polynoidae, Sigalionidae and Spionidae) in the diet. Mollusca are present in only 18% of the stomachs. When comparing feeding of crabs from different classes of sizes (CW = 5-15 mm, 16-26 mm, 26-35 mm, 35-73 mm), food type is found to be related to the size of individuals. Unlike the adults, no Echinodermata was found in the diet. More than 36% of the individuals ingested spicules of sponges which seems to indicate that the early benthic stages of C. opilio ingest a certain amount of sediment while feeding.

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Physiological Energetics of the Snow Crab, *Chionoecetes opilio*

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ABSTRACT

Measurements of the rates of oxygen uptake, ammonia excretion and food consumption were made at -1°C for male and female snow crabs, *Chionoecetes opilio*, fed an excess of mussel flesh. All three variables were positively correlated with body weight. Absorption efficiency was 74% and independent of body weight. Under these conditions, crabs weighing 200 g or less were in negative energy balance, but in larger individuals energy input exceeded maintenance demands.

INTRODUCTION

Despite the economic importance of the snow crab *Chionoecetes opilio* in eastern Canada, very little is known of the physiological energetics of this species, or indeed of other spider crabs (Majidae). McLeese and Watson (1968) measured oxygen uptake in *C. opilio*, but the most comprehensive studies are those of Paul and Fuji (1989) for the tanner crab *C. bairdi* and Foyle et al. (1989) for *C. opilio*, which both included measurements of energy input and estimates of energy balance. Foyle et al. (1989) focussed on the physiological responses of *C. opilio* to a wide temperature range, since their objective was to determine whether metabolic limitations are responsible for confining the species to the cold waters (< 5°C) in which it is found. These authors worked exclusively on "morphometrically mature" males, as defined by Conan and Comeau (1986), and they also considered the metabolic costs of activity. The approach of Paul and Fuji (1989) was to relate growth, reproductive output and energy balance to body size in *C. bairdi* at ambient temperatures (4-7°C), thereby providing data from which calculations could be made of prey requirements of the tanner crab and of energy transfer from the crab to its predators.

In Conception Bay, southeast Newfoundland, *C. opilio* is common at depths up to 240 m, at which temperatures rarely, if ever, exceed minus 1°C (unpublished observations). The population supports a commercial fishery. Our purpose in this study was to determine oxygen uptake, ammonia excretion rate, ingestion rate and absorption efficiency at -1°C for males and females of various sizes, and to calculate an energy balance for individual animals. The objective was to provide an insight into the physiological mechanisms operating at the whole organism level that allow *C. opilio* to function at this extremely low temperature, and to provide information on physiological energetics that can be integrated with existing data on population structure and dynamics to allow more efficient management practice.

MATERIALS AND METHODS

Collection

Snow crabs (*Chionoecetes opilio*) were collected on four occasions between March and September 1989 in commercial crab traps lined with 25 mm mesh, baited with squid and deployed for 24 hrs at 180 m to 230 m depth in Conception Bay, Newfoundland. To collect smaller crabs and increase the size range of the sample, a scallop dredge lined with 25 mm mesh was employed in September. It was towed for 10 min at 146 m depth.

Crabs were immediately transferred from the deck of the ship to coolers filled with crushed ice to minimise the physiological stress associated with capture. The animals were then transported to the laboratory in the dark and transferred to holding tanks.

Holding

The crabs were kept at -1°C in well-insulated holding tanks (volume 300 l) supplied with running seawater. The tanks were covered to keep the crabs in darkness. A surplus of fresh mussel meat (*Mytilus edulis*) was always available to the crabs. Excess food was removed every 2 to 3 days and replaced with fresh food.

Tags were attached to the carapace to identify individual crabs. The carapace was blotted dry and a Dymo label then attached with cyanoacrylate glue.

Oxygen uptake

Crabs were placed in acrylic respiration chambers of the appropriate size, ranging from 130 ml to 13 l. Each respiration chamber was immersed in a water bath at -1°C and positioned on top of a submersible stirrer. The decrease in oxygen tension was measured over a period of 1 to 2 hours using a Radiometer pO_2 electrode (E5046) coupled with a PHM71 Mk2 acid-base analyzer fitted with a PHA934 oxygen module and connected to a chart recorder. The oxygen electrode was calibrated daily in sea water obtained from the surface of the holding tank and equilibrated with the atmosphere.

Ammonia excretion

Crabs were incubated in chambers of the appropriate volume in darkness at -1°C. Water samples were taken every half hour for 3 hours from each chamber and from a 300 ml control, and ammonia concentration determined by the phenol-hypochlorite reaction (Bayne et al., 1985). Ammonia concentration was plotted against time and excretion rate calculated from the slope of the line. Some crabs excreted ammonia at an abnormally high rate immediately after being placed in the chambers, but this was always followed by a period in which ammonia accumulated as a linear function of time, providing a more meaningful estimate of excretion rate under steady-state conditions. The ratio of oxygen consumed to nitrogen excreted was calculated as described by Bayne et al. (1985).

Feeding experiments

Ingestion rates were determined for crabs held at -1°C in individual containers in a flow-through system for 14 days. A weighed portion of fresh mussel meat was placed in each container every 2 days. At the same time, the unconsumed portion from the previous feeding was removed. The wet weight of the food was determined after blotting to remove surface water.

For the determination of absorption efficiency, faeces were collected separately from each crab every 2 days and pipetted onto combusted, preweighed glass fibre filters (Whatman GF/C) and dried to constant weight at 90°C. The samples were cooled in a desiccator and weighed. The dry samples were then combusted at 450°C and reweighed after being allowed to cool in a desiccator. Dry weight and ash weight were also determined individually for a sample of 12 mussel meats. Absorption efficiency was then calculated as described by Conover (1966).

Energy balance was calculated by subtracting oxygen uptake from absorbed energy, assuming that 1 ml oxygen = 20.3 J (Bayne et al., 1985) and 1 g dry tissue of *Mytilus edulis* = 21.8 kJ (Bayne and Worrall, 1980). This is sometimes termed "scope for growth", especially in the literature on bivalves (Bayne et al., 1985), but since there is a cessation of growth after the terminal moult in male *Chionoecetes opilio* (Conan and Comeau, 1986), we will avoid semantic difficulties by referring to energy balance, which does not distinguish between growth *per se*, reproductive output and the synthesis or utilisation of energy reserves. Excretory losses were not considered, since they accounted for a very small fraction (less than 2%) of the energy budget.

RESULTS AND DISCUSSION

Oxygen uptake

The rate of oxygen uptake (VO_2) of *Chionoecetes opilio* at -1°C was an increasing function of body weight (Fig. 1). No difference was observed between males and females, and there was no evidence of seasonality in VO_2, so the data from the four collections have been pooled. Although our study on *C. opilio* was not designed to investigate cyclical fluctuations, we were aware of the literature

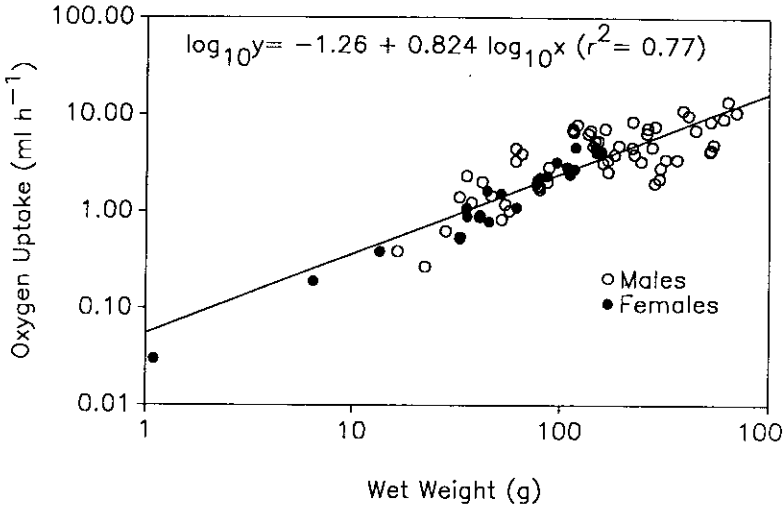

Figure 1. The rate of oxygen uptake as a function of body weight in *Chionoecetes opilio* at -1 °C.

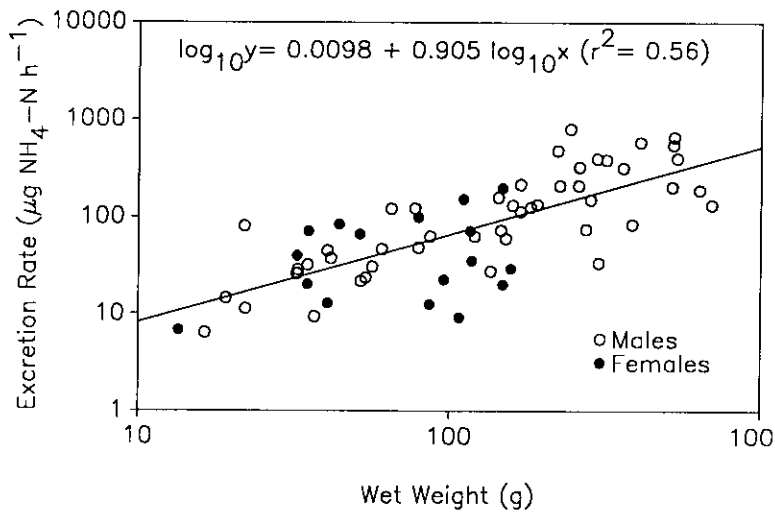

Figure 2. The rate of excretion of ammonia-nitrogen as a function of body weight in *Chionoecetes opilio* at -1 °C.

describing metabolic rhythmicity in decapod crustaceans, including the closely-related species *Maia squinado* (Aldrich, 1975), but we found no evidence for this when making our measurements on the snow crab, and the high correlation (r^2=0.77) between routine VO_2 and body weight is consistent with this.

Our values for crabs fed to satiation are consistent with published data for *C. opilio* and *C. bairdi* in similar physiological states. According to McLeese and Watson (1968), a fed snow crab (*C. opilio*) of 760 g live weight consumes 30 mg O_2 kg^{-1} hr^{-1} at 5°C and high pO_2, which is equivalent to 15.9 ml O_2 $crab^{-1}$ hr^{-1}. This compares with a value of 13.0 ml O_2 $crab^{-1}$ hr^{-1} predicted for a 760 g crab at -1°C from our regression equation. Foyle et al. (1989) recorded a routine oxygen uptake of 13 mg kg^{-1} hr^{-1} at 0°C for *C. opilio* males of wet weight 250-370 g, which is 2.73 ml O_2 $crab^{-1}$ hr^{-1} if one assumes a live weight of 300g. This is considerably lower than our predicted value (6.06 ml hr^{-1}) for an individual of this weight, but in the experiments described by Foyle et al. (1989), oxygen uptake almost doubled after feeding, and their estimates for fed crabs are therefore very similar to ours. In the tanner crab *C. bairdi*, Paul and Fuji (1989) also observed a substantial increase in the rate of oxygen uptake when starved animals were fed. According to these authors, an unfed crab weighing 100 g consumed 1 ml O_2 hr^{-1} at 3°C, but a 68% increase in oxygen uptake was recorded when a single meal equivalent to 3% of body weight was provided. This corrected value of approximately 1.7 ml hr^{-1} for *C. bairdi* at 3°C compares with our estimate of 2.4 ml hr^{-1} for a 100 g *C. opilio* at -1°C.

Ammonia excretion

The rate of ammonia excretion of *Chionoecetes opilio* at -1°C was also an increasing function of body weight (Fig. 2), although the correlation was less strong than that between oxygen uptake and wet weight. As with oxygen uptake, there were no differences between males and females or between crabs from different collections, so the data were pooled and a single regression equation calculated. In contrast, Paul and Fuji (1989) found that excretion rate was independent of size in *C. bairdi*.

The ratio between oxygen consumed and nitrogen excreted (O:N) in *C. opilio* varied from 27 for a crab weighing 500 g to 55 for an individual weighing 10 g. In the absence of comparable data for this or related species, it is difficult to interpret these O:N values, but in the mussel *Mytilus edulis*, for which there is a considerable body of data, O:N ratios less than 30 suggest that protein catabolism is high relative to lipid and carbohydrate, a condition normally associated with environmental stress, whereas values greater than 50 are indicative of high lipid and carbohydrate catabolism relative to protein, a situation normally found in unstressed individuals (Bayne et al., 1985). According to Mayzaud (1973) the minimum value possible is approximately 7, which occurs when a protein substrate alone is catabolised. The O:N ratio is particularly sensitive to nutritional status, and we conclude that since the crabs used in our study were fed to satiation, the O:N values that we recorded are likely to be characteristic of *C. opilio* in good physiological condition, but more data are required on different populations under a wider range of conditions before the full potential of the O:N ratio as a physiological index of stress will be realised in these spider crabs.

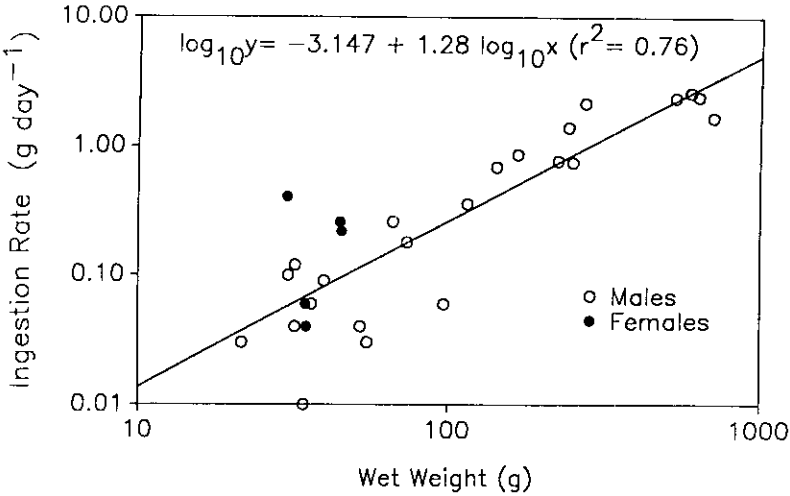

Figure 3. Ingestion rate as a function of body weight in *Chionoecetes opilio* at -1°C.

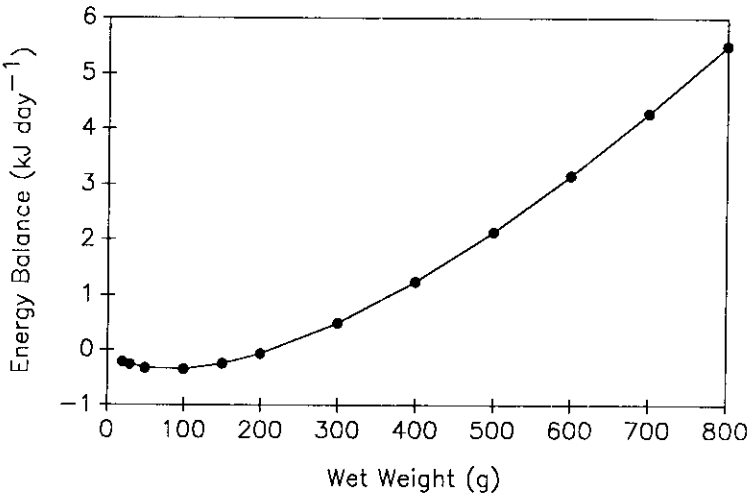

Figure 4. The relationship between energy balance and body weight in *Chionoecetes opilio* at -1°C.

Energy input

Ingestion rate in *Chionoecetes opilio* also increased with body weight, and data for males and females from all collections were pooled in a single regression (Fig. 3). In the experiments undertaken by Foyle et al. (1989), satiated snow crabs at 0°C consumed approximately 1 kcal kg^{-1} body weight day^{-1}, which is 300 cal (=1.25 kJ) per individual per day for crabs of 300 g live weight. The regression equation that we obtained yields a predicted value for ingested ration of 1.07 g wet weight day^{-1} for a 300 g crab at -1°C. Assuming a water content of 80% for meat from *Mytilus edulis* (own unpublished observations) and a caloric value of 21.8 kJ g^{-1} dry weight for *M. edulis* tissue (Bayne and Worrall, 1980), this is equivalent to 4.3 kJ day^{-1}, greater than was observed by Foyle et al. (1989). However, ingestion rate may be sensitive to factors such as the nature of the food and the frequency with which it is presented, both of which differed between the studies. Foyle et al. (1989) found that food consumption was a maximum (2.9 kJ day^{-1}) at 6°C, which approximates our estimate for crabs at -1°C. It is possible that the crabs from Conception Bay are adapted to colder water than those from eastern Cape Breton Island which were used by Foyle et al. (1989), so that the temperature optimum is lower in the former population, but this requires further study, since differences in experimental procedures may also be responsible. It is likely that the higher routine rates of oxygen uptake observed in our study are partly attributable to the greater food consumption which we observed.

There was no correlation between absorption efficiency and body weight in *C. opilio*, which agrees with observations by Paul and Fuji (1989) on *C. bairdi*. We obtained a mean value of 0.74 (s.d.= 0.11, n=29) for crabs continually fed an excess ration, compared with an absorption efficiency of 0.95 recorded by Paul and Fuji (1989) for crabs starved before and after a single feeding event, a situation which is likely to provide maximum values. According to Paul and Fuji (1989), the limited data available suggest that absorption efficiency in cold-water decapods is usually high.

Energy balance

Snow crabs exceeding 200 g wet weight were in positive energy balance at -1°C when fed to satiation, but in smaller individuals energy losses exceeded energy input (Fig. 4). This is partly a consequence of the underlying allometric relationships, since the slope of the equation relating ingestion rate to body weight was greater than that of the equations relating metabolic losses to body weight, but the relationship between energy balance and body weight is also greatly influenced by ration level. Thus Widdows (1978) found that in *Mytilus edulis* scope for growth decreased with larger body size at low ration levels, but increased with size at high ration. This is consistent with our observations on *Chionoecetes opilio*. The reason for a negative energy balance in small snow crabs fed to satiation is not apparent, since this cannot continue indefinitely in the natural environment, but it may be a consequence of artificial conditions in the laboratory (Foyle et al., 1989).

According to Foyle et al. (1989), male snow crabs of approximately 300 g body weight are in negative balance at temperatures below 1°C, which is paradoxical

since they commonly encounter such conditions. In our experiments energy balance was positive in crabs of this size, but whether this represents physiological adaptation by a cold-water population or a response to a good food supply is a matter for conjecture at present. Our metabolic rate values do not take into account any activity costs that may occur in the natural environment, which would tend to decrease the energy available for growth and reproduction.

One major challenge for future work on the physiological energetics of *C. opilio* lies in establishing what is an ecologically meaningful food ration, both in qualitative and quantitative terms, and in making the appropriate physiological measurements under more natural conditions. It may be possible to obtain reasonable determinations of routine metabolic rate by measuring the oxygen uptake of crabs soon after capture, provided that the animals are collected by means other than conventional trapping, or are caught in traps deployed for a very short period. An estimate of foraging activity will also be necessary, to facilitate the interpretation of laboratory measurements on active crabs. The measurement of a corresponding ingestion rate will probably require a synthesis of data from several approaches, combining behavioural observations using photographic and telemetry techniques, for example, with physiological data obtained in the laboratory.

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Nov. 1989, Anchorage, Alaska

A Temperature-Dependent Growth Model for Juvenile Red King Crab, *Paralithodes camtschatica*, in Kodiak, Alaska

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ABSTRACT

Growth rates for some crustaceans are highly dependent upon ambient temperature. A temperature-dependent growth model was calculated for juvenile red king crab collected by divers in Kodiak during 1986-89, using continuously recorded *in situ* temperature data. Studies have concentrated on 3 year-classes of crabs during their first two years of life, and are unique because all crabs were collected from a localized area, with replacement, often from a single pod of several hundred to thousands of crabs. These data show a strong linear relationship between the log of mean carapace length (CL) and the log of cumulative degree-days (dC); the equation derived was Ln(CL) = -10.787 + 1.702(Ln dC). This model should allow more accurate estimation of crab age when combined with historical temperature data for a given region. Additional temperature data were used to estimate the age of maturity for Kodiak Island and eastern Bering Sea female red king crab, and the results are compared to published estimates for both locations.

INTRODUCTION

Growth of the red king crab, *Paralithodes camtschatica*, has been studied by a number of authors (Weber 1967; Vinogradov 1968; Matsuura and Takeshita 1976; McCaughran and Powell 1977). Most have described growth via a simple age-length key (Incze et al. 1986), and assumed that mature crabs molt annually. However, older males tend to molt less frequently (skipmolt), and there is no clear evidence that molting occurs at regular intervals after maturity. Thus age-length keys can be misleading. Additionally, growth rates calculated by various authors differ widely (Stevens In Press), with both growth rates and size at maturity decreasing with increasing latitude.

Numerous mathematical models have been developed to describe the growth of Decapod crustaceans (Mauchline 1977). One of the most useful of these is the Hiatt diagram (Hiatt 1948), in which postmolt measurements are plotted against

premolt measurements. This technique was extensively applied to the study of a variety of crustaceans, including *Paralithodes camtschatica*, by Kurata (1962), who concluded that growth of larvae, and to some degree postlarvae, was a function of temperature. Stevens (In Press) expanded on this concept and derived a model for growth of juvenile king crab based on data from Unalaska, Alaska (Weber 1967), and used the resulting equation to predict growth of juvenile crabs at temperatures found in the Bristol Bay region of the eastern Bering Sea (EBS), and back-calculate their age by comparing predicted sizes to those observed by National Marine Fisheries Service surveys of the EBS (Stevens and MacIntosh 1989). He concluded that, as a result of geographic temperature differences, crabs in Bristol Bay matured at ages greater than those at Unalaska (Weber 1967) or Kodiak, Alaska (McCaughran and Powell 1977), and that age at maturity varied with seawater temperatures. However, those conclusions were based on limited or partially estimated water temperature data.

The present study was undertaken to obtain better data with which to verify Stevens' (In Press) conclusion regarding the relationship of carapace length to temperature, to improve the parameter estimates for the equation, and to compare the results with other models of growth.

METHODS AND MATERIALS

Development of the model

Kurata (1961) derived a general growth formula applicable to any crustacean instar, of the form:

$$CL = ab^s \tag{1}$$

where CL is carapace length in mm, s is stage (instar), and a and b are constants. Equation (1) can alternatively be expressed as

$$\mathrm{Log}(CL) = \mathrm{Log}(a) + s\mathrm{Log}(b) \tag{1.1}$$

and since both a and b are constants,

$$\mathrm{Log}(CL) = A + Bs \tag{1.2}$$

where A = Log(a) and B = Log(b). Thus, length is an exponential function of instar number.

Both Kurata (1960, 1961, 1962) and Nakanishi (1974, 1987) studied the effects of temperature on growth of larval and juvenile *Paralithodes camtschatica*, concluding that intermolt period for a given instar decreased exponentially with temperature, providing an equation of the form:

$$d = k/C \qquad \text{or, equivalently,} \qquad dC = k \tag{2}$$

where d is days in the intermolt period, C is degrees C, and k a constant. Equation (2) shows that the value dC, commonly referred to as "degree-days", is a constant. Nakanishi (1987) also showed that dC for the intermolt period increased for each larval stage of *Paralithodes camtschatica*, and that for each stage it was more or less constant over the temperature range of 5-18°C, except for zoeal stage IV (Z4) at 8°C.

If dC is constant for any single intermolt period, then for any continuous series of intermolt periods, the sum of these constants should also be a constant. Thus the total degree-days required to reach any given instar should be a constant. In support of this, Kurata (1960) showed that the number of degree-days required by *Paralithodes camtschatica* to pass through all larval stages from hatching to the first postlarval stage averaged 463 dC. We calculated similar values of 468 dC and 453 dC from data in Nakanishi (1974) and Nakanishi and Naryu (1981), respectively. Using data from Weber (1967), Stevens (In Press) determined that instar number was a linear function of log(dC), but since stage cannot be estimated precisely, the resultant equation was of little predictive value. However, the equation derived was of the form:

$$s = m + n[\log(dC)] \tag{3}$$

where s is stage or instar number, and m and n are derived constants.

If CL is a function of instar number (s), and stage or instar number is a function of degree-days, then it follows that length should be a function of cumulative degree-days, i.e.,

if $\log(CL) = A + B(s)$ Equation (1.2)

and $s = m + n\log(dC)$ Equation (3)

$$\begin{aligned} \text{then } \log(CL) &= A + B[m + n\log(dC)] \\ &= A + Bm + Bn\log(dC) \\ &= A' + B'\log(dC) \end{aligned} \tag{4}$$

where $A' = A + Bm$, and $B' = Bn$.

Data Collection

Juvenile red king crab (*Paralithodes camtschatica*) were collected by scuba in depths ranging from 5 to 17 m. Most collections were made in Women's Bay, Kodiak, AK (Lat. 57°43.5' N, Long. 152°31.5' W), near or under an abandoned wooden pier (Marginal Pier). Occasional other collections were made approximately 1 km across Women's Bay from Marginal Pier, and from Dog Bay or Trident Basin, approximately 8 km from Marginal Pier, but these accounted for less than 2% of the total number of crabs sampled. Age 0+ crabs were found by looking under rocks and debris, or on sea stars (primarily *Asterias amurensis* or *Evasterias troschelli*). Some very small crabs were collected from sediiments with an airlift suction sampler. Age 0+ crabs were returned to the laboratory, where they were measured under a binocular dissecting microscope with a calibrated ocular micrometer. Carapace length (CL) was measured to the nearest 0.01 mm from the rear of the right orbit to the middle of the rear margin of the carapace. All crabs were returned to the area of capture within several days. Sampling was conducted once monthly or more often.

In November 1987 a pod of about several hundred age 1+ crabs appeared near Marginal Pier, and it was repeatedly sampled for carapace lengths until June, when it disappeared (Dew In Press). A second pod formed in the same area in fall of 1988, and it, too, was repeatedly sampled until the crabs left the area. In 1989, crabs were repeatedly sampled from one or more aggregations which formed around pilings under Marginal Pier. Age 1+ crabs were measured to the nearest 0.1 mm

on shore near the site of capture, after which they were immediately returned to the location of capture. Approximately 10-20% of the podded crabs were measured at each collection, and it is likely that numerous crabs were measured more than once, on subsequent collections.

Small samples of <10 crabs of the same age group which were collected within a single 10 day period were occasionally combined to form minimum sample sizes of 10 crabs, in order to increase the precision of calculation of mean length.

Water temperature was continuously recorded by a thermograph placed approximately 9 m below mean lower low water (MLLW) near the south end of Marginal Pier. From 1 January 1986 to 4 July 1987, a strip-chart recorder was used, but we subsequently found that sampling dates could not be determined accurately, so it was replaced by a digital recorder which recorded temperatures at 2 h intervals. Additional water temperatures were collected by a similar thermograph placed at a depth of 11 m in Trident Basin by the Alaska Department of Fish and Game. Data missing from the Women's Bay data series were estimated by regressing Women's Bay temperatures on Trident Basin temperatures. Data recorded at 2 h intervals were used to calculate daily mean temperatures. Cumulative degree-days were determined for each year-class from the estimated date of hatching (31 March) by summing the daily mean water temperatures.

Age 0+ and 1+ crabs were treated separately, as their frequency distributions showed no overlap. For each collection date, the natural log (ln) of the mean CL was regressed on the natural log of cumulative degree-days (in days-Celsius, dC) calculated from the estimated date of hatching.

RESULTS

Temperatures in Women's bay were recorded for almost four years, and ranged from a high of about 12.5°C to a low of -1.6°C, although average winter temperatures were normally 3.5-4.0°C during this period (Fig. 1). Water temperature began to increase in April or May, and began to decline in September of each year. The average annual number of degree days calculated from 31 March to 30 March over this period was 2210, and varied little from 1986 to 1989, with the exception of a very cold period in February 1989. Trident Basin was about 0.5-1.0°C warmer than Women's Bay in mid-winter, and about 0.2-0.5°C cooler at the summer peak. Temperatures for the two bays were within +/- 0.5°C during the periods of increasing or decreasing temperature (the times for which missing data were recreated for Women's Bay).

Age 0+ crabs were usually first found in small numbers (<10 per dive) during the fall of each year, at sizes of 5-7 mm CL. Upon reaching sizes of 10-15 mm CL in the spring and summer, they were found in greater numbers (10-50 per dive), and were more frequently found in association with the sea stars *Asterias amurensis* and *Evasterias troschelli*. Aggregative behavior began when crabs reached sizes of 18-20 mm CL in the following autumn, as discussed by Dew (In Press). Growth was followed only up to a mean size of about 40 mm CL (Fig. 2), after which the crabs could no longer be found, and probably left the area. A total of 3079 crabs were measured. Sample sizes ranged from 1 to 283 crabs, with a mean of 62.8 crabs. No significant differences in mean length were detected between male and female crabs for any sample (unpaired two-sample t-test, $p=0.05$).

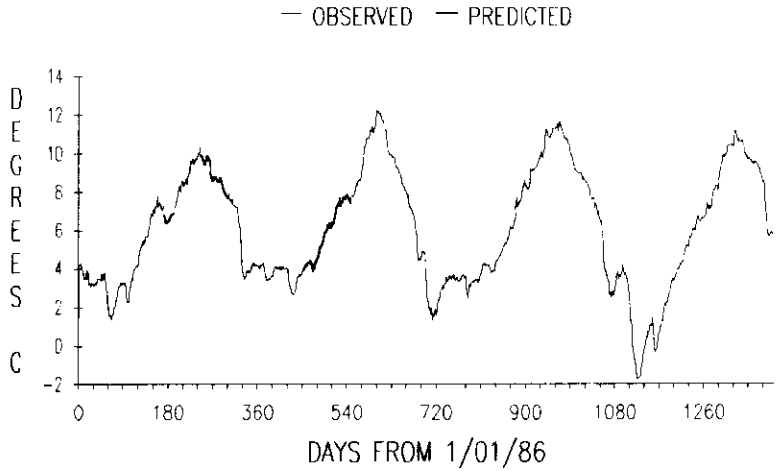

Fig. 1. Water temperature at a depth of 9 m (MLLW) in Women's Bay, Kodiak, Alaska, from 1 January 1986 to 3 November 1989. Heavier line near days 180, 270 and 450-540 are temperatures estimated from regression of Women's Bay data on Trident Basin data.

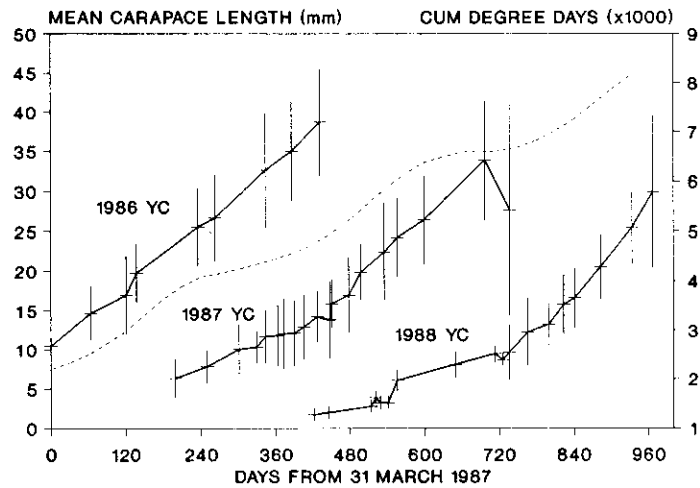

Fig. 2. Mean carapace length, ± 2 s.d., of red king crabs collected from Women's Bay, Kodiak, Alaska, from 31 March 1987 to 19 October 1989. Dotted line is cumulative degree days, from 31 March 1986, the estimated hatching date for the 1986 yearclass (YC) crabs. Note day numbers do not correspond to those in Fig. 1.

Data from all three year-classes of crabs were combined for regression analysis using Equation 4. The relationship between mean CL and degree days was determined to be:

$$\text{Ln(Mean CL)} = -10.787 + 1.702(\ln dC)$$

with $r^2 = 0.970$, and 46 degrees of freedom (Fig. 3). A single early instar crab (1.98 mm CL) was collected from Dog Bay in June 1988; it was excluded from the regression equation, but is shown in Fig. 3, along with the predicted location of a first instar crab (C1), based on the size (1.75 mm CL) and degree-days (460 dC) estimated by Kurata (1960) from laboratory rearing experiments.

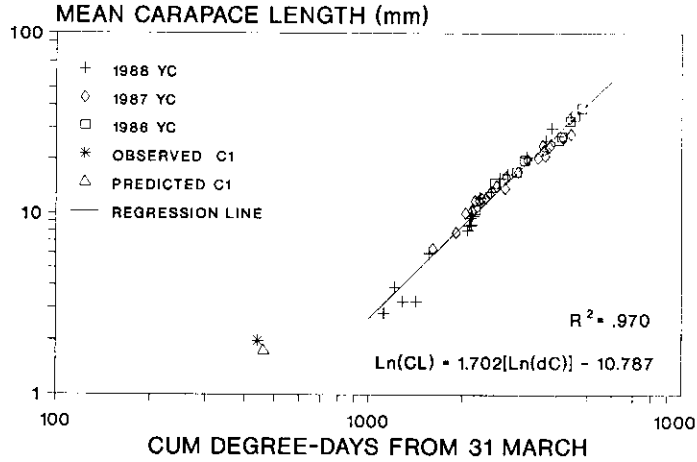

Fig. 3. Log-log plot of mean length of Women's Bay red king crab versus cumulative degree days. Both variables were transformed to natural logs for regression analysis, but are shown here as $\log_{10}$ transformed. "Observed C1" is smallest crab collected during study, and was omitted from regression equation. "Predicted C1" is shown at size (1.75 mm CL) and location (460 degree-days) determined by Kurata (1960), for laboratory reared king crab.

Sizes at ages 1-7 were predicted for female king crab for both Women's Bay and a site in the eastern Bering Sea, and compared (Fig. 4) for the years 1986-92. Temperature data for the EBS were collected at a site where early instar crabs had been observed in the past (INPFC 1959), using a thermograph placed there in 1987 (authors unpublished data).

The total annual degree days from 27 May 1987 to 26 May 1988 at the EBS site were 1518 dC. Degree-days for the EBS site for years other than 1987-88 were estimated based on the ratio of EBS to Kodiak degree-days.

The growth model on which these results are based entailed two steps. First, growth

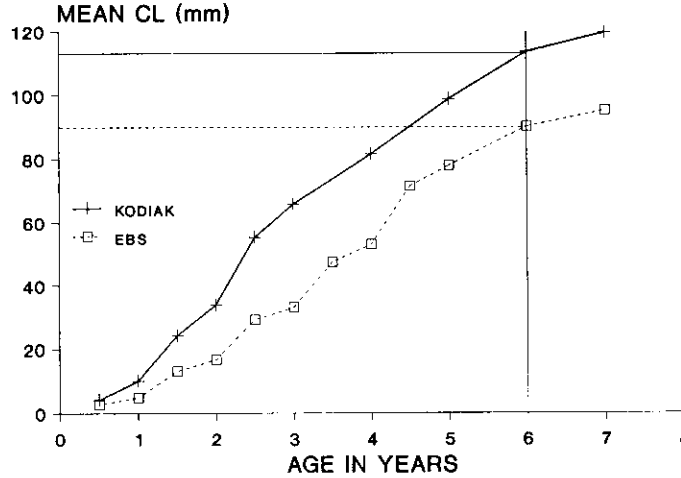

Fig. 4. Growth of female red king crabs in Kodiak and Bristol Bay, eastern Bering Sea, as predicted by model. Model includes early growth according to temperature regression, and secondary growth by annual molting increments assumed to be different for each location (see text for details).

was calculated according to the temperature-based regression equation up to a critical size at which molting was assumed to occur once annually, and to become largely temperature independent. The second step was to add annual molting increments based on published growth studies. Both the critical size and later growth increments differed between Kodiak and the EBS, and the predicted sizes are greatly dependent upon the following assumptions made about growth.

For Kodiak crabs growth was assumed to be temperature dependent up to a size of 65 mm CL. Growth beyond this size was modeled according to Powell (1965), who concluded that annual molting began at this size, and that growth increments for the next 3 molts were 24%, 21%, and 15%, after which the crabs reached 113 mm CL, approximately the size at maturity for female king crab in Kodiak (Powell et al. 1973). After reaching maturity, female crabs would be expected to grow only 5-6 mm for each of the next few molts (Powell 1965).

Weber (1967) concluded that king crab in the EBS also started to molt annually at sizes above 60 mm, although most of his conclusions were based on research done at Unalaska, for crabs <60 mm. However, he presented data showing a mode of female crabs at 78 mm occurring in the EBS in July of several consecutive years, and concluded that the next molt was annual with an increment of 12 mm. Therefore, we assumed that growth was temperature dependent up to a size of 78 mm, after which an annual increment of 12 mm was added to reach 90 mm CL, equivalent to the mean length at 50% maturity for EBS female king crab over the period 1976-89 (Otto et al. 1989). We assumed a post-maturity molt increment of 5 mm, as suggested by Weber (1967).

This model of growth predicts that female RKC currently reach sexual maturity at the age of 6 years in both Bristol Bay and Kodiak, although at different sizes.

DISCUSSION

Temperature has a strong influence on the growth of juvenile *Paralithodes camtschatica*, at least up to the size of 40 mm CL. Temperature also influences the development rate of external embryos; data for EBS king crab (Otto et al. 1989) indicate that hatching occurs later in years with lower June bottom temperatures. Since this is probably the result of differences in total annual degree days, it follows that the hatching date in Kodiak probably varies with total annual degree days accumulated. Fortunately, during the period of study, total dC have not varied greatly, so the assumption of a constant hatching date of 31 March in each year may not have been too erroneous for this period. Examination of Fig. 3 does not reveal any obvious discrepancies from this assumption for any of the 3 year-classes observed.

The locations in Fig. 3 of the predicted first instar crab (C1), and the single first instar collected from Dog Bay were very close, and both fell well away from the predicted regression line. This could be the result of several possibilities: Data which was derived in laboratory situations by Kurata (1960) and Nakanishi (1987) may not be representative of growth in the marine environment, where more than 460 dC might be required to reach the first postlarval instar; hatching probably occurs over a protracted period, and the single observed early postlarva might have hatched earlier than expected; and the hatching date assumed for all samples might be incorrect, although Powell (1965) concluded that hatching occurred around 15 April in Kodiak (although his conclusion was representative of the early 1960's, it may not be far off for the present). Additionally, it is not known whether the smallest crab captured in this study was a first (C1) or second (C2) instar; it occurred exactly 440 dC following our assumed hatch date (i.e., right on schedule if it were a C1). However, due to the small sample size, no conclusions can be drawn about this discrepancy without additional data on the size of first instars and timing of settlement.

The utility of this data in determining the age of crabs is greatly dependent upon assumptions made about the size or age at which molting becomes an annual event. Since females are known to molt annually for reproductive purposes, their growth was modeled. Additionally, it is easy to determine the point of 50% maturity by the presence or absence of external embryos, so a physiologically important milestone can be compared between populations. Although there is more published data concerning the growth of male crabs, interpretation is confounded by the phenomenon of skip-molting or anexuviation, which is difficult to determine or predict precisely, although both Balsiger (1976), and McCaughran and Powell (1977) present transition matrices desinged to account for it. Furthermore, estimates of the size of male sexual maturity vary widely and are dependent upon the method used and the definition employed, whether physiological, morphometric, or functional. For these reasons, modeling the growth of crabs is much more prone to error for males than for females.

In the present model, the predicted sizes at each age for Kodiak red king crabs closely match those of Powell (1965). Weber (1967) concluded (probably correctly) that an 80 mm crab at Unalaska was 4 years old, and therefore assumed (probably incorrectly) that a similar sized crab in the EBS was also 4 years old. The present model predicts that such a crab would be almost exactly 5 years old (using temperature data estimated for recent years), and the next molt, if annual, would occur prior to 1 June, exactly the correct time for molting and mating. For these reasons, it seemed appropriate to assume that annual molting would start at this size and age. The present model predicts that EBS red king crab would reach a size of

65 mm sometime in midsummer of their 5th year, about 4.25 years post-hatching. If annual molting started at this size and time, they would be out of synchrony with the known mating and molting period, which occurs in late spring (March-June). In order for crabs to reach the known size of maturity at about 90 mm CL with one molt of about 12 mm as indicated by Weber (1967), the starting point must be at 78 mm the previous June, which, fortuitously, was exactly the size predicted by the temperature-dependence model. However, other interpretations are possible if different assumptions are employed concerning the molt increment or the point at which molting becomes an annual event.

Using a similar growth model derived from data of Weber (1967), and assuming the onset of annual molting to occur at about 60 mm CL, Stevens (In Press) concluded that the age at maturity for EBS red king crab averaged 8.5 years during the mid 1970s, but had decreased to about 7.5 years in the early 1980s due to warming in the EBS. The value predicted by the present model (6 years) is slightly lower due both to use of females, more recent and more accurate temperature data for the EBS, and to the use of different assumptions about the size at which annual molting begins.

Growth of juvenile king crab up to 60 mm has been fairly well documented by Weber (1967), and Powell (1965). Growth of crabs larger than 80 mm has likewise been well studied both in the EBS (Weber 1974, Weber and Miyahara 1962; Balsiger 1976) and at Kodiak (Powell 1965). However, there is very little published data concerning the growth of crabs in the range of 60-80 mm, because crabs over 60 mm are not abundant close to shore where diving studies can be conducted, and crabs less than 80 mm CL are too small to tag properly. Therefore, most authors have simply assumed either that annual growth increments are similar between those size ranges, or that annual molting begins at some point in that range. This is an important transition point, however, and the construction of any growth model will be greatly influenced by the assumptions made about it, until further data becomes available concerning this aspect of growth.

Determining the age of crustaceans has always been a difficult problem due to the lack of hard parts from which a record of growth may be derived. Attempts have been made to use integumental layers (Farmer 1973), external tags, internal ferro-magnetic tags (Bailey and Dufour 1987), "living tags" (Shelton and Chapman 1987), or chemical techniques (Ettershank 1984). None of these methods has been very succcessful, either due to variablility induced by a laboratory environment, the large effort and low recovery rates associated with tagging studies, or the requirement for sophisticated laboratory instruments. None are amenable to remote field sampling of large numbers of animals. For the majority of crustaceans supporting large commercial fisheries, the major technique for studying growth has been length frequency analysis (Cassie 1954), assuming that large, persistent modes which progress with time represent individual year-classes, or in the case of juveniles, perhaps instars. Widespread availability of computers has lead to improved methods for identifying and separating modes (MacDonald and Pitcher 1979), but this method still requires long term studies in order to determine the annual progression of modes.

Improved knowledge of the relationship between size and temperature history, as demonstrated in this report, could be used to back-calculate the age of a given cohort of crabs, using historical data on temperature conditions experienced by the population. Such calculation requires a long-term record of water temperatures for the region of interest, and will be most precise (for red king crab) up to 60 mm CL. Extrapolation to larger sizes cannot be done precisely until better information is

available concerning the frequency of molting for larger crab.

ACKNOWLEDGEMENTS

We are greatly indebted to C. Braxton Dew for marking and tracking the two pods which provided a large portion of the measurements for this study, and to him and Peter Cummiskey for assistance in collecting and measuring crabs. Forrest Blau, Alaska Department of Fish and Game, provided Trident Basin temperature data.

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Nov. 1989, Anchorage, Alaska

Trophic Relationships of Crabs, Shrimps, and Fishes of the Western Bering Sea

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A reduction has been recently observed in the abundance of commercial shrimps and crabs in the northwest Bering Sea. *Paralithodes platypus* abundance has decreased by approximately 3 times and *Chionoecetes opilio* and *Ch. bairdi* abundance by almost 8 times. Undoubtedly, stock reductions were partially caused by the fisheries, but environmental influences, including biotic factors, must not be ruled out. The most abundant shrimp species of this area is *Pandalus goniurus* and starting from the late 1970s its abundance has significantly decreased as well (Ivanov and Zgurovsky, 1988). We will attempt to estimate the consumption of *Pandalus goniurus* and crabs by the most abundant fish species of this region during their feeding migrations (June to August). The estimates will employ our data on fish and crustacean abundance in the area, as well as the frequency of the prey in fish stomachs, per cent of prey in the food and the published data on fish feeding rates.

Humpy shrimp and crabs play a very significant part in the diet of the abundant and active consumers: Alaska pollock, cod and sculpins. We calculated that total consumption of the humpy shrimp by pollock and cod may amount to approximately 280,000 tons. The main components of the diet of sculpins is juvenile tanner crabs; Alaska pollock and cod also actively feed on them. The total consumption of *Ch. opilio* in June to August, 1988 was about 300,000 to 600,000 tons.

The main goal of consumption estimation is to assess the daily rations of the fish and the rate of the food digesting. Nevertheless, taking into consideration our previous calculations, it is clear that the crustaceans and fin fish fisheries should be regulated as a unit. They show us the necessity of developing ecosystem research in this region.

A reduction has been recently observed in the stocks of commercial shrimps and crabs in the northwest Bering Sea. *Paralithodes platypus* abundance decreased by approximately 3 times, that of *Chionecetes opilio* and *Ch. bairdi* by almost eight times. The abundance of those species was clearly influenced by rather intensive exploitation by Soviet and Japanese fishermen in the area, but the influence of environmental factors cannot be denied either, including biotic influences. Stocks of the most abundant shrimp species, *Pandalus goniurus*, have significantly decreased as well (Ivanov, Zgurovsky 1988).

Thus, we had the task of attempting to estimate the influence of fish predation during their feeding migration into the northwest Bering Sea upon the local shrimp and crab stocks.

MATERIALS AND METHODS

The data were collected in summer and autumn of 1982 to 1988 on board the R/V *Gidrobiolog*, *Gidronavt*, *Gorny* and *Conchak*. Bioanalysis of the catches included opening of fish stomachs to determine the qualitative and quantitative composition of the food bolus. Based on trawl survey results, the distribution of the following major fish species was mapped: *Theragra chalcogramma*, *Gadus morhua macrocephala;* Cottidae: *Myoxocephalus* and *Hymnocantus geni.* The abundance of each separate concentration was then estimated (Figs. 1, 2, 3).

The trophic ranges and data on the amount of crustaceans consumed were related only to the specific concentration of individuals that were sampled. Employing information on the average sizes of fish in the catches, average body weight was calculated using equations cited from Pereira et al., (1976). Based on the daily ration of Alaska pollock (Savicheva,1981) and that of cod (Gordeeva, 1952) in summer and the data of Vinberg (1956), Shorygin (1952), Dwyer et al., (1986) and Dulepova (in press), and employing the frequency and average percentage of each type of prey in the food samples collected by the authors of the present paper (Table 1), daily consumption by the above fish was calculated. Upon determining the abundance of fish in the individual stocks and assuming a 3-month feeding duration by the fish, we obtained figures for the consumption of shrimp (Tables 2 and 3), the interannual dynamics of shrimp consumption (Table 4), and the consumption of tanner crabs as well (Tables 5, 6 and 7).

Studies on feeding by *P. goniurus* have shown that this species has a varied diet, and that it feeds on both bottom and nektonic organisms. In addition, it tends to be a scavenger (Ivanov, Zgurovsky, 1989). Thus, the population growth of this shrimp does not appear to be food limited in any way. Nevertheless, biotic factors, in particular high predation rates, seem to play a significant part in the processes affecting the abundance of this shrimp. Humpy shrimp in its most abundant years (summer 1981, for example) was a significant part of the diet of the following major fish species: Alaska pollock, cod, sculpins. Less numerous fish species contained it as well: black halibut, skates, eelpout, saffron, cod, snailfish and even Pacific halibut.

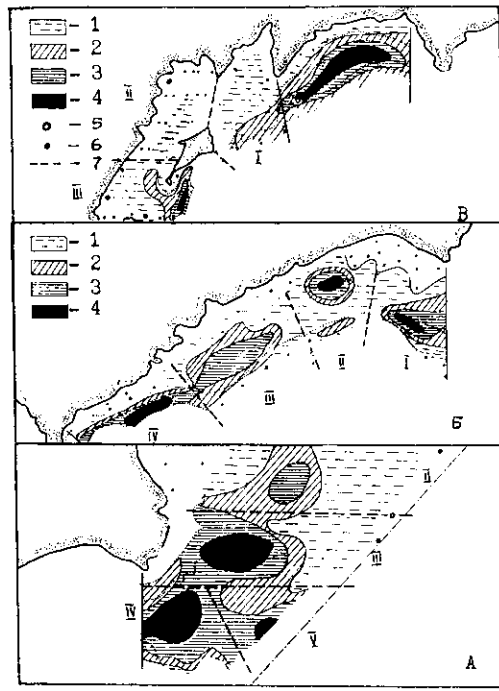

Figure 1. The pollock distribution in the Anadyr (A), Korfo-Karaginsky and Olyutorsky Gulfs (C) and at the Koryak shelf (B) in July - September 1988; (1) 25 individuals/trawling hour; (2) 5-250; (3) >250; (4A) >625; (4B) >2,500; (5) juveniles; (6) catches unavailable; (7) area borders.

Starting from 1982, the frequency of shrimp in the stomachs of fishes considerably decreased, and then increased again in 1986 (Table 4). The shrimp were replaced by euphausiids in the diet of pollock, by small fishes in that of cod, by juvenile tanner and spider crabs in sculpins, by bivalves and amphipods in eelpout. The quantity of shrimp in fish stomachs varied from 1 to several dozen. The stomachs of cod, pollock and sculpins were frequently filled with shrimp, while in the stomachs of the halibut, eelpout and flounder, shrimp seldom exceeded 1-3 individuals. The importance of shrimps in the cod and pollock diets increases as those fishes migrate into the Gulf of Anadyr for feeding. The quantity of shrimps in the fish stomachs depends on the predator's size as well.

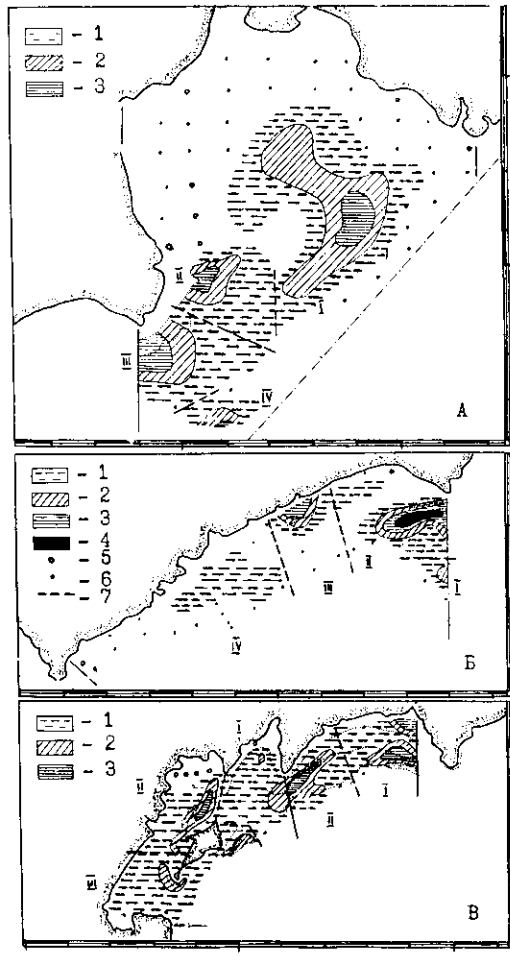

Figure 2. The cod distribution in the Anadyrsky (A), Karaginsky and Olyutorsky Gulfs (C) and on the Koryak shelf (B). Legend as in Figure 1.

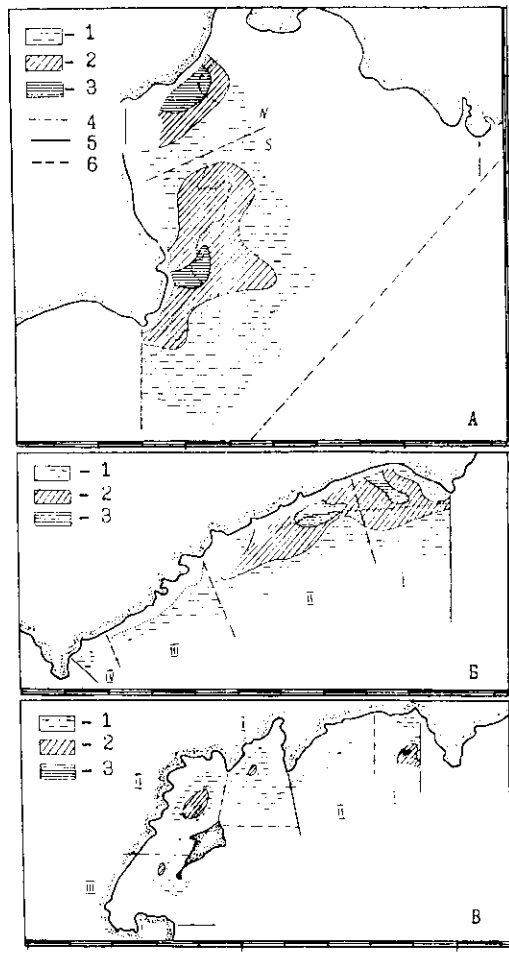

Figure 3. Sculpin distribution in the Anadyrsky (A), Olyutorsky and Karaginsky Gulfs (C) and on the Koryiak shelf (B) in July - September 1988: (1) 25-75 individuals/trawling hour; (2) 75 - 250; (3) >250; (4) fisheries zone; (5) Gulf border; (6) area border.

Table 1. Frequency and percentage of the main food items in diets of the major fish species in the Anadyrsky Gulf in summer 1988.

Species	Shrimps		Snow crabs		Euphausiids		Fishes		Rest		TOTAL
	fr	%	fr	%	fr	%	fr	%	fr	%	
Cod	62	44	30	0.5	-	-	29	7.5	20	53.5	186
Pollock	86	99	3	100	12.6	60	11	78	1.5	43	230
Cottidae	12	57	93	90	-	-	-	-	14	48	44

Note: "Fr" is the frequency in percent; "%" is the percent in the food.

Table 2. Consumption of *P. goniurus* by cod in summer 1988. (ration: min - 5%; max - 8%).

	Anadyr Gulf	Koryak Shelf	Olyutor Gulf	Karagin Gulf
FISH:				
Body length (cm)	55.2	57.3	65.8	60
Body weight (g)	2,140	2,390	3,750	2,890
Quantity (millions)	77.5	50.0	17.5	29.6
SHRIMP:				
Frequency (%)	56	20	42	18
% in food	17	0.3	4.2	3.0
Consumption (thousand tons)	71-115	0.3-0.5	5.1-8.3	2.1-3.4

Table 3. Consumption of *P. goniurus* by Alaska pollock in summer 1988 (ration: min - 0.4%; max - 5.6%).

	Anadyr Gulf	Koryak Shelf	Olyutor Gulf	Karagin Gulf
FISH:				
Body length (cm)	53.8	46.2	39.1	55.2
Body weight (g)	1,100	700	400	1,200
Quantity	132.5	65.3	246.3	45.5
SHRIMP:				
Frequency (%)	43	45	5	25
% in food	78	28	41	1
Consumption (thousand tons)	17-238	2-28	0.7-10.4	0.1-0.7

Table 4. Interannual dynamics of *P. goniurus* consumption by Alaska pollock and cod.

Fish Species	Frequency (%)					% in the food					Number of stomachs analyzed				
Year	81	82	83	86	88	81	82	83	86	88	81	82	83	86	88
Cod	100	60	53	62	38	*	*	50	44	9	33	70	100	176	602
Pollock	100	39	35	78	23	60	50	40	99	46	62	194	125	230	596

Note: *No data obtained

Table 5. Consumption of *Ch. opilio* by cod in summer 1988 (ration: min - 5%, max - 8%).

	Anadyr Gulf	Koryak Shelf	Olyutor Gulf	Karagin Gulf
FISH:				
Length (cm)	55.2	57.3	65.8	60.1
Abundance (millions)	77.5	50.0	17.2	29.6
Weight (g)	2,140	2,390	3,750	2,890
CRAB:				
Frequency (%)	19	32	26	15
% in food	40	70	60	30
Consumption (thousand tons)	57-91	121-193	45-72	17-28

Table 6. Consumption of *Ch. opilio* by Alaska pollock in summer 1988 (ration: min - 0.4%; max - 5.6%).

	Anadyr Gulf	Koryak Shelf	Olyutor Gulf	Karagin Gulf
FISH:				
Length (cm)	53.8	46.2	39.1	55.2
Abundance (millions)	132.5	65.3	246.3	45.5
Weight (g)	1,100	700	400	1,200
CRAB:				
Frequency (%)	3	-	-	-
% in food	100	-	-	-
Consumption (thousand tons)	1.5-22.0	-	-	-

Table 7. Consumption of *Ch. opilio* by sculpins in summer 1988.

	Anadyr Gulf	Koryak Shelf	Olyutor Gulf	Karagin Gulf
FISH:				
Biomass (thousand tons)	21.7	17.2	1.7	7.7
Abundance (millions)	14.5	8.5	0.9	3.1
CRAB:				
Frequency (%)	93	7	30	57
% in food	90	55	60	45
Consumption (thousand tons)	40	13	1	4

Principally, pollock and cod larger than 40-45 cm fed upon shrimps. Taking this into consideration, we employed the data on the abundance of pollock and cod larger than 45 cm in size in areas of high shrimp concentrations. The data on *Myoxocephalus* and *Hymnocantus*, the most numerous species in the area, were used for determining the consumption of tanner crabs. Analysis of feeding by the major fish species also shows that tanner crabs are very important in the diets of benthos-feeding species. Juvenile tanner crab occur with the humpy shrimp in the cod diet, and are the main component in the diet of sculpins (Table 1). Also, tanner crabs are significant in the diet of skates, although the latter are not highly abundant. We shall attempt to estimate the consumption of tanner crabs (*Ch. opilio* and *Ch. bairdi* by the major fish species in the area mentioned above. The contribution of *Ch. bairdi* to the fish diets is not crucial and does not exceed 7-8% of the total quantity of tanner crabs in their stomachs.

As data on the daily ration of pollock is controversial, the resulting estimates of its consumption of humpy shrimp vary by more than an order of magnitude (20-280 tons). We consider the ration obtained by Savicheva (1981), 4%, as most realistic. Thus, pollock consumption of shrimps in the northwestern Bering Sea can amount to approximately 200,000 tons. The estimated biomass of *P. goniurus* consumed by cod in summer 1988 varied from 80,000 to 130,000 tons. Thus, those two fish species annually consume hundreds of thousands of tons of humpy shrimp. Bearing in mind that their abundance variations seem to be asynchronous, and shrimps vary their abundance more than an order of magnitude, then predation can significantly influence the humpy shrimp population in the western Bering Sea.

Our preliminary calculations indicate that the total consumption of *Ch. opilio* by the most numerous fish species of the northwestern Bering Sea in summer 1988 was approximately 300,000-600,000 tons.

Thus, the tanner crab abundance variations can also be related to the biomass dynamics of predators feeding in this area (Figs. 1, 2, 3). Consideration that at present, the cod has reached its abundance maximum, and sculpins are not commercially harvested, it can be postulated that those predator species and the fisheries combined significantly influence the population dynamics of tanner crabs, especially in their "nursery" area in the Gulf of Anadyr. From June to August 1988, the major fish species consumed about 100,000-150,000 tons of tanner crab juveniles. As for the blue crab (*Paralithodes platypus)*, its consumption is difficult to assess due to its low abundance. But we have observed three cases of blue crab in cod stomachs in the Olyutorsky Gulf.

The main difficulty in determining the amount of crustaceans consumed involves determination of the rate that they are consumed, since all published data are extremely controversial. But even now it is clear that management of commercial fisheries on crustacean and fish stocks should be conducted in concert, which leads us to the vital necessity of expanding ecosystem investigations in the western Bering Sea.

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Proc. Int. Symp. King & Tanner Crabs
Nov. 1989, Anchorage, Alaska

Feeding Habits of Southern King Crab, *Lithodes santolla* (Molina), and the False King Crab, *Paralomis granulosa* Jacquinot, in the Beagle Channel

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ABSTRACT

Stomach contents from 245 Lithodes santolla and Paralomis granulosa ranging in size from 40-100 mm CL, from the Beagle Channel near Ushuaia, were analyzed. Capture was made by SCUBA diving at depths from 4 to 36 m. Vacuity, repletion and frequency indexes were calculated.

The dominant food groups in terms of frequency of occurrence in L.santolla were: gastropods, Foraminifera, Algae, Bryozoa and echinoids. Crabs, isopods and amphipods were found exclusively in this species. Fed taxa in P.granulosa were: Algae, Foraminifera, Bryozoa, bivalves and gastropods. Barnacles, ascidians and Polychaeta were exclusive taxa for this species. Prey groups in southern king crab consist in more mobile organisms than those consumed by the false king crab.

Non-significatly differences in terms of food wt/animal wt between sexes for each of both species were observed. Smaller crabs consumed significantly more food than larger crabs.

INTRODUCTION

The southern king crab, Lithodes santolla (Molina), and the false king crab, Paralomis granulosa Jacquinot, commonly named "centollón", are the most important commercial shellfish in Tierra del Fuego, Argentina and in the XII° Región, Chile. Both species represent important organisms in the Beagle Channel, the Magellan Strait and other localities in the South Pacific and South Atlantic oceans.

In order to manage a fishery efficiently, knowledge of crabs distribution and abundance, their reproductive biology and behavior of the involved species are major requisites. The

early life history, size and growth, and reproductive biology of L.santolla have been described (Campodónico, 1971 Geaghan, 1973; Boschi, et al., 1984; Vinuesa, 1984; Bertuche, et al., 1985; Vinuesa et al., 1985;1989). Little is known in P.granulosa; early life history (Campodónico and Guzmán, 1981; Vinuesa, et al., MS) and some population studies (Campodónico, et al., 1983) were carried out.

Feeding habits for both species are poorly known. Only few isolated stomach analysis were previously performed in L.santolla (Scelzo, et al., 1974; Guzmán and Ríos, 1985). In P.granulosa food intake was largely unknown.

In this study we analyzed the stomach contents in L.santolla and P.granulosa to determine the diet of the species and to compare them to determine a possible niche overlapping.

MATERIAL AND METHODS

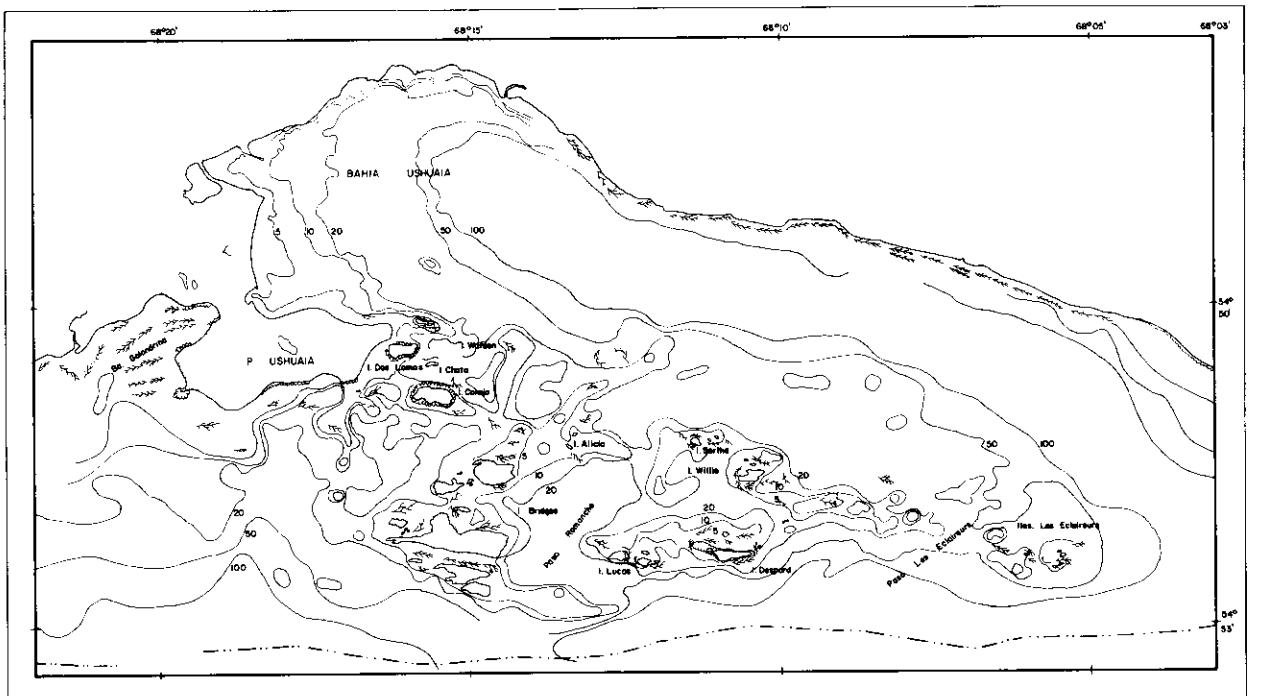
Specimens ranging in size from 40-100 mm carapace length (CL) of Lithodes santolla and Paralomis granulosa were monthly collected in the Beagle Channel, near Ushuaia, by SCUBA diving during 1988. Sampled areas include the Ushuaia Bay and the Golondrina Bay. Depths of captures were 4 to 36 m approximately (Figure 1).

Crabs were measured (carapace length, in mm) weighed (wet weight, in g) and categorized by sex. CL is defined as the distance from the posterior margin of the orbital indentation to the mid-point of the posterior marginal indentation. Both L.santolla and P.granulosa were categorized in one of 6-10mm incrementd size classes. Stomachs were removed from esophagus to the proximal part of the intestine. Then, stomach contents were removedand weighed to the nearest 1/100 g and they were fixed in 10% neutralized formaline. Stomach contents were sorted to the lowest possible taxonomic level. Skeletal material was here considered as food.

A frequency index (F) (Arnaud and Miquel, 1985) for identified prey taxa in stomachs was calculated as $F = n \times 100 / N'$; where n is the number of stomachs containing a particular taxon and N' is the number of stomachs with preys. A vacuity index (V) (Arnaud and Miquel, 1985) was calculated as $V = Es \times 100 / N$; where Es is the number of empty stomachs and N is the total number of stomachs examined. Also a food index (K) (Takeuchi, 1968) was calculated as $K = FW / BW$; where FW is food weight and BW is the wet weight of the crab. It was used in order to relate the weight of food to weight of crab from which the food was taken.

As the weight of stomach contents was not normally distributed, the median weight value rather than the aritmethic mean was used as the measure of central tendency. Two statistical procedures were used in analyzing the food of crabs. Mann-Whitney-Wilcoxon test was employed to test the null hypothesis that there is no difference in amount of food consumed between sexes (Daniel, 1978). The second

FIGURE 1: Area where Lithodes santolla and Paralomis granulosa were collected for stomach analyses, 1988.



procedure, the Kruskal-Wallis Test (Daniel, 1978) was used to determine feeding differences between crab size classes. A probability value was calculated and, if it was found to be less than 0.05, multiple comparisons using rank sums, was employed.

RESULTS

Lithodes santolla

Stomach contents of 127 specimens of Lithodes santolla were examined; 20,47% were empty. From the total of empty stomachs, 30.67% were females and 69.33 were males. From the total of the postmolt-shell conditioned crabs (N=15) the 73.11% of the stomachs were empty or showed trace food. All size classes were represented in the same percentage (Chi-square = 10.28; $P < 0.05$) (Table 1). Sex ratio was 1:1 (Chi-square test; $P < 0.05$).

Items Gastropoda, Foraminifera and Filamentall algae were the dominant food groups in terms of frequency of occurrence. Items Bryozoa and the echinoid Pseudechinus magellanicus were the next most important groups. Gastropods, Laminar Algae, the anomuran Munida sp. and isopods consumed by females showed a greater frequency of occurrence than those in males (Figure 2).

The effect of sexes on weight of consumed food was tested by Mann-Whitney-Wilcoxon method and non significant differences were observed; thus data from both sexes were assembled (Table 2). The effect of the crab size on weight of consumed food was tested by the Kruskal-Wallis method. Food weight is significantly different among size classes. Smaller crabs consumed major amounts of food than larger ones (Groups 40-49.9 > 90-99.9 mm CL and 50-59.9 > 90-99.9 mm CL differ significantly; multiple comparison, $P < 0.20$) (Table 3).

TABLE 1: Percentage of animals by size classes in L.santolla and P.granulosa.

SIZE CLASS (mm)	Lithodes santolla (%)	Paralomis granulosa (%)
40-49.9	14.17	4.24
50-59.9	25.19	10.17
60-69.9	16.54	32.20
70-79.9	20.47	38.10
80-89.9	14.17	14.40
80-89.9	7.87	0.85

FIGURE 2: Lithodes santolla. Frequency of occurrence of food items in 127 stomachs.

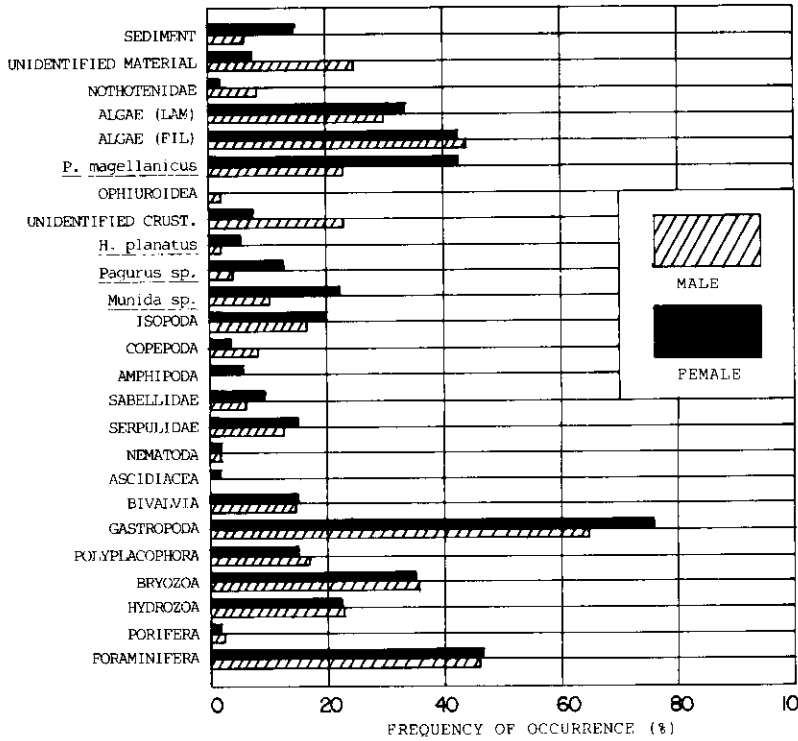


TABLE 2: Lithodes santolla. Mann-Whitney Wilcoxon for food wt and sex.

SEX	STOMACHS WITH FOOD No	RANK SUM OF CONTENTS	AVERAGE RANK SUM OF CONTENTS
MALES	46	2353.99	51.173
FEMALES	55	2796.990	50.855

* Test statistic = -0.05114
* P-value = 0.959

TABLE 3: Lithodes santolla. Kruskal-Wallis One-Way ANOVA for food wt to crab size groups.

CARAPACE LENGTH (mm)	STOMACHS WITH FOOD No	RANK SUM OF CONTENTS	AVERAGE RANK SUM OF CONTENTS
40-49.9	12	735.99	61.33
50-59.9	26	1488.50	57.25
60-69.9	18	900.00	50.00
70-79.9	20	1039.50	51.98
80-89.9	15	627.00	41.80
90-99.9	9	259.00	28.78

* Test statistic = 9.55707
* P-value = 0.089 (assuming a Chi-square distribution with 5 DF)
* Pairs significantly different ($P < 0.20$): 40-49.9 > 90-99.9
50-59.9 > 90-99.9

Paralomis granulosa

Stomach contents of 118 specimens of P.granulosa were examined; 89% of the stomachs contained food. From the total of empty stomachs, 61.54% were males.

The distribution of size classes was significantly different (Chi-square = 69.11, $P < 0.005$) (Table 1). Groups 3 and 4 (60-80 mm CL) were the most frequently sampled. Sex ratio was 7:3 for males and females respectively. This results are due to a spatial segregation between sexes and sizes observed.

In males Algae, Gastropoda and barnacles were the dominant food groups, regarding to frequency of occurrence. In females the most important groups were Bivalves and Hydrozoa (Figure 3).

Non-significant differences were observed between sexes using Mann-Whitney-Wilcoxon test; thus, data from both sexes were combined (Table 4).

Weight of consumed food was significantly different among different size groups (Kruskal-Wallis test)(Table 5). The pairs significantly different were 40-49.9 > 80-89.9 and 40-49.9 > 70-79.9 (multiple comparison, $P < 0.20$).

Differences between species

The little crab Halicarcinus planatus, isopods and amphipods are exclusively present in L.santolla while barnacles and ascidians were only consumed by P.granulosa (Figure 4). Organisms consumed by false king crab are proved to be less mobile than those fed by southern king crab. These facts could be related to the movements of the studied species: P.granulosa exhibits slow movements and it has tendency to burrow into the substrate, while L.santolla is a mobile animal.

FIGURE 3: Paralomis granulosa. Percentage Frequency of occurrence of food items in 118 stomachs.

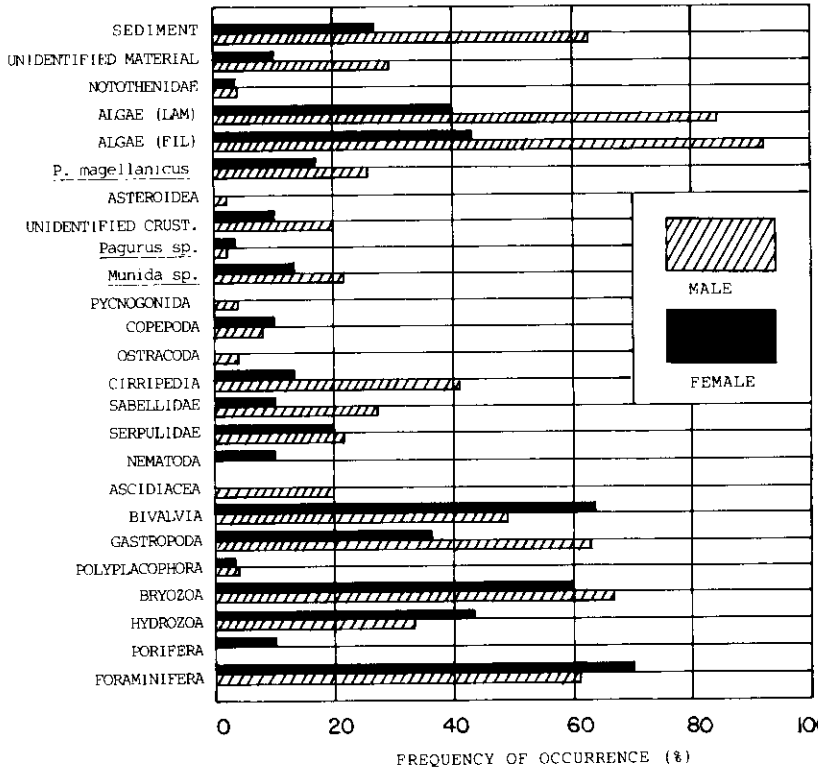


TABLE 4: Paralomis granulosa. Mann-Whitney-Wilcoxon for food wt and sex

SEX	STOMACHS WITH FOOD No	RANK SUM OF CONTENTS	AVERAGE RANK SUM OF CONTENTS
MALES	78	3984.9966	51.0897
FEMALES	27	1579.9995	58.5185

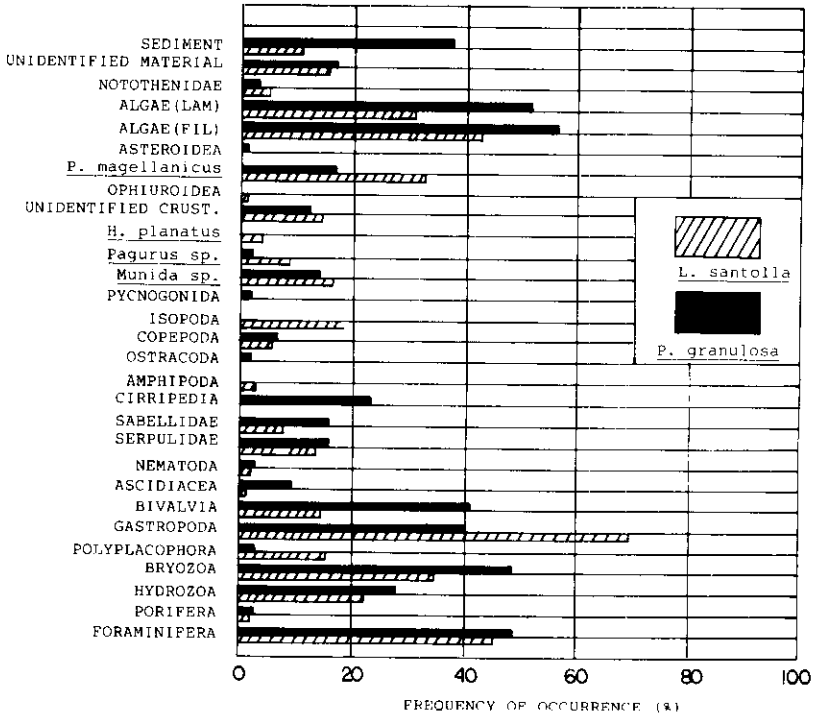
* Test statistic = 1.08877
* P-value = 0.2763

TABLE 5: Paralomis granulosa. Kruskal-Wallis One-way ANOVA for food wt relative to crab size groups.

CARAPACE LENGTH (mm)	STOMACHS WITH FOOD No	RANK SUM OF CONTENTS	AVERAGE RANK SUM OF CONTENTS
40-49.9	5	412.00	82.40
50-59.9	10	627.00	62.70
60-69.9	35	1934.99	55.29
70-79.9	39	1828.00	46.87
80-89.9	15	658.00	43.87

* Test statistic = 8.94055
* P-value = 0.063 (assuming a Chi-square distribution with 4 DF)
* Pairs significantly different ($P < 0.20$): 40-49.9 > 80-89.9
  40-49.9 > 70-79.9

FIGURE 4 : L.santolla and P. granulosa. Percentage of occurrence for both species.



DISCUSSION

Few studies in natural diet of lithodids in the Southern Oceans were carried out. Stuardo and Solís (1963) mention the dominance of bryozoans and crustaceans in the diet of Lithodes antarcticus from the Magellan Strait based on 25 stomachs of which 20 were empty. In contrast, the diet of the North Pacific king crab Paralithodes camtschatica has been much studied (see literature cited in Jewett and Feder, 1982). This species reflect a high variation in composition and in the dominance of prey groups: bivalves, gastropods, cirripeds and echinoderms are largely present. These items are mostly sedentary and thy are well represented in P.granulosa as well as in other studied lithodid from the Southern Indic, Lithodes murrayi (Arnaud and Miquel, 1985). At the other hand L.santolla was found to be a mobile-organisms predator.

Regarding to food weight relative to crab size groups, intermediate sizes of P.camtschatica (120-139 mm CL) consume significantly more food than other size classes (Jewett and Feder, 1982). In L.santolla and in P.granulosa it was observed that smaller crabs consumed significantly more food than larger ones. It could be assumed that these crabs increased food ingestion to equilibrate the expended energy in molting. At least, juveniles L.santolla molt more frequently than larger crabs. (Vinuesa et al., 1989).

Both, sediments and Foraminifera were taken inderectly with food. Although Foraminifera appears to be one of the dominant food groups in terms of frequency of occurrence, their contribution to the total biomass in the stomach content is not significantly important: it was observed few specimens per stomach.

Taking into account the commercial importance of these species, additional information are essential to understand their feeding biology. Some parameters that should be included: the time required for the passage of food along the digestive tract, maximun stomach volume, tamporal patterns of feeding, caloric content of preys, importance of foods containing Calcium relative to molting stage and interactions (prey-predator; competition) with other benthic decapods.

In the Beagle Channel the sympatric species Lithodes santolla and Paralomis granulosa seem to be competitors, occupying a similar trophic niche. Consuming mobile or sessile preys could be a tactic to avoid trophic niche overlapping. Much studies should be done in this sense.

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Mortality

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Influence of Cold Air Exposures on Ovigerous Red King Crabs (*Paralithodes camtschatica*) and Tanner Crabs (*Chionoecetes bairdi*) and Their Offspring

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ABSTRACT

Ovigerous red king, *Paralithodes camtschatica*, and Tanner, *Chionoecetes bairdi*, crabs are often caught incidentally in the males-only fishery for these crabs. Effects of low air temperature on ovigerous crabs and their developing larvae were simulated by exposing groups of crabs to cold air (-20 to +5°C) from 0 to 40 minutes. Response to cold air was best described when the units of exposure were the product of temperature (°C) and duration of exposure (h). Short exposure at low temperatures caused the same effects as long exposure at high temperatures when the units of exposure (degree•hours, °h) were equal. Exposure to cold air reduced vigor (measured by the ability of a crab to right itself when placed on its back), feeding rates (Tanner crab), and growth (king crab). Exposure also caused limb autotomy in Tanner crabs, and mortality in both species in severe situations. Median lethal exposures, measured 128 days after emersion, were -8 ± 2°h for king crabs. Median lethal exposure stabilized after 16 days for Tanner crabs at -4.3 ± 0.5°h. Righting times were reduced immediately after exposure and in sublethal treatments; median exposures causing half the crabs to cease righting immediately after exposure were -8 ± 2°h (king crab) and -2.1 ± 0.3°h (Tanner crab). Mean limb autotomy ranged up to 11% for Tanner crabs; some severely treated king crabs lost legs at ecdysis. During ecdysis, severely exposed king crabs often died. Tanner crab feeding rates were depressed ($P < 0.001$), and king crab growth was reduced ($P = 0.02$). However, if the adult crabs survived, hatch timing, percent hatch, and zoeal viability were not affected.

INTRODUCTION

Current Alaska fishing regulations require release of undersized male red king, *Paralithodes camtschatica*, and Tanner, *Chionoecetes bairdi*, crabs and all female crabs. (*P. camtschatica* will be referred to synonymously as king crab in this paper). The minimum legal size for male king crabs is 121-180 mm, depending on the management area, and 140 mm for Tanner crabs. Incidentally caught crabs may be exposed to cold air for various periods of time before being returned to the sea. Commercial fishing seasons range from September through February (king crab) and from January through April (Tanner crab) (ADF&G, 1989a-c). During these seasons normal daily minimum air temperatures in coastal Alaska range down to -21°C (NOAA, 1987). There is also an ice-based king crab fishery in Norton Sound where mean temperatures range from -14° to -16°C from December through March, and mean wind speeds range from 17 to 19 km/h (NOAA, 1987). Exact exposure duration of incidentally caught crabs to air on deck is unknown, but may approach 15 minutes. Exposure may result in mortality to crabs and developing larvae.

A few studies on the effects of aerial exposure have been reported for other commercially harvested decapod crustaceans, but nearly all of these have been conducted on species inhabiting lower latitudes (Schlieder, 1980; Brown and Caputi, 1983, 1985, and 1986; Vermeer 1987; Taylor, 1989). The only study of which we are aware on either king or Tanner crab was by Nakanishi (1974), who found that heart rate in *P. camtschatica* can be depressed during aerial exposure and that changes in heart rate may depend on water temperature.

The purpose of our experiment was to investigate the effects of exposure to cold air on ovigerous king and Tanner crabs and their developing larvae. Our objectives were to determine the effects of low air temperature on 1) survival of adults, 2) sublethal responses of adults including limb autotomy, ecdysis, righting response, feeding rate and growth, 3) survival of developing larvae, 4) zoeal production and viability, and 5) egg extrusion.

METHODS

All experimental animals were caught in crab pots. King crabs were caught at a depth of about 55 m in Auke Bay, Alaska (lat. 58°21'N, long. 134°41'W) from 1 December 1986 to 23 January 1987. Tanner crabs were caught north of Auke Bay near the mouth of Eagle River (lat. 58°31'N, long. 134°48'W) and Lena Point (lat. 58°24'N, long. 134°47'W) in Favorite Channel on 11 February 1988.

Carapaces were measured to the nearest millimeter from the posterior margin of the right ocular orbit to the midpoint of the carapace posterior margin. Live weights were measured to the nearest 0.1 g. A cinch tag was placed around the base of the third walking leg of each king crab. Crabs were maintained in 500 L tanks at ambient seawater temperatures (4.9-5.2°C for king crabs and 5.3-6.0°C for Tanner crabs) until exposure and were returned to the same tanks for 30 to

35 days of observation following treatment. Water temperatures in holding tanks after exposure were 4.4-5.2°C for king crabs and 4.7-5.2°C for Tanner crabs.

Crabs were exposed in a modified chest freezer (Fig. 1). The freezer was divided into two compartments with a wooden baffle. Infrared heat lamps were placed on one side of the baffle for temperature control. Air was drawn from one compartment, the exposure chamber, with a small fan inserted in the bottom of the baffle (air flow = 45 ± 5 cm/sec) and circulated over the baffle to distribute air uniformly; circulating air reentered the exposure chamber at the top. Temperature was measured with a thermister located in the exposure area near the fan and was regulated manually by switching the heat lamps on or off. Temperatures were controlled to ±0.1°C after the chamber had cooled to the desired temperature. Crabs were exposed to cold air on plywood at the bottom of the chamber.

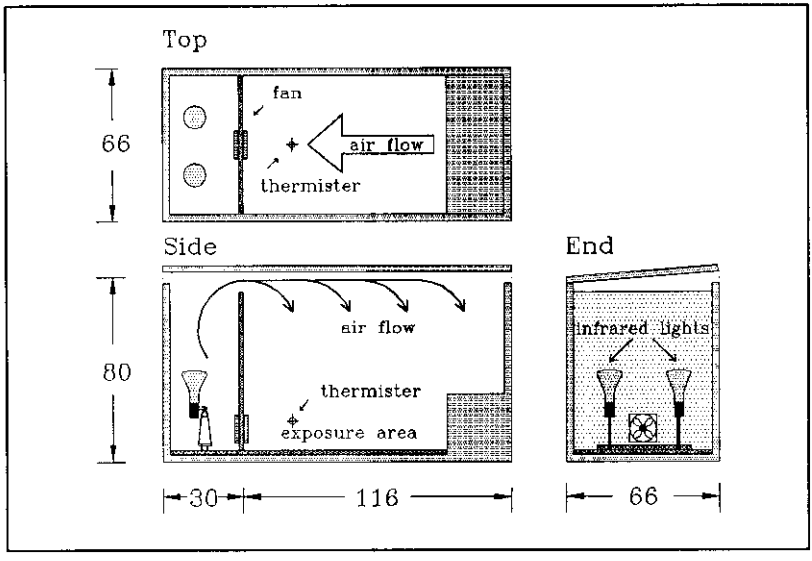

Figure 1.--The chamber used for experimental aerial exposure. Lights were each 250 W. Units = cm.

Evaporative loss was estimated in a separate experiment by measuring the reduction in the mass of 5 mL of seawater enclosed in paired, dried crab carapaces at -10°C. We did not measure evaporation directly from living crabs because variable water loss owing to drainage from the branchial chamber and other water retention sites on the exoskeleton combined with increased evaporative rates of the drained water would have confounded the estimates of evaporative loss made in this way. Evaporative loss was initially 0.18 g/L/min becoming asymptotic in about 10 minutes at 0.60 g/L/min. The freezing rate of seawater in identical

containers was greatest in small volumes; fluid temperatures decreased in a nonlinear fashion ($T = ae^{b*m}-10$, where T = temperature in celcius and m = mass in grams).

Crabs were placed haphazardly in 20 groups (including controls) in a complete two factor (temperature by length of emersion) design. In the king crab experiment most groups contained 5 crabs (3 crabs per group at +5°C). King crab treatment temperatures were +5.0 ± 0.2°C, -4.8 ± 0.2, -9.6 ± 0.1, and -18.9 ± 0.4°C; exposure times were 0, 10, 20, 30, and 40 minutes. King crabs were exposed on 5 February 1987, 13-36 days after capture. In the Tanner crab experiment each group contained 7 to 8 crabs. Treatment temperatures were 5.1 ± 0.1°C, -3.1 ± 0.1, -8.2 ± 0.1, -13.1 ± 0.1, and -19.7 ± 0.2°C; exposure times were 0, 4, 8, 16, and 32 minutes. Tanner crabs were exposed on February 16 and 17, about 6 days after capture.

Mortality and limb autotomy were observed daily. Crabs were judged dead when scaphognathite movement stopped. Dead crabs were generally rechecked the following day before they were removed from test tanks. The number of legs missing on each crab was counted and autotomized legs were removed from the tanks.

Righting response (the time it took a crab to turn over when placed on its back under water on the bottom of the holding tank), which we considered to be a measure of vigor, was timed with a stop watch immediately after aerial exposure and 1, 2, 4, 8, 16, 24, and 32 days thereafter. Crabs that could not right themselves after 2 minutes were recorded as "not righting" and placed upright until the next observation.

After righting responses were recorded, all king crabs and a subset of 40 Tanner crabs were isolated in covered 70 L tanks which overflowed into 19 L buckets containing conical 363 μm mesh nets designed to trap zoea. The flow rate of seawater through the tanks was maintained at about 1.5 L/min with a 95% turnover time of 2.3 h. Water temperatures ranged from 4.2 to 5.5°C for king crabs and from 5.2 to 5.9°C for Tanner crabs during zoeal release (Table 1).

Table 1.--Hatching times for king and Tanner crab zoeae. The king crab hatch was bimodal because zoeae hatched earlier from smaller, presumably primiparous, crabs.

Hatch Date	King Crab	Tanner Crab
Start	March 12	April 11
Median(s)	March 25, April 20	April 25
End	May 18	May 9

Feeding rates were measured before and after zoeal release while the Tanner crabs were individually isolated. Crabs were fed mussels, *Mytilus edulis*, ad libitum during each measured feeding period. Living mussels were cut in half and

drained tissue-side down on paper towels for 5 minutes, weighed, then placed in the tanks. Twenty-four hours later the remaining food was removed, drained and weighed as before. At each feeding, four food portions were placed in tanks without crabs to act as controls. Consumption was corrected for the mean changes in the control portions. Feeding observations were repeated every 1 to 3 days, from 41 to 60 and 85 to 98 days after exposure.

King crab zoeae were collected daily, rinsed from the nets, filtered to remove excess water, and fixed in 5% Formalin. The content of each net was subsampled with a Folsom plankton splitter. The zoeae in each subsample were counted and the remainder of the sample was weighed (wet) after debris removal. Samples were preserved a minimum of one week prior to weighing. Estimates of the number of zoeae in each sample were extrapolated from the counts in the subsamples or from total sample weights divided by zoeal wet weight (1.1 ± 0.06 mg/zoea).

Tanner crab zoeae were collected daily, rinsed from the nets, and subsampled with a plankton splitter designed to subsample zoeae quickly and accurately (Fig. 2). The splitter drained samples to a constant volume. An outer cylindrical container mounted on a level platform controlled the water height. Excess water drained through a wide orifice, which was covered after excess water overflowed. Volumes (76-845 mL) were determined by selecting one of eight cylidrical specimen holders with bottoms of plankton net (mesh size 363 μm.) The specimen holder containing the sample was placed inside the larger cylindrical container. After the excess water over-

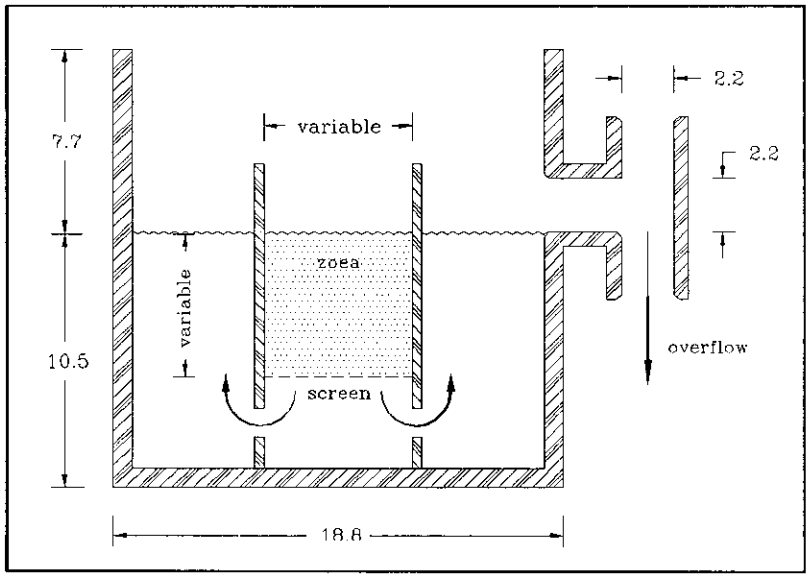

Figure 2.--Cross section of plankton splitter.

flowed, samples were mixed to distribute zoea randomly and a subsample was withdrawn with a Hensen-Stemple pipette (5 or 10 mL). Data in this paper are based on the first subsample withdrawn. Subsamples were fixed in 5% Formalin for subsequent counting. The occasional large subsample was divided with a Folsom plankton splitter before counting. Samples were fixed a minimum of one week prior to weighing.

After hatching was complete, debris from each tank bottom was collected with a siphon and preserved. Eggs and zoeae in this debris were counted. After ecdysis the remains of each king crab egg clutch were removed from the exoskeleton and preserved. Eggs in these remnant clutches were counted. Difficulties (death, prolongation of ecdysis, or leg loss) encountered by king crabs during ecdysis were recorded.

Responses of the crabs were related to aerial exposure expressed as the product of air temperature (°C) and length of exposure (h). The units of exposure used here are therefore degree·hours hereafter abbreviated as "°h". See results section for data supporting the use of exposure in °h as the independent variable in our analyses. Regression techniques and logit analysis were used to relate response variables to exposure. Log-likelihood ratio tests were used to compare median lethal responses (Fujioka, 1986). Multiple regression in conjunction with dummy variables was used to test for differences in the slopes of regression lines and to adjust for covariates. Parametric correlation was used to relate selected response variables to one another. Comparisons of treatment means were tested with Tukey's or Dunnett's *a posteriori* multiple comparsion tests at the P = 0.05 level following one-way analysis of variance. Arcsine transformations were used on proportional data. All error ranges reported below are ±95% confidence limits.

RESULTS

The weights of king crabs tested ranged from 688 to 2908 g ($\bar{x}$ = 1405 ± 109 g) with carapace lengths 9.12 to 16.35 cm ($\bar{x}$ = 11.9 ± 0.4 cm). Tanner crab weights ranged from 182 to 533 g ($\bar{x}$ = 329 ± 8 g) with carapace lengths 6.5 to 9.6 cm ($\bar{x}$ = 8.0 ± 0.1 cm). Crab lengths and weights did not differ among treatment cells.

Response to aerial exposure was analyzed as a function of air temperature (°C) and length of exposure (h) in °h because shorter emersion at lower temperatures caused the same effects as longer emersion at higher temperatures where °h were the same. For example, king crab righting times and percent not righting were not significantly different within the following three groupings: $R_{(-5°C,20\ min)} \approx R_{(-10°C,10\ min)}$, $R_{(-10°C,40\ min)} \approx R_{(-20°C,20\ min)}$, and $R_{(-5°C,40\ min)} \approx R_{(-10°C,20\ min)} \approx R_{(-20°C,10\ min)}$, where R = response and subscripts are exposure conditions (Table 2). King crab mortality and percentage of king crabs not molting were similar within these groupings and also show similar responses to equivalent exposures. Tanner crab data could not be similarly grouped to determine equivalent responses because test temperatures and times did not produce any equal exposures.

Table 2.--Several combinations of temperature and duration of emersion produced the same results: for example, king crab death observed 128 days after emersion, and number not righting observed 32 days after emersion. N = number of deaths, number not molting, or number not righting; M = total number observed; and SE = standard error.

Exposure			Death	Molt	Righting	
°C	Minutes	°h	N/M	N/M	N/M	Sec ± SE
-10	40	-6.7	2/5	2/4	1/5	30 ± 33
-20	20	-6.7	3/5	2/4	1/5	59 ± 87
- 5	40	-3.3	1/5	0/4	1/5	3 ± 3
-10	20	-3.3	0/5	0/5	0/5	4 ± 1
-20	10	-3.3	1/5	0/4	0/5	11 ± 16
- 5	20	-1.7	0/5	0/5	0/5	2 ± 1
-10	10	-1.7	0/5	0/5	0/5	4 ± 2

Death of king crabs caused by exposure was delayed; 2 days after exposure only one crab had died, and mortality did not exceed 50% until 19 days after exposure at -12.7°h. Mortality was inversely proportional to exposure and increased sharply below -4.6°h; $r^2_{logit} = 0.70$, n = 10, measured 128 days after exposure (Fig. 3a). The median lethal exposure was -13.4 ± 4.0°h 16 days after exposure, but rose to -7.8 ± 1.8°h 128 days after exposure.

In contrast, Tanner crabs died soon after exposure; up to 50% of the deaths occurred within the first 24 h. Mortality was inversely proportional to exposure and increased sharply below -3°h; $r^2_{logit} = 0.84$, n = 17 (Fig. 3a). Nearly all deaths occurred within 8 days after exposure. Median lethal exposures rose from -7.2 ± 1.6°h measured 1 day after exposure to -4.3 ± 0.5°h 16 days after exposure, and differed significantly from the king crab median lethal exposure ($P < 0.001$, n = 13). No Tanner crabs died after day 16.

King crab mortality often occurred during ecdysis; correlation between mortality during ecdysis and total mortality was high ($r^2 = 0.88$, n = 13). Below -4.6°h the percentage of crabs experiencing difficulty during ecdysis increased sharply. Crabs that encountered difficulty generally died during ecdysis. The median exposure causing death during ecdysis was -8 ± 2°h. Because female Tanner crabs undergo terminal anecdysis at puberty we could not examine mortality during ecdysis in this species.

King crabs began molting on March 23 and continued through June 4, although 90% had molted by May 16. One crab receiving an exposure of +3.4°h, observed until Sept. 18, did not molt. Although the lone surviving severely treated crab (-12.7°h) was the last to molt (June 4), molt timing and exposure were uncorrelated ($r^2 = 0.09$, n = 69).

Righting times were reduced by aerial exposure and were inversely proportional to exposure. Righting times and the percentage of crabs not righting increased sharply below -4.6°h for king crabs and -2.2°h for Tanner crabs (Fig. 3b). Crabs ceased righting entirely after exposure to ≤-12.7°h (king crab) and ≤-6.9°h (Tanner crab). The percentage of crabs unable to right themselves was a function of exposure; $r^2_{logit} = 0.83$, n = 13 for king crabs, and $r^2_{logit} = 0.70$, n = 22 for Tanner crabs. Median righting responses of king and Tanner crabs differed significantly (-10.9°h vs -3.8°h respectively on day 32; $P < 0.001$, n = 13). The percentage of crabs unable to right themselves immediately after exposure correlated with mortality ($r^2 = 0.83$, n = 13 for king crabs and $r^2_{\sqrt{x}} = 0.67$, n = 22 for Tanner crabs). The percentage of king crabs unable to right themselves correlated with the percentage of crabs experiencing molting difficulty ($r^2 = 0.95$, n = 13) and molt increment ($r^2 = 0.39$, n = 13). The percentage of Tanner crabs unable to right themselves correlated with limb loss ($r^2_{ln} = 0.85$, n = 22). Righting times of crabs tended to improve during the first 8 days after exposure, but this recovery was generally not statistically significant. Recovery of severely affected king crabs was often temporary. In a few cases the percentage of crabs not righting declined significantly over time, but generally data were scattered and fits were poor.

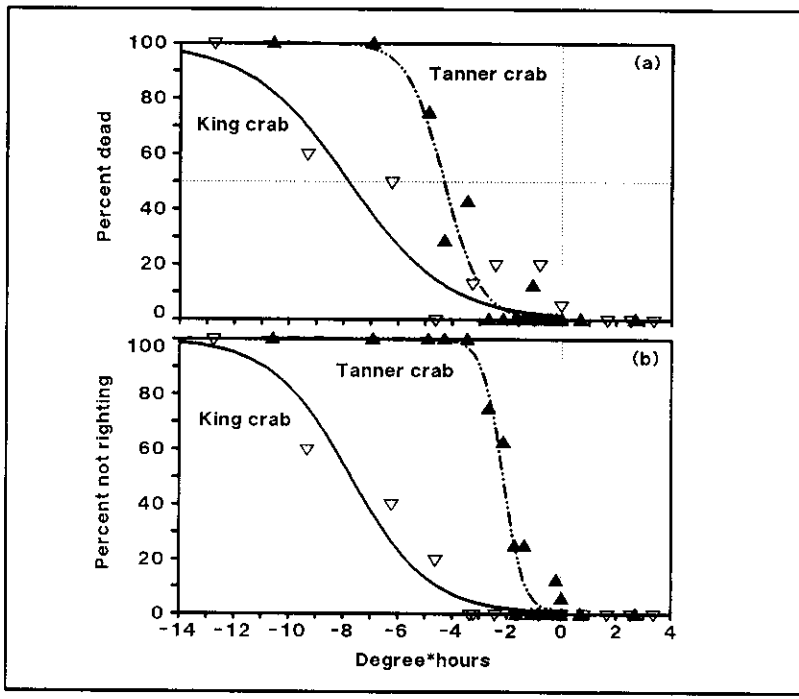

Figure 3a.--Percent mortality 128 days after aerial emersion as a function of exposure (°h). 3b.--Percent crabs not righting immediately after emersion as a function of °h.

Aerial exposure caused limb autotomy in Tanner crabs, and induced limb loss during ecdysis in king crabs. The percentage of Tanner crab limbs lost per treatment was linearly related to exposure; $P < 0.001$, $r^2 = 0.85$, $n = 19$ (Fig. 4). Autotomy was most frequent immediately after exposure and correlated with mortality ($r^2 = 0.81$, $n = 19$). King crabs that survived exposure at -9.3°h lost a significant percentage of walking legs during ecdysis (Dunnett test) (Fig. 4). Severely affected crabs frequently had difficulty withdrawing legs from their old exoskeletons.

Feeding rates of adult female Tanner crabs were depressed by exposure ($P_{ANOVA} < 0.001$, Fig. 5). In general, crabs exposed to ≤-2.7°h (62% of the median lethal exposure) fed significantly less than controls (Tukey test). Feeding rates [(mg/g/d)/(°h)] measured shortly before zoeal release (41 to 60 days after exposure) were significantly less for all crabs than feeding rates measured after zoeal release (85 to 98 days), but the slopes between treatments did not differ ($P > 0.50$, Fig. 5). The frequency of feeding also increased after zoeal release but was significantly related to aerial exposure before and after larval release ($P_{linear} < 0.001$). The most severely exposed crabs (-4.9°h) did not feed prior to zoeal release, but ate 57% of the time after release.

King crab growth, measured by molt increment and live weight, was a function of initial crab size and exposure (Figs. 6 and 7). Molt increments of controls declined with increasing crab size; $P < 0.001$, $r^2 = 0.68$, $n = 18$ (Fig. 6). Molt increments of king crabs in subzero exposures were less than controls after adjusting for crab size with multiple regression ($P = 0.020$, $n = 63$). Weight change decreased with increasing crab size; $P < 0.001$, $r^2 = 0.44$, $n = 71$; $r^2 = 0.62$ after removal of 4 outliers (Fig. 7). Changes in weight of king crabs with exposure did not depend on whether the crabs extruded eggs (41 crabs extruded infertile eggs after

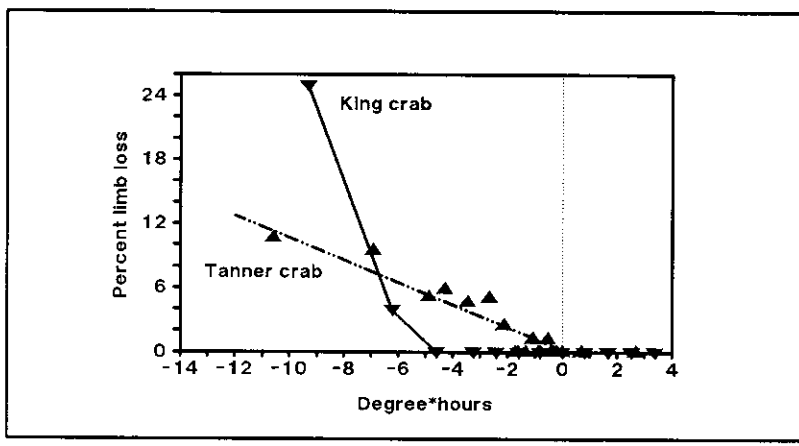

Figure 4.--Limb loss as a function of exposure (°h).

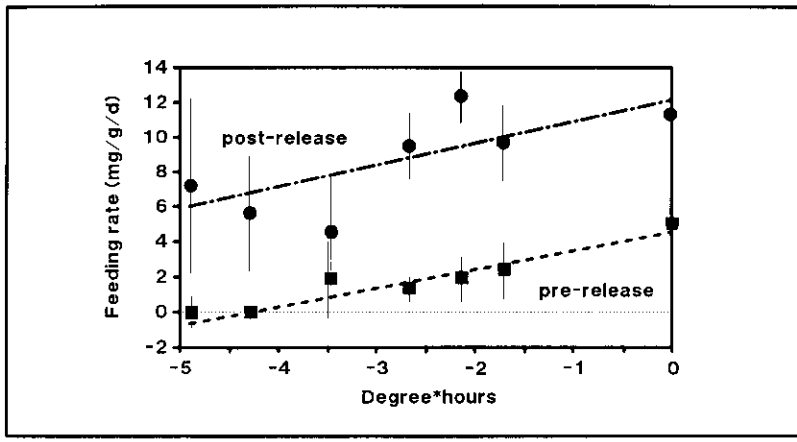

Figure 5.--Feeding rates (mg/g/d) of Tanner crab before and after zoeae release plotted against exposure (°h). Error bars are ±95% CI.

molting). The slopes and positions of the regression lines relating weight change to exposure did not differ regardless of whether the crabs extruded eggs or not ($P > 0.75$, n = 61 for position and slope, multiple regression). Weights of king crabs emersed at subzero temperatures declined with decreasing exposure; $P < 0.001$, n = 61 after adjusting for crab size (Fig. 7). Crabs emersed at temperatures greater than freezing showed no trend in growth with exposure. Tanner crab weights did not correlate with exposure ($r^2 \leq 0.08$, n = 44).

Exposure of ovigerous crabs generally did not affect eggs or subsequently released zoeae unless the female died; all eggs died if the female died. Timing of initial zoeal release, duration of release, and median release dates did not vary with exposure; $r^2 \leq 0.17$, $n_{king} = 80$, $n_{Tanner} = 44$ (Table 1). Zoeae placed in separate containers for 2 days continued swimming (83 ± 6% for king crabs, 87 ± 3% for Tanner crabs), and were not significantly affected by exposure ($P \geq 0.425$, $r^2 \leq 0.02$, $n_{king} = 70$, $n_{Tanner} = 43$). Larval viability measured by the percentage of zoeae which sank to tank bottoms and died (5 ± 5% for king crabs and 0.4 ± 0.2% for Tanner crabs), did not vary with the amount of exposure ($r^2 < 0.04$, $n_{king} = 32$, $n_{Tanner} = 44$).

Although 42% of the king crabs molted before their clutches had completely hatched, neither the percentage of eggs remaining in the clutches (36 ± 15%) nor the percentage of eggs that hatched (57 ± 15%) was affected by exposure ($P_{ANOVA} = 0.433$, n = 37). Tanner crab hatching success may have been very slightly affected. The percentage of eggs hatching in the -5.3°h treatment differed significantly from the control (Dunnett test), but the differences were minor (99.1% versus 99.8% hatching).

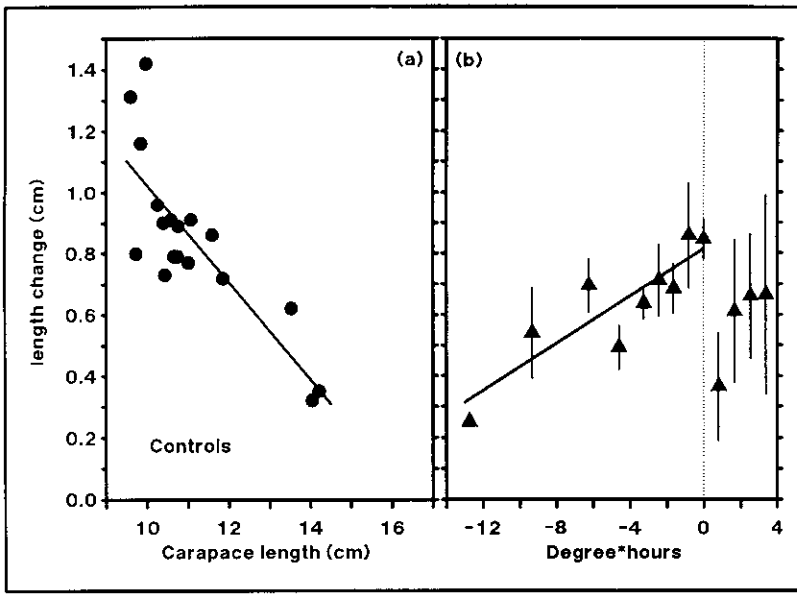

Figure 6.--King crab carapace growth as functions of initial carapace length and exposure (°h). Error bars are ± 1 standard error. Fitted curves include only negative degree hour exposures plus controls.

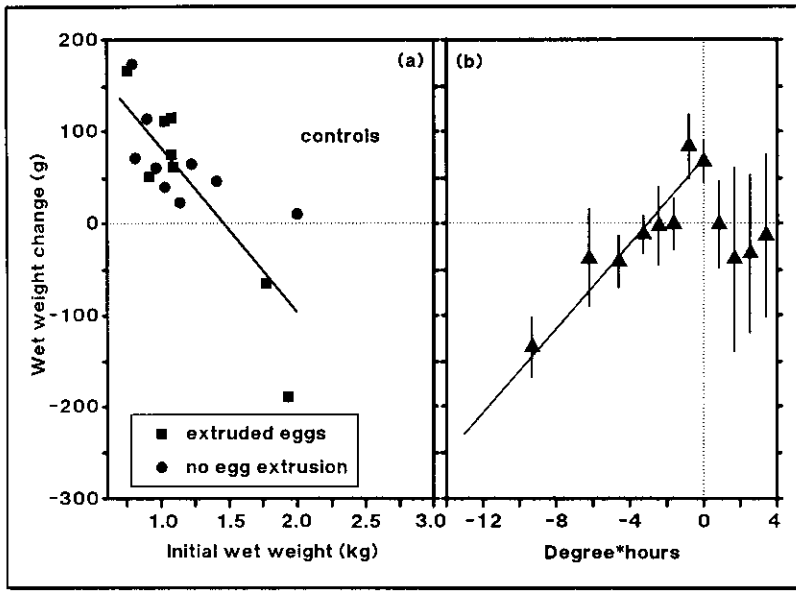

Figure 7.--Weight change as functions of a) initial wet weight and b) exposure (°h).

Exposure may have affected egg extrusion in both species, but the data were inconsistent. The percentage of king crabs extruding eggs tended to vary directly with the amount of exposure, but the data set was small and points were fairly scattered (P_{linear} = 0.031, $P_{lack\ of\ fit}$ = 0.746, r^2 = 0.31, n = 15). The timing of king crab egg extrusion, 9-32 days after ecdysis (May 2 ± 4 days), and number of days infertile eggs were carried (66 ± 17 days) were not affected by exposure ($P \geq 0.26$, $r^2 \leq 0.01$, n = 26). Exposure did not affect the percentage of Tanner crabs extruding eggs (93%), but the time to egg extrusion tended to vary directly with exposure albeit the fit of the regression line was poor; P_{linear} = 0.011, $P_{lack\ of\ fit}$ = 0.700, but r^2 = 0.16, n = 41. Tanner crab egg extrusion generally occurred 2 days (median) after zoeal release, but ranged from 0 to 18 days: only crabs in the lower two treatments (≤-4.3°h) exceeded 9 days (P_{linear} = 0.005, $P_{lack\ of\ fit}$ = 0.719, but r^2 = 0.19, n = 41).

DISCUSSION

Aerial exposure of ovigerous crabs was lethal under extreme conditions. Following sublethal exposure king crabs exhibited a slowed righting response, delayed completion of ecdysis, and reduced growth. The sublethal responses of Tanner crabs included slowed righting response, autotomy of pereiopods and depressed feeding rates.

Temperature and exposure duration were both critical factors in determining how exposure affected crabs in our experiment. The response of crabs to exposure was most clearly seen when exposure was defined as the product of temperature and the length of time the crabs were exposed. Shorter exposure at lower temperatures caused the same effects as longer exposure at higher temperatures. However, our approach may not be generally applicable. When we reanalyzed the exposure data of a study similar to ours by Brown and Caputi (1983) on percentage mortality of sublegal-sized western rock lobsters (*Panulirus cygnus*) the response was not related to exposure as we define it. Body size may also be an important factor, but over the restricted size range tested in the present experiment significant differences did not occur. An experiment involving a broad size range of conspecific individuals is needed to test whether sensitivity to exposure is size-dependent in crabs.

Mortality of king crabs was significantly greater below -4°h and vigor (speed of righting response) was reduced below -3°h compared to control crabs. Exposures this severe probably occur infrequently except during cold spells in winter on the fishing grounds in the northern Gulf of Alaska and Bering Sea and during the Norton Sound through-the-ice fishery. Tanner crabs were adversely affected by less severe conditions (mortality was significantly greater below -3°h and vigor was reduced below -2°h compared to controls). Data on the time female crabs remain on deck before being released are lacking, but that time period probably varies widely. Larger vessels employing assembly line techniques probably process crabs much more rapidly than smaller vessels. Poor handling of culls may combine with prolonged exposure to further reduce the survival of incidentally caught crabs.

Mortality and injury due to aerial exposure have been reported for commercially harvested decapod crustaceans that inhabit lower latitudes. For example, the western rock lobster, *Pandalus cygnus*, was significantly affected by ≥15 minutes of warm temperature exposure; recapture rates were lower than for unexposed controls, and the probability of mortality due to predation rose (Brown and Caputi, 1983). In the only published data on king and Tanner Crab aerial exposure, Nakanishi (1974) found that heart rate in *Paralithodes camtschatica* can be depressed during aerial exposure and that changes in heart rate may depend on water temperature. Nakanishi's exposures lasted 7 h and although he did not list the air temperatures to which his crabs were exposed, presumably the air temperatures were close to his experimental water temperatures which were 5, 8, 10, 11, and 14°C.

Warm temperature exposure might also adversely affect king and Tanner crabs, but our observations in a separate experiment indicate unrealistically warm temperatures would be necessary to reduce survival. King crabs survived exposure at 10°C for 24 h with almost no effect (unpublished data). Nakanishi (1974) recorded death in one of eight *P. camtschatica* following 1-day exposure at 8°C, one of three crabs at 11°C, and the only crab held at 14°C. However, because he reports only water temperatures the role of the presumably higher air temperatures associated with the elevated water temperatures cannot be assessed.

We do not know what physiological mechanism(s) caused the abnormal events during ecdysis that often resulted in death in the king crabs. O'Brien et al. (1986) induced apolysis (the separation of integumentary tissues from the exoskeleton during proecdysis) in several species of brachyurans by packing the crabs in ice. Tissue separation occurred within 1 h in most cases, and was not caused by crab death (O'Brien et al, 1986). O'Brien et al (1986) did not observe ecdysis in their experimental crabs therefore one cannot be certain how apolysis might affect the timing, duration and success of ecdysis in crabs. Although ecdysis in king crabs was prolonged by exposure in our study, the onset of ecdysis was not affected.

The ability of crabs to right themselves after they were placed on their backs proved to be a sensitive measure of crab viability. Righting response data collected immediately after exposure correlated strongly with less immediate responses such as mortality, the frequency of abnormal ecdysis, and growth.

Aerial exposure reduced growth in king crabs, but Tanner crab weight changes did not vary with exposure. The Tanner crabs became anecdysial at maturity and therefore did not molt. The absence of significant changes in Tanner crab weights is puzzling because feeding rates were significantly depressed by exposure. Growth of the western rock lobster was also reduced by exposure (Brown and Caputi, 1985).

Surprisingly, aerial exposure did not measureably affect the developing larvae of exposed females unless the female died.

Surviving crabs produced normal zoeae. Moreover, the timing of larval release, larval swimming ability and viability in both species, and the percentage of king crab eggs remaining in the clutch at ecdysis were not affected by exposure. We do not know if the eggs froze during exposure or if they have an inherent resistance to freezing. Longer term responses such as survival past the first molt and zoeal growth were not examined. Exposure may have reduced the hatching success (by less than 1%) of Tanner crab eggs and possibly affected egg extrusion in both species, but these responses did not vary strongly with exposure. Schlieder (1980) reported a 13% reduction in hatching success in the stone crab, *Menippe mercenaria*, compared to controls when the crabs were exposed to air for 2 h. Hatching success was reduced further by a 5 h exposure and by autospasy.

In summary, although severe environmental conditions may not be common on the fishing grounds, low temperature aerial exposure during fishing operations can adversely affect incidentally captured red king and Tanner crabs. Exposure reduced crab vigor, feeding rates (Tanner crab), and growth (king crab). Exposure also caused limb autotomy in Tanner crabs, and mortality in severe situations. Progeny died if exposure killed ovigerous females, but otherwise larvae were not measureably affected.

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Trace Metal Concentrations in Red King Crab from Norton Sound

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ABSTRACT

During March of 1986, 1987, 1988 and 1989, a total of 200 red king crab (Paralithodes camtschatica) were collected off Nome in Norton Sound as part of the WestGold NPDES environmental monitoring program for the Nome Offshore Placer Project. Collection sites were located nearshore between Nome and the mouth of the Penny River, located approximately 11 km to the west. Crabs were collected by pots fished through the ice in water depths between 6 and 15 meters. Samples of white muscle tissue, hepatopancreas, and carapace (shell) were analyzed for arsenic, cadmium, chromium, copper, lead, mercury, nickel, and zinc.

During the four years of data collection, trace metal concentrations for hepatopancreas tissue in mg/kg dry weight ranged from 3.26 to 33.18 (medians) for arsenic; from 7.53 to 12.60 (medians) for cadmium; from 0.22 to 0.57 (means) for chromium; from 64.4 to 184.4 (means) for copper; from 0.010 to 0.218 (medians) for lead; from 0.017 (median) to 0.135 (mean) for mercury; from 1.13 to 2.79 (means) for nickel; and from 92.0 to 130.4 (medians) for zinc. Trace metal concentrations for white muscle tissue in mg/kg dry weight ranged from 12.69 to 28.00 (means) for arsenic; from 0.06 (median) to 0.56 (mean) for cadmium; from 0.40 to 1.90 (medians) for chromium; from 55.2 to 96.7 (medians) for copper; from 0.005 to 0.406 (medians) for lead; from 0.014 (median) to 0.075 (mean) for mercury; from 0.45 (median) to 3.40 (mean) for nickel; and from 170.7 to 188.1 (medians) for zinc. Carapace median trace metal concentrations in mg/kg dry weight analyzed in 10 crabs collected in 1989 were: arsenic - 5.03, cadmium - 0.07, chromium - 1.70, copper - 19.06, lead - 0.291, mercury - 0.020, nickel - 12.76, and zinc - 18.2.

The only trace metals to show increases through time in the hepatopancreas and white muscle tissue were arsenic and nickel. Sex differences did not account for these year to year differences. The observed increases in arsenic concentrations appeared to be a direct result of the evolving analytical techniques. Nickel concentrations were approximately one-fourth the concentration found in carapace shell, indicating that king crab may have an effective mechanism for purging their systems of nickel when molting.

INTRODUCTION

The Nome Offshore Placer project, the largest offshore gold placer mining operation in the world, commenced operation in 1985. During the permitting process for this mining operation, it became apparent that potential heavy metal contamination of subsistence seafood resources was a major concern of local residents. Virtually no information existed on trace metal levels in marine plants and animals from Norton Sound to address this concern or to establish a baseline from which to assess perceived project impacts. Therefore, a monitoring program was implemented, concurrent with project startup, to evaluate trace metal concentrations in a major subsistence animal, the red king crab (Paralithodes camtschatica) and principal prey species. The heavy metal of primary concern was mercury; but seven other metals (arsenic, cadmium, chromium, copper, lead, nickel, and zinc) were monitored as well. The results of the trace metals monitoring program for red king crab are presented in this paper.

A review of the literature revealed that very little published information existed anywhere on trace metal concentrations in king crab. Most literature on trace metals dealt with acute and chronic toxicity testing of organisms rather than measurement of naturally occurring levels of these metals in their tissues. However, a major summary of baseline trace metal concentrations in invertebrates, fish, marine mammals, and birds was published by NOAA (Hall et al., 1978). This work included reference to three studies of red king crab conducted in major commercial fishing areas from the Alaska Peninsula to the Gulf of Alaska. Information on mercury in related species and other freshwater and marine plants and animals is contained in a review by Eisler (1987) and in a treatise by Mitra on mercury in the ecosystem (Mitra, 1986). Most recently, studies by Pastorak (1988) and Tetra Tech (1988) have stressed the health risks of contaminants, including trace metals, in marine foods and determined safe levels of risk to humans for ingestion of marine organisms which may have higher than background levels of specific contaminants.

The purpose of the present study was first to assess whether naturally occurring trace metals in red king crab are at levels that would pose a health risk to residents consuming this marine resource; second, assess whether trace metal concentrations change over time concurrent with mining activity; and finally, determine if any changes observed in trace metal concentrations can be related to mining activities or specific biological parameters. The program design resulted in a large database of trace metal concentrations in one species, presenting a unique opportunity to evaluate appropriate statistical methodology for data interpretation and significance of numerical information generated by these kinds of studies. This paper focuses on the statistical analyses and methodology used to evaluate the red king crab trace metals data set.

METHODS

Field Methods

Red king crab were collected in 1986, 1987, 1988, and 1989 with commercial pots fished through the ice at sample stations located offshore of Nome, Alaska within mining lease boundaries (Figure 1). Crabs were collected during March and April all four years. Pots were located in water depths of 6 to 15 meters (m). Each pot was typically baited with two, 1-quart perforated plastic containers filled with chopped, frozen herring. The bait was changed every 24 to 48 hours. The crab pots were located in both mined and unmined areas. In 1986, crabs were not collected at specific stations; instead, they were collected by Alaska Department of Fish and Game (ADF&G) personnel and a commercial fisherman at a variety of locations.

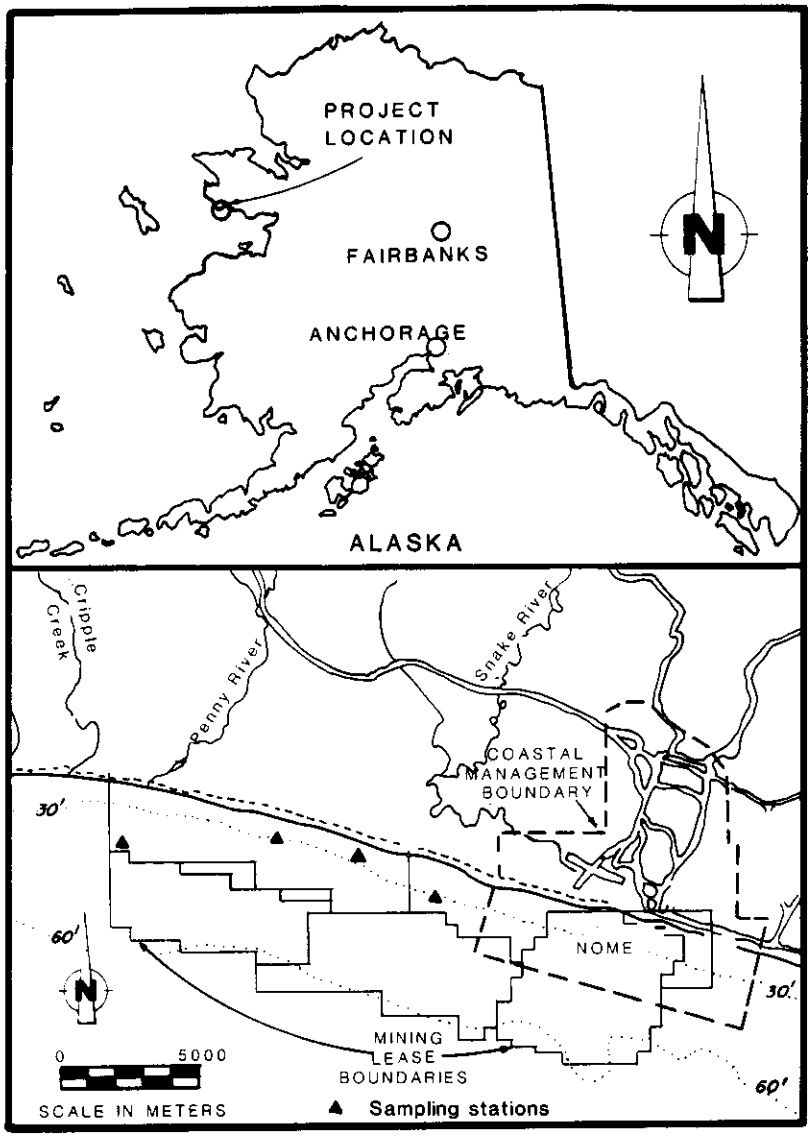

Figure 1. Area location map.

From 1986 through 1989, white muscle and hepatopancreas tissues were collected from each crab. Carapace length, shell condition, sex, and weight were recorded for each individual. In 1989, shell carapace samples were also collected for trace metals analysis. Tissue samples were placed in Whirl-Pac bags, labelled, and then frozen. Following completion of the field program, tissue samples were air-shipped frozen to an analytical laboratory. In 1986, tissue samples were analyzed by Northern Testing Laboratories, Inc. in Fairbanks, Alaska. Crabs collected in 1987, 1988, and 1989 were analyzed by AmTest, Inc. in Redmond, Washington.

Laboratory Methods

Freshly thawed king crab tissue samples were acid digested and analyzed for eight priority trace metals: arsenic, cadmium, chromium, copper, lead, mercury, nickel, and zinc. Digestion methods and modifications are summarized in Table 1; procedures were as specified by the U.S. Environmental Protection Agency (EPA, 1983 and 1986).

Detection limits for each element were calculated with consideration for the average sample weight, the dilution factor once the sample was digested, and the instruments' detection limits as established by the EPA.

Statistical Analyses

The red king crab trace metals data set was challenging to analyze statistically for two reasons.

1) For almost all metals, the data formed a "censored" data set as described by Gilbert (1987) in which a number of observations were known to occur below some calculated value (the laboratory detection limit or DL). This resulted in the data set being "censored on the left" (i.e., values below the DL were not available). In fact, for some of the metals (e.g., lead, mercury), a majority of the observations occurred at or below the DL.

   Gilbert (1987) noted that "these missing data make it difficult to summarize and compare data sets and can lead to biased estimates of means, variances, trends, and other population parameters. Also, some statistical tests cannot be computed, or they give misleading results."

2) Because of the large, multi-year data set, often more than one DL occurred for a given trace metal. This resulted because samples were analyzed at different times in different laboratory runs and therefore were subjected to different run conditions (e.g., instrument voltage, quantity of tissue digested, etc.).

These two characteristics of the data set required that a series of statistical analyses be performed; each step of the analytical process was dependent on the outcome of the previous step. Figure 2 shows a general flow diagram of the analytical process.

Statistical Theory

When data values are reported as below the DL, Gilbert (1987) noted that biased estimates of the population mean and variance can be computed in one of the following ways:

a) Compute statistics using all the data values, including the DL values; or

b) Compute statistics after deleting all DL values from the data set; or

Table 1. Summary of analytical techniques used for trace metal analysis of Red King Crab tissue samples from 1986 through 1989. PE = Perkin Elmer; TJA = Thermo Jarrel Ash.

Laboratory/ Year	Element	Digestion Method	EPA Method	Analytical Instrument	Detection Limit (ug/g)
Northern Testing Laboratories, Inc. 1986	Arsenic	3020	7060 (206.2)	PE 603 w/HGA 2200	0.00105
	Lead	3020	7421 (239.2)	PE603 w/HGA 2200	0.0001
	Cadmium	3020	7130 (213.2)	PE603 w/HGA 2200	0.0001
	Chromium	3020	7190 (218.1)	PE2380 w/HGA 400	0.003
	Copper	3020	7210 (220.1)	PE2380 w/HGA 400	0.002
	Nickel	3020	7520 (249.1)	PE2380 w/HGA 400	0.004
	Zinc	3020	7950 (289.1)	PE2380 w/HGA 400	NA
	Mercury	----	7471 (245.1)	PE603	NA
AmTest, Inc. 1987	Arsenic	3005	206.2	PE603 w/HGA 5100	0.10
	Lead	3005	239.2	PE603 w/HGA	0.05
	Cadmium	3005	213.2	PE603 w/HGA 5100	0.025
	Chromium	3005	218.1	PE 2380	2.5
	Copper	3005	220.1	PE 2380	1.5
	Nickel	3005	249.1	PE 2380	2.5
	Zinc	3005	289.1	PE 2380	0.50
	Mercury	----	245.1	PE Coleman Model 50	0.01
AmTest, Inc. 1988	Arsenic	3005	206.2	TJA 551	0.05
	Lead	3005	239.2	TJA 551	0.05
	Cadmium	3005	213.2	TJA 551	0.02
	Chromium	3005	200.7	TJA ICP 61	0.50
	Copper	3005	200.7	TJA ICP 61	0.15
	Nickel	3005	200.7	TJA ICP 61	0.50
	Zinc	3005	200.7	TJA ICP 61	0.10
	Mercury	----	245.1	PE 603	0.01
AmTest, Inc. 1989	Arsenic	3005	206.2	Varian 3007	0.05
	Lead	3005	239.2	Varian 3007	0.05
	Cadmium	3005	213.2	Varian 3007	0.02
	Chromium	3005	200.7	TJA ICP 61	0.50
	Copper	3005	200.7	TJA ICP 61	0.15
	Nickel	3005	200.7	TJA ICP 61	0.50
	Zinc	3005	200.7	TJA ICP 61	0.10
	Mercury	----	245.1	PE 603	0.01

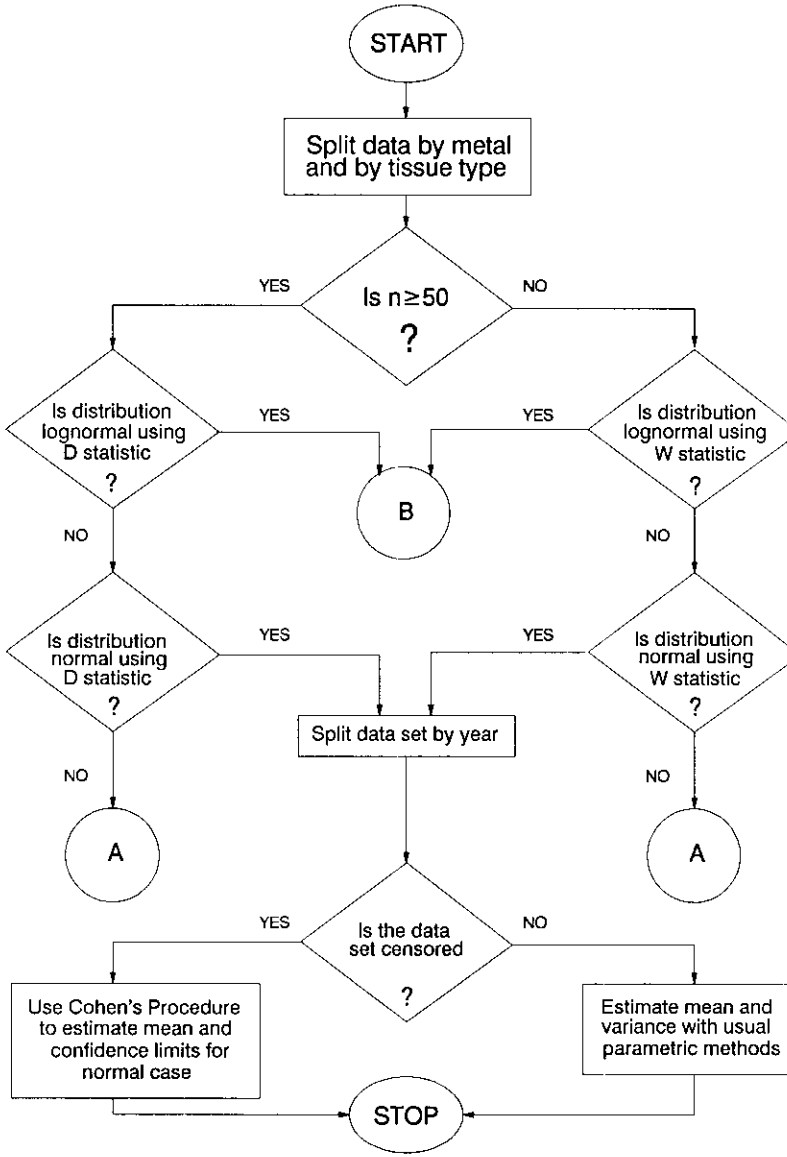

Figure 2. Statistical flowchart used for the analysis of red king crab trace metals data.

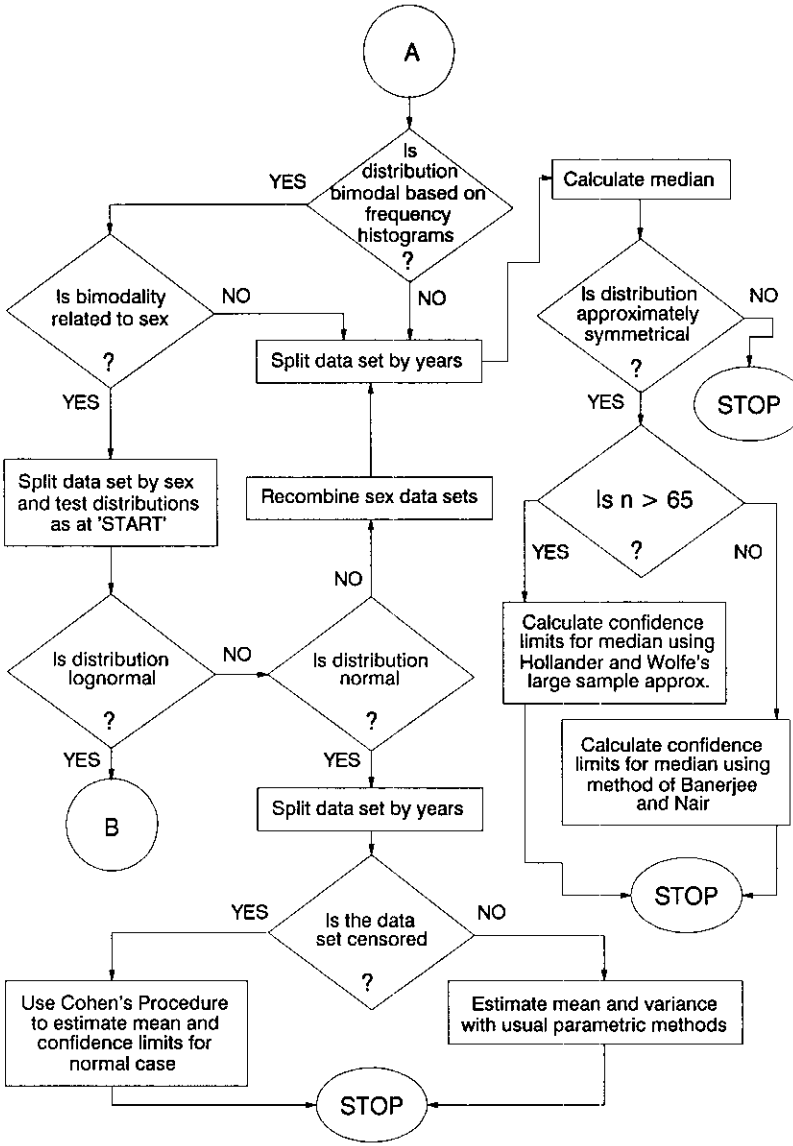

Figure 2 (cont'd). Statistical flowchart used for the analysis of red king crab trace metals data.

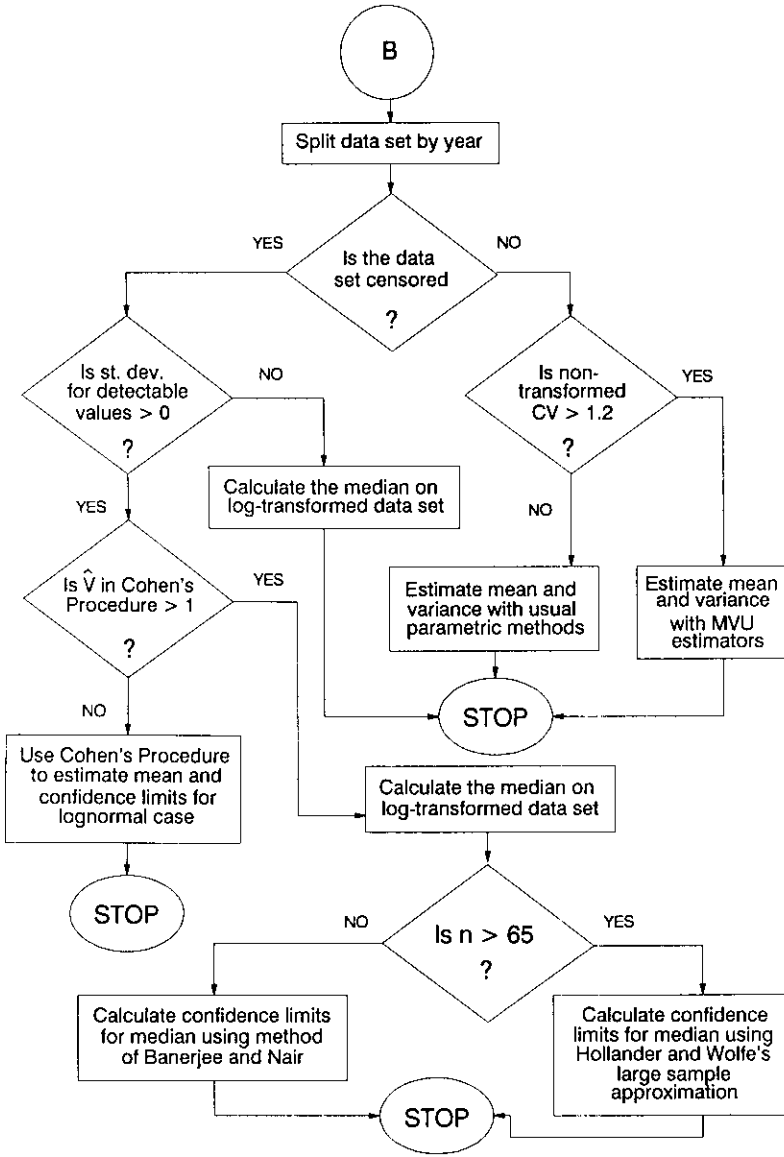

Figure 2 (cont'd). Statistical flowchart used for the analysis of red king crab trace metals data.

c) Compute statistics after replacing all DL values by zero; or

d) Compute statistics after replacing all DL values with one-half DL.

The first three methods are biased for both population mean and population variance. The fourth alternative can be an unbiased estimator of the population mean, but will still always be a biased estimator for the population variance (Gilbert, 1987).

As a result, Cohen (1959 and 1961, as cited in Gilbert, 1987) developed a method for estimating the population mean and variance when only a censored data set from a normal or lognormal distribution is available. This enhanced statistical technique (Cohen's Procedure) was used on the crab trace metal data whenever applicable.

Analytical Process

Statistical tests were performed on a Compaq 386 personal computer using the following commercial software packages: SYSTAT statistical software developed by SYSTAT, Inc. of Evanston, Illinois; SYGRAPH graphics software developed by SYSTAT, Inc.; and Lotus SYMPHONY database management software developed by Lotus Development Corporation of Cambridge, Massachusetts.

Statistical tests used in the analytical process (Figure 2) were D'Agostino's D Statistic (Gilbert, 1987); Shapiro and Wilk's W Statistic (Gilbert, 1987); Cohen's Maximum Likelihood Estimators for a left censored data set (Gilbert, 1987); parametric estimators of mean, variance, and confidence limits (Dixon and Massey, 1969); the coefficient of variation (Sokal and Rohlf, 1981); and confidence limits for medians as described by Banerjee and Nair (Dixon and Massey, 1969) and Hollander and Wolfe (Daniel, 1978).

The king crab trace metals data set was analyzed for year to year differences to determine if there was an increasing trend (i.e., bioaccumulation). Secondly, the data set was analyzed with sex variation as a differentiating criterion to determine if any of the year to year differences could be accounted for due to the sex of the crabs.

Year to year differences. As shown in Figure 2, the first step in the statistical analysis was to determine if a given data set followed a lognormal, normal, or other underlying distribution. For the distribution analysis, the four years of data were combined to produce the largest data set possible; each trace metal by tissue type was analyzed separately. The first null hypothesis tested was whether the distribution was lognormal. If the null hypothesis was rejected ($\alpha = 0.05$), then the null hypothesis for normal distribution was tested.

For the distribution analysis, all DL values were deleted. Initially, the distribution analysis was run with DL values treated in three different ways: DL values set equal to DL; DL values set equal to one-half DL; and DL values deleted. The three DL treatments showed how each affected the analytical result. The first two treatments ultimately biased the results so much that the results of null hypothesis testing for a lognormal distribution directly contradicted the results of testing for a normal distribution. Ideally, a treatment of the DL's would have distributed the values over the entire range of possible values between zero and the DL. None of the DL treatment methods accomplished this; however, the deletion of DL values produced distribution hypothesis test results that were not contradictory. Therefore, the deletion of DL values was adopted for the distribution analyses.

If the underlying distribution was determined to be normal or lognormal for a given metal in a particular tissue type, then the data sets were split by year and individual means and 95 percent confidence limits were calculated. If the underlying distribution was lognormal, then the data were transformed with a lognormal transformation before

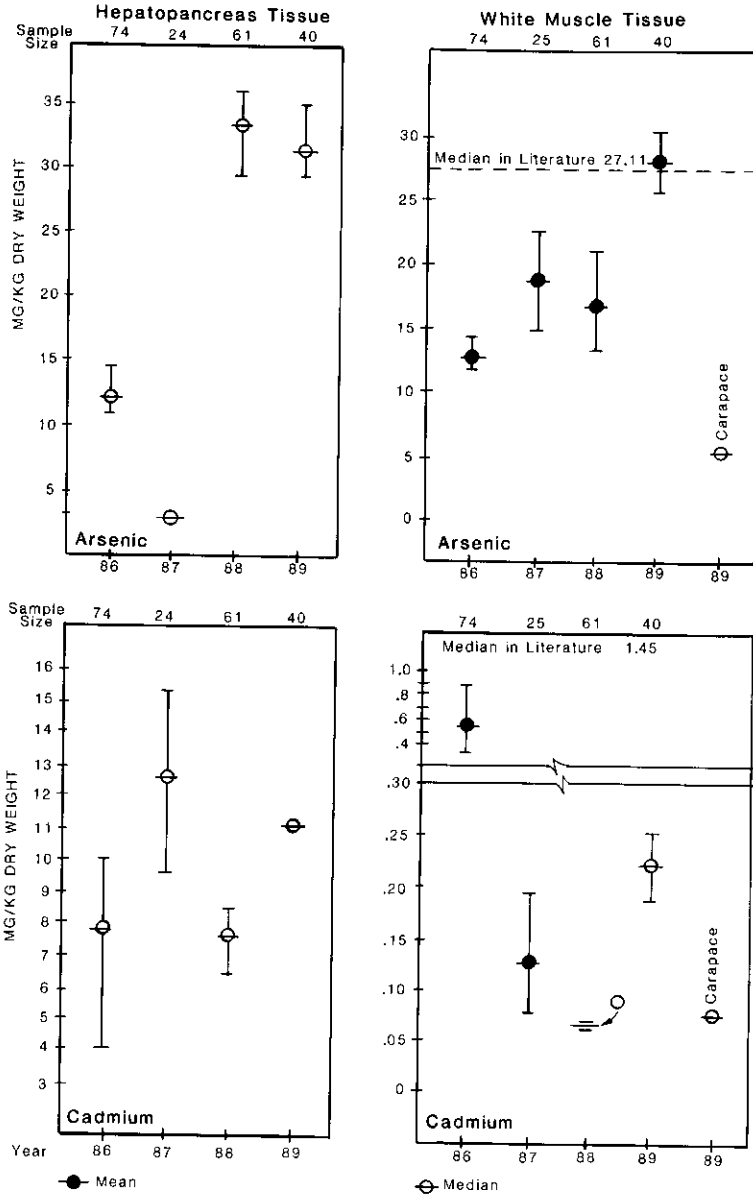

Figure 3. Arsenic and cadmium concentrations in red king crab tissues. Mean, median and 95% confidence intervals are shown where applicable. See text discussion on median in literature.

the means and confidence limits were calculated. If data sets contained DL values, Cohen's Procedure for estimating means and variances of censored data sets (lognormal or normal distribution) was used. For censored data sets in which more than one DL value was present, all DL values were set equal to the DL median value since Cohen's Procedure could utilize only one censored value per data set.

For those data sets having neither a lognormal nor normal distribution, the data sets were separated by year, and individual medians were calculated. To compute the least-biased estimator (refer to Statistical Theory discussion), all DL values were set equal to one-half DL. Confidence limits were estimated for the median if the data were approximately symmetric based on frequency histograms.

Sex differences. The data set was split by metals and sex and then analyzed to determine if a given data set followed a lognormal, normal, or other underlying distribution. All DL values were deleted in the distribution analysis and analyzed as described previously under Year to Year Differences.

Individual means, medians, and confidence limits for each sex were analyzed as described previously under Year to Year Differences.

RESULTS

During the four years of sampling from 1986-1989, 165 male and 35 female crab were collected. In most instances, for each tissue type 74 crab (49 males, 25 females) were analyzed in 1986; 24 (20 males, four females) in 1987; 61 (59 males, two females) in 1988; and 40 (36 males, four females) in 1989. Of the 200 crab, 181 had "new" shells (i.e., shells molted within the first year) and 19 had "old" shells. The carapace sizes (lengths) ranged from 55 mm to 130 mm with a mean of 93.4 mm and a standard deviation of 18.1 mm. The minimum recorded crab weight was 0.120 kg and the maximum weight was 1.709 kg with a mean weight of 0.676 kg and a standard deviation of 0.424 kg.

The results from the analysis of red king crab tissues (hepatopancreas, white muscle, and carapace shell) collected in Norton Sound off Nome, Alaska from 1986 through 1989 are reported by individual trace metal. Carapace shell analysis was limited to 10 male crab, selected at random by analytical laboratory personnel, from the 40 crab used in 1989 for hepatopancreas and white muscle tissue analyses. The eight metals analyzed were arsenic, cadmium, chromium, copper, lead, mercury, nickel, and zinc.

For each metal, year to year differences and sex differences were investigated. The results were compared to the median of minimum and maximum values reported in previous literature for Alaskan red king crab white muscle tissue. Refer to Rusanowski et al. (1987) for a thorough literature review. No previous data from other investigations were available on trace metal concentrations in red king crab hepatopancreas tissue or carapace shell.

Year to Year Differences

Arsenic. Median arsenic concentrations in hepatopancreas tissue fluctuated from 3.26 to 33.18 mg/kg dry weight (Figure 3). Due to the nature of the data set (Figure 2), confidence limits could not be calculated for 1987. The highest values occurred in 1988 and 1989 which may indicate an increasing trend. Hepatopancreas tissue had the highest level of arsenic for the three tissue types analyzed.

Mean arsenic concentrations in white muscle tissue increased from 12.69 mg/kg dry weight in 1986 to 28.00 mg/kg dry weight in 1989 (Figure 3). However, the median reported in previous literature for red king crab (27.11 mg/kg dry weight) still fell within the mean's 95 percent confidence interval for the 1989 muscle tissue data set.

The median arsenic concentration in carapace shell was 5.03 mg/kg dry weight.

Cadmium. Median cadmium concentrations in hepatopancreas tissue fluctuated from 7.53 to 12.60 mg/kg dry weight (Figure 3). Due to the nature of the data set (Figure 2), confidence limits could not be calculated for 1989. Cadmium values indicated no increasing trend through time. Hepatopancreas tissue had the highest level of cadmium for the three tissue types analyzed.

Cadmium concentrations in white muscle tissue fluctuated from a median of 0.06 mg/kg dry weight to a mean of 0.56 mg/kg dry weight (Figure 3). The highest values occurred in 1986. However, in no year did muscle concentrations exceed the median reported in previous literature for red king crab (1.45 mg/kg dry weight).

The median cadmium concentration in carapace shell was 0.07 mg/kg dry weight.

Chromium. Mean chromium concentrations in hepatopancreas tissue fluctuated from 0.22 to 0.57 mg/kg dry weight (Figure 4). Chromium values indicated no increasing trend through time.

Median chromium concentrations in white muscle tissue fluctuated from 0.40 to 1.90 mg/kg dry weight (Figure 4). The highest values occurred in 1987 and indicated no increasing trend with time. Muscle tissue concentrations fluctuated widely from year to year as indicated by each year's 95 percent confidence interval in which no two overlapped. In 1987, the median concentration and approximate 95 percent confidence interval exceeded the median reported in previous literature for king crab muscle tissue.

The median chromium concentration in carapace shell was 1.70 mg/kg dry weight.

Copper. Mean copper concentrations in hepatopancreas tissue decreased from 184.4 mg/kg dry weight in 1986 to 64.4 mg/kg dry weight in 1989 (Figure 4).

Median copper concentrations in muscle tissue fluctuated from 55.2 mg/kg dry weight to 96.7 mg/kg dry weight (Figure 4). Muscle tissue median values indicated fluctuations through time. In 1986, 1987 and 1989, approximate 95 percent confidence intervals for copper exceeded the median reported in previous literature for king crab muscle tissue.

The median copper concentration in carapace shell was 19.06 mg/kg dry weight.

Lead. At initial inspection, median lead concentrations in hepatopancreas tissue and white muscle tissue appeared to show some increasing trends through time (Figure 5) from 0.005 mg/kg dry weight in 1986 to 0.406 mg/kg dry weight in 1989. However, approximately 90 percent of the values were near or at the laboratory DL. With the exception of one crab collected in 1986, all 200 muscle tissue values were lower than the median reported in previous literature for king crab muscle tissue (3.59 mg/kg dry weight).

The median concentration of lead in carapace shell was 0.291 mg/kg dry weight.

Mercury. Mercury concentrations in hepatopancreas tissue fluctuated from a median of 0.017 mg/kg dry weight to a mean of 0.135 mg/kg dry weight (Figure 5). The hepatopancreas had the highest level of mercury for the tissue types analyzed.

Mercury concentrations for white muscle tissue fluctuated from a median of 0.014 mg/kg dry weight to a mean of 0.075 mg/kg dry weight (Figure 5). Due to the nature of the muscle tissue data set, a mean could only be calculated in 1986. These data indicated no increasing trends through time for mercury. With the exception of one

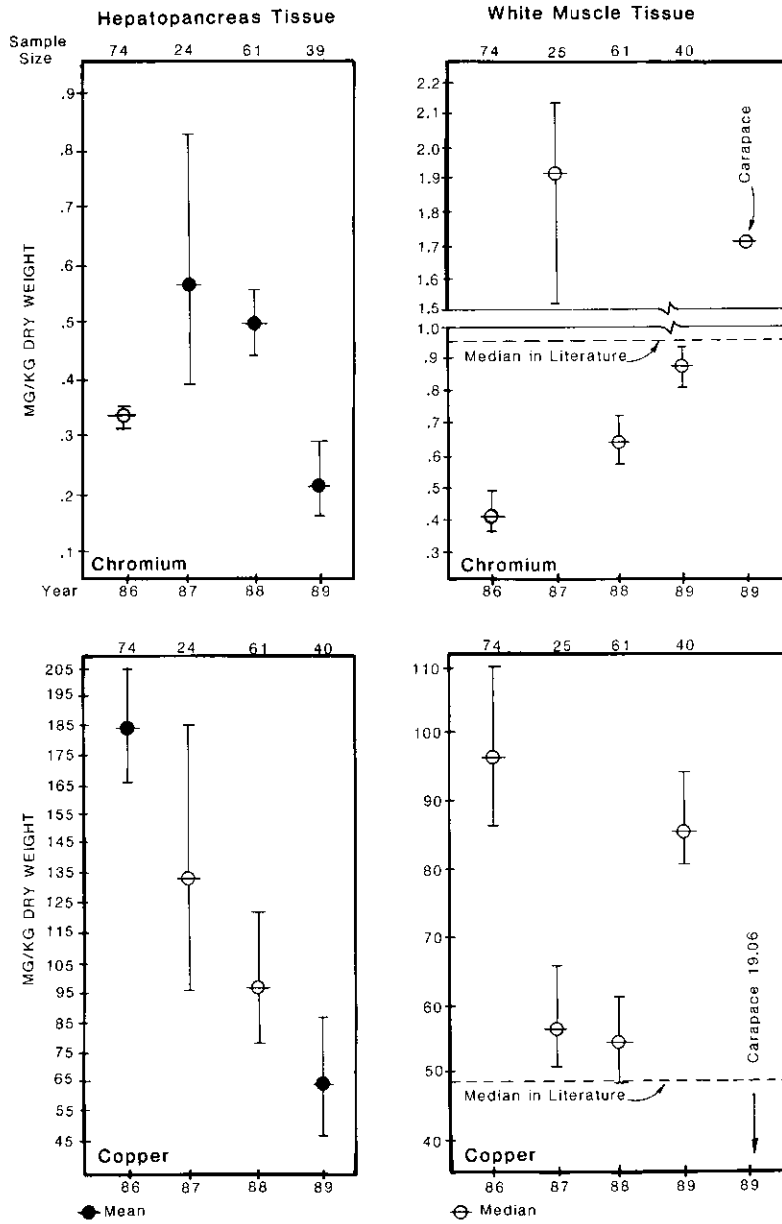

Figure 4. Chromium and copper concentrations in red king crab tissues. Mean, median and 95% confidence intervals are shown where applicable. See text discussion on median in literature.

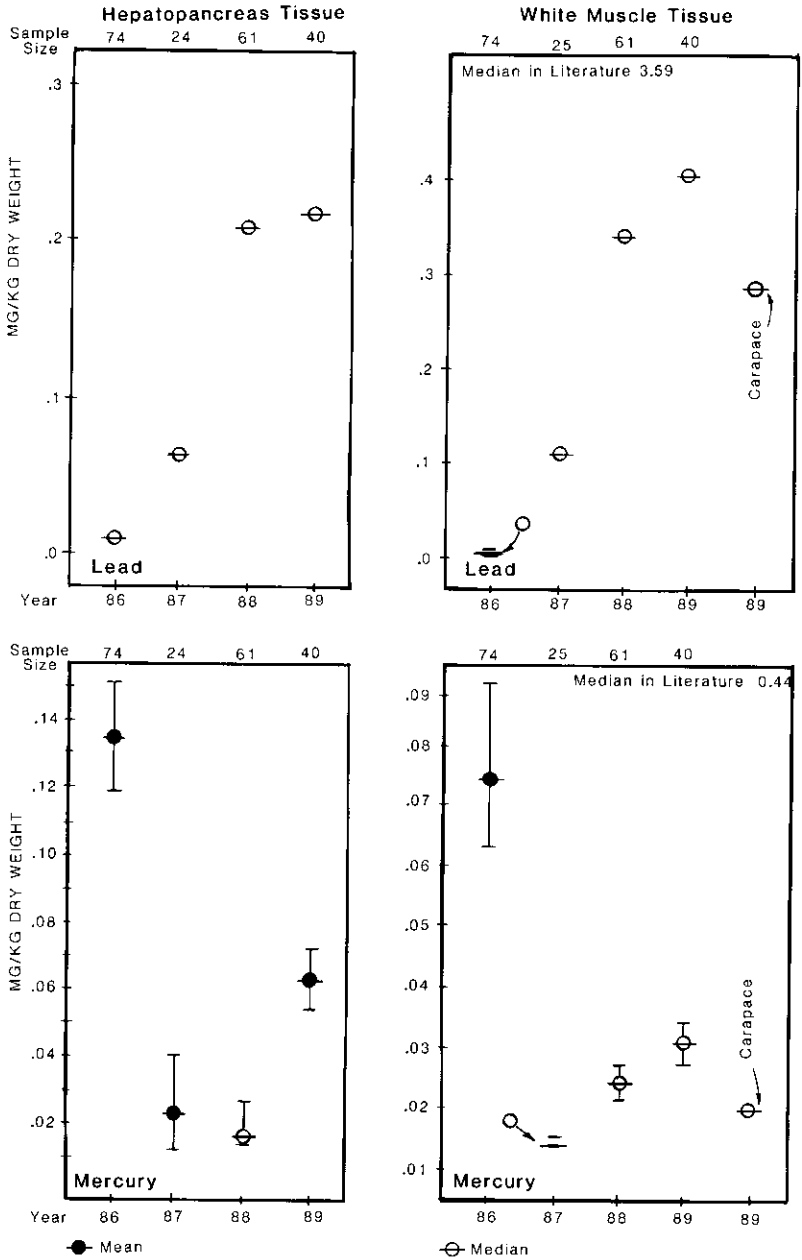

Figure 5. Lead and mercury concentrations in red king crab tissues. Mean, median and 95% confidence intervals are shown where applicable. See text discussion on median in literature.

crab collected in 1986, 199 of 200 mercury muscle tissue values were lower than the median reported in previous literature for king crab muscle tissue (0.44 mg/kg dry weight).

The median concentration of mercury in carapace shell was 0.020 mg/kg dry weight.

Nickel. Mean nickel concentrations in hepatopancreas tissue fluctuated from 1.13 mg/kg dry weight to 2.79 mg/kg dry weight (Figure 6). The highest values occurred in 1987 and therefore indicated no pronounced increasing trend with time.

Nickel concentrations for white muscle fluctuated from a median of 0.45 mg/kg dry weight to a mean of 3.40 mg/kg dry weight (Figure 6). The highest value occurred in 1989 which was also the only year in which nickel concentrations exceeded the median reported in previous literature for king crab muscle tissue. However, these values were almost an order of magnitude lower than that reported for carapace shell (median = 12.76 mg/kg dry weight).

Zinc. Median zinc concentrations in hepatopancreas tissue remained at approximately 130 mg/kg dry weight, except in 1987 when values decreased (Figure 6).

Median zinc concentrations for white muscle fluctuated from 170.7 to 188.1 mg/kg dry weight (Figure 6). These data indicated no increasing trends through time for zinc in muscle tissue. All zinc muscle tissue values were well below the median reported in previous literature for king crab (466.7 mg/kg dry weight). White muscle tissues had the highest level of zinc for the tissue types analyzed.

The median zinc concentration in carapace shell was 18.2 mg/kg dry weight .

Sex Differences

For each of the eight priority trace metals, sex was also investigated as a differentiating criterion to determine if any of the year to year differences could be accounted for by this factor. Table 2 shows the mean or median calculated and the 95 percent confidence interval where appropriate for each metal by sex and tissue type.

In both hepatopancreas and white muscle tissue, copper and mercury concentrations were significantly higher (no overlap of confidence intervals) in females than males while lead concentrations were lower. In white muscle tissue, zinc concentrations were also higher in females than males while chromium concentrations were lower.

DISCUSSION

Many variables can have a potential effect on trace metals concentrations in marine organisms. The age of the organisms; the temperature, salinity and turbidity of the water; and the stage of the sexual cycle of the organism all may have an effect on the metabolism of trace metals in king crab. The different chemical properties and available amounts of the trace metals in the physical environment are also responsible for the variability of trace metal concentrations in crab. In addition, levels can also be affected by variable field and laboratory techniques, field sampling contamination, and/or laboratory contamination.

All of the trace metals analyzed in this study bioconcentrate in the tissues of crabs, but only cadmium, lead, and mercury biomagnify in the food chain (T. Scheuhammer, personal communication, Canadian Wildlife Service, National Wildlife Research Center, Quebec). For this reason, the latter three metals are of greatest concern biologically. None of the three metals is known to be biologically essential or beneficial. Cadmium is a known teratogen and carcinogen (Eisler, 1985). Lead is known to have deleterious effects on many aspects of life cycles (Eisler, 1988) with those effects being most

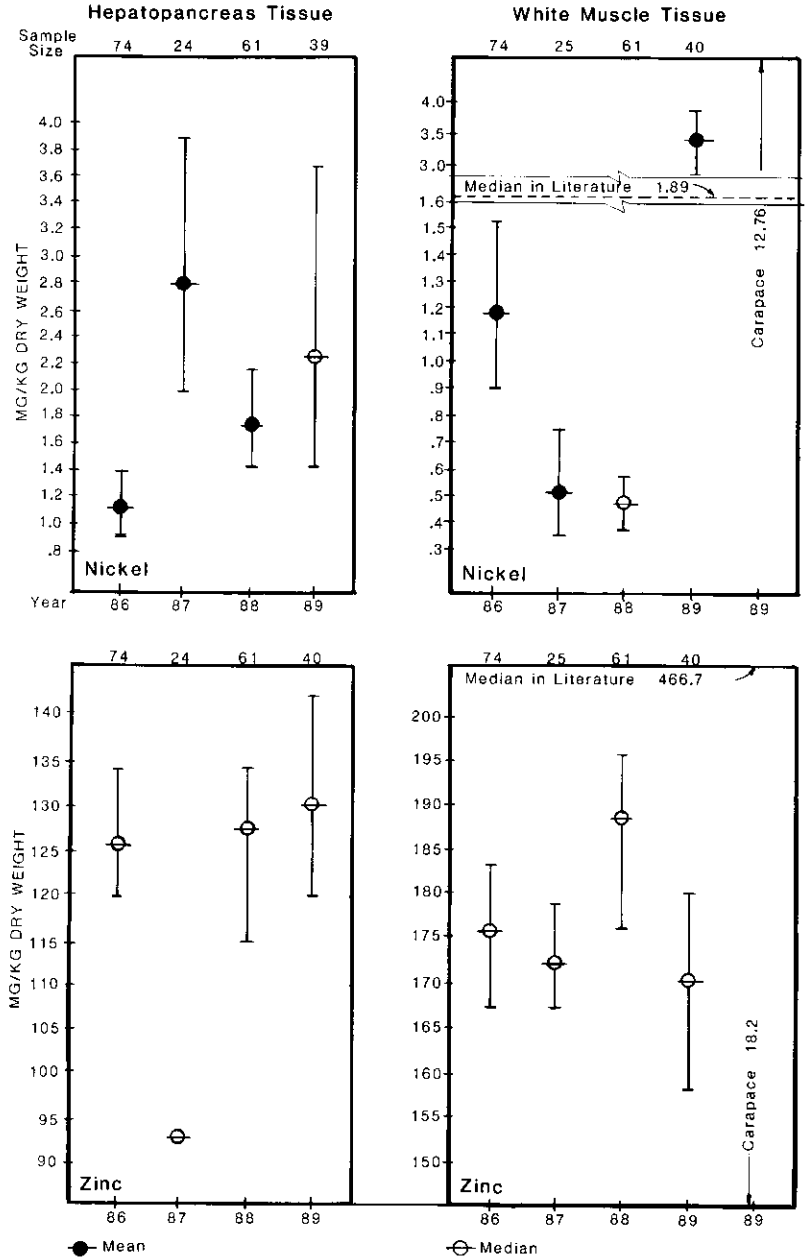

Figure 6. Nickel and zinc concentrations in red king crab tissues. Mean, median and 95% confidence intervals are shown where applicable. See text discussion on median in literature.

Table 2. 95 percent confidence intervals for red king crab trace metal results by sex. For medians, the confidence interval is approximately 95 percent.

Element	Male (n = 165) Confidence Interval			Female (n = 35) Confidence Interval		
	Lower	Mean/Median	Upper	Lower	Mean/Median	Upper
Hepatopancreas Tissue						
Arsenic	17.967	21.729*	26.613	11.535	14.585**	18.441
Cadmium	7.667	8.497*	9.206	3.333	10.400*	15.667
Chromium	0.408	0.435*	0.487	0.350	0.547*	0.767
Copper	91.212	103.493**	117.427	187.394	231.829**	286.800
Lead	0.129	0.160*	0.192		0.01000*	
Nickel	1.499	1.713**	1.959	0.832	1.248**	1.870
Zinc	119.500	125.762*	130.000	102.813	115.955**	130.776
Mercury	0.041	0.048**	0.056	0.090	0.133*	0.167
White Muscle Tissue						
Arsenic	15.550	17.348**	19.355	13.369	15.944**	19.015
Cadmium	0.125	0.168**	0.226	0.109	0.225**	0.466
Chromium	0.888	1.022**	1.177	0.487	0.623*	0.733
Copper	67.039	73.292*	78.000	92.317	106.208**	122.189
Lead	0.304	0.335*	0.364		0.0125*	
Nickel	0.613	0.859*	1.111	0.867	1.267*	2.033
Zinc	169.536	173.333*	176.667	191.260	203.548**	216.624
Mercury	0.027	0.031*	0.034	0.036	0.049**	0.065

* Median ** Mean

pronounced at elevated water temperatures and after long exposures. Mercury's presence is potentially hazardous to an organism but occurs in many forms with varying toxicity levels; under certain environmental conditions, the forms are interchangeable through processes such as bacterial methylation. Results from this study indicated that none of the three metals of primary biological concern showed increasing trends through time for the tissues analyzed.

The only metals that showed increases through time in the tissues analyzed were arsenic and nickel. Arsenic concentrations appeared to increase in 1988 for hepatopancreas tissue and in 1989 for hepatopancreas and white muscle tissues (Figure 3). Sex differences did not account for these year to year differences. Instead, these increases appeared to have resulted from variable laboratory techniques (Table 1). In 1986, samples were analyzed for trace metals by a different laboratory than in subsequent years; laboratory techniques were also slightly different in 1986 wherein percent moisture content values were not reported by the laboratory for each individual sample. Therefore, to make unit conversions in 1986 from mg/kg wet weight to mg/kg dry weight required the use of an average moisture value per species. Although the digestion procedures and the EPA analytical methods used by AmTest during 1988 and 1989 remained the same, AmTest changed to a more sensitive instrument in 1989 (Table 1).

These analytical changes ultimately complicated the comparisons between years, particularly for arsenic. This was because, as explained by AmTest (M. Fugiel, personal communication, AmTest, Redmond, WA.), "arsenic is one of the most difficult among all of the metals to analyze. It has a relatively low analytical wavelength, it is volatile, and it is somewhat unstable. The analytical signal is subject to both positive and negative interferences from other elements. Furthermore, the presence of high salt concentrations typically results in signal suppression. The use of matrix modification and background absorption can eliminate many of these problems." This was the reason AmTest upgraded to an analytical instrument with Zeeman Background Correction in 1989 (Table 1).

To facilitate comparison between arsenic data sets of different years, AmTest estimated through indirect analytical methods that a conversion factor of 2.5 could be applied to AmTest arsenic data sets prior to 1989. However, AmTest emphasized that their computation of the correction factor was not done using a straightforward approach (i.e., comparing measured values versus determined values of standard reference materials) since the laboratory no longer used the standard reference materials of earlier years. AmTest warned that the conversion factor, when applied to the 1987 and 1988 arsenic data sets, would be an approximation at best. AmTest did note, however, that the arsenic concentrations reported in 1989 reflected the best possible estimates of arsenic concentration in tissues with current technologies. The apparent increases in arsenic concentrations could, therefore, be a direct result of the evolving analytical techniques.

Nickel in white muscle tissue was the other trace metal that appeared to increase in 1989 (Figure 6). Sex differences did not account for the higher values in 1989. However, nickel concentrations in white muscle tissue were approximately one-fourth the concentration found in carapace shell (Figure 6), indicating that king crab may have an effective mechanism for purging their systems of nickel when molting.

Sex differences were observed in trace metals concentrations in hepatopancreas and white muscle tissue. For both tissues, copper and mercury concentrations were higher in females than males while lead concentrations were lower. In white muscle tissue, zinc concentrations were also higher in females than males while chromium concentrations were lower. However, analysis of crab size indicated that these results

could also be due to size differences since female crab were all less than 85 mm carapace length. There were insufficient juvenile males in the same size range as the females to discriminate whether size was a factor in accounting for these trace metal differences.

CONCLUSIONS

Of the eight priority trace metals analyzed in red king crab tissues, three metals (cadmium, copper, mercury) occurred at their highest levels in hepatopancreas tissue. Zinc had highest levels in white muscle tissue while nickel had highest levels in carapace shell. Approximately 90 percent of lead values were near or at the laboratory DL for both hepatopancreas and white muscle tissues.

Only arsenic and nickel showed some increases through time in hepatopancreas and white muscle tissue. Sex (or size) differences did not account for these year to year differences. The observed increases in arsenic concentrations appeared to be a direct result of the evolving analytical techniques, although arsenic levels were still comparable or below the median level reported in previous literature for red king crab. Nickel concentrations in hepatopancreas and white muscle tissues were approximately one-fourth the concentration found in carapace shell, indicating that king crab may have an effective mechanism for purging their systems of nickel when molting.

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A Method for Estimating Survival Rate of Male Zuwai Crab (*Chionoecetes opilio*) in the Western Japan Sea

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ABSTRACT

To better understand the dynamics of the Zuwai crab stock, *Chionoecetes opilio*, exploited by Danish seiners in the Japan Sea, a method is described for estimating survival rate of the male crab in consideration of the terminal molt. Among 1985 to 1988 samples, two clearly distinguishable carapace width groups were seen: a large group (mean size 130.1 mm ranging from 116 to 150 mm) and a small group (mean size 103.3 mm ranging from 96 to 116 mm). The morphometric data showed that a two-fold carapace width range (about 60 to 120 mm) over which a morphometric switch to positive allometric growth was reached was not exceptional. In the small and large groups, 47.8% and 98.7% of the crabs were evaluated to be morphometrically mature, respectively. The survival rate of the legal-sized crab was estimated to be 0.58 to 0.67 per year, using 1986-1988 male crab carapace widths.

INTRODUCTION

The Zuwai crab, *Chionoecetes opilio*, is a valuable species exploited mostly by Danish seiners in the western Japan Sea. For the Danish seine fishery, the net catches various sizes of crabs in front of the gear mouth, and the size and male-female composition of the cod-end are not acceptable. Continuous fishing mortality on prerecruits is likely occurring (Sinoda *et al.*, 1987). It is doubtful that the illegal male crabs less than 90 mm carapace width and female crabs carrying orange-colored eggs discarded at sea will eventually recruit to legal size and will fully contribute to a stock with reproductive potential.

According to recent findings, male crabs have a terminal molt as females and the

molt may be reached at any size between 60 and 120 mm carapace widths in eastern Canada (Conan and Comeau, 1986). However, it is not known what determines the size at which a male undergoes its terminal molt and there is no consensus about the concurrence of the onset of maturity and terminal molt of this species. In the Japan Sea, it is generally agreed that there is a switch to positive allometric growth of male chela at 55 to 65 mm carapace widths (Ito, 1957). However, the assumption that male Zuwai crab keep growing and change morphometrically after the terminal molt hasn't been confirmed.

The purpose of this paper is to demonstrate a method for estimating the survival rate of both the illegal- and legal-sized male crabs with regard to the terminal molt.

MATERIALS

A total of 772 male crabs were collected by three fishing gears, longline trap (pudding-shaped trap), beam trawl with an 8 m wide mouth, and commercial Danish seine (14.9 gross tonnage) at 220 to 290 m depths from November 1988 to June 1989. Longline trap fishings and beam trawlings were carried out by the R/V Heian-maru (229 gross tons) in the sea off Kyoto Prefecture, over the fishing grounds used by commercial Danish seiners.

In addition, data on carapace width of male crabs collected by a series of experimental trap fishings by the R/V Heian-maru from 1985 to 1988 were used. A total of 4,458 male crabs were trapped at 230 to 350 m depths in the sea off Kyoto Prefecture.

METHODS

Carapace Width Frequency Distribution

Carapace width composition is shown in Figure 1. Clearly five distinguishable groups are seen in the composition and the normal distribution curves are fitted to them by Tanaka's method (Tanaka, 1956). Groups R, A, B, C, and D symbolized here are recognized as five molt classes as shown in Figure 1 (lower). Miller and O'Keefe (1981) and Conan and Comeau (1986) suggested that a relatively large number of males less than 95 mm carapace width reached a terminal molt. Conan and Comeau (1986) concluded that spermatophores were present in the vasa deferentia of all males larger than 60 mm carapace width and the molt to morphometric maturity occurred at carapace widths ranging from 60 to 120 mm. Based on this finding, five groups can be defined as follows:

- Group R - Premolt crabs to morphological maturity of males smaller than 45 mm carapace width

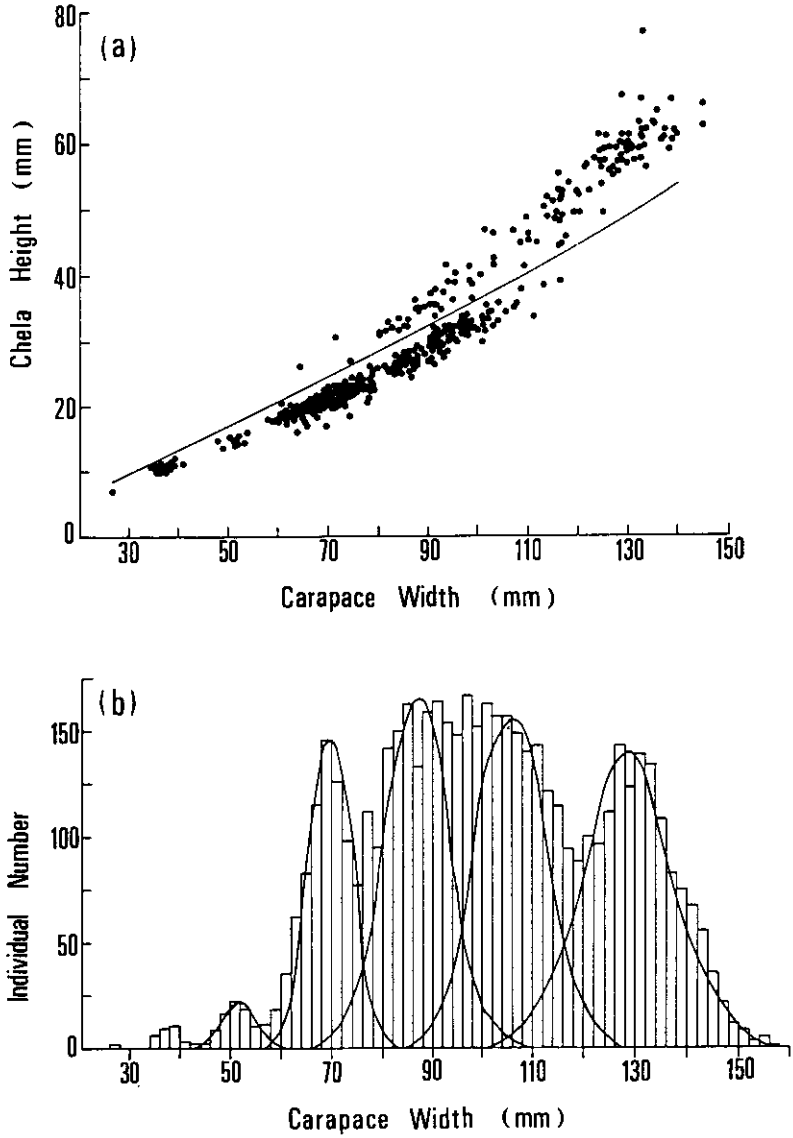

Figure 1. (Upper) The allometric relationship between chela height and carapace width of male tanner crabs, N = 772, from the sea off Kyoto Prefecture and the dividing line separating the two swarms of points. (Lower) Overall size distribution of male crab, N = 4,453, caught by beam trawl, longline trap and Danish seine, with fitted normal curves to distribution by Tanaka's method (Tanaka, 1956).

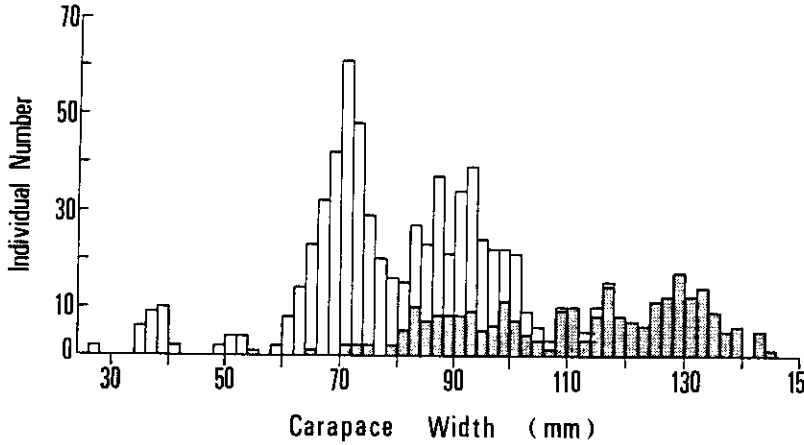

Figure 2. Carapace width distributions of male tanner crabs, N = 772, classified into the two groups (morphometrically mature and immature crabs) by discriminate analysis based on the dividing line in Figure 1.

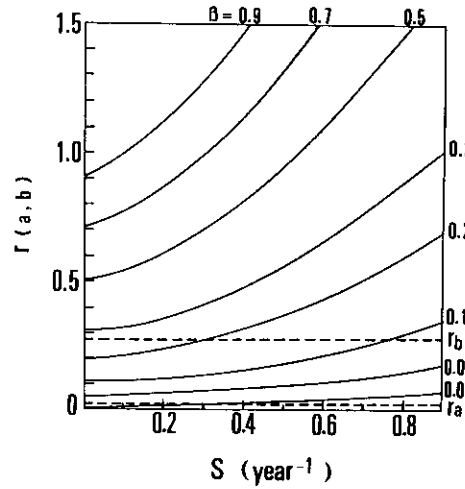

Figure 3. Relationship between r_a, r_b and S at $\beta \left(= \frac{n_a}{n'_b} \text{ or } \frac{n_b}{n'_b}\right) = 0.01 - 0.9$.

- Groups A, B, C – Three molt classes contained morphometrically immature and mature crabs at carapace width ranging from 58 to 116 mm.

- Group D – The largest molt class contained only morphometrically mature crabs larger than 116 mm carapace width.

Relationship Between Carapace Width and Chela Height

Carapace width and chela height measurements were made to the nearest millimeter using a vernier caliper. We used discriminate analysis on log transformations of the measurements to identify the area by a specific dividing line equation which effectively separates the two swarms of data.

Estimates of Survival Rates of Illegal and Legal-Sized Males

As the numbers of morphometrically mature crabs, N'_A, N'_B, in the groups A and B are considered to contain more than one year-class, the accumulated numbers may be represented by the following equations (Sinoda, 1968):

$$N'_A = n_a \frac{1 - S^{(\Delta t+1)}}{1 - S} \qquad [1]$$

$$N'_B = n_b \frac{1 - S^{(\Delta t+1)}}{1 - S} \qquad [2]$$

where h_a and h_b are the numbers of the youngest crabs after terminal molt into each group A and B, respectively, S is the survival rate per year of illegal-sized crabs and Δt is the life span in years after terminal molt in four groups A, B, C, and D. Numbers for morphometrically immature crabs, N' and N'_b, before terminal molt in groups A and B can be given by separating two swarms of chela-carapace sizes. That is, ratios, r_a and r_b are expressed by N'/n'_a and N'_B/N'_b, respectively from the equations [1] and [2].

$$r_a = \frac{n_a}{n'_a} \cdot \frac{1 - S^{(\Delta t+1)}}{1 - S} \qquad [3]$$

$$r_b = \frac{n_b}{n'_b} \cdot \frac{1 - S^{(\Delta t+1)}}{1 - S} \qquad [4]$$

The ratios, r_a and r_b, can be evaluated directly by measuring the chela sizes in a given carapace range in groups A and B. The life span, Δt, after the entrance into morphometrically mature groups is estimated to be three years from the results of tagging experiments (Appendix). Parameters n_a/n'_a and n_b/n'_b are said to be proportional to the molting probabilities conditional on whether a crab terminally molted or nonterminally molted in the previous molt

group R for n_a/n'_a and in group A for n_b/n'_b.

For group C, in which carapace width ranges approximately from 96 to 118 mm, there are morphometrically immature and mature males. With N'_c and n'_c denoting mature and immature males in group C, respectively, a total number of crabs, N_c, can be represented as follows:

$$N_c = N'_c + n'_c = n'_c(1 + r_c) \quad [5]$$

where r_c is the ratio N'_c/n'_c. If all the morphometrically immature crabs in group C undergo terminal molt to group D, in which carapace width is larger than 116 mm, the total number of crabs in group D, N_d, would be represented by

$$N_D = n_d \frac{1 - S_m^{(\Delta t+1)}}{1 - S_m} \quad [6]$$

where r_d is the number of the youngest crabs after the last molt into the group D and S_m the survival rate per year of legal-sized crabs. Then, the following equation would be expressed:

$$\frac{N_D}{N_C} = \frac{n_d}{n'_c} \cdot \frac{1}{1+r_c} \cdot \frac{1-S_m^{(\Delta t+1)}}{1-S_m} \quad [7]$$

As all the morphometrically immature crabs in group C are equally likely to molt into group D, the number of newly molted crabs, n_d, may be given as:

$$n_d = n'_c \cdot P \quad [8]$$

where P is the probability of successfully molting into group D. The equation [7] is rewritten as:

$$\frac{N_D}{N_C} = \frac{P}{1 + r_c} \cdot \frac{1 - S_m^{(\Delta t+1)}}{1 - S_m} \quad [9]$$

Some parameters in equations [3], [4], and [9] for estimating S and S_m can be estimated using the data collected at sea and in fish markets, except descriptive parameters P and Δt.

RESULTS

Plots of chela height versus carapace width were presented on an arithmetic scale in Figure 1 (upper), and carapace width frequency distribution of male crab was shown in Figure 1 (lower). In Figure 1 (upper), the line separating the two swarms was estimated for the Zuwai crab, *C. opilio*, in the western Japan

Sea following the discriminate function,

$$Y = -18.9321 \ln Cw + 17.1271 \ln Ch + 38.3594$$

where Cw is carapace width in mm, Ch is chela height in mm, and the discriminate boundary value was calculated as $Y = 0.838528$. Although there has been no evidence on a functional maturation of males coincident with chela allometric growth, it seemed that two groups were indicated morphometrically (Figure 1), mature crabs above the line and immature crabs below the line. As tentatively defined for the five groups (R, A, B, C, and D), molt to morphometric maturity might occur from 65 to 120 mm.

From modes in Figure 1 (lower), mean carapace widths corresponding to the five groups could be estimated at 50.9, 66.8, 82.9, 103.3 and 130.1 mm, respectively. Relative numbers of immature and mature crabs in each group and estimated values of r_a, r_b, and r_c were tabulated as below.

Group	Mean Size in mm	Immature Crab in %	Mature Crab in %	Ratio (r)
R	50.9	100.0	0	—
A	66.8	97.8	2.2	$r_a = 0.022$
B	82.9	78.9	21.1	$r_b = 0.267$
C	103.3	52.2	47.8	$r_c = 0.916$
D	130.1	1.3	98.7	—

The value of $N_d/N_c = 0.663$ was simply obtained from size frequency distribution which was separated into molt classes as groups C and D. From equations [3] and [4] for illegal-sized crabs and equation [9] for legal-sized crab, values of S and S_m could be evaluated for various descriptive parameters of n_a/n'_a, n_b/n'_b, and P as shown in Figures 3 and 4. For the life span after terminal molt as mentioned above, it was assumed in this paper that $\Delta t = 3$ years at least based upon the results of tagging experiments in the western Japan Sea.

For estimating the survival rates, S and S_m, the parameters of n_a/n'_a, n_b/n'_b and P should be conditioned for some reasons. We have no appreciation of these parameters, n_a/n'_a and n_b/n'_b : ratios in number of the youngest crabs terminally molted into groups A and B to number of morphometrically immature crabs in each group, P : probability of successful molt into the largest

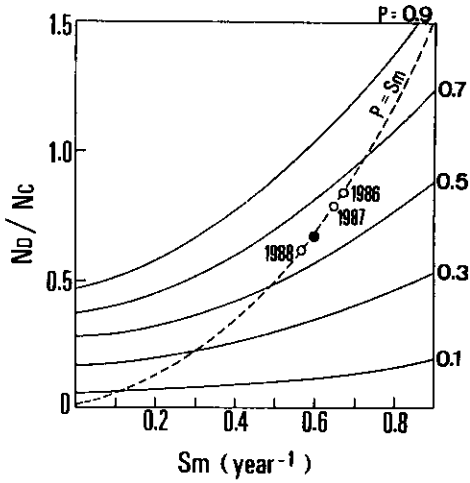

Figure 4. Relationship between N_D/N_C and S_m at P = 0.1 - 0.9 in consideration of terminal molt in Group C.

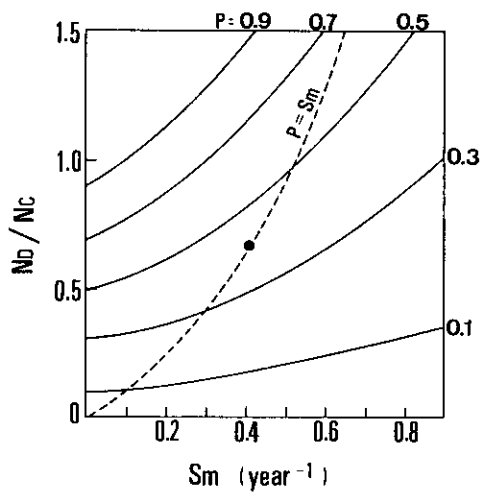

Figure 5. Relationship between N_D/N_C and S_m at P = 0.1 - 0.9 without consideration of terminal molt in Group C.

molt class (group D). Based on estimated values of $r_a = 0.022$ and $r_b = 0.267$, it is implied that the number of youngest crab newly terminally molted in groups A and B was a small minority comprising only about 1% of the immature crabs in group A and about 10-20% of crabs in group B, respectively. However, we could not assign definite values to n_a/n'_a and n_b/n'_b, corresponding to values of S as accurately as Figure 3 permit were ranged 0.30>S>0.75 per year for illegal-sized crabs in both groups A and B.

Similarly for legal-sized crabs in groups C and D, since the assigned value of $N_d/N_c = 0.663$ could not define the probability P, the corresponding value of S_m was not estimated without any specific conditions. From a practical fisheries point of view, P was considered to be close to S_m. Namely, crabs in group C molt during the period from July to November in the western Japan Sea (Ito, 1970); at the same time, Danish seines start heavy exploitation of newly molted and hard-shelled crabs. Therefore, the probability of successful molt was tied to escaping Danish seining. Under this assumption, $P = S_m$, the value of the survival rate could be estimated at $S_m = 0.60$ per year. Based on the annual values of N_d/N_c in three fishing periods from 1986 to 1988, values of S_m separate by year indicated an upward trend of total mortality in legal-sized crab population, $S_m(1986) = 0.67$, $S_m(1987) = 0.65$, $S_m(1988) = 0.58$, as shown in Figure 4.

DISCUSSION

Male *C. opilio* in the eastern Canadian waters are considered to have a terminal molt, based on extensive research on morphological measurements (Conan and Comeau, 1986, Conan *et al.*, 1987), physiological function (Beninger *et al.*, 1988) and biological observation (Ennis *et al.*, 1988). It is doubted that male crabs in the Japan Sea have a terminal molt, based on the duration of each stage of development to the post-maturity molt. Sinoda (1968), Kon (1969) and Ito (1970) estimated the duration of crabs larger than VII molt stage, ranging from 55 to 70 mm carapace widths, to be around 12 months, mainly based on the appearance of soft-shelled crabs every July to November. Therefore, the perception of male crab growth has been based on the uncertainty of whether the crab population as a whole has an annual molting cycle. Since there were few data from tagged male crabs that have been recaptured after two or three years in tag-recapture experiments, it was considered that all the male crabs had lost their tag at molt during the one-year period after release to fishing grounds. Only Niwa's report (Niwa, 1967) implied intermolt time longer than one year, but not with regard to a morphometric change in chela size. On the other hand, from the result of measurement of shell conditions, Ito (1970) stated that crabs larger than 128 mm carapace width did not indicate any molting time in a year due to a large individual variation in measuring shell hardness. Also, in his paper, the monthly changes in appearance of the double-carapaced crab (new and old carapaces) were not described for male crabs larger than 128 mm carapace width but for crabs smaller than 127 mm carapace width. Based on the published data taken in the Japan Sea, it is doubted that all male crabs larger than about 60 mm carapace width molt year by year, and it is probable that they undergo a terminal molt

at allometric change of chela growth.

If male growth continues after the molt to morphometric maturity, all crabs in group C recruit into group D. The survival rate S_m in group D may be represented using the same symbols mentioned above as follows:

$$\frac{N_D}{N_C} = P\frac{1 - S_m^{(\Delta t+1)}}{1 - S_m} \qquad [10]$$

Under the condition of $S_m = P$ and $\Delta t = 3$ years, it can be estimated from Figure 5 that 40% of the crabs in group D survive annually. There is a large difference in estimated S_m between two assumptions whether male crabs have a terminal molt or not. As implications on male terminal molt could not be fully established in this paper, because of a lack of biological information collected from the Zuwai crab population in the western Japan Sea, we must leave it for future research.

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Appendix

Results of Western Japan Sea tagging experiments on male crab recaptured more than 12 months after release.

Recapture Date	Release Date	Carapace Width at Release (mm)	Days at Large
9 Nov. 1986	25 Jul. 1985	112	472
15 Nov. 1986	25 Jul. 1985	96	478
7 Jan. 1987	23 May 1985	97	594
21 Jan. 1987	10 Apr. 1985	93	652
28 Jan. 1987	8 Mar. 1985	100	691
10 Feb. 1987	10 Apr. 1985	103	671
6 Nov. 1987	15 Oct. 1986	135	386
	17 Sep. 1986	135	415
7 Nov. 1987	23 May 1986	129	533
9 Nov. 1987	15 Oct. 1986	120	390
18 Nov. 1987	17 Sep. 1986	97	427
26 Nov. 1987	15 Oct. 1986	100	406
30 Nov. 1987	25 Jul. 1985	119	858
7 Dec. 1987	23 May 1986	108	563
8 Dec. 1987	15 Oct. 1986	113	419
21 Feb. 1988	10 Feb. 1987	131	377
27 Feb. 1988	10 Feb. 1987	131	383
29 Feb. 1988	10 Feb. 1987	131	385
14 Mar. 1988	10 Feb. 1987	121	398
17 Mar. 1988	15 Oct. 1986	114	519
7 Nov. 1988	14 Jul. 1987	128	482
8 Nov. 1988	24 Apr. 1987	97	564
	24 Apr. 1987	127	564
9 Nov. 1988	27 Mar. 1986	89	958
	15 Oct. 1986	126	756
	10 Feb. 1987	131	638
	14 Jul. 1987	126	484
	21 Aug. 1987	77	445
	22 Sep. 1987	103	414
22 Nov. 1988	16 Jun. 1987	131	525
23 Nov. 1988	14 Jul. 1987	142	498
1 Dec. 1988	24 Apr. 1987	117	587
2 Dec. 1988	26 Nov. 1987	135	372
3 Dec. 1988	20 Feb. 1987	102	662
	14 Jul. 1987	131	508
25 Dec. 1988	26 Nov. 1987	135	395
29 Dec. 1988	14 Jul. 1987	121	534
6 Jan. 1989	26 Nov. 1987	144	407
20 Jan. 1989	14 Jul. 1987	138	556
23 Jan. 1989	26 Nov. 1987	130	424
24 Feb. 1989	26 Nov. 1987	121	456

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Diet Influences Cannibalism in Laboratory-Held Juvenile Red King Crabs (*Paralithodes camtschatica*)

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Auke Bay, Alaska USA

ABSTRACT

Groups of 10 juvenile (1-yr-old) red king crabs (*Paralithodes camtschatica*) were maintained on either a high-growth or low-growth diet to determine whether diet quality affected the incidence of cannibalism. Over the 112 days of the study, crabs that ate the high-growth diet (mussels) grew to twice the weight of the crabs on the low-growth diet (shrimp tails). Cannibalism was consistently more common in groups that ate the low-growth diet; by the end of the 112 days, 45% of those crabs had been eaten by tank-mates, while only 8% of the crabs that ate the high-growth diet had been eaten. Additional crabs maintained in isolation on the low-growth diet had significantly longer intermolt periods than those in groups that ate low-growth diets and each other. When the diets of crab groups were reversed after 112 days, the trends in cannibalism reversed as well. Tests using 2-yr-old crabs showed similar results. We conclude that captive crabs limited to a low-growth diet, supplement that diet with cannibalism, and that doing so improves their growth rate.

INTRODUCTION

Red king crabs are opportunistic omnivores, reported to feed on dozens of species from at least nine phyla (Sundberg and Clausen, 1979; Pearson et al., 1984; Fukuhara, 1985) and very different food items, depending on season and location (Jewett and Feder, 1982; Pearson et al., 1984). Food is not generally considered a limiting factor for king crabs because of their all-inclusive eating habits; however, we have observed that different diets fed to laboratory-held crabs support different rates of growth (Rice et al., 1988). Juvenile red king crabs are prone to cannibalism in the

laboratory and are especially vulnerable to predation when molting. We undertook this study to determine whether diet quality (as defined by growth-rate supported) was a factor influencing the incidence of cannibalism among communally-held juvenile red king crabs.

METHODS

Groups of 1-yr-old and 2-yr-old crabs were maintained on high-growth and low-growth diets for 112 days and cannibalism was monitored. Diets were then reversed and monitoring continued for 40 more days. The selected diets were whole mussels (*Mytilus edulis*) and shrimp tails (Penaeid shrimp). For 1-yr-old crabs, six groups of 10 crabs each were held communally, and 16 additional crabs were maintained in isolation, on each diet. In tests on 2-yr-old crabs, three groups of 8 crabs each were held on each diet.

The crabs tested were red king crabs from Auke Bay in northern Southeast Alaska. The 1-yr-old crabs were obtained from the low intertidal area (below the -.7-m tide level) in early spring--a little more than 1 year after hatching and a little less than 1 year after settling out of the water column (Freese and Babcock, Proceedings, this symposium). The 2-yr-old crabs were collected by divers from the subtidal area; these crabs were of the size that form pods.

Crab groups were held outdoors in long rectangular fiberglass tanks that were divided by screen partitions. Seawater flowed in at one end, passed through all sections of the tank, and overflowed through a standpipe at the other end. Tanks had 2-cm washed sand on the bottom to provide the crabs traction and a more natural substrate. Tank sections for the 1-yr-old crabs were 20 x 55 x 40 cm, with six sections/tank, and for the 2-yr-old crabs were 40 x 55 x 40 cm, with three sections/tank. There were two tanks for each size of crab. Tanks had translucent covers that allowed crabs exposure to a natural photoperiod. Isolated crabs were maintained in individual compartments in modified fish-egg incubators (Arasmith et al., In press). All crabs were maintained in running Auke Bay seawater at ambient temperature (6-10°C).

Crabs were fed ad libitum three times/week; uneaten food was removed before each feeding. Mussels used were collected from the Auke Bay intertidal zone in areas away from boat moorage to reduce the likelihood of contamination. They were split open and given to the crabs whole. Shrimp tails used were a frozen aquaculture product. Both the meat and shell of the tails were given to the crabs.

Crabs were monitored daily, and all deaths, incidences of cannibalism, and molting noted. Individual crabs in each group were identified by 2-mm colored glass beads attached to their carapaces with cyanoacrylate glue. Two to 7 days after any crab molted, it was weighed (live wet weight) and measured (carapace length), and it's colored bead replaced.

Statistical significance of differences between groups was determined by one-way ANOVA, with arcsine transformation applied to proportional data before analysis.

RESULTS

A diet of mussels induced much faster growth in king crabs than a diet of shrimp. Initial mean length of the 1-yr-old crabs was 10.4 mm. Over 155 days, crabs that ate mussels grew to a final mean length of 25.0 mm while the crabs that ate shrimp grew to just 18.6 mm. At the end of our study, crabs that ate mussels weighed more than twice what crabs that ate shrimp weighed--11.32 g and 4.59 g, respectively. Initial mean length of the 2-yr-old crabs was 25.9 mm. Crabs that ate mussels grew to a mean of 39.6 mm and 44.2 g, while those that ate shrimp grew only to 30.2 mm and 20.0 g. Diet-associated differences in final lengths and weights for both ages of crabs were significant at $P << .0001$.

Most deaths were associated with cannibalism. Typically, we first discovered a death by finding a crab eating a dead crab; however, we occasionally found that a crab being eaten was not dead, which supports our conclusion that cannibalism was the cause of death rather than an after-the-fact occurrence. We observed one incidence of a crab attacking an apparent healthy crab, and killing it. At least three members of the group ate some part of the victim. Some crabs (14% of losses for 1-yr-old crabs, and a single 2-yr-old crab) disappeared entirely. Although disappearances were probably due to being completely consumed, we have conservatively based all calculations of significance on numbers of partially eaten crabs actually observed. Eleven percent of deaths among 1-yr-old crabs followed a different pattern. Affected crabs had a swollen abdomen for several days before death, and after death were very stiff--unlike the limp remains of cannibalized crabs; these crabs were never cannibalized by surviving crabs. The first such death occurred 92 days into the study, and most of them occurred in one tank. The period of stress before death, the late onset, and the clustering of occurrences of these deaths are consistent with disease, and we consider these to have been disease-caused mortalities.

Cannibalism was significantly more prevalent among groups of crabs that ate the slower-growth diet of shrimp than among groups that ate the faster-growth diet of mussels (Fig. 1). After only 40 days, each 1-yr-old group on the shrimp diet had lost a mean of 1.5 (0.5-2.5, 95% confidence interval) crabs to cannibalism, while groups that ate mussels had lost a mean of 0.3 (0-0.8) individuals. The 2-yr-old groups that ate shrimp had lost a mean of 2.3 (1.2-3.5) individuals while groups that ate mussels had no mortality. Diet-related differences were significant at $P < .05$ for both ages after 40 days. After 112 days, 1-yr-old groups that ate shrimp had lost 4.5 (2.3-6.7) crabs to cannibalism, while those that ate mussels lost 0.8 (0.1-1.6). The 2-yr-old groups that ate shrimp had lost 4.7 (1.6-7.8) to cannibalism, while those on mussels lost 0.3 (0-1.5). Differences were significant at $P < .01$ for both ages after 112 days.

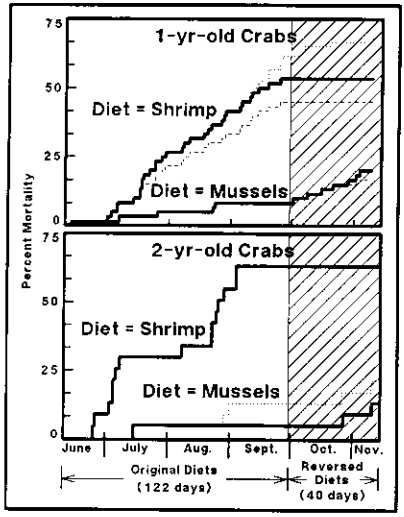

Figure 1.--Cumulative numbers of deaths of juvenile king crabs. Solid lines = probable cannibalism (both known and disappearances). Dashed lines = known cannibalism only. Dotted lines = total deaths.

There can be little doubt that diet was the variable causing the difference in degree of cannibalism. The diets were reversed 112 days into the study (crabs that were eating mussels were switched to shrimp and vice versa), and the trends in cannibalism immediately reversed as well (Fig. 1). During the 40 days after diets were reversed, differences in cannibalism for both ages of crabs were significant at $P < .001$. No crabs of either age that were switched to the mussel diet were cannibalized, while 7 (~1/group) of the 1-yr-old crabs and 2 (.7/group) of the 2-yr-old crabs that were switched to the shrimp diet were eaten.

The most notable difference between the grouped and the isolated 1-yr-old crabs on the shrimp diet was the considerably longer intermolt period of the isolated crabs. The mean intermolt times for all grouped and isolated crabs eating mussels were similar, 40.6 and 39.7 days, respectively, but the mean intermolt time of 48.4 days for grouped crabs eating shrimp (and each other) is considerably less than the 72.2 day intermolt time for isolated crabs eating only shrimp. Of the 3 isolated crabs that died during this experiment (all on the shrimp diet), 2 had molted only once and survived inordinantly long periods, 109 and 131 days, between molting and dying. Availability of even relatively small amounts of crab meat to augment the shrimp diet of grouped crabs apparently went a long way toward balancing a nutritional deficit that delayed molting in the isolated crabs.

DISCUSSION

Our conclusion is that cannibalism among captive juvenile red king crabs is mediated by their diet. Crabs limited to a slow-growth diet supplement that diet by eating each other; doing so improves their growth and molting rate. A similar phenomenon may occur in lobsters; Van Olst et al. (1975) report that feeding lobster meat to juvenile lobsters promotes faster growth, and they speculate that some cannibalism among communally reared lobsters may serve to improve growth.

There is little evidence in the literature to indicate whether cannibalism by king crabs occurs to a significant degree in the field. The most tantalizing hints are reported by

Pearson et al. (1984), who experimented with immunoassays to identify stomach contents (unrecognizable when examined visually) of juvenile king crabs. One antigen they developed and tested was to king crab tissues. Many of the stomach-content samples tested for presence of king crab tissues showed initial precipitation lines, but not confirming lines of identity, which meant the presence of king crab tissue in the stomachs was neither indicated nor eliminated. Pearson et al. (1984) do report one occurrence of tissue visually identified as king crab in a red king crab stomach. Any further analysis of king crab diets in the wild should include checks for cannibalism.

If seasons of suboptimal prey variety do occur in the wild, causing cannibalism among juvenile red king crabs, the phenomenon could have both positive and negative impacts on recruitment. On one hand, if diets adequate for good growth rate are not available, individual crabs would be doubly at risk; their growth would be limited at the same time that the risk of predation by their own species increased. On the other hand, the year-class could be partially protected from disastrous lack of food items necessary for good growth rate if the stronger individuals could survive by improving their diets through cannibalism. Further studies that shed light on the question of what food items are necessary for good growth and molt rates could help determine the likelihood of food availability having adverse impact on natural recruitment. Food availability certainly cannot be dismissed as a possible major factor in king crab population fluctuations.

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Some Implications of Egg Mortality Caused by Symbiotic Nemerteans for Data Acquisition and Management Strategies of Red King Crabs, *Paralithodes camtschatica*

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ABSTRACT

Analyses of egg masses from 772 red king crabs (Paralithodes camtschatica) collected at 28 Alaskan localities from 1983 to 1985 demonstrated the widespread presence of several species of symbiotic nemertean egg predators. Nemertean intensity was correlated with significant egg mortality. At some localities nearly all crab eggs were consumed. Carcinonemertes regicides was the most abundant of the nemertean egg predators. Its abundance was markedly seasonal.

A visual estimate of the percentage of the maximum volume of eggs that a female red king crab of a given size could carry was recorded as percent clutch size. It provided a rapid, semiquantitative, evaluation of fecundity. The fourth pleopod was collected from ovigerous crabs for a more detailed analysis of the abundance of symbionts in the egg mass. Pleopod fecundity was estimated based on the dry weight of a counted subsample of eggs. Egg mortality was expressed as the percentage of dead embryos based on counts of 1,000 eggs attached to the egg-bearing setae.

Percent clutch was significantly associated with the number of living embryos ($r = 0.92$). At extreme values (0% or 90%-100%) percent clutch was in close agreement with percent egg mortality. However, percent clutch estimates from 20% to 80% were but weakly associated with percent egg mortality. This variation was apparently due to the relative contributions of two sources of reduced egg counts; either few eggs were oviposited (or retained on pleopods), or heavy embryo mortality occurred (after a full clutch was oviposited). Thus, the correlation between percent clutch and the number of dead embryos was relatively low ($r = 0.71$), and the number of dead embryos in pleopod egg mass samples with a percent clutch of 2.0% ranged from 8,000 -

38,000 (full clutches ranged from 40,000 - 80,000 living eggs).

The outbreak of symbiotic nemertean egg predators was geographically localized. Epidemic levels were usually reached in enclosed fjords and passages. Larval development of red king crabs appears to be considerably longer than that of the nemertean, C. regicides. Hence, these epidemiological systems may consist of hosts with an open recruitment pattern and infectious agents with a closed recruitment pattern. Under such conditions effective management might entail fishing out the infested hosts rather than protecting infested stocks. More detailed studies of larval crab movements, recruitment to juvenile populations and nemertean larval development and transmission should precede implementation of such a radical management strategy.

Active management of the Alaskan red king crab fishery requires regular surveys yielding information on productivity and recruitment. Inclusion of egg mortality information can be readily accomplished and will enhance interpretation of reduced percent clutch observations. We propose specific and simple sampling procedures to estimate egg mortality, intensity of nemertean infestations and other infectious diseases of the eggs. Such samples would enhance retrospective studies of crab fecundity, brooding seasonality, and the systematics and abundance of clutch symbionts. Most importantly, a routine pleopod sampling program would provide a basis to assess the frequency and causes of future reproductive events.

INTRODUCTION

Initial evidence, based on percent clutch observations of Alaska Department of Fish & Game (ADF&G) and U.S. National Marine Fisheries Service (NMFS) surveys, indicated that brood losses of red king crabs, Paralithodes camtschatica, were unusually high in some Alaskan management areas (Blau 1983 1986; Wickham et al. 1985). These indications were confirmed in an extensive quantitative analysis (Kuris et al. 1990) covering 28 locations from 1983 to 1985. These losses generally occurred three to six months into the brooding season (June to September) and were caused by the predatory activity of very high intensities of at least two species of symbiotic nemertean egg predators, Carcinonemertes regicides (Shields, Wickham & Kuris, 1989) and an undescribed small eyeless species designated "form #4" by Wickham & Kuris (1988). Other predatory nemerteans have been recovered but are neither as widespread nor as abundant as are C. regicides and form #4. One of these species, Alaxinus oclairi, has recently been described (Gibson et al. 1989).

Kuris et al. (1990) showed that these egg predators were widespread over much of the geographic range of red king crabs in Alaska. An outbreak of these symbionts to epidemic levels occurred in certain regions; most notably in Kachemak Bay, certain locations in the Kodiak Archipelago, Southeastern Alaska and near Dutch Harbor. Brood losses were very substantial in these areas. At some places such as Kachemak Bay (Cook Inlet Management Area), Uganik Bay and Terror Bay (Kodiak Management Area) brood losses were nearly total in the 1983/84 brood season; all ovigerous females lost nearly all their eggs by September (hatching usually occurs in March). In several samples from different locations nemertean intensities exceeded 100,000 worms per crab. This outbreak subsided in 1985/86 brood season.

Other symbionts were present in the egg masses of red king crabs. A species of turbellarian was abundant, but it did not kill crab embryos. An amphipod (Ischyrocerus sp.) was often present and was an egg predator. At three locations it may have been sufficiently abundant to have a significant impact on egg survival. Its overall importance remains to be assessed.

Red king crab stocks are actively managed (Jamieson 1986) with annual restrictions on catch. Active management of the red king crab fisheries in Alaska is based on a program of repeated surveys (preferably annual) of red king crab stocks. Sex ratios, reproductive condition, egg output, and population size and structure are assessed (Blau 1983 1986). As the key reproductive statistic in ADF&G and NMFS surveys, biologists routinely record a visual estimate of the size of the clutch relative to the size of the female. This is recorded as percent clutch, the relative proportion of a hypothetical full clutch of eggs retained by the brooding female crab.

To improve our ability to acquire information on brood mortality in red king crabs, we present a correlation analysis of the percent clutch statistic with the percentage of egg mortality caused by nemertean egg predators, the total number of eggs present (both living and eaten by nemerteans), the number of living eggs, and the number of dead eggs. We also consider some management implications of brood losses caused by infectious agents, discuss how egg mortality studies complement other components of the continued study of Alaskan red king crab fisheries, and then suggest some future lines of research.

MATERIALS AND METHODS

Our general sampling procedure was detailed in Kuris et al. (1990). Briefly, pleopod egg samples were obtained from crabs collected by baited crab pots or eastern otter trawls at 28 localities ranging from Adak Island to Southeast Alaska, with most samples being obtained from the Kodiak and Cook Inlet Management Areas during the 1983/84 to 1985/86 brooding seasons.

To provide a sample to quantify egg mortality and the abundance of nemertean worms and other symbionts, the fourth pleopod of each randomly selected ovigerous female crab was excised at its base and preserved immediately in a vial containing 5% formalin in sea water. Of the six pleopods present, the fourth was chosen since it is located near the center of the clutch and it carries a large proportion of the eggs. Carapace length, estimate of percent clutch size, depth and location of capture were recorded for each female sampled. Percent clutch is a visual estimate of the percentage of the maximum volume of eggs that a female of such a size could carry (Blau 1986). It provides a semiquantitative record of fecundity. For the statistical analysis of the association between percent clutch and the laboratory egg mortality estimates we used samples collected in the Kodiak Management Area, June to September, 1984, a time and place with high egg mortality (41 to 84 percent) and predatory nemerteans were shown to be the cause of most of the mortality (Kuris et al. 1990).

Symbionts present in a pleopod sample were extracted by agitation of the pleopod. Symbionts were then identified, counted and preserved in 5% formalin in sea water. If the number of extracted worms exceeded

about 2,000, a subsampling procedure was used to estimate the number of worms per pleopod sample. The worms were poured into a petri dish with a 1 cm^2 grid. Worms were counted in 6 randomly selected squares. The mean number of worms per cm^2 was then multiplied by the area of the dish (in cm^2) for the estimated total number of worms per pleopod.

To assess egg mortality on individual crabs, all of the egg-bearing setae of each sampled pleopod were carefully removed from the pleopod and a subsample of approximately 1,000 eggs were counted as described in Wickham (1979). Crabs whose clutches were in the process of hatching, or had already hatched, were excluded from this analysis as egg mortality could not be distinguished from hatched eggs. Intact eggs containing normally developing embryos were counted as live, while eggs containing abnormal embryos, or eggs partially or completely devoid of their contents were counted as dead. Nearly all the dead eggs had slit outer membranes and were empty, indicating that nemerteans had killed the embryos and consumed the contents (Wickham 1978; Roe 1984; Shields and Kuris 1988b). Egg mortality was expressed as the number of dead eggs per total number of counted eggs. Crab fecundity per pleopod was estimated by dividing the total weight of the eggs by the weight of a counted subsample, then multiplying the quotient by the number of eggs in the subsample. The weight of the dead eggs in a pleopod or subsample potentially biased the fecundity per pleopod estimate when mortality was moderate to high (10-100%). To correct for this bias, the mean weight of a dead egg, 0.40×10^{-4} gm ($\pm$ 0.48×10^{-4} SD, range = $0.09 - 2.09 \times 10^{-4}$ gm) and the mean weight of a live egg, 1.89×10^{-4} gm ($\pm$ $0.19\ 10^{-4}$ SD, range = $1.50 - 2.37 \times 10^{-4}$ gm) was estimated and the proportional weight of dead eggs (PWD) in a subsample was calculated as follows:

$$PWD = \frac{D_{\#}\ D_{wt}}{(L_{\#}\ L_{wt}) + (D_{\#}\ D_{wt})};$$

where $D_{\#}$ and $L_{\#}$ represent the number of dead and live eggs in the subsample, and D_{wt} and L_{wt}, the weight of a dead and live egg. Then, the product of the total weight of the eggs and PWD was divided by the mean weight of a dead egg to give the total number of dead eggs on the pleopod. Similarly, the product of the total weight of the eggs and (1-PWD) was divided by the mean weight of a live egg to give the total number of live eggs on the pleopod. The corrected fecundity estimated the total number of live plus dead eggs.

Margolis et al. (1982) defined "prevalence" as the proportion of infested individuals in the host population, and "mean intensity" as the mean number of symbionts per infested host. Worm density as defined in Wickham (1979) represents the estimated number of worms per 1,000 crab eggs and is used here for comparisons with other carcinonemertid-host systems. Statistical analyses were computed with the aid of SAS (1982) as per Sokal and Rohlf (1981). Correlation analyses were run on data with and without log-transformation. A value of $P<0.05$ was accepted as significant.

RESULTS

Using samples collected in the Kodiak Management Area from June to

September 1984, a correlation matrix was developed to examine the predictability of the percent clutch statistic for the number of living eggs, the number of dead eggs, the total number of eggs (live plus dead), and percentage egg mortality (Table 1). Percent clutch was highly correlated with the number of living eggs (r = 0.92). It was also significantly correlated with the total number of eggs (both living and dead) and was also an excellent predictor of the percentage of egg mortality (r = -0.93) and the number of dead eggs.

Table 1. Correlation matrix for percent clutch, total number of eggs, number of living eggs, number of dead eggs and the percentage of egg mortality in the pleopodal samples from the egg masses of red king crabs, Paralithodes camtschatica (N = 59) collected from the Kodiak Management area from June to September, 1984; **P<0.01, *0.01<P<0.05.

	Total Number of Eggs	Number of Living Eggs	Number of Dead Eggs	Percentage Egg Mortality
Percent Clutch	0.80*	0.92**	-0.71**	-0.93**
Total Number of Eggs	-	0.94**	-0.33*	-0.72**
Number of Living Eggs		-	-0.64**	-0.88**
Number of Dead Eggs			-	0.80**

Further examination, using samples from many Alaskan localities throughout the year (N = 418) provided a correlation of r = -0.78, (P < 0.01), for percent clutch and the percentage of egg mortality. Figure 1 shows the regression of the percentage of egg mortality on percent clutch (mortality = 68.6 - 0.752 percent clutch). Table 2 shows that for percent clutch values $\leq$ 10%, egg mortality generally exceeded 75%. For percent clutch values $\geq$ 70% egg mortality was usually 10% or less. This suggested that when high percent clutch values (70-90%) were recorded there was little mortality due to nemerteans. The shipboard observers may have been recognizing differences in the number of eggs oviposited or lost to other mortality causes.

Figure 1 also compared summer samples (May to September) with winter samples (October to March). In general the summer outlier values fell above the regression line indicating that heavy egg mortality from nemertean predation was sometimes not detected by the shipboard observers, perhaps because the early egg mass retained its full shape even though many eggs were killed. In contrast, the outlier winter values generally fell below the regression line, suggesting that, late in the breeding season, some clutches may be smaller due to mortality factors other than worm predation.

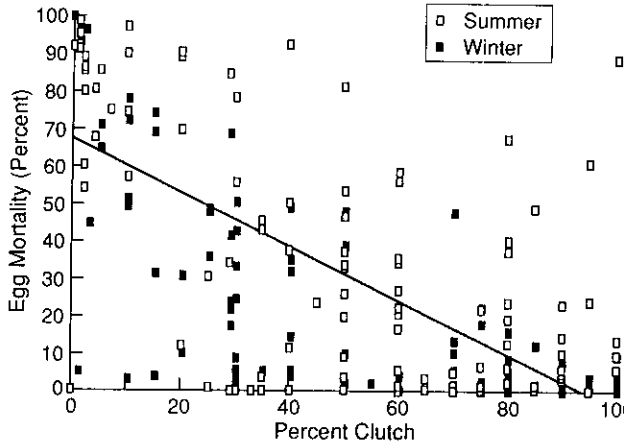

Table 2. Frequency of levels of egg mortality observed for different values of the percent clutch statistic.

Percent Clutch	Percentage of Egg Mortality							
	0	1-10	11-25	26-74	75-90	91-99	100	Total
0	3	0	0	0	0	3	26	32
10	0	2	0	11	9	9	0	31
20	0	2	1	5	1	1	0	10
30	0	9	4	12	2	0	0	27
40	2	5	2	7	0	1	0	17
50	4	9	2	8	1	0	0	24
60	5	9	3	5	0	0	0	22
70	5	26	2	1	0	0	0	34
80	13	42	7	3	0	0	0	65
90	13	44	4	2	0	0	0	63
100	33	58	1	0	1	0	0	93
Total	78	206	26	54	14	14	26	418

DISCUSSION

Relationship between Brood Mortality, Percent Clutch and Reduced Catch

Overall, the percent clutch statistic overestimated egg mortality from worm predation, particularly when egg mortality was high. A possible explanation for this discrepancy is that the percent clutch statistic includes other sources of egg mortality (or more generally, reduced brood size) that cause the complete detachment of eggs from the egg-bearing setae. Documented causes of such egg loss for red king crabs in Alaska include sloughing of infertile eggs (McMullen and Yoshihara 1969) and egg predation by Ischyrocerus sp. (Kuris et al. 1990).

Male red king crabs enter the fishery seven to nine years after they hatch (Powell 1967; Jamieson 1986). It is tempting to try to identify the year in which reduced egg numbers, perhaps caused by nemertean egg predators, may have become a problem for certain Alaskan red king crab fisheries by examining summary data on percent clutch statistics (e.g., Blau 1983). This data set covers 1972-1989 and provides percent clutch estimates for thousands of female red king crabs. However, sampling regions and dates sometimes varied between years. Since Kuris et al. (1990) have shown that egg mortality due to nemertean predation varies between districts of the Kodiak Management Area and that only dates late in the summer survey will detect this source of brood loss, these areawide data are not suitable for a comparison of different years. However, we suggest that a district-by-district annual summary of the distribution of the percent clutch statistics may help identify where and when the outbreak to epidemic levels of predatory nemerteans occurred. As Blau (1983) has noted, certain locations, such as Uganik & Viekoda bays, had much lower proportions of females with full clutches (Blau 1983). These locations were consistently and heavily impacted by nemertean egg predation in 1983 to 1986 (Kuris et al. 1990).

Kuris et al. (1990) have shown that brood losses caused by nemertean worms will be substantially underestimated unless samples are taken in the latter half of the brooding season. Worm intensity does not attain high levels until July or August, and egg mortality lags behind worm intensity, often peaking in September for those years in which outbreaks reached epidemic proportions. When outbreaks are less severe peak egg mortality may not be observed until very late in the brooding season, i.e., November to January. Late fall and winter surveys are infrequent generally because weather is inclement.

Reduced egg output, perhaps beginning in the 1970s in some districts, could have contributed to declining catches in the Kodiak Management Area from 1983 to the present. If so, its effects will continue to be a factor until at least 1993, (7 years after our last egg mortality observations in 1986). Unlike other reported episodes of reduced reproductive output (Powell and Lebida 1968; Otto et al. 1983, this volume) the current reduction in egg production appears to be a prolonged event, induced by egg predation.

Recommendations for Improved Assessment of Reproductive Output

Our analysis of the percent clutch statistic shows that it is a valuable predictor of the potential reproductive output of female crabs. As presently recorded, it cannot, however, distinguish between very different causes of egg loss.

The inclusion of an additional sampling procedure in a regular survey or catch monitoring program necessarily competes with the limited resources available to management agencies. To obtain a substantial benefit at minimum cost, it is desirable to focus a new sampling program on probable areas of concern. Additional information on the condition of the egg mass should be sought whenever the mean percent clutch of a location drops below an agreed upon threshold. The percent clutch statistics presented above and in Blau (1983) suggest that detection of less than 70% of the females having full clutches (90% to 100%) should trigger further inquiry. The geographic survey of brood mortality and intensity of nemertean egg predators (Kuris et

al. 1990) suggests that crab stocks fished in partially enclosed embayments, fjords, and passages are notably at risk and should have priority for a regular egg mortality/egg predator sampling program.

To distinguish causes of reproductive failure and quantify nemertean abundance we suggest that samples of red king crabs in Alaska be taken twice in the brooding season. An early sample, taken in the spring, after oviposition, will enable causes of egg loss, such as breeding failure, to be recognized (Mc Mullen and Yoshihara 1969; Kuris et al. 1990). It will also provide a baseline to evaluate later causes of egg loss. A second set of samples, taken no sooner than August or September, should be sufficient to document the intensity of nemertean infestations and resultant egg mortality. Nemertean populations appear to reach their peak levels at this time, and egg mortality is already substantial (Kuris et al. 1990).

The following is a suggested simplified protocol for additional monitoring of crab reproduction. Sampling for the presence of nemerteans and the quantification of nemertean intensity and brood mortality should involve excision and preservation of an egg-bearing pleopod from females selected in a randomized sampling design. Random samples from Kachemak Bay showed relatively moderate levels of variation for egg mortality and intensity of nemerteans (Kuris et al. 1990). Thus, counts from relatively few pleopods (n = 25) would provide a simple and adequate sample to estimate brooding success. The similarity in egg mortality and nemertean infestations from locations in close proximity revealed that samples from such sites may be grouped for analysis.

Pleopodal samples may be processed as detailed in Kuris et al. (1990). Briefly, egg mortality due to nemertean egg predators may be directly estimated by the proportion of empty egg membranes retained on the egg-bearing setae, and worms may be separated from the egg mass by agitating a pleopod suspended in water. The only aspect of this protocol that requires some experience is the separation of the predatory nemerteans from the symbiotic turbellarians which may also be abundant. The latter do not kill crab eggs (Kuris 1991). In fresh samples the living worms are readily distinguished by color, shape, size and behavior. The symbiotic nemerteans of the red king crab are pink or pink suffused with white, cylindrical (or slightly flattened) and do not have a posterior adhesive gland. They may or may not be contained within a parchment sheath. The adult female nemerteans may also be recognized by the alternating arrangement of the pink gut and the white gonads. Length of the nemerteans is variable and depends on the species encountered; but at least some adult females are often fairly long, exceeding 2 mm. Turbellarians are orange, white or transparent, often laterally expanded at mid-body, generally flattened, temporarily adhere to surfaces using a posterior adhesive gland and not ensheathed. Turbellarians are always small, less than 2 mm long. The eggs of these symbionts are also readily recognizable. Nemertean eggs are white and oviposited in clusters of dozens to hundreds contained within a sac. Turbellarian eggs are deposited singly on hard surfaces, often on crab eggs. In preserved samples the nemerteans retain their cylindrical shape. The turbellarians are usually expanded posteriorly and are more variable in shape than are the nemerteans. Brief transfer of preserved worms to glycerine permits confirmation of the identity of these two types of worms. The complete gut, proboscis and ladder-like arrangement of the gonads of

nemerteans contrast with the central pharynx and the laterally displaced vitellaria of the turbellarians. Further details are reported in Shields et al. (1989), Gibson et al. (1989), and Fleming and Burt (1978).

Mortality estimates based on samples obtained prior to hatching underestimate the ultimate impact of egg predation and other time-dependent mortality factors. Shields and Kuris (1988a) provide a method for calculating total mortality based on the length of the remaining period of embryogenesis, worm intensity, and per capita feeding rates of the worms. The first two parameters are readily estimated from the suggested sampling procedure. Worm feeding rates have been calculated for a variety of symbiotic nemertean egg predators using both in vitro techniques and Ricker's (1975) method to separate concurrently operating mortality causes (Wickham 1979; Roe 1984; Okazaki, 1986; Kuris and Wickham 1987; Shields and Kuris 1988b). The estimates have all been similar: about one egg eaten per day for male worms and 1-3 eggs per day for female worms.

Management Implications

The additional sampling procedures described above, triggered by low values in the percent clutch statistic, could benefit the active management of red king crab stocks. Firstly, causes of egg mortality may be readily separated, and these causes may have different management implications. For instance, if breeding failure has occurred, restricted fishing would be needed to protect sufficient males and achieve a high proportion of mated females. If high intensities of nemertean infestations are the principal cause of egg loss, then the fishery may not be the direct source of the problem, and management implications are less certain, requiring further study. Secondly, high intensity nemertean infestations and resultant egg mortality are geographically localized. Certain localities are repeatedly impacted. Since the marked increase in intensity during the brooding period suggests that larval dispersal of *Carcinonemertes regicides* is brief, perhaps worm recruitment is generally restricted to confined bodies of water.

If worm recruitment is geographically restricted, then one possible management strategy might be to increase fishing pressure on these stocks by including ovigerous females in the catch. This might ultimately decrease worm abundance (Dobson and May 1987). However, if these stocks are identified as important contributors to larval recruitment of crabs over a broader geographic region, then increased protection of the brooding females in such stocks may be indicated. We have demonstrated (Kuris 1986; Kuris and Wickham unpublished observations) that nemerteans may be rapidly killed on living Dungeness crabs by a brief emersion of the infested host in fresh water or dilute solutions (0.5%) of formalin in sea water. Neither the crabs nor their embryos were harmed by this procedure. A stockwide manipulation to reduce the abundance of predatory nemerteans has never been attempted. But, it would seem feasible to dip or otherwise treat and release ovigerous females captured incidental to the fishery. The several bays around Kodiak Island and Cook Inlet, where nemertean infestations are intense, might be suitable for such an experiment.

Future Research

If mortality of red king crab embryos continues to be substantial coordinated studies of reproductive output and brood mortality with studies of larval dispersal and recruitment may be useful. Larval dispersal clearly depends on oceanographic conditions and larval crab behavior (Incze et al. 1986; Shanks 1983; 1986; 1988; McConaugha 1988; Clancy and Epifanio 1989). Some adult populations may contribute disproportionately to the successful recruitment of juvenile crabs, while other adult populations are effectively expatriate, being dependent upon larvae produced elsewhere for population persistence (O'Day & Nafpaktitis, 1967). Thus, it would be of interest to assess the reproductive output of the exporting populations and examine whether this productivity predicts subsequent larval, and ultimately juvenile, abundance in specific geographic locations. The Kodiak Management Area includes numerous geographically distinct bodies of water for which catch statistics are separately gathered (e.g., Blau, 1983). These districts and "crab schools" may provide a data base to search for patterns of nemertean abundance, egg mortality, larval abundance and juvenile recruitment.

Studies of nemertean infestations, of the recently recognized bitter crab disease of *Chionoecetes* spp. caused by a parasitic dinoflagellate (Meyers, et al., this volume; Eaton et al., this volume) and of the rhizocephalan parasite, *Briarosaccus callosus* of king crabs (Sloan 1984; Meyers and Short, this volume) all indicate that infectious diseases may be very important, geographically localized, mortality causes. We suggest that the geographical mosaic of such infestations provides an opportunity to conduct some innovative experiments to try and reduce or eliminate these mortality causes.

The predatory nemerteans are an appropriate first target as their pattern of infestation has been most extensively studied and their impact on egg mortality has been most thoroughly quantified. As external symbionts, they are also accessible to removal by appropriate helminthicides. Field manipulations of the red king crab fishery in locations such as Kachemak Bay or the Uganik-Viekoda-Terror bays system might include an experimental fishery on female crabs or an attempted reduction of nemertean abundance on ovigerous female crabs caught and released incidental to the fishery on male crabs. The latter experiment would require further work on methods to kill nemertean worms without harming female crabs or their embryos. Additional study is needed to develop the most suitable helminthicide. Possibilities include fresh water, dilute formalin, malechite green and praziquantal, a drug now in widespread use against trematode and cestode parasites of humans. Methods of application to be explored include dips, sprays, and slow release pellets that adhere to ovigerous crabs. Rapid shipboard handling procedures need to be developed.

CONCLUSION

Brood mortality of red king crabs has been nearly complete in some areas and years (e.g., Uganik and Kachemak Bays in the 1983/84 brood season) (Kuris et al. 1990). No other life history stage of the red king crab has been shown to suffer such high mortality even when the impact of commercial fishing is included. Although the symbiotic nemertean egg predators that caused this egg mortality have

doubtlessly coexisted with red king crabs for a very long time, their presence and impact has escaped detection until recently (Wickham et al. 1985). It is likely that some past episodes of poor clutch conditions (e.g., Powell and Lebida 1968) have been caused by these symbionts. Crab surveys by ADF&G and NMFS have generally been conducted prior to the increase in symbiont intensity and resultant egg mortality in the autumn. Novel approaches, including experimental manipulation of certain local fisheries now merit careful consideration. It may be possible to substantially reduce the abundance of these mortality agents and perhaps increase the abundance of some red king crab stocks.

Figure Legend

Figure 1. The relationship between the percent clutch statistic and the percentage of eggs killed by predatory symbiotic nemerteans in clutches of the red king crab in Alaska during the 1983/84 brooding season. Egg masses collected early in the brood season, May to September, (summer) are distinguished from those collected later in the brood season, October to March, (winter). The depicted regression equation is percentage of egg mortality = 68.6 - 0.752 (percent clutch); N = 418 crabs.

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Brood Mortality Estimation and Role of Symbionts in Egg Mortality of the Tanner Crab *Chionoecetes bairdi* in Alaskan Waters

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ABSTRACT

Samples from egg clutches of the tanner crab, Chionoecetes bairdi, were obtained from waters in the Gulf of Alaska and Bering Sea and analyzed for density of nemertean and turbellarian symbionts and for mortality of host eggs. Infestations by nemerteans of the genus Carcinonemertes ranged from high levels in certain Cook Inlet and Kodiak Island populations to a virtual absence in the Bering Sea. No nemerteans were recovered from C. opilio. Turbellarians were most abundant in southeastern Alaska and Cook Inlet. They were also present along the Alaska Peninsula, in Bristol Bay and the Bering Sea. In general the geographic pattern of abundance of nemerteans on C. bairdi paralleled the geographic distribution of these worms on the red king crab, Paralithodes camtschatica. Percent clutch, the visual estimate of clutch size recorded by shipboard fisheries biologists, was not correlated with direct laboratory counts of egg mortality caused by nemertean worms because nearly all samples were collected too early in the brooding period for substantial egg mortality to accrue.

INTRODUCTION

Infestations of decapod crustaceans by symbiotic nemertean egg predators are now known to be common (Wickham and Kuris, 1985). For some host species nemertean intensities can be high enough to cause a substantial reduction in the survival of the eggs (Wickham, 1986). Dramatic instances of such mortality occur in populations of the Alaskan red king crab, Paralithodes camtschatica, which are infested by several species of nemertean symbionts (Wickham, et al., 1985; Shields et al., 1989, this volume; Gibson et al., 1990; Kuris et al.,

1990). During the course of red king crab studies in Alaskan waters it was noted that some populations of the tanner crab, Chionoecetes bairdi, also harbored dense infestations of symbiotic nemerteans.

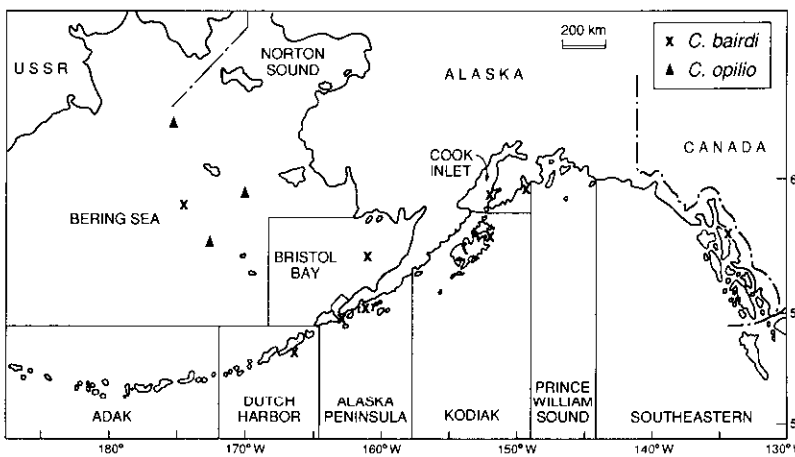
We report here on sampling that has been conducted from a range of tanner crab populations in the Gulf of Alaska and the Bering Sea to determine the extent of infestation by nemerteans.

MATERIALS AND METHODS

Egg bearing female Chionoecetes bairdi and C. opilio were captured by trap during operations by the Alaska Department of Fish and Game and the National Marine Fisheries Service. Field agents removed the third egg bearing pleopod from the left side of captured crabs and preserved them in a 5% solution of formalin and seawater. These were forwarded to us for laboratory analysis. Symbiotic organisms were removed from the sample, enumerated and identified where possible. A subsample of from 500-1,000 eggs was counted for live and dead eggs. Dead eggs were recognized by empty membranes still attached to the pleopod setae. The subsample was dried and weighed. The rest of the sample was dried and weighed and the total number of eggs in the sample was calculated from the weight per egg and total sample weight. Worm density was expressed as the number of worms per 1,000 crab eggs. Prevalence and intensity are defined as in Margolis et al. (1982). Egg mortality was expressed as percent dead eggs in the sample.

Areas sampled included Kodiak Island, along the Alaska Peninsula and near Dutch Harbor in the Gulf of Alaska, Kachemak Bay in Cook Inlet and several locations in the Bering Sea including Bristol Bay and areas near the Pribilof Islands. Additional observations on living worms were made on crabs collected from Resurrection Bay (Cook Inlet Management Area) and Auke Bay (Southeastern Alaska Management Area). At Kodiak, Alaska Peninsula and Dutch Harbor small samples of crabs were obtained from several localities. These small samples were combined by month of collection for statistical analysis. (Figure 1).

SAMPLE LOCATIONS OF TANNER CRABS FOR NEMERTEANS



RESULTS AND DISCUSSION

Samples of Chionoecetes bairdi in 1984 and 1985 from Kachemak Bay, Kodiak Is., Resurrection Bay and Auke Bay demonstrated the presence of nemertean worms. Egg mortality attributed to these predators was also recorded (Table 1). Carcinonemertes regicides was the most abundant symbiotic nemertean but the small, eyeless, undescribed species, form #4 of Wickham & Kuris (1988), was also recovered. Turbellarians were observed at Kodiak Is. and Auke Bay but not at Kachemak Bay.

Table 1. Egg mortality and abundance of symbionts in the egg masses of tanner crabs, Chionoecetes bairdi (B) and C. opilio (C) in Alaskan waters. N is sample size; P, prevalence; I, intensity (± standard deviation); +, present, not quantified; *, data missing.

Location	Date	Crab Species	N	Nemerteans P	Nemerteans I	Turbellarians P	Turbellarians I	Percentage Egg Mortality (%)
Resurrection Bay	8/82	B	5	100	+	100	+	+
	8/85	B	16	100	+	100	+	+
Auke Bay	8/82	B	4	100	+	100	+	+
	12/89	B	6	100	+	100	+	+
Kachemak Bay	11/84	B	10	100	40±48	-*	-	49.2
	6/85	B	11	100	+	0	-	+
Kameshak Bay	6/85	B	4	100	+	100	+	+
Kodiak I.	7/84	B	9	89	100±205	0	-	2.0
	8/84	B	8	100	407±69	0	-	16.2
	7/85	B	8	100	40±61	0	-	3.82
	8/85	B	9	78	18±20	11	41	1.14
Bristol Bay	7/87	B	29	0	-	14	11±16	0.0
Dutch Harbor	8/85	B	11	0	-	-*	-	0.0
Alaska Peninsula	7/85	B	20	0		90	18±28	0.4
Bering Sea	7/87	B	20	0	-	16	10±21	0.2
	7/87	O	24	0	-	8	6	0.0
	7/87	O	25	0	-	4	9	0.0
	7/87	O	12	0	-	0	-	0.0
			241					

In the Bering Sea no nemerteans were recovered. Mortality of tanner crab eggs was likewise absent. This supports our earlier findings that nemertean predation was generally the predominant source of mortality to crab eggs (Wickham, 1979; Shields & Kuris, 1988b; Kuris et al., 1990). Unidentified turbellarians, similar to those found on other crab hosts, were present on Bering Sea tanner crabs but did not contribute to egg mortality.

The geographic pattern of infestation of C. bairdi by nemerteans is similar to the geographic distribution of these worms on the red king crab, Paralithodes camtschatica (Kuris et al., 1990). The most common worm on both species appears to be Carcinonemertes regicides (Shields et al., 1989). Form #4 has been found on both crabs from the Kodiak Is., Resurrection Bay and Auke Bay. For both host species, nemerteans are rare or absent in Bristol Bay, the Bering Sea and along the Alaska Peninsula. They are abundant in the Kodiak Archipelago, and Kachemak Bay (Cook Inlet Management Area). An interesting exception to this consistent pattern of co-occurrence is the presence of nemertean worms on tanner crab but not red king crab from Kamishak Bay in the Cook

Inlet Management Area. Nemerteans have not been recorded from Chionoecetes opilio. This is probably due more to geography than host specificity as all C. opilio collections are from the Bering Sea where nemerteans are also absent from red king crabs and C. bairdi. Recently, one of us (AMK) has collected an additional undescribed species of nemertean on C. bairdi from Auke Bay. These worms were large and adult males lacked eyes.

The correlation between nemertean density and crab egg mortality ranged from r=.11 (n.s.) in Kachemak Bay samples to r=.24 (n.s.) in Kodiak 1985 and r=.90 (P<.001) in Kodiak 1984. This was also similar to the correlations between nemertean abundance and egg mortality of king crabs in these waters (Kuris et al., 1990). The postulated annual cycle of infestation by C. regicides on king crabs begins with the arrival of worms in crab egg clutches in June to July. But these worms do not begin to substantially impact egg survival until they have infested the eggs for a month or two. Hence, high correlations between nemertean density and egg mortality only occur late in the brooding season.

Comparing the July sample with the later August 1984 Kodiak sample showed an increase in nemertean density from 1.94 to 16.25. Mortality likewise increased from an average of 2% to 16.0% during that period. We suggest that mortality would eventually reach much higher levels. Our observations on other nemertean-host systems (Wickham 1979, 1986; Kuris and Wickham, 1986; Kuris et al., 1990) project a density of 16.5 worms/1000 crab eggs prior to hatching of C. bairdi eggs in April/May (Hilsinger, 1976). Using the method of Shields & Kuris (1988a) we project total mortality by the end of the brood period to be about 35%.

The samples obtained in Kachemak Bay in November are consistent with observations on king crabs; indicating that nemerteans begin to disappear from host egg clutches late in the fall. Egg mortality was relatively high (49.2%), even though worm density was only 3.26 worms/1000 crab eggs. The correlation between worm density and egg mortality was not significant (r=.11). As with C. regicides on king crabs, worms on tanner crabs appeared to leave the egg mass (or die) after causing extensive mortality to the eggs.

Correlations between the shipboard visual estimate of percent clutch and laboratory counts of the percentage of egg mortality were not significantly correlated. This was not unexpected as most of the samples were taken too early in the brooding season for nemertean egg predation to have impacted egg survivorship. Also, in most samples, nemertean intensity was too low to significantly impact egg mortality. Thus, as with evaluation of the percent clutch statistic for red king crabs (Shields et al., this volume), we note that the impact of egg loss caused by predatory nemertean symbionts will be not detected, or be significantly underestimated, unless percent clutch observations are available from late in the brooding season.

Nemertean infestations of tanner crabs in the Gulf of Alaska are similar to those found on red king crabs in terms of presence of nemertean egg predators, their species composition and the relative intensity of the infestations. We suggest that where both host species are present they may serve as alternative hosts for the population of predatory symbionts. High levels of egg mortality can

be attributed to symbiotic nemerteans in these populations and it may be high enough to make this a major source of mortality in C. bairdi. This information warrants greater attention to the contribution of egg mortality to population dynamics of tanner crabs.

The epidemiological importance of two host species, C. bairdi and P. camtschatica, for these predatory symbionts is presently unclear. One possible factor is suggested by the inferred short larval period of Carcinonemertes regicides and the possible accumulation of worms on individual crab hosts via autoinfection (Kuris et al., 1990). If this life history pattern is confirmed, then the presence of ovigerous crabs of either species throughout the year ensures a source of ovigerous hosts for transmission. Both crab species have very long reproductive periods (Powell & Nickerson, 1967; Hilsinger, 1976) and the period between eclosion and oviposition of the next brood is brief (about one month). However, the timing of this period without eggs is not synchronous. In the red king crab it usually occurs in February or March while in C. bairdi it is in April or May. Usage of two host species may diminish the scarcity of hosts for these worms in the late winter and early spring.

We also note that this system provides an example of low host specificity for two symbiotic nemertean egg predators (C. regicides and form #4). We have shown (Wickham & Kuris, 1985) that most symbiotic nemertean egg predators of crustacean hosts appear to be restricted to a single host or a few closely related species. In the present circumstance two very unrelated hosts, one an anomuran and the other a brachyuran, appear to be suitable.

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FIGURES

Figure 1. Locations for collections of tanner crabs, Chionoecetes bairdi and C. opilio, where pleopod egg samples were examined for symbiotic nemerteans and turbellarians. In the Kodiak Archipelago, at Dutch Harbor and Sand Point a single symbol represents several small collections of C. bairdi from the general area.

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Diseases of King Crab Species in Southeast Alaska

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The commercial king crab industry in southeast Alaska has been supported primarily by three king crab species. Surveys of these feral crab species by the F.R.E.D. and Commercial Fisheries Divisions of the Alaska Department of Fish and Game (ADF&G) and the University of Alaska-Southeast have identified four diseases, two of which are caused by potentially significant pathogenic organisms (Meyers et al., in press). Crabs were collected by commercial crab pots and maintained in flowing seawater tanks until necropsies could be performed. Briarosaccus callosus, a parasitic barnacle, infects male and female red (Paralithodes camtschatica), blue (P. platypus) and golden (Lithodes aequispina) king crabs causing gonadal sterilization with reduced growth in male blue and golden king crab hosts (Hawkes et al., 1986a, 1987). The prevalence of this parasite varies with host species and geographic area, the highest level (76%) occurring in blue king crabs (Hawkes et al., 1986b) from Glacier Bay. The fecundity of king crab populations having such high prevalences of B. callosus is undoubtedly reduced. A second disease agent associated with holding mortality in two king crab species (blue and golden) is an intracellular Gram negative prokaryotic rod-shaped organism infecting the hepatopancreas and anternnal glands. Infected tissues are indurated and friable with granulomatous foci and caseous necrosis. The prevalence of this disease within king crab populations is still under investigation. The ciliate, Paranophrys sp. can also produce systemic infection and mortality in king crabs (blue and golden). Grossly visible gelatinous nodules and diffusely scattered white foci comprised of the organism are presenting signs within the visceral mass of infected crabs. Generalized tissue necrosis and displacement by the protozoan are microscopic features. This disease may result from injury and secondary invasion while in captivity as often occurs in captive Dungeness crabs (Armstrong et al., 1981). Ultrastructural examination of antennal glands from one blue king crab having two nodular neoplastic-like foci within the right organ showed virus-like particles of the size and morphology of birnaviruses. Whether the virus was incidental or associated with the tumor is being investigated. The significance of the virus or the putative neoplasm regarding effects on the host are not known.

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Bitter Crab Dinoflagellate Disease: Overview of the Causative Agent and Its Importance and Distribution in the Alaskan Tanner Crab (*Chionoecetes bairdi, C. opilio*) Fisheries

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Bitter crab disease was first discovered in one-third of the major commercially exploited southeast Alaskan Tanner crab (Chionoecetes bairdi) populations in 1985. The causative agent is a dinoflagellate hemolymph parasite that produces a chronic wasting disease resulting in poor meat quality and 100% mortality of infected crabs. Field and laboratory data suggest that the disease is cyclical with vegetative stages of the parasite occurring from October through July followed by sporulation and reinfection of new crab hosts putatively by one or both of two types of bimotile dinospores. Most crabs die during the vegetative phase of the disease but those surviving die soon after sporulation of the parasite. Metabolites filling large vacuoles within the vegetative parasite are most likely responsible for the breakdown of meat texture and the bitter flavor imparted to cooked meats. In the summer of 1988, samples of deadloss crabs from the Bering Sea C. opilio fishery showed hemolymph smears with an identical appearing dinoflagellate parasite (Meyers, in press). The current distribution of this parasite in the southeast Alaska bairdi fishery in 1989 again encompassed 1/3 of the total subdistricts commercially fished with areas in upper Lynn Canal having disease prevalence of 80-90%. The distribution of the agent in the Bering Sea opilio crab fisheries during 1988 ranged from 0 to 14% with increasing prevalence northward. Successful management of this disease, when considering the apparent cyclical nature of this parasite's life cycle, may be possible by setting earlier harvest dates to allow crabs to be taken earlier in the infection cycle when meat quality would be more marketable. This may eliminate the necessity of widespread sorting of infected crabs, thus increasing the marketable pounds of meat and decreasing the numbers of crabs to be disposed of. Further control of the transmission of the disease needs to be exercised by increasing the awareness of fishermen regarding recognition of the problem and by proper disposal of parasitized crabs and meats through burial or incineration. Cooking of infected meats would be an alternative method if seawater discharge of wastes is necessary.

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Preliminary Results on the Seasonality and Life Cycle of the Parasitic Dinoflagellate Causing Bitter Crab Disease in Tanner Crabs

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ABSTRACT

Since 1985 a disease syndrome known as bitter crab disease has been occurring in increasing numbers of tanner crabs from southeast Alaska. The disease is caused by a parasitic dinoflagellate, possibly of the genus *Hematodinium*. Crabs affected with this syndrome have a pink carapace and milky hemolymph while the meat has a chalky texture and a bitter aspirin-like flavor. The bitter flavor appears to result from the release of extensive amounts of an unknown extracellular compound found in the cytoplasm of the parasite. The parasite has been found in three forms; a non-motile vegetative stage (containing excessive amounts of foamy cytoplasm presumed to be composed of the unknown compound causing the bitter flavor), and two different types of motile dinospores, a large, slow-moving one and a smaller, faster-moving one.

For the last year, research has been conducted at the Juneau Center for Fisheries and Ocean Sciences, with the assistance of the Alaska Department of Fish and Game, to elucidate the life cycle of the parasite and to determine whether there is a seasonal increase in the incidence and intensity of the parasite in tanner crabs from the Sullivan Island area in upper Lynn Canal, approximately 50 miles north of Juneau.

The results from the Sullivan Island samples suggest there is a definite seasonality associated with the parasite. Infection levels in crabs sampled from Sullivan Island were clearly highest in the summer months from June through August, 1988, as 84-99% of the crabs sampled were infected with the parasite at an infection level of 2.8-3.0+. Both the incidence and intensity of infection decreased from October 1988, (55%, 2.2+) through February 1989, (46%, 2.0+) then again increased in March (53%, 2.2+) and May 1989 (60%, 2.4+).

The year-long in vivo laboratory experiments have identified possibly six different stages of the parasite based on size, nucleus to cytoplasm ratio, nuclear density, tendency of the cells to form plasmodia, and staining properties. The results from this work also suggest that although either of the two spore types can be infectious, crabs injected with both spore types developed two different stages of the parasite not seen in crabs injected with either the large or the small spore type. In addition, crabs injected with both spore types developed a visible infection over 100 days before any infection was evident in crabs injected with either spore type.

Much more work is needed to determine where in the life cycle of the parasite these different stages occur and to verify the seasonality of the infection in wild crabs. When this can be accomplished, management steps can be taken to attempt to reduce the prevalence and the spread of this industry-threatening disease.

Population Structure and Dynamics

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Population Structural Variation of the Southern King Crab, *Lithodes santolla*, of the Beagle Channel, Argentina, from 1975 to 1989

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ABSTRACT

The structural variation of the fraction of the southern king crab **Lithodes santolla** biomass vulnerable to the fishing gear, in the Argentine zone of Beagle Channel through period 1975-1989, is described. Collection of data was discrete in the mentioned period owing to economic constraints. Analyses of available information allows to conclude upon a decrease in abundance of the king crab biomass recruited to the gear, particularly affecting bigger size classes of both sexes. A concordant decrease in the total number of sexually mature king crab together with a decrease in recruitment level is also noticeable. Non-observance of legislation in force with landing of illegal specimens could be a determinant of this situation. A commission integrated by fishing companies managers, scientists and state managerial authorities is suggested to be urgently convoked in order to define a proposal of solution to present resource state. A binational strategy with Chile ought to be elaborated owing to species distribution in both jurisdictions. Strong restriction to fishing effort is suggested in western side of the Argentine zone of Beagle Channel jointly with promotion and expansion of fishing in the eastern side of Beagle Channel and Atlantic coast where unexploited fishing grounds are still to be found. The need to start research on pre-recruits as well as diseases and parasites as causes of probable mortality in any ontogenic stage, and environmental and pollution effects on fishery, is emphasized.

INTRODUCTION

The fishery of the southern king crab **Lithodes santolla** of Beagle Channel (Argentina) is a typical semi-artisanal fishery, dating from about 60 years ago. This resource supports fishing industry in Tierra del Fuego Territory (Figure 1).

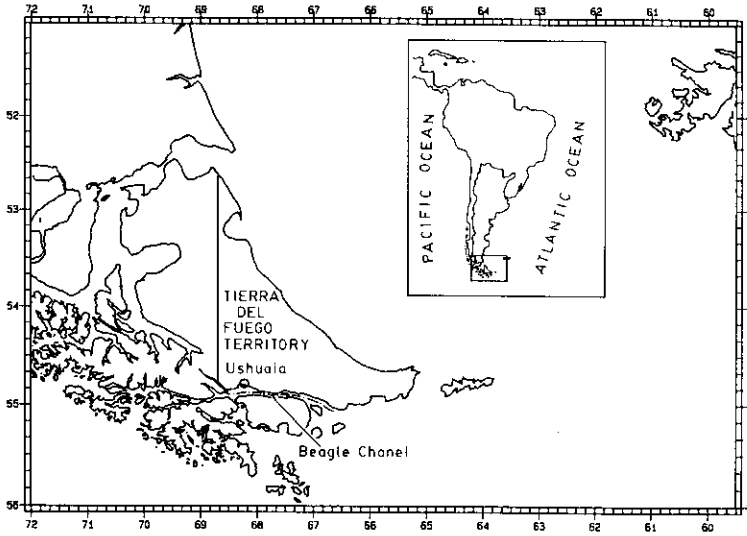

Figure 1: Southern extreme of Argentina. Tierra del Fuego Territory and Beagle Channel.

Low yields in commercial catches (Table 1) provoked certain alarm in fishing community in the last years.

Table 1: Declared landings of southern king crab **Lithodes santolla** (a) and softshell red crab **Paralomis granulosa** (b), in metric tons. Argentine jurisdiction.

	1978	79	80	81	82	83	84	85	86	87	88	89
a	370	62*	77*	194	203	179	201	188	175	153	120	74#
b	0	0	0	8	52	74	94	159	168	153	161	98#

* Extraordinary restrictions to fishing existed in the area
\# Up to month of August.

This decrease cannot be easily ascribed to over-harvesting owing to an increase in fishing effort applied, since this remained constant or even decreased. Furthermore, fishing time dedicated to softshell red crab (or false king crab) **Paralomis granulosa** has increased from 1981 up to present time. Instead, the non-observance of legislation in force preventing landing of all females and males with carapace length smaller than 110 mm, is suspected to be the cause of decrease in landings. In the last years, and due to polytic and/or economic reasons, extraordinary exceptions to the closed fishing season were authorized. A closure to fishing of king crab rules annually from October through December, critical period of hatching, females molting and mating. The landing of illegal size king crab males has also been mentioned for the Chilean fishery (Hernandez et al., 1986; Diaz, 1987) as a negative element in reproductive potential.

Ushuaia city (Argentina) has grown spectacularly in the last years as a consequence of a special promotion regime for industrial settling. This urban and industrial expansion has increased pollution in adjacent waters. At present there exists no research program to assess consequences of pollution for fishing resources in the area, but a correlation between contamination and low yields of king crab is yet not to be discarded.

Fishing industries in surveyed area are not important in macro-economic terms, but they do have a great regional incidence. Recently, strategy of fishing companies settled in Ushuaia has been the search of joint ventures with foreign companies, in order to meet a significant expansion jointly with diversifying of production. In the particular case of southern king crab, fishing is trying to be expanded towards new fishing grounds in the eastern side of the Beagle and Moat Channels, and eastern coast of Tierra del Fuego Territory. In the Southwest Atlantic area, South of 50 latitude, the commercial fishing vessel Hoshin Maru N 2 of Hoko Fishing Co. carried out exploratory fishing in the search of profitable king crab fishing grounds during 1986, with no encouraging results. It seems possible however, that grounds with interesting yields of king crab and softshell red crab exist in the coastal area between San Jorge Gulf and Mitre Peninsula (Province of Santa Cruz, Argentina) for small vessels to operate.

A brief review of the fishery and all biological information of **Lithodes santolla** available, can be searched for in Boschi et al., 1975; Boschi et al., 1984; Bertuche et al., 1985; Vinuesa, 1982,1984, 1985; Vinuesa et al., 1982; Vinuesa et al., 1989.

The INIDEP (National Institute of Fisheries Research and Development) is the only scientific institution adviser of National Government with respect to management of fishing resources of the Argentine Sea. The generalized alarm in the fishing community of Tierra del Fuego Territory owing to Beagle Channel southern king crab fishery state made necessary to analyze existent information in order to

implement a new and perhaps a moreeffective management proposal.

The fishery biology research on this crustacean, as well as scientific research in general, presents strong constraints to its normal development owing to poor financial support, mainly due to economic situation in Argentina. With regard to southern king crab fishery, the most important consequence of this circumstance is the lack of continuity in sampling surveys in the area. However, during some periods collection of basic information was reasonable, allowing to obtain results supporting legislation in force in the Argentine Zone of the Beagle and Moat Channels (Boschi et al., 1984). In order to obtain evidence of probable causes of decrease in commercial yields of southern king crab in the Argentine zone of Beagle Channel, an analyses of the structural variation of recruited fraction of the biomass through the last 15 years (1975-1989), is attempted in this paper.

Periods during which processed data were collected were: 1975-1976, 1978-1982 and 1987-1989, owing to different cooperation agreements between INIDEP (formerly Marine Biology Institute), Government of Tierra del Fuego Territory, FAO and local fishing companies. Of these periods, years with more complete and/or reliable data chosen for analyses were: 1975, 1981, 1988 and 1989. The Argentine zone of Beagle Channel between the Chilean boundary and Gable Island, has been defined in 1984 as the Fishery Conservation Zone (FCZ), subdivided for managerial purposes into subareas I to V, (Bertuche et al.,1985).

MATERIAL AND METHODS

From annual information obtained during years taken into account, only data from three-months period June-July-August were considered. These months do not include any critical period in the post-recruitment phase of the southern king crab life cycle such as periods of maximum probability of molting of males (March-April) or hatching, molting of mature females and mating (September through December), in which distortions in estimates of parameters refering to population structure, could be introduced (Boschi et al.,1984; Bertuche et al.,1985). Consequences of recruitment produced in this temporal lapse were not taken into account.

Methodology used to compare means of different variables among years was the following: raw or transformed data were tested for homoscedasticity and comparisons of means wer made through single classification ANOVA or approximate test of equality of means when variances were heterogeneous (Sokal & Rohlf, 1969,1981). Unplanned comparisons among pairs of means using the Student-Newman-Keuls test or the Games and Howell method were applied to data when ANOVA or approximate test indicated significant differences (Sokal & Rohlf, op.cit.; Tamhane, 1969).

Abundance Estimates

Information was collected aboard of commercial fishing vessels operating at random in a previously defined area. Fishing gear was always the same (Boschi et al., 1984; Bertuche et al., 1985). Only information from areas II and III, adequately representing the whole Fishery Conservation Zone, could be analyzed.

Abundance instantaneous estimates in number of male and female king crab were calculated from samples collected at random. Methodology applied assumed a patchy distribution of king crab in a previously defined area S. Assuming n fishing operations distributed at random in area S could be carried out in the least time possible, then n results, in number of crabs per potline would be obtained. The probability function of results can be associated to a negative binomial distribution (Fisher, 1941; Haldane, 1941; Bliss, 1953; Scheaffer, 1976). Parameters of this distribution were estimated by the maximum likelihood method (Fisher, 1953) and their confidence intervals taking into account Anscombes transformation (Anscombe, 1949; Taft, 1960). The area of action of a potline (a) and the coefficient of catchability (q) were determined through experiences with tagged specimens and autonomous diving (Boschi et al., 1984; Bertuche et al., 1985). Then, solving: $\Sigma t.p_t .q^{-1}.s.a^{-1}$, an instantaneous estimate of the number of king crab composing the fraction recruited to the gear in area S, is obtained, with p_t being the probability of each result t.

In order to compare estimates among different years, raw data were transformed according to model $y = k.\sinh^{-1}(\sqrt{x}.k^{-1})$ (Bartlett, 1947), with k as the coefficient of contagion, and grouped according to sex and area.

Structure of The Recruited Fraction of Southern King Crab Biomass

A structural comparison was also attempted analyzing mean carapace length (CL) of male and female southern king crab catches, percentage of males from total catch, percentage of legal size males from total male catch (LSM), and percentage of ovigerous females from total female catch (OF), through different years analyzed. Size data were normally distributed. Mean CL of male and female king crab of areas II and III from different years were compared through methodology described. As for percentages (males, LSM and OF), consonance intervals were constructed for each one of the observed frequencies (Easterling, 1976), in order to check for an overlapping between them so as to withdraw statistically valid conclusions.

Catch per Unit Effort

Independently of abundance estimates, CPUE of the same three-months period of years 1975, 1981, and 1989 were compared. The catch per unit effort is defined as number of king crab caught per pot 48 hours fishing and standardly

baited (Boschi et al., 1984; Bertuche et al., 1985). In this case, only cruises operating with main objective being maximizing economic returns, were considered. Data with no records of sex or size structure, from areas II, III and IV were available. CPUE data from three-months period were pooled and assumed to have a normal distribution. Means of untransformed data of different years were compared through methodology previously described.

RESULTS

Abundance Estimate Variations

Table 2: Abundance instantaneous estimates of southern king crab males (m) and females (f) of areas II and III, in number of crab *E+04.

		AREA II		AREA III	
		estimate	CI limits	estimate	CI limits
1975	(m)			83.7	69.9/112.4
	(f)			102.2	81.7/139.7
1981	(m)	20.2	16.2/27.4	68.8	59.5/86.1
	(f)	24.6	19.8/34.0	90.1	78.0/110.8
1988	(m)	14.2	12.1/17.9	60.5	53.6/73.9
	(f)	15.7	13.4/19.7	82.4	71.1/99.7
1989	(m)	12.3	10.7/15.2	65.0	57.2/78.2
	(f)	14.5	12.4/18.2	71.6	64.4/83.0

Table 2 shows abundance estimates of different years (three-months period June-July-August). Previously published abundance estimates were not taken into account owing to bias in data collection. Transformed data were grouped according to sex and area (Group 1: male king crab, area II; Group 2: female king crab, area II; Group 3: male king crab, area III and Group 4: female king crab, area III). For area II, available information was from years 1981, 1988 and 1989. For area III, there were also data from year 1975. ANOVA or approximate test of equality of means results were the following: Group 1: $F = 17.07$, df= 2; 897; Group 2: $F = 20.44$, df= 2; 519; Group 3: $F = 23.33$, df= 3; 865 nd Group 4: $F = 16.66$, df= 3; 865. Unplanned comparisons among pairs of means showed following results: for Group 1, no significant differences could only be found among means of years 1988 and 1989 ($P>0.05$). Highly

significant differences among pairs of means of 1981-1988 and 1981-1989 were found, ($P<0.01$). Group 2 presented similar results. In area III, Group 3 showed no significant differences among means of years 1988-1989 but highly significant differences among other pairs of means. Group 4 showed no significant differences among pair of means 1981-1988 and significant differences among means of 1988-1989, ($0.01<P<0.05$). Highly significant differences were found among other pairs of means.

CPUE Variations

Table 3: CPUE of areas II, III and IV. n: number of cruises considered.

Areas	II			III			IV		
	$\bar{\bar{x}}$	s	n	$\bar{\bar{x}}$	s	n	$\bar{\bar{x}}$	s	n
1975	11.13	5.48	9	11.98	5.74	7			
1981	8.93	4.02	27	9.57	3.89	29	11.54	5.21	10
1989	5.48	2.89	23	4.88	2.93	20	7.28	3.80	12

Means, s.d. and sample sizes of CPUE data, in number of king crab per pot are shown in Table 3. Results of ANOVA showed highly significant differences among means of different years ($P<0.01$) for areas II ($F = 8.53$, df= 2; 56) and III ($F = 12.66$, df= 2; 53) and significant differences among means for area IV ($F = 4.91$, df= 1; 20), ($0.01<P<0.05$). Results of unplanned comparisons among pairs of means were similar for areas II and III: no significant differences could be found among means of years 1975 and 1981, but highly significant differences were found among pairs of means of 1975-1989 and 1981-1989.

Structural Variations of the Recruited Fraction

Size data of male and female king crab, as well as structural data (percentages of males, LSM and OF) of different years taken into account, are summarized in Table 4. In the size structure variation analysis, data were grouped as for abundance estimates comparisons. ANOVA results showed in all cases highly significant differences among mean CL, (Group 1: $F = 367.69$, df= 2; 6,086; Group 2: $f = 304.65$, df= 2; 6,574; Group 3: $f = 245.83$, df= 3; 7,711 and Group 4: $F = 385.96$, df= 3; 8,953),($P<0.01$). Unplanned comparisons among pairs of means showed in all cases no significant differences ($P>0.05$) among means of years 1988-1989, but highly significant differences among other pairs of means, ($P<0.01$).

Temporal variation in size frequency distributions of male and female king crab of the recruited fraction in area III

is plotted in Figures 2 and 3.

Table 4: Mean CL (mm) and structure of recruited fraction of southern king crab biomass of areas II and III. M: percentage of males from total catch, LSM: percentage of legal size males from total male catch, and OF: percentage of ovigerous females from total female catch. Range of sample sizes: 900-7500. (m):males, (f):females.

Areas	II					III				
	CL(m)	CL(f)	M	LSM	OF	CL(m)	CL(f)	M	LSM	OF
1975	-	-	-	-	-	108.2	93.5	45.0	46.6	-
1981	103.2	90.5	45.1	21.7	87.3	102.7	89.7	43.3	26.5	85.2
1988	93.4	84.4	47.5	12.4	75.1	96.3	83.5	42.3	14.5	77.9
1989	92.8	83.9	45.8	11.9	78.8	95.7	83.2	47.6	13.3	81.2

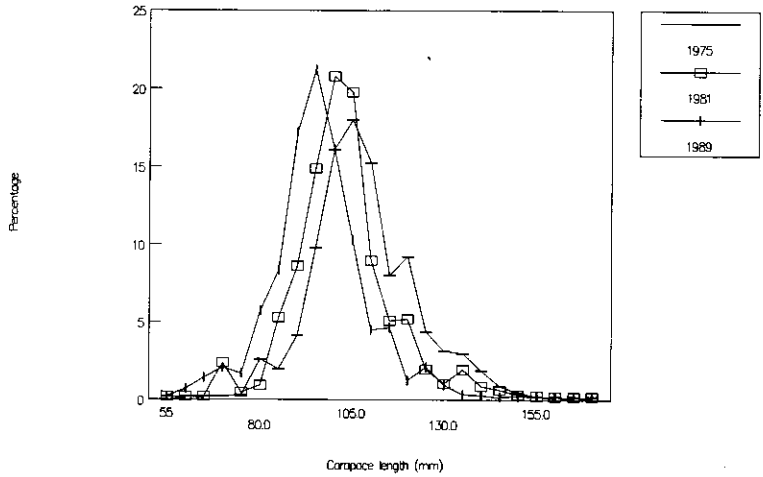

Figure 2: Temporal variation in size structure of male southern king crab. Area III.

As for percentages (males, LSM and OF), consonance intervals were constructed for each of the observed frequencies, (Easterling, 1976). No overlapping of intervals was found in any case. Large sample sizes

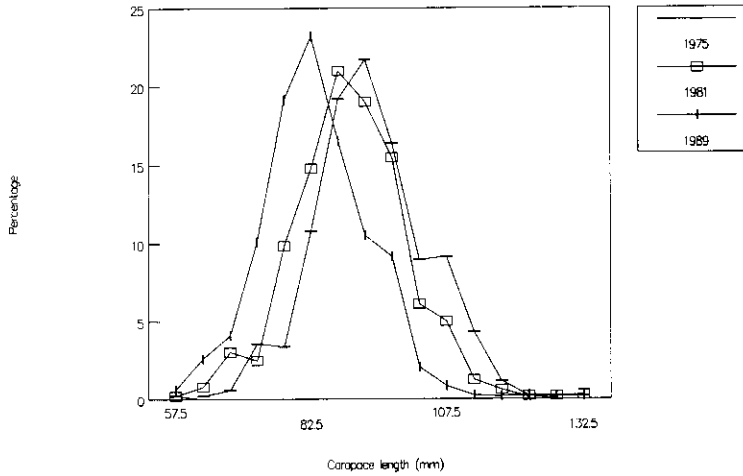

Figure 3: Temporal variation in size structure of female southern king crab. Area III.

allowed to conclude that even frequencies of years 1988 and 1989, were significantly different between each other.

DISCUSSION

The following can be asserted from these results. With respect to abundance estimates, comparisons among pairs of means allow to find a highly significant decrease from 1981 through 1989 for area II and from 1975 through 1989 for area III in male and female king crab abundance. No differences could be found between estimates of years 1988 and 1989, except for females of area III. This group showed no differences between mean abundance estimates of years 1981 and 1988. The situation described allows to conclude that there existed a statistically significant decrease in the abundance of the king crab biomass recruited to the gear in the Argentine zone of Beagle Channel, from 1975 through 1989, taking into account that areas II and III are representative of the whole FCZ.

Results of comparisons among pairs of mean CL, Table 4 and Figures 2 & 3 allow to make a simple qualitative analysis of the size structure of the recruited fraction in the mentioned areas. A highly significant decrease in mean CL of male and female king crab, can be observed from 1975 in area III and 1981 in area II through 1989, with no significant differences among means of years 1988 and 1989 in all cases (males and females, both areas). Temporal variation of size structure of the recruited fraction (Figures 2 & 3), shows an increase of small size class

frequencies with a concordant decrease of big size class frequencies, in male as well as female king crab, in the analyzed period. Although figures refer to area III, area II showed similar results in years analyzed. Those results, associated to a decrease in abundance estimates would indicate that decrease in abundance is mainly affecting big size classes of both sexes. If the cause of abundance decrease were fishing, then it seems evident that regulatory measures are not observed, and there is no sexual discrimination in harvests. At this point, it can be added the decrease observed in LSM from 46.56% in 1975 to 26.52% in 1981, 14.49% in 1988 and 13.26% in 1989, in area III and from 21.66% in 1981 to 12.37% in 1988 and 11.93% in 1989, in area II of the FCZ. Sex ratios seem not to have varied significantly according to calculated percentages of males from total catch (Table 4).

Size at maturity for male king crab in the surveyed area has been set between 91 amnd 99 mm of CL (Boschi et al., 1984). As for female king crab, published data are variable (Vinuesa, 1984; Vinuesa et al., 1989). Nevertheless, the decrease of bigger size class frequencies shown for males and females, concordant with a decrease in abundance estimates of the fraction of the king crab biomass vulnerable to the gear, allow to infer that there exists a decrease in total number of king crab sexually mature. The question to be answered is: how did the OF fraction vary during the period analyzed? Unfortunately, no reliable data of 1975 were available. Information which allowed for results presented was collected during 1981, 1988 and 1989. Figures 4 & 5 show variation in percentage of OF as a function of size class in years 1981 (Figure 4) and 1988/1989 (Figure 5).

Curves plotted in each figure correspond to percentage of OF per size class in different three-months periods of the same year: January-February-March (JFM) when maximum percentage of OF per size class is reached, and June-July-August (JJA). Decrease of OF percentage in smaller size class females in JJA is due to recruitment to the fishing gear and/or area of non-ovigerous females. Curve corresponding to JFM variations remains almost inaltered through different years. There are no reliable data for JFM of year 1989 but there is no reason to think that this curve will significantly vary from ones of the same temporal lapse of years 1981 and 1988. Curves resulting from OF percentage per size class of lapse JJA in years 1988 and 1989 are above the one representing JJA variations of 1981, indicating that relative recruitment in the same 6-months period has been lower, since OF percentages per size class have decreased less. Given that an abundance decrease cannot be rejected, if recruitment levels of non-ovigerous females had remained constant through period 1981-1988 in absolute terms, curves of OF percentage per size class corresponding to months period JJA of 1988/1989 would have been below the one of JJA of 1981. JJA curves of Figure 5 clearly show that recruitment has also significantly decreased in relative as well as in absolute terms. No evidence was found up to now of

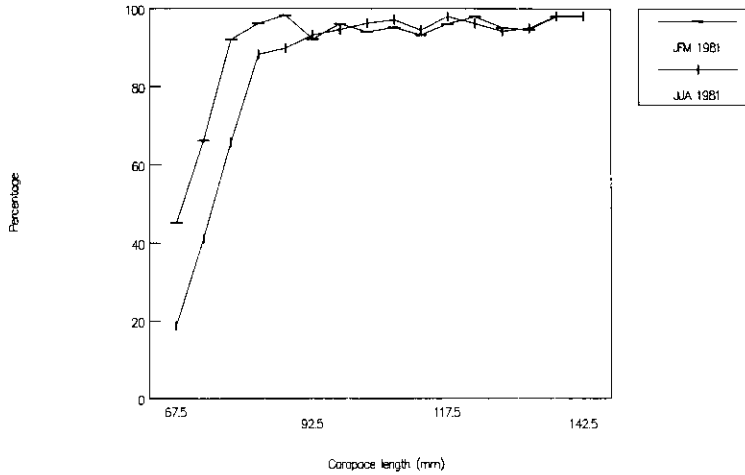

Figure 4: Percentage of ovigerous females from total female catch (OF) per size class. Three-months periods of JFM and JJA of 1981.

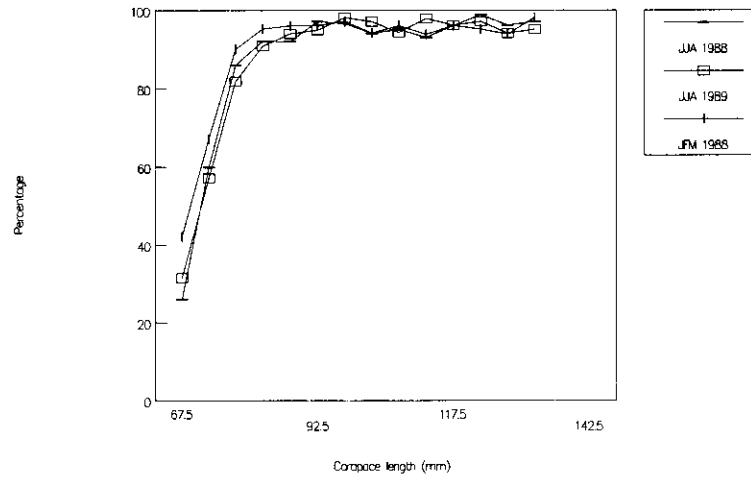

Figure 5: Percentage of ovigerous females from total female catch (OF) per size class. Three-months periods of JFM of 1988 and JJA of 1988/1989.

diseases or parasites affecting OF, and fishing mortality affects similarly OF and non-ovigerous females.

Since sex ratios have not varied significantly in the period analyzed (1975-1989), it is possible to assume that decrease in recruitment has also occured in male king crabs. If environmental factors were not affecting recruitment, which cannot be checked because of the lack of sufficient data, the decrease in abundance of sexually mature king crab would lead to an increase of the probability of lower recruitment, in relative or absolute terms.

As for CPUE, refering to the total king crab catch per pot, with no records of size or sex structure of the landed catch, results of unplanned comparisons showed no significant differences among CPUE means of 1975 and 1981 for areas II and III, but highly significant decreases from year 1981 through 1989. Hypothesis intending to explain this is that in 1981 harvest levels remained still relatively inaltered owing to new fishing grounds added to commercial harvesting, situation that could not be sustained through analyzed period, and in 1989 consequences of a decrease in abundance clearly appear with decrease in commercial yields.

CONCLUSIONS

Although analyses were tentatively carried out based on a discrete data base owing to the lack of continuity in sampling program due to poor financial support, the situation described leads to consider that the southern king crab resource state in the Argentine zone of Beagle Channel (specifically the FCZ) is at least complex and alarming. A general conclusion can be attempted: the resource presents evidence of decrease in abundance, being this effect particularly noticeable in bigger size classes of both sexes. Concordantly, the capability of generation of new recruits to the fishery seems to be seriously affected, situation becoming worse in the short term.

An important fact to be taken into account is the absence still of a fluent interchange of information by institutional ways with Chile, with respect to the southern king crab fishery in the Chilean zone of Beagle Channel, as well as in the area of Lennox, Picton and Nueva Islands. In spite of international boundary being in several parts of the Beagle Channel situated at a depth where king crab catches are unfrequent (200 m), seeming difficult therefore to imagine a significant king crab transfer from one jurisdiction to the other; population continuity cannot be denied. In Mackinlay Path, the Beagle Channel East of Gable Island and Moat Channel, situation is quite different since international boundary is localized at lower depths (15-80 m). Although transfer of juvenile and adult king crab is not massive, dispersion of larval stages seems to be important owing to strong currents observed in the area. The lack of studies on pre-recruitment stages and the small duration of a tagging program carried out during 1981 needs to be remarked. Transfer of king crabs from one jurisdiction to the other could not be irrefutably

demonstrated. Notwithstanding, transfer of big size male king crab seems evident in a certain period each year (September through December) from deeper waters towards area I of the Argentine FCZ (Lapataia Bay).

Other species with distributions including Argentine and Chilean jurisdictions are present in the area. These are still little or not harvested at all: softshell red crab **Paralomis granulosa**, mussels **Mytilus chilensis** and **Aulacomya ater**, Malvinas (Falkland) herring **Sprattus fueguensis**, king klip **Genypterus blacodes**, **Salilota australis**, hoki **Macruronus magellanicus**, hake **Merluccius hubbsi**. This situation adds groundwork to the idea of setting an institutional binational coordination in research and management of fishing resources in the area.

Searching for hypothesis attempting to explain the southern king crab resource present state, a set of ideas can be mentioned. Firstly, fishing effort has remained constant in the last ten years and even decreased. Also, fishing time dedicated to softshell red crab **Paralomis granulosa** has increased. In second term, it needs to be emphasized that landing of female king crab of all sizes and males under the minimum legal size is apparently frequent. A similar situation is also stated for Chile (Diaz, 1987), where in some areas of their king crab distribution, landing of females and illegal size males has become a generlized practice.

The lack of information on environmental factors in the surveyed area, mainly due to economic constraints already mentioned, is also to be taken into account. An analyses of environmental variations and relationship with recruitment levels is essential in the search of other causes affecting large scale temporal variations in the recruited fraction of the king crab biomass. Temperature and salinity recorded in some periods show no significant variations. Maximum temperatures are normally registered in January-February- March, with 9.0 °C-10.5 °C at surface and 9.0 C-9.8°C at the bottom, together with lower salinity registers: 26‰-29‰ and 27‰-29‰ respectively. Surface temperatures recorded in the months of June- July-August were 6.0 °C-6.5 °C, bottom temperatures were 6.1°C-6.6 °C (10-60 m deep) and salinity surface and bottom winter registers show values of 29‰-30‰.

An adequate program to study the obviously alarming symptoms of urban and industrial pollution in Ushuaia Bay and its probable correlation with fishing resources conditions in Beagle Channel, needs to be implemented. In the short term, consequences of pollution levels reached in the area have to be studied, and this should be a subject of priorital treatment in institutional levels of both countries: Argentina and Chile.

Research on pre-recruitment king crab stages as well as environmental incidence on the fishery; and studies on diseases and parasites as probable causes of mortality at different ontogenic stages needs also to be started.

On the base of analyses of available data of the southern king crab fishery in the Argentine zone of Beagle Channel, here described, the following was proposed:

1) A discussion forum should be set including fishing companies managers, state managerial authorities and scientists in the search for practicable solutions to present situation.

2) Owing to possible over-harvesting of **Lithodes santolla** in the western side of the Argentine Beagle Channel, and low fishing levels in the eastern side, Moat Channel and Atlantic coast, legislation in force ought to be changed with the onset of new regulatory measures with strong restrictions or even a whole close to fishing in the western side, and fishing promotion and allowance in the eastern side.

3) Landings ought to be efectivelly controlled, in order to make sure that legislation in force is actually observed.

4) Regulatory measures should be applied also to **Paralomis granulosa** resource in the Argentine zone of Beagle Channel, similar to those applied in Chile (Hernandez et al.,1986; Diaz, 1987).

5) Strategy of fishing companies should be diversifying of fishing and expansion eastwards of Beagle Channel.

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Proc. Int. Symp. King & Tanner Crabs
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A Note on Population Structure in the Eastern Bering Sea Adult Red King Crab, *Paralithodes camtschatica*

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ABSTRACT

Seasonal changes of population structure in adult red king crab in the eastern Bering Sea were examined in relation to seasonal migration of the crabs based upon the release-recapture data.
In winter, adult males aggregated in the offshore area and some part of them molted. Prior to the following spring, males migrated to inshore area for breeding, while high proportion of newly molted crabs did not take part in the inshore migration. Males that migrated to inshore area joined adult females that migrated during winter-spring from intermediate area between offshore and inshore area, and made up the breeding population. During summer-autumn, a high proportion of males in the breeding population migrated from inshore to offshore area, to join molters that remained in the offshore area. In course of this offshore migration, adult females appeared to be segregated from adult males.
The molting as well as the mating is apparently an important factor in the seasonal inshore-offshore migration of adult red king crabs.
The proportion of adult males that migrated from offshore to inshore area was calculated to be approximately 50 %.

INTRODUCTION

It is well-known that adult red king crabs aggregate inshore area to breed in spring, and then move to offshore area during seasons from summer to autumn. It is also well-known that adult females molt annually in spring just before mating, while adult males molt in winter and molting frequency of adult male changes according to ages, from annual molt to biennial, triennial and even quadrennial

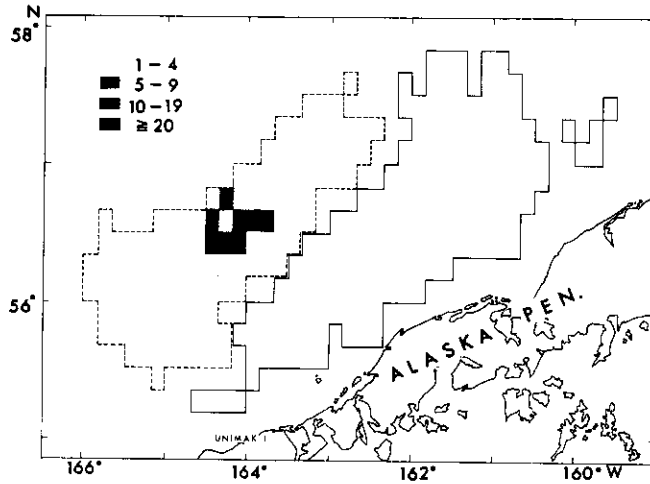

Figure 1. Relative distribution of tag recovery of adult male king crabs by autumn operation in 1966, released in offshore fishing area in 1966 (Fujita et al., 1973). Area confined by dotted and solid line indicates offshore and inshore area respectively. Solid circle indicates tagging site.

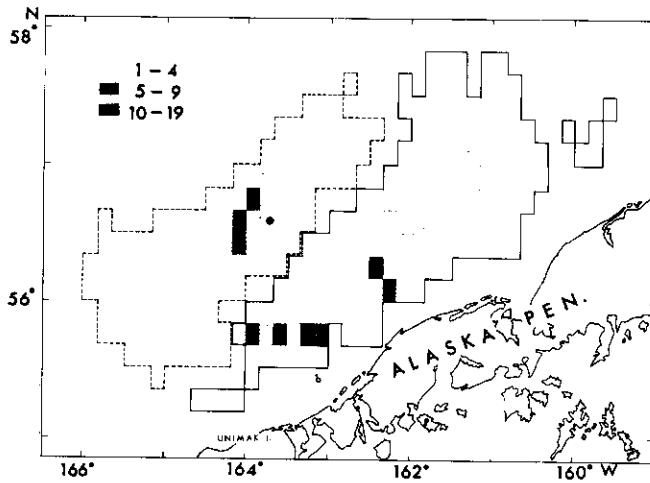

Figure 2. Relative distribution of tag recovery of adult male king crabs by spring and autumn operation in 1967, released in offshore fishing area in 1966 (Fujita et al., 1973).
Area confined by dotted and solid line indicates offshore and inshore area respectively. Solid circle indicates tagging site.

molt.
The primary purpose of this study is to describe the relation of changes in population structure to the seasonal migration and molting in adult males, based upon our release-recapture data for the years 1966-1967, reported previously (Fujita et al., 1973).

SEASONAL MIGRATION OF ADULT MALES

According to the records of the Japanese king crab fishery, 1964-'68, two fishing areas were recognized in the tangle net grounds, the inshore area for spring operations (March-June) and the offshore area for autumn operations (July-September). Tagging stations were established in the respective areas, in order to describe the movement of adult males between the areas (Figure 1). The successive recapture data for the offshore release in autumn showed that adult males migrated from the offshore area to the inshore area during winter-spring months and also from the inshore area to the offshore area during summer-autumn months (Figures 1 and 2). The recapture data for the inshore release also showed the inshore-offshore migration during summer-autumn months.

RELATIONSHIP BETWEEN MIGRATION AND MOLTING

The seasonal recapture data for the offshore release in autumn showed that majority of the spring recaptures was skipmolters, in contrast with considerably high percentage of molters in the autumn recaptures (Table 1). In addition, trawl survey data indicated that adult males newly molted (new shell crabs) distributed widely in the offshore area even in spring (Wallace et al., 1949; Fisheries Agency of Japan, 1960).

Table 1. Recapture data of adult male red king crabs released in the offshore area in the eastern Bering Sea*1

	Release year		The next year			
Recapture period (Season)	0 (Autumn)		1 (Spring)		2 (Autumn)	
Area	Offshore area		Inshore area		Offsore area	
Molters	(r_{0M})	0	(r_{1M})	11	[$r_{2(M+M')}$]	61
Skip molters	(r_{0S})	136	(r_{1S})	102	(r_{2S})	34
Total		136		113		95

*1 Data from Fujita et al. (1973). A total of 1,003 crabs was released.

According to these findings, the high proportion of adult males that newly molted in the offshore area may not take part in the inshore migration in spring and remain in the offshore area. In autumn of the next year, those molters remaining in the offshore area were considered to join the migrating crab from the inshore area to reorganize the adult male population.
As to the adult females, molting occurred just before mating in spring when crabs aggregated rather exclusively in the inshore area.

POPULATION STRUCTURE IN ADULT CRABS

Population structure in adult crabs are summarized in relation to seasonal migration in Figure 3. In winter, adult males inhabit in the offshore area and a part of them molts to grow. In the following spring, males mainly skipmolters migrate to inshore area to make breeding population with adult females. Females migrate probably from intermediate area between the offshore and the inshore area. After breeding season, males of breeding population migrate to the offshore area to reorganize male population by joining molters remained in the offshore area. In the course of this offshore migration, females are dissociated from males to make up each sexual assemblage.

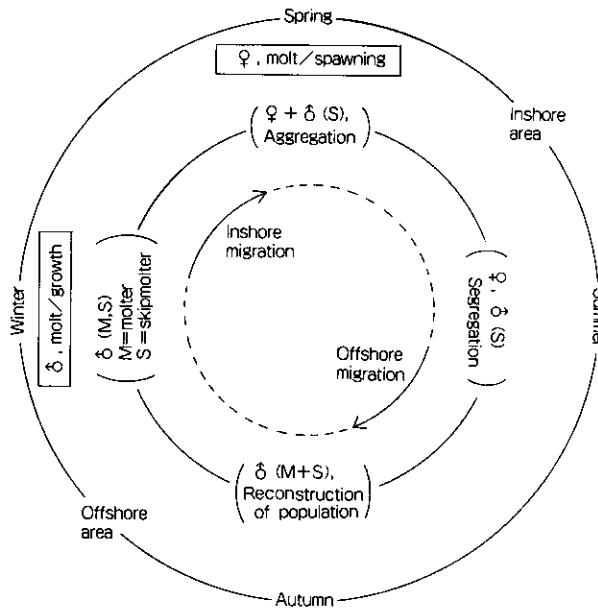

Figure 3. Schematic representation of seasonal migration and changes of population structure in adult king crabs.

AN ANALYSIS OF POPULATION STRUCTURE IN ADULT MALES

Seasonal changes of population structure in adult males were schematically presented in Figure 4. In autumn and winter, population consist of skip molters (S) and molters (M and M'). In the following spring, S and M migrate to the inshore area, while M' remains in the offshore area. In the next autumn, S and M migrate to the offshore area and join to M' to reorganize the population.

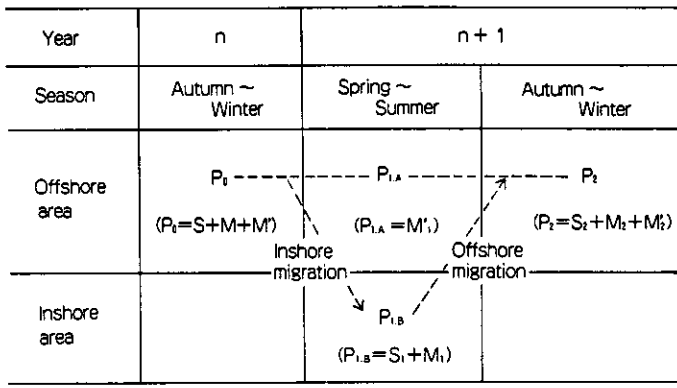

Figure 4. Schema for seasonal changes of population structure in adult male king crabs.
P: Population, S: Skipmolter, M and M': Molter.

The component ratio of the population, an essential population attribute, was estimated as to the skipmolters (S) and molters (M and M'), based on the release-recapture data for the autumn tagging shown in Table 1.

For R_1,

$$R_1 = R_0(1-d)-r_0 \qquad \text{- - - - - (1)}$$

For R_{1S},

$$R_{1S} = (R_{2S}+r_{1S})/(1-d) \qquad \text{- - - - - (2)}$$

$$R_{1M'} = R_1-(R_{1S}+R_{1M}) \qquad \text{- - - - - (3)}$$

R_{1S} in equation (2) can be obtained, using R_{2S} derived from the following equation (4)

For R_{2S},

$$R_{2S}/R_2 = r_{2S}/\{r_{2S}+r_2(M+M')\} \qquad \text{- - - - - (4)}$$

R_{1M} in equation (3) can be obtained from the following equation (5), using R_{1S}.

$$R_{1M}/R_{1S} = r_{1M}/r_{1S} \qquad \text{- - - - - (5)}$$

$R_{1M'}$ in equation (3) can be obtained, using R_{1S} and R_{1M} thus obtained.

Notations for equations (1) to (5) are as follows:

- d: Natural mortality per 0.5 year.
- R_0: Initial number of crabs tagged released in the offshore area in autumn.
- R_1: Number of tagged crab at liberty, at the beginning of the following spring.
- R_2: Number of tagged crabs at liberty, at the beginning of the next autumn.
- R_{1S}: A part of R_1, number of skipmolters that migrated to the inshore area.
- R_{2S}: A part of R_1, number of skipmolters that migrated to the inshore area and to the offshore area.
- R_{1M}: A part of R_1, number of molters that migrated to the inshore area in the following spring.
- $R_{1M'}$: A part of R_1, number of molters that remained in the offshore area in the following spring.
- r: Number of recaptures, suffix is same as that in the other notations.

The results of estimation were listed in Table 2, under several mortality rates, and the ratio of M'_1 to total population can be evaluated as approximately 50 %.

Table 2. Population structure of adult male red king crabs in the eastern Bering Sea, at various natural mortality rates*1

d	R_1	R_2	R_{2S}	R_{1S}	R_{1M}	$R_{1M'}$	$R_{1M'}/R_1$(%)
0.00	1,003	890	318	42	45	538	53.5
0.05	946	786	281	403	44	499	52.7
0.10	889	687	246	386	42	461	51.9
0.15	832	594	213	371	40	421	50.6

*1 Calculated, based on the release-recapture data by Fujita et al. (1973).
R_0=1,139, r_0=136, r_1=113, r_{1S}=102, $r_{1M'}$=11 (see Table 2 and text).
d: Natural mortality per 0.5 year.
R: Number of tagged crabs at liberty.
r: Number of recaptures.
The other notations are shown in text.

The results thus obtained are compatible with the field observations that the abundance of females is obviously higher than that of males in the breeding population in inshore waters (Table 3).

Molting is apparently an important factor in the seasonal migration of adult male king crabs, in addition to mating. The population structure in adult male red king crabs may

relate to sex ratio in the breeding population, furthermore to polygamous behavior in the red king crabs.

Table 3. Sex ratios of spawning red king crabs by shell conditions, based on trawl survey in the Kodiak Island area, Alaska.*1

Male Carapace length	60-99	100-139	140-169	170-199	Total
New shell	1	55	11	3	70
Old shell	0	0	42	28	70
Female Carapace length	70-99	100-119	120-129	130-169	Total
New shell	0	51	79	76	206
Old shell	0	7	17	56	80

Sex ratio	Total males to total females	Large males to total females	Old shell males to total females
Male : Female	1 : 2.1	1 : 3.4	1 : 4.1

*1 Quoted from Gray and Powell (1966).

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Effect of Hydrological Conditions on Harvest of Populations of the King Crab (*Paralithodes camtschatica*)

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ABSTRACT

Some deviations from normal reproductive processes have been observed while examining material collected on the western Kamchatka population of the king crab (*Paralithodes camtschatica*). Comparisons of these data with previous data have led the authors to conclude that low-yielding crab generations can occur both in cold and warm years. The displacement of biological processes in populations is a function of hydrological conditions the previous year.

The king crab population inhabiting the western Kamchatka shelf has been studied for a long time. Distribution, migration and spatial structure of the population have been thoroughly studied (Vinogradov, 1945, 1968, 1969; Rodin, 1967, 1969, 1985; Fedoseev, Rodin, 1986). Fluctuation in stock abundance of migrating groups from year to year (Rodin, 1985) and some factors causing low-yielding generations (Rodin, Lavrentyev, 1974) have been revealed. Our information supplements basic material and provides some new insights into factors regulating stock abundance in the populations.

Some deviations from normal reproductive processes in the king crab population have been observed while examining sample material. Having compared the data we obtained with previous data, the authors have concluded that low-yielding crab generation can occur both in cold and warm years. Displacement of biological processes in populations is a function of hydrological conditions the previous year.

MATERIAL AND METHODS OF COLLECTION

The material was collected by an observer on board the *Sergey Lazo* factory ship and by a TINRO expedition on board the *Permskoye* which was working on the western Kamchatka shelf from May 16 to June 16, 1987. Mature male and female crabs with carapace width over 130 mm were taken as objects of study. Mature females were identified by having developed gonads and eggs and by carapace width no less than 90 mm (Fedoseev, Rodin, 1986). All the samples were collected using trawls. Thirty minute trawls were made at speeds of 2.5-3.0 knots on a standard station grid (Rodin, 1979).

Biological stages were visually identified for each female. These were as follows: eyed eggs, clearly visible embryo (ES); larvae are "released," the gonads are violet colored (LR); eggs are "violet" (EV); eggs are "brown" (EB); "initial eyed" stage of eggs, the embryos barely visible (IE); a nonbreeding female (NB), white gonads, no eggs. Intermolt male crabs were identified by the following features: II -- the shell is white and there are no scratches on it; early III -- the shell is darker than that of II, with or without barely visible fouling; late III -- dark shell with fouling, the sternum is badly frayed and there are many brown scratches on it; IV -- the shell is badly fouled and has many dark scratches, new shell has already formed underneath the old one and is exfoliating from it, the sternum is brown, almost black.

Two seasonal groups were distinguished from the male crabs under study. The intermolt crabs of II and early III categories were referred to group I, those of late III and IV categories were referred to group II.

Data are given for the Hairuzov, Itcha, Kolpakov and Kihtchik migration groups separately.

RESULTS

Some unique features were revealed during the investigation. Male crabs of group I concentrated at a depth of 50-75 m in the Itcha region. They had clean shells, which had appeared about two months before, i.e., approximately in April. The route of the spring migration (shoreward) indicates that molting of this group took place in deeper waters. Group II individuals that were getting ready for molting in June or July had a fouled shell and upon collection had concentrated near shore at a depth less than 30 m. They probably would have molted there too. Thus, these two groups of the male crabs differed in the time and place of molting. While the male crab of group II were observed at similar depths all the way along the western Kamchatka shelf, depth distribution of the group I male crabs varied in different regions (Fig. 1). They were farthest from the shore in the Hairuzov region, but the majority of the soft-shelled crabs were closer to shore in the areas to the south. There were no clear differences in the location of male crabs of different biological stages in the most southern Kihtchik region.

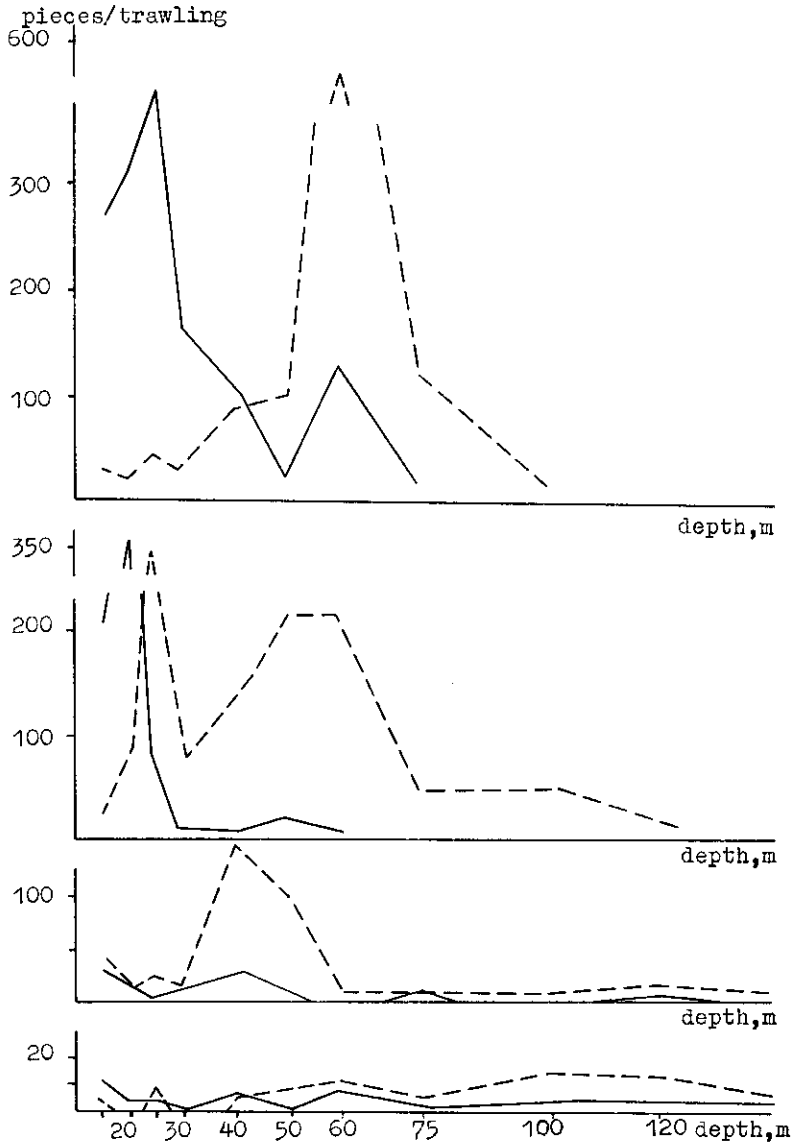

Figure 1. Average harvests of the groups I (dashed line) and II (solid line) Kamchatka crab on the western Kamchatka shelf in May - June, 1987.

Thus, a different degree of separation of the individual groups was observed all the way along the shelf. The separation was not observed in the southern region, but was the most distinct in the northern region.

The female crab concentrated near pods of male crabs; i.e., they had a similar spatial distribution.

A large number of females with recently spawned eggs were marked. This suggests that the males of both groups participated in spawning. Considering the spatial separation of the male crabs, each group of males must have had its own spawning ground and harem of mating females as well.

Not only were the spawning locations different, but also the spawning period. While practically all the female crabs that were concentrated near the pods of group I males had spawned in all the regions except the Kihtchik region, the percentage of LR females was still high in shallow waters (Table 1). In addition an increase in the percentage of EB females (i.e., females that had spawned much earlier than the others) was observed from shallow to deep waters. Combining the groups yields an increase in total spawning duration of the population in comparison with conventional estimates. The above observation is confirmed by presence of ES females (previous year spawning, 1986) and IE females (current year spawning) in the catch. They spawned within an interval of 4 to 6 months. Thus, in 1987, two spawning groups formed which differed in place and time of spawning.

While the male crabs could be easily divided into groups, the female crabs could not be divided with much certainty. For example, there were females with "violet" eggs both in deep and shallow waters; this is apparently explained by a coincidence between the end of the first group spawning and the beginning of the second group spawning. Proceeding from the actual distribution of male crabs, we postulate that the first group spawned in the Hairuzov region at a depth of over 50 m., and in Itcha and Kolpakov regions at a depth of over 25-30 m. We included in this group the female crabs with "violet" eggs, that had been observed in deeper waters, and those with later "brown" eggs and with eggs in IE stage. The latter had spawned in March and April and partially reached shallow waters where temperature conditions are the most favorable for embryonic development. This group had practically finished spawning at the time of collection.

The female crabs that had mated with the group II males were observed at a depth less than 40 m in the Hairuzov region, and at a depth less than 25 m in the Itcha and Kolpakov regions. The majority of the females had already spawned. A considerable number of LR females had finished spawning in late June.

The time and duration of larval hatching from eggs spawned the previous year may be estimated by circumstantial data. The presence of female crabs that had spawned early indicates that larval hatching took place earlier than usual in 1987. Hatching probably began in late February or early March. Because some ES females were observed during sample collection, we assume that the larval

hatching period lasted until late May or early June. The female crabs of the first spawning group released their larvae in February and March, probably at depths of over 100 m. The females of the second spawning group released larvae from April to June, mostly at a depth of 40 - 60 m.

Thus, in contrast with the usual molting and reproductive processes in the western Kamchatka population, in 1987 some biological abnormalities were observed that eventually led to some deviations in the reproduction of the population. First, "winter" molting of the male crabs took place in the northern part of the shelf. There has never been strong evidence of winter molting previously and it does not conform to the annual king crab cycle as determined by Rodin (1985) for that region. Second, a number of females began spawning earlier than usual, which led to an increase in total duration of spawning of up to four months (from March to June in contrast to the traditional spawning period which lasted two months, from late April to mid-June). Third, the duration of larval hatching also increased, with partial hatching taking place in deep waters.

DISCUSSION

The examined spawning groups differed, first of all, in order of molting and spawning. The biological processes in the group spawning in shallow waters were normal (i.e., molting of the males took place after total spawning of the female crabs) while in deep waters the male crabs molted during spawning.

Molting of the males resulted in an interruption in the spawning of the female crabs that influenced their reproductive function. Molting is accompanied by large expenditures of energy (Hartnoll, 1978), and for two weeks energy is mainly expended on hardening of the chitinous shell. We therefore believe that there was a temporary lack of males capable of reproduction in April. The majority of the females that spawned during molting of the males couldn't be fertilized and their eggs fell off. This hypothesis is supported by the fact that the highest percentage of "nonbreeding" females were observed where group I males concentrated, and the percentage gradually decreased shoreward (Table 1). Thus "nonbreeding" of a large number of the female crab caused by an interruption in spawning is certain to affect the magnitude of reproduction by the population the following year.

Early larval hatching has a negative impact on the year class. In favorable years, larval hatching takes place in warm shallow waters of the coastal zone in the summer months (Vinogradov, 1945). Pelagic larvae are moved by currents northward and settle in southwestern Shelikov Bay where the juvenile part of the king crab population forms. Positive temperatures and currents favorable for larval settlement in the bay provide for optimum larval survival (without predation taken into consideration). The farther from Shelikov Bay that larval hatching takes place, the greater the number of larvae that scatter and die due to unfavorable conditions. If larval hatching takes place at depths over 50-60 m, the majority of larvae fail to reach their usual habitat before settling. Consequently,

Table 1. Bathymetrical distribution of the Kamtchatka female crabs depending upon their biological stage.

Depth m	BIOLOGICAL STAGE ES	LR	NB	EV	EB	IE
1	2	3	4	5	6	7
Hairuzov Region (June 10-15)						
15	-	46/18.0	6/2.3	198/77.7	5/2.0	-
20	1/0.4	37/15.7	13/5.5	178/75.9	6/2.5	-
25	-	78/24.8	15/4.8	219/69.8	2/0.6	-
30	-	15/5.1	22/7.4	250/84.5	9/3.0	-
40	-	29/11.4	31/12.2	189/74.1	6/2.3	-
50	-	11/13.6	11/13.6	52/64.2	7/8.6	-
60	-	5/1.3	123/32.8	230/61.4	17/4.5	-
75	-	2/6.2	3/9.4	22/68.8	5/15.6	-
100	-	1/12.5	1/12.5	6/75.0	-	-
120	-	-	-	-	-	-
REGION TOTAL	1/+	224/12.1	225/12.2	1344/72.6	57/3.1	-
Itcha Region (June 2-9)						
15	-	61/36.1	1/0.6	105/62.1	2/1.2	-
20	-	23/30.7	5/6.7	41/54.6	4/5.3	2/2.7
25	-	9/33.3	5/18.5	10/37.1	3/11.1	-
30	-	2/9.1	4/18.2	13/59.1	3/13.6	-
40	-	8/17.4	3/6.5	21/45.7	13/28.2	1/2.2
50	1/2.3	2/4.5	6/13.6	21/47.8	14/31.8	-
60	-	1/4.5	4/18.2	10/45.5	7/31.8	-
75	-	-	2/22.2	6/66.7	1/11.1	-
100	-	-	3/13.6	9/40.9	10/45.5	-
120	-	-	2/66.7	-	1/33.3	-
150	-	-	-	-	-	-
REGION TOTAL	1/0.2	106/24.1	35/8.0	236/53.8	58/13.2	3/0.7

Table 1. (Continued) Bathymetrical distribution of the Kamtchatka female crabs depending upon their biological stage.

Depth m	BIOLOGICAL STAGE ES	LR	NB	EV	EB	IE
1	2	3	4	5	6	7
Kolpakov Region (May 22-25)						
15	1/3.6	22/78.6	-	3/10.6	1/3.6	1/3.6
20	-	2/100	-	-	-	-
25	-	2/100	-	-	-	-
30	-	11/84.6	-	1/7.7	1/7.7	-
40	2/20	2/20	2/20	3/30	1/10	-
50	-	4/40	3/30	1/10	2/20	-
60	-	-	-	-	-	-
75	-	1/14.3	2/28.6	3/42.8	1/14.3	-
100	-	-	-	1/100	-	-
120	-	1/12.5	1/12.5	1/12.5	5/62.5	-
150	-	3/25	-	3/25	6/50	-
REGION TOTAL	3/3.6	48/51.6	8/8.6	16/17.2	17/18.1	1/1.2
Kihtchik Region (May 16-21)						
15	2/18.2	9/81.8	-	-	-	-
20	1/50	1/50	-	-	-	-
25	-	4/100	-	-	-	-
30	-	1/100	-	-	-	-
40	-	4/100	-	-	-	-
50	-	-	-	-	-	-
60	1/25	3/75	-	-	-	-
75	1/50	1/50	-	-	-	-
100	-	1/100	-	-	-	-
120	-	1/50	-	1/50	-	-
150	1/50	1/50	-	-	-	-
REGION TOTAL	6/18.2	26/78.8	-	1/3.0	-	-

NOTE: Individuals as numerator
Percent as denominator
Dash (-): Weren't found at all
Plus (+): Their quantity was small number of "summer" spawning

in 1987 the majority of the larvae may have died without forming the juvenile part of the population.

Considering the effect of the above-mentioned abnormalities in the reproductive processes, we divided the spawning period into two parts: "winter" spawning and "summer" spawning. The approximate time that male crabs finished their winter molting (late April) serves as a temporal boundary. We consider the female crabs that had spawned earlier than usual to be "winter" spawning females. At the time of collection some were "nonbreeding" due to the reasons stated above. The others had "brown" eggs and IE eggs attached to their pleopod. The LR female crabs and the females with "violet" eggs were assigned to the group of "summer" spawners. These females were observed at a depth of 15-75 m. In our opinion, the first group of females, which had spawned in deeper waters, isn't homogeneous and consists of both "winter" and "summer" spawning individuals.

The effects of the abnormalities are mostly expressed in the "winter" spawning females. First, they had maximum scattering of larvae after hatching; second, they had the highest percentage of "nonbreeding" females. Those females that had spawned after "winter" molting of the males had the usual percentage of "nonbreeding" individuals, but the majority of the larvae died. The female crabs of the second group released larvae and spawned without any apparent negative consequences.

We believe the reasons that females occur in "winter" or "summer" spawning groups are different. The reason is temporal for the "winter" spawning females and is based upon accelerated maturation of oocytes, i.e., on physiological readiness of the females to spawn earlier than usual. But for the "summer" spawning females, the reason is behavioral; prespawning females are attracted to a large concentration of males. Apparently, "winter" spawning females had spawned in deep waters due to their inability to continue their migration and a number of "summer" spawning females stopped their migration shoreward and stayed in deep waters near pods of males.

The effects of the abnormalities are different between the northern and southern regions. The percentage of "winter" spawning females increases from the Hairuzov region to the Kolpakov region (Table 2). This indicates that spawning starts later in the northern region than in the southern region. The percentage of winter molting males increases with the same regularity (Fig. 1).

In the southern regions, cold water masses from the sea of Okhotsk proper are quickly washed away by the warm Western Kamchatka current resulting in positive bottom temperatures on the shelf earlier than in the northern regions (Moroshkin, 1966). Although the biological processes in the southern region are accelerated with respect to those in the northern regions, the percentage correlation of reproductive damage was less than in the northern regions. Thus, the percentage of "nonbreeding" females is lower in the Kolpakov region, though

Table 2. Regional percentage correlation of "winter" and "summer" spawning female Kamchatka crabs depending upon depths.

Depth, m	I	II	III	IV
15	4/96	2/98	7/93	0/100
20	8/92	15/85	0/100	0/100
25	5/95	30/70	0/100	0/100
30	11/89	32/68	8/92	0/100
40	15/85	37/63	27/73	0/100
50	22/78	46/54	50/50	-
60	37/63	50/50	-	0/100
75	25/75	33/67	43/57	0/100
100	13/87	59/41	0/100	0/100
120	-	100/0	75/25	0/100
150	-	-	50/50	0/100
Average	16/84	40/66	37/74	0/100

Note: Regions:

I - Hairuzov
II - Itcha
III - Kolpakov
IV - Kihtchik

Percentage of "winter" spawning as numerator
Percentage of "summer" spawning as denominator

"winter" spawning females comprise a large part of the group (Tables 1, 2). Apparently, this is a result of lesser separation between the "winter" molting males and "summer" ones. It was therefore easier for the females to redistribute for spawning during the early molting of group I males. It's remarkable that there was no "winter" molting in the most southern Kihtchik region, where the molting cycle of the males corresponded to the typical cycle of the king crab observed in the Kihtchik region. In our opinion, this is due to the effect of the Western Kamchatka Current. Rapid warming of waters by the current with a constant positive temperature results in a similarity between years as indicated by Vinokurova (1964). The effects of the current weaken between the Kihtchik and Kolpakov regions (54°N), and persistent cold temperature "spots" form to the north (Tchernyavsky, 1981). Therefore adaptation of the king crab to

comparatively constant hydrological conditions leads to a consistent optimum period for molting and spawning.

Rodin and Lavrentyev (1974) consider that the reason for the low-yielding generation is that there was wide scattering and death of larvae due to unfavorable conditions. They considered such a situation to be possible only in cold years when the females are not able to move shoreward because of the cold temperature "spots" with bottom temperatures below 1.0°C. Bottom temperatures were positive and cold "spots" were completely washed away in 1987, a typical warm year (Vinokurova, 1964). Nevertheless, a low-yielding generation occurred during 1987 as well. In our opinion, the low yield was caused by temperature conditions the previous year.

It has been demonstrated that the most rapid embryonic development takes place in late spring and summer when the females are in a warm water zone (Fedoseev, Rodin, 1986). The development may be accelerated or delayed by the hydrological conditions of the year. According to hydrological survey data, 1986 was a typically warm year. The cold "spots" had been washed away by early May and positive temperatures established along the shelf. Therefore, early maturation of oocytes and early development of embryos under the influence of warm temperature conditions could cause early larval hatching and "winter" spawning in 1987. This might also have caused changes in the molting period of a number of the males. However, it is still unclear why a portion of the males and females were unaffected by the temporal displacement of biological processes.

Thus, our observation indicates that both typically cold and warm years have a negative effect on the king crab year classes. The time of maturation of reproductive products and, consequently, the degree of displacement of biological processes are determined by the previous year's temperature conditions. The formation of the current year class is therefore influenced by the temperature regime of both the current and previous years or perhaps by several of the previous years.

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Evaluation of Some Errors in Estimating Recruitment for the Bristol Bay Red King Crab Stock-Recruit Relationship

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ABSTRACT

The stock-recruit relationship estimated for Bristol Bay red king crabs provides information needed for management regarding the appropriate level of harvest given the current state of the spawning stock. This study examines the effect of potential innaccuracies in the recruit data on the estimation of the spawner-recruit relationship. Errors may stem from indirect age determination, or from assuming a constant growth schedule when growth of recruits may be variable due to a variable temperature regime. Simulations indicate that variations in recruitment and mortality will bias estimates of recruits calculated indirectly from growth curves, and corrections are introduced based on a knowledge of the extent and direction of the bias. Similarly, recruit data can be adjusted for variations in the time lag before recruitment. Effects of aging bias on the spawner-recruit data set appear to have been minor, but the assumption of temperature-dependent growth would lead to differing management implications.

INTRODUCTION

The crab fisheries of Alaska form a significant part of the fisheries of the north Pacific, as well as contributing considerably to world crab landings (Otto 1981). The southeastern Bering Sea, which includes Bristol Bay, has historically been a top producer of the red king crab, Paralithodes camtschatica, which is the predominant commercial king crab in Alaska. The Bristol Bay fishery for red king crabs typically occurs in the fall of the year, when the crabs are approaching maximum meat fullness, and is prosecuted with large modern vessels using

individually-bouyed pots (traps). Several management measures are used to ensure the reproductive viability of the stock: female crabs are not landed, but returned to the sea when encountered; sublegal males, smaller than the minimum carapace width limit of 6.5" (165mm), are likewise returned to the sea; seasons are set to avoid the spring molting and mating period; and quotas are set based on stock abundance and desired exploitation rates.

Regarding the establishment of quotas, abundance estimates for the Bristol Bay stock of red king crabs are provided by an annual summer trawl survey (Stevens,MacIntosh and Stahl-Johnson 1987). Area-swept estimates (Alverson and Pereyra 1969) of legal males, as well as other stock components, are used to make annual quota determinations. In addition, estimates of spawner and recruit abundance from the survey data go back to 1968, and were first fit by stock-recruit models in Reeves and Marasco (1980). Stock-recruit models hold potential for providing guidance in the adjustment of exploitation rates as the spawning stock fluctuates with reference to its optimum level. The time series of abundance estimates available for the Bristol Bay stock has permitted an estimation of S(max) for the Ricker model, to which the current level of spawners may be compared. The result of this comparison can provide guidance on adjustment of the rate of exploitation. If the current level of spawners is below S(max), a lower rate may be most prudent; at higher spawner levels more liberal rates of exploitation may be allowed.

The spawner-recruit relationship for Bristol Bay red king crabs relates five-year old male recruits to the female spawning stock. Although the fishery harvests only males, the rate of exploitation may impact females through handling mortality or reduced clutch size. Annual spawning abundance and population fecundity, which is expressed in terms of an average population clutch size, is assessed following the mating period. Abundance of mature females is adjusted for clutch size thereby implicitly accounting for the effect of changing sex ratios, to the extent that less-than-full clutches are the result of low abundance of mating male crabs. External fertilized clutches are carried for approximately one year before hatching. Male recruits are considered adequately recruited to the survey trawl gear (Incze,Otto and McDowell 1986) rather than to the fishing gear, such recruitment occurring several years later. They are further considered to be age 5 and are related to the spawning stock six years earlier, due to delayed hatching.

The purpose of this paper is to assess the effects of errors in the estimation of recruits on the form and parameters of the stock-recruit curve. Two types of errors are considered: (1) bias related to the inability to age crabs accurately because there are no known hard parts to record growth history annually, and (2) bias in the time lag between spawners and recruits caused by variable growth of pre-recruit crabs. In the first situation, error arises when a growth equation determined from modal analysis and tagging is solved for t (age) but does not account for error around

the curve. The effect of variation in length at age on these indirect estimates of "age 5" recruits is assessed by simulation of crab growth characteristics. In the second case, The hypothesis proposed by Stevens (1989) relating growth of sublegal male crabs to their temperature environment is evaluated. If growth is temperature dependent as proposed, then the lag between spawners and resulting recruitment is larger and more variable than growth based on modal analysis and tagging studies would indicate.

BIAS DUE TO INDIRECT AGE ESTIMATION

In this section, the procedure for estimating age 5 recruits from a von Bertalanffy growth curve is given, as well as an evaluation of the resulting estimates based on a model of king crab growth. Corrected recruit data resulting from this evaluation are then used to re-estimate the spawner-recruit relationship. The current spawner-recruit relationships for Bristol Bay red king crabs, employing indirect estimates of age 5 male recruits, is shown in figure 1 (years of recruit estimates shown) with the plotted data given in table 1. These curves represent fits of the Ricker model,

$$R(i+6) = aS(i)e^{-bS(i)} .$$

It should be noted that the solid curve of figure 1 represents an improved nonlinear fit to the data compared to log-transformed fit, based on R-squared values of table 2, which are defined according to expression (1) of Kvalseth (1985). Although transformed data have been used in earlier analyses (Reeves and Marasco 1980;Reeves 1982;Jamieson 1986), untransformed nonlinear fits of the Ricker model will be used for comparisons in this study.

Recruit estimation

Indirect estimates of recruits are based on the study by Weber(1967), who utilized modal analysis to derive a growth curve for immature crabs,and Balsiger's(1974) analysis of tagging data for mature male king crabs. The latter utilized information on molting frequency and growth increment per molt to construct growth curves for tagging periods in the 1950's and 1960's. Carapace length-at-age data for these two studies were combined and fit with a von Bertalanffy growth curve having the following parameter estimates:k=0.16, Linf=190mm, to=0. The growth function is then solved for t as a function of carapace length in mm, and approximate (rounded to the nearest 5-mm) equidistant intervals around each whole age value are established. This process is shown diagramatically for age 5 recruits in figure 2, indicating a 95-109mmm interval for this age group.

Evaluation of recruit estimates

A growth simulation model developed by Somerton (1981) was used to evaluate estimates of age 5 recruits. The GROW model

Table 1. Spawner-recruit data for Bristol Bay red king crabs.

Year i	Female spawners (millions) >89mm	Percent full clutch (2	Adjusted for clutch size	Age 5 male recruits (millions) in year i+5 (1 Un-corrected	Corrected for year class variation	Corrected for temp. dep. growth
1968 (3	53.7	67%	36.0	15	15	24
1969 (3	28.5	67%	19.1	18	18	29
1970	13.0	62%	8.1	27	24	12
1971(3,4	12.6	67%	8.4	45	55	5
1972	12.1	49%	5.9	21	14	13
1973	76.8	52%	39.9	11	11	7
1974	72.0	88%	63.4	15	15	24
1975	58.9	77%	45.4	17	17	13
1976	71.8	61%	43.8	20	20	14
1977	150.1	36%	54.0	11	11	5
1978	128.4	89%	114.3	15	16	5
1979	110.9	96%	106.5	6	2	0
1980	67.6	67%	45.3	7	9	
1981	67.3	81%	54.5	7	7	

(1 Lag is variable for data corrected for temperature-dependent growth
(2 Calculated after Reeves (1988), using all shell age categories
(3 Missing clutch size value replaced with average for the series (67%)
(4 Missing abundance estimate replaced with average of adjacent years

Table 2. Nonlinear regression estimates for four red king crab spawner-recruit data sets.

Parameter estimates	Log transform	No transform	Year class corrected	Growth corrected
b	0.036	0.070	0.069	0.042
Smax (1/b)	28	14	14	24
95% CI(Smax)	10-38	11-18	9-19	14-34
var(Smax)*	24.5	3.7	5.5	26.6
var(b)	4.11E-05	8.86E-05	1.24E-04	8.20E-05
a	2.27	6.29	6.19	2.26
var(a)	0.660	2.053	2.900	0.527
R sq.	-0.46	0.25	0.25	0.36

* Approximated by the delta method

Table 3. Base parameters for GROW model simulations.

Initial cohort numbers	1000
Mean size (mm)	70
Variance (mm)	25
Annual survival	0.9
Hiatt parameters:	
Intersection point (mm)	100
Lower intercept (mm)	15.0
Lower slope	1.0
Upper intercept (mm)	13.0
Upper slope	1.0
Variance	6.9

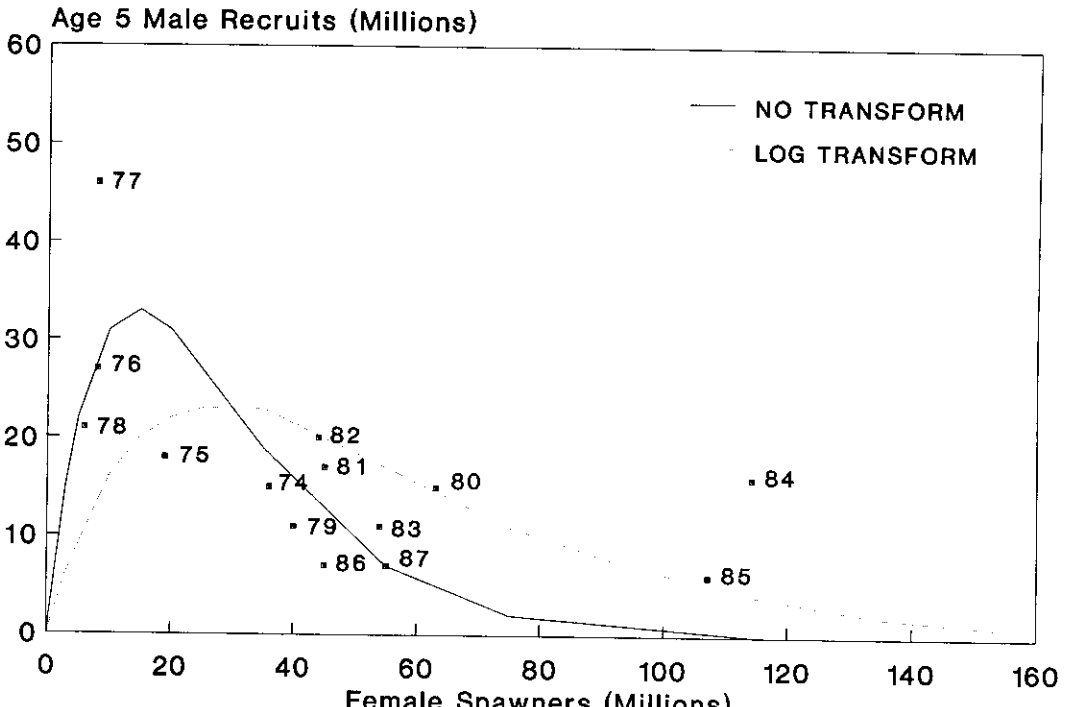

Figure 1. Uncorrected spawner-recruit relationships for red king crabs.

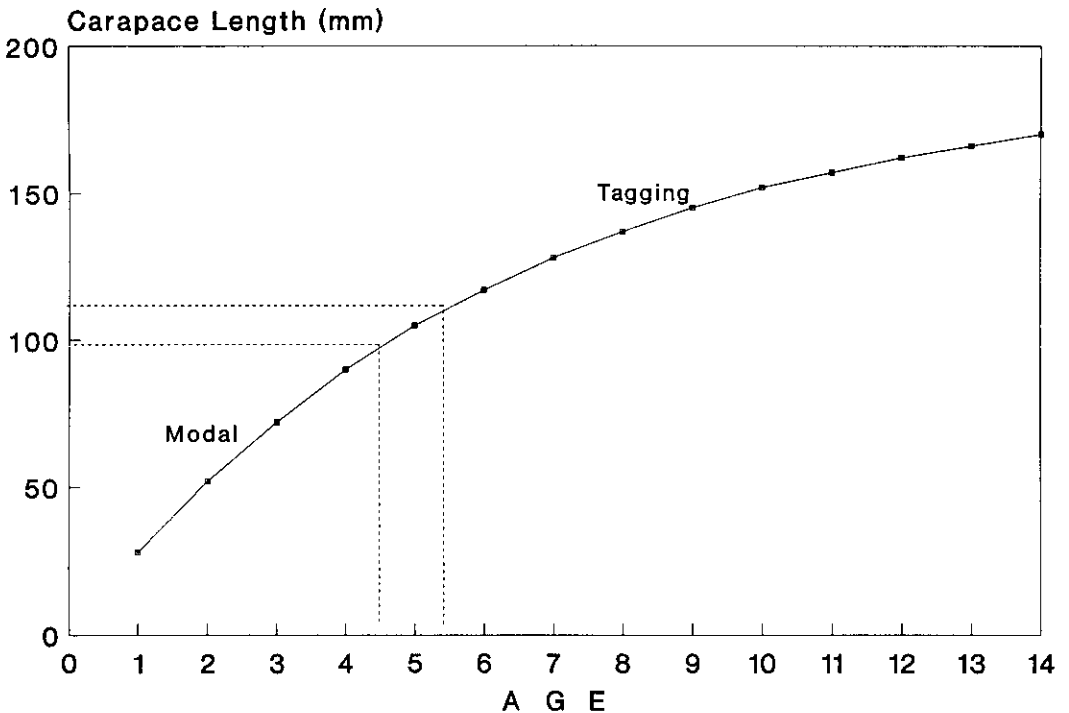

Figure 2. Von Bertalanffy growth curve for red king crab males.

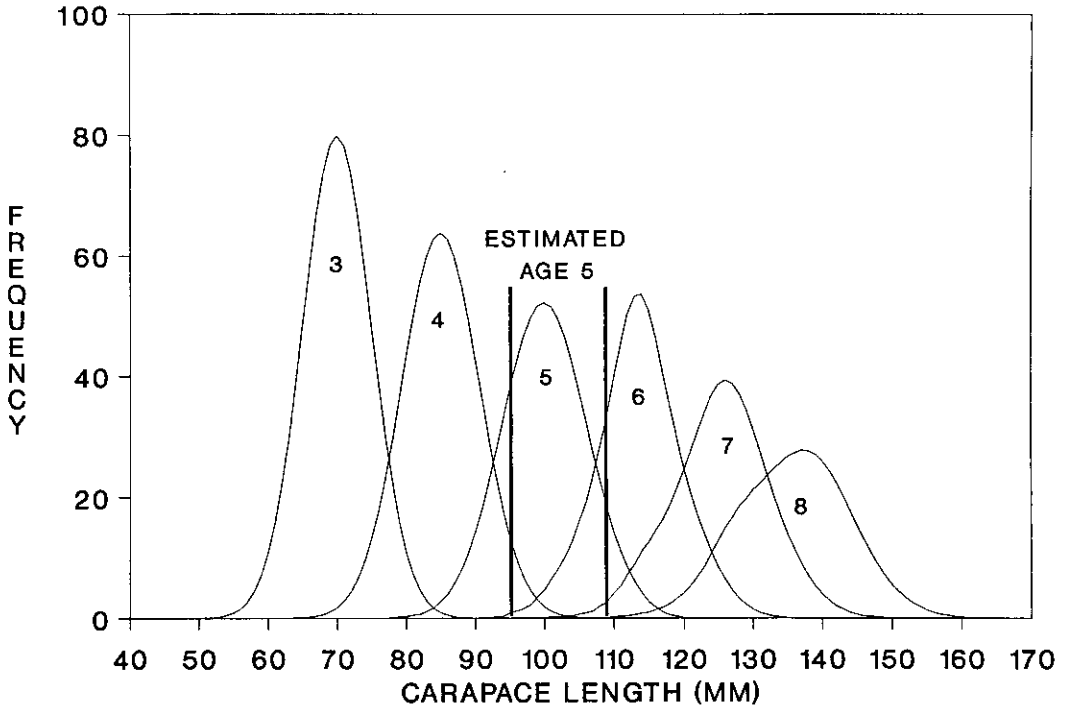

Figure 3. Simulated size distributions for age 3-8 crabs, with estimation interval.

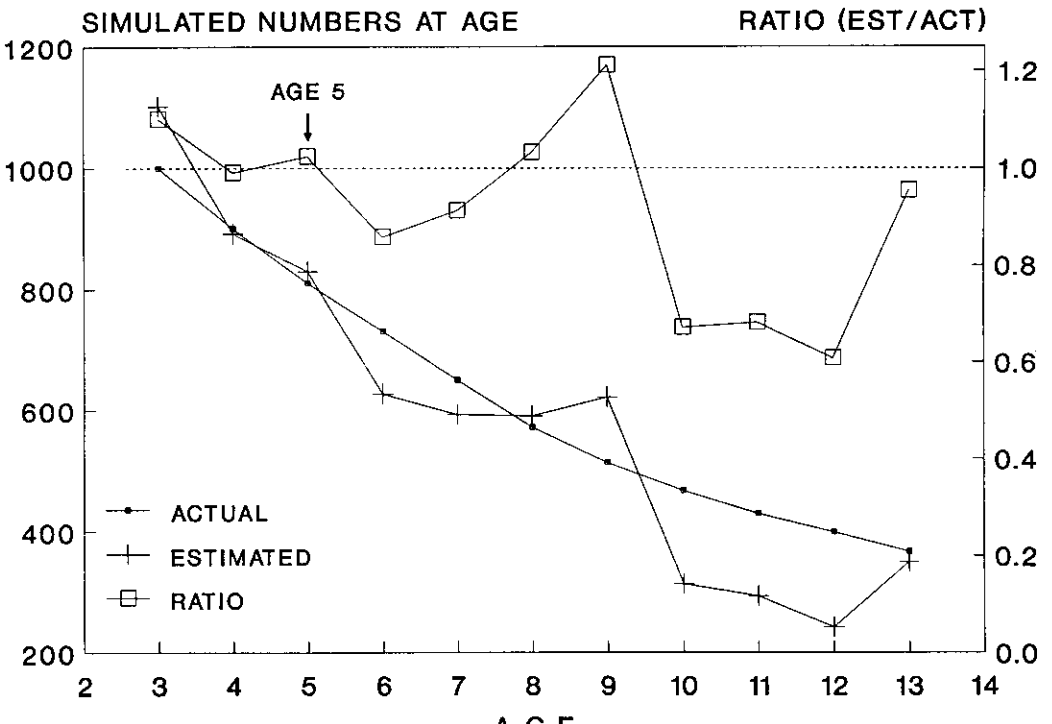

Figure 4. Bias in age estimated from Von Bertalanffy growth.

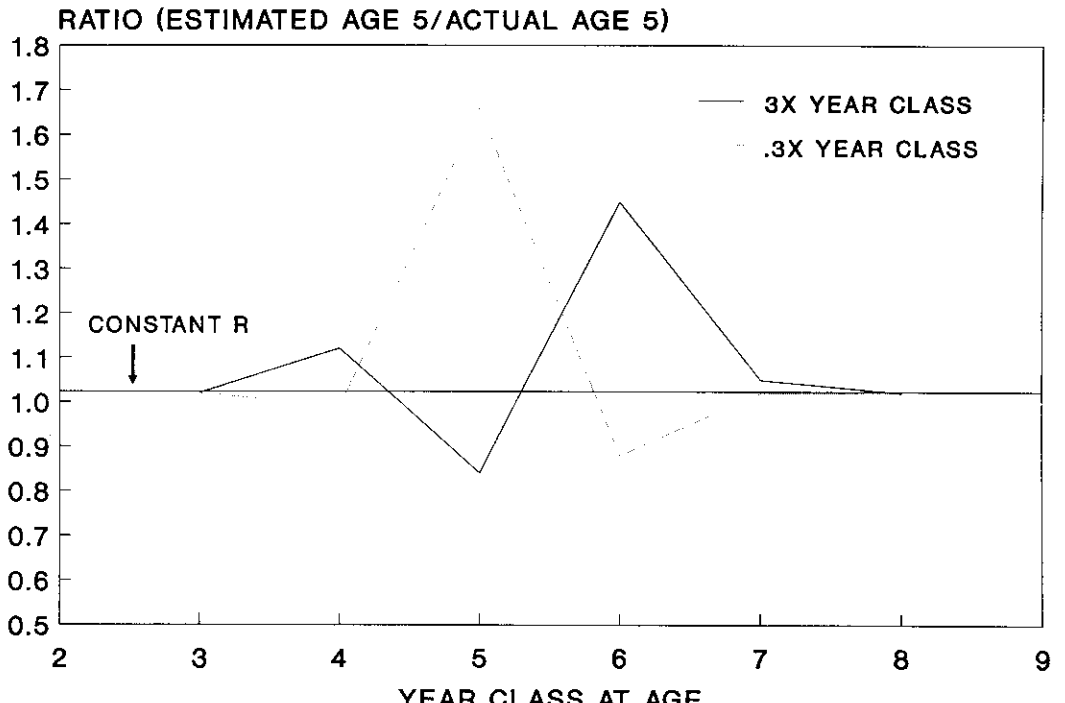

Figure 5. Changes in age 5 bias related to strong and weak recruitment.

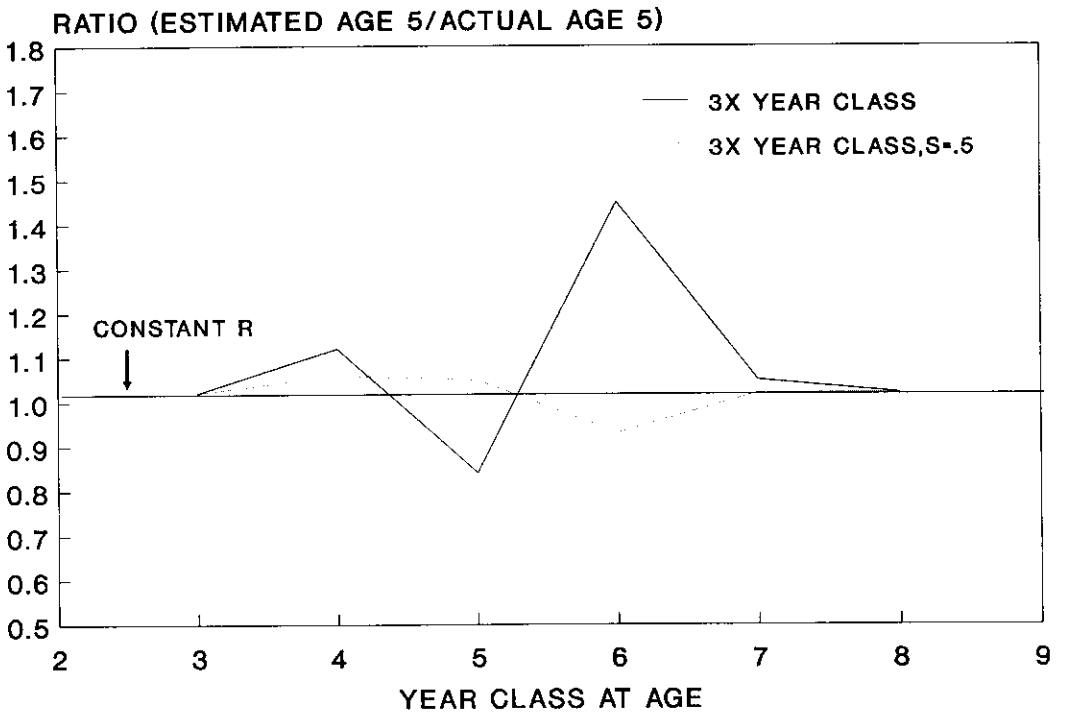

Figure 6a. Effect of higher mortality on age 5 bias related to strong recruitment.

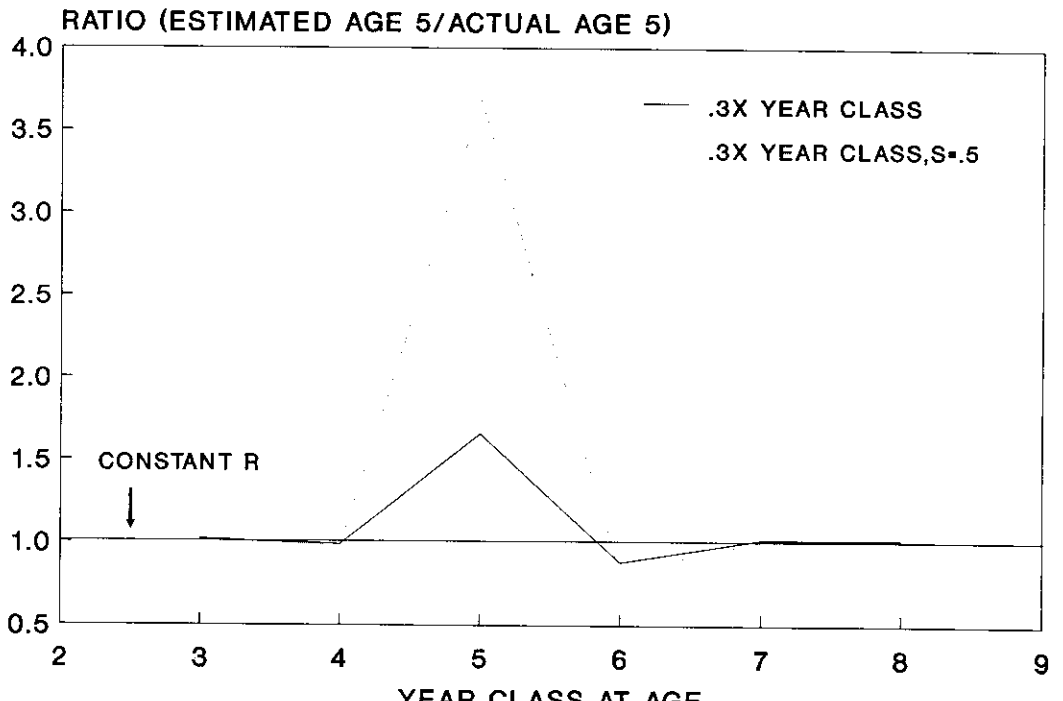

Figure 6b. Effect of higher mortality on age 5 bias related to weak recruitment.

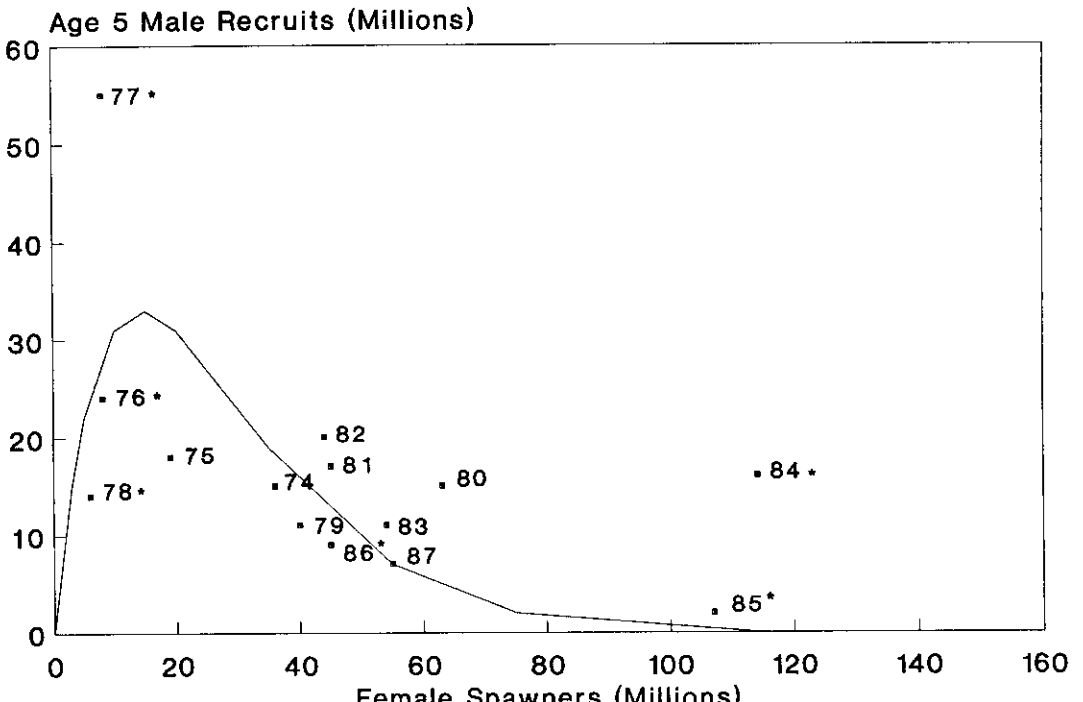

Figure 7. Recruit values corrected for year class strength, indicated by asterisks.

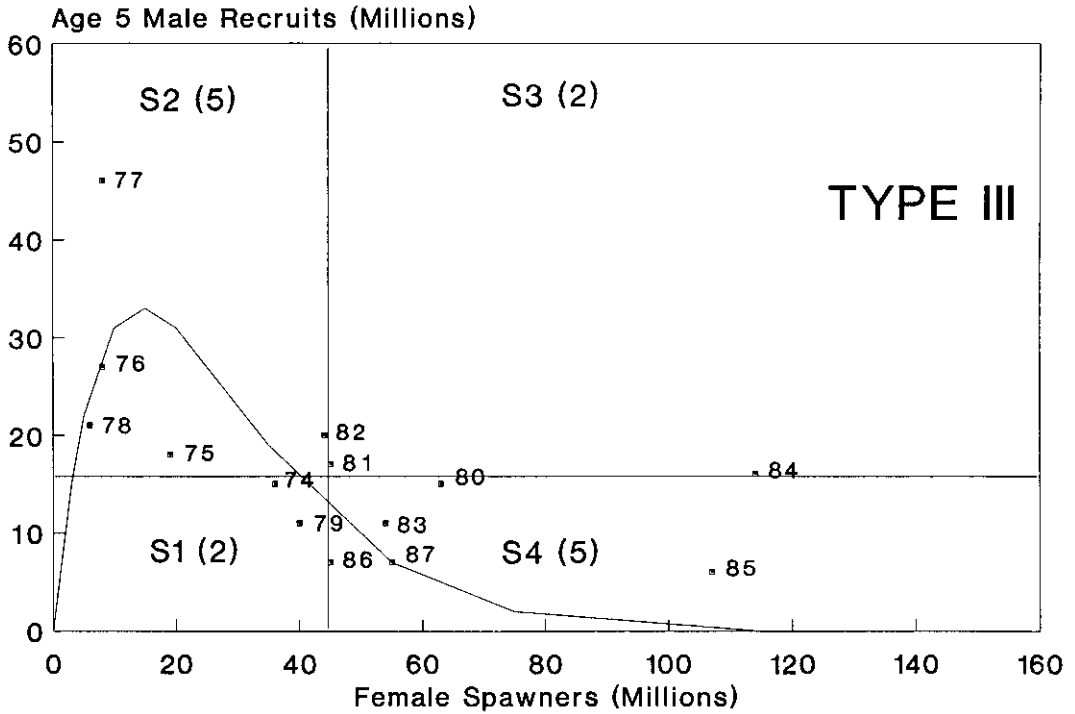

Figure 8a. Non-parametric classification of uncorrected spawner-recruit data.

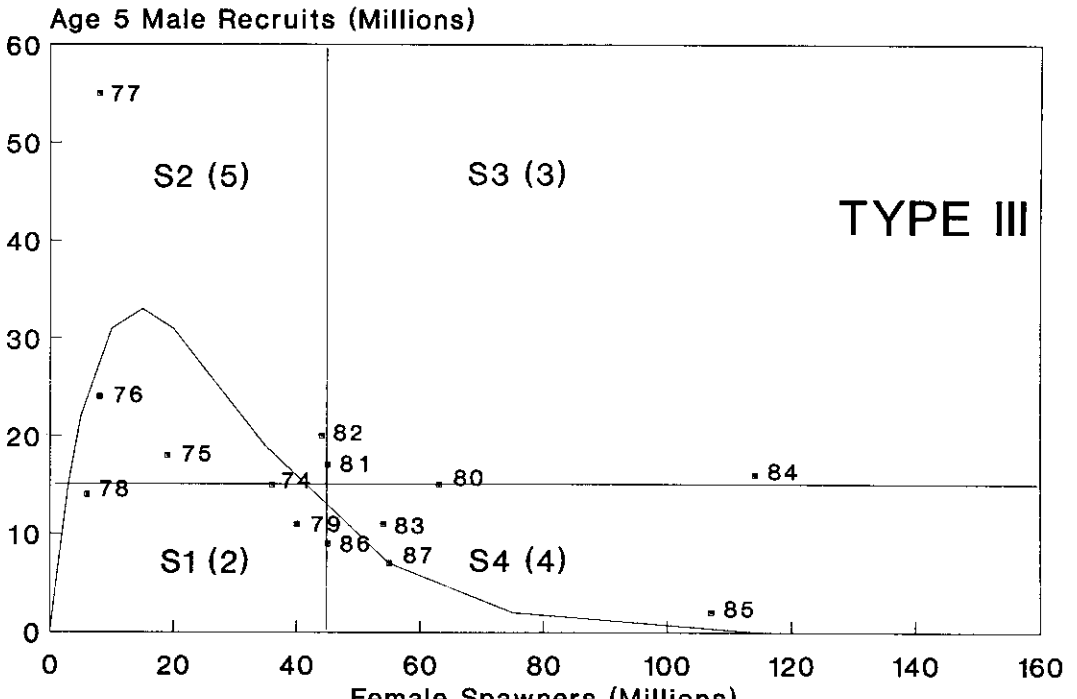

Figure 8b. Non-parametric classification of data corrected for year class strength.

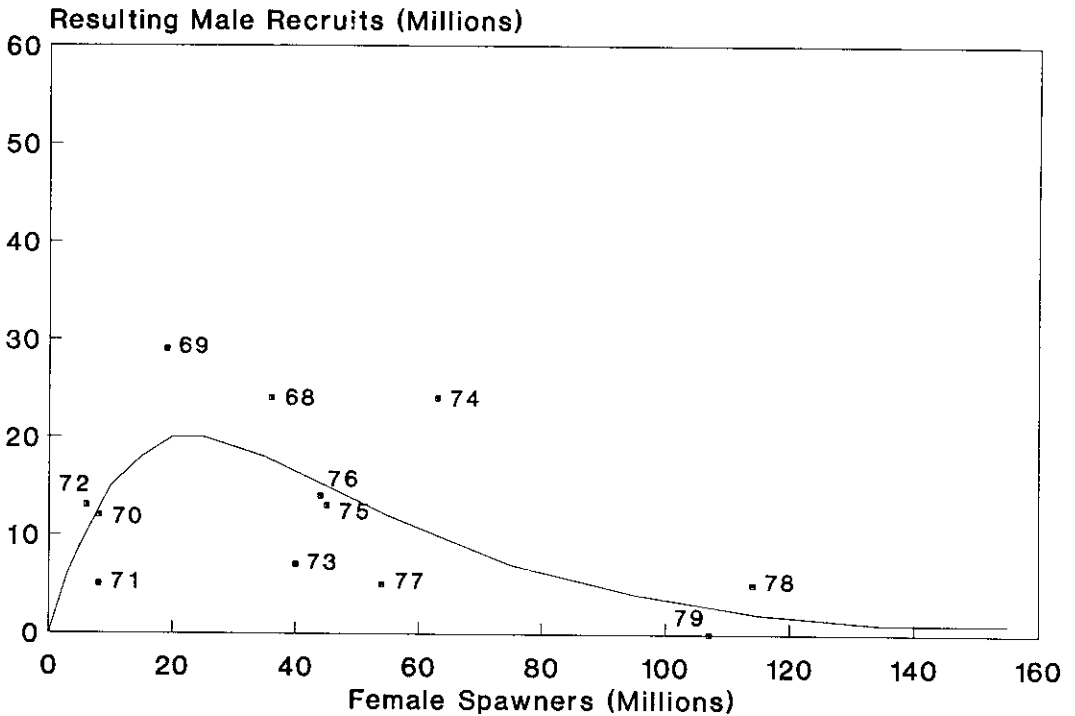

Figure 9a. Recruit values based on temperature-dependent growth (Stevens 1988).

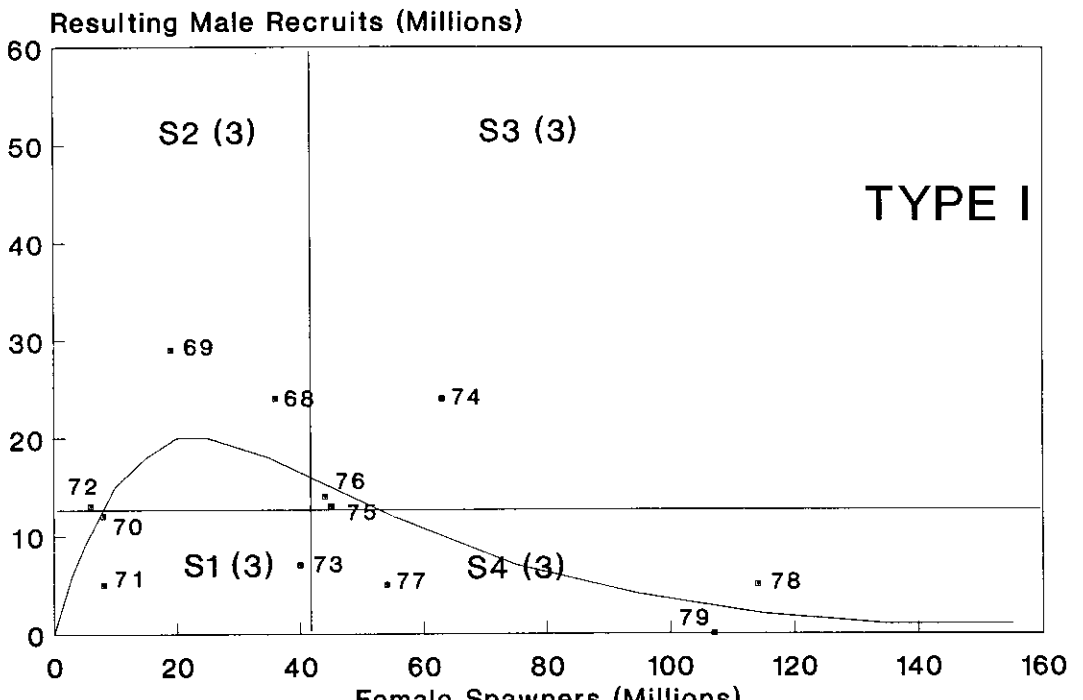

Figure 9b. Non-parametric classification of data based on temperature-dependent growth.

incorporates estimates of molting probabilities, growth per molt and survival to compute size distributions by age for given cohorts of crabs. Size distributions of initial cohorts are computed from input values for mean size and variance and initial number in the cohort. In successive simulation years the number of crabs within each 1-mm size interval is determined by molting probabilities,growth increment and survival for that interval. Growth increments are determined by means of Hiatt plots relating postmolt size to premolt size. Simulation output includes annual size distributions, specified by molting history, of a cohort over its lifespan, as well as the number alive and mean size for each simulation year.

Base parameters for evaluation of recruit estimates are given in table 3, with the exception of molting probabilities which were calculated as the average of the two sets of molting probability functions in Balsiger(1974). Mean size represents age 3 determined from the von Bertalanffy growth curve, its variance having been calculated from data given by Stevens(1989) for crabs of that size. Annual survival is based on an average value calculated from survey age compositions derived from the growth curve. Hiatt parameters were selected to reflect the growth curve, and represent the situation where the increment per molt (year) changes from 15 to 13mm at a size of 100mm. Figure 3 shows distributions for ages 3 through 8 generated by the basic parameter set. During simulations, such "actual" size-at-age distributions were generated and then age groups were estimated from them by taking sections of the overall length range corresponding to growth curve size-at-age intervals, and summing crabs of all ages in each section. As an example, the age 5 recruit length interval estimated from the von Bertalanffy curve is superimposed on the distributions in figure 3.

Simulated actual and estimated numbers at age are shown in figure 4 for the case of constant recruitment. Bias, indicated by the ratio of estimated to actual values, increases with age. It is relatively minor through age 8 and insignificant for ages 4 and 5, but increases at age 9 and above, leading to a tendency of increasing underestimation with age. This tendency is caused by the increasing overlap of size distributions with increasing age. The age of interest in this study is age 5, but it should be noted in passing that age 3-13 Z is overestimated, being .14 for the estimated data set compared to.10 for the actual data. The approximate 95% confidence interval on the estimate includes the actual value, however.

The effect of fluctuating recruitment on the estimates of age 5 males was examined by inducing changes in year class strength similar to those actually observed, as indicated by the uncorrected age 5 index of table 1. The average for this data series is 17 million crabs, with a range of 6-46 million. Thus, simulated year classes were followed through the population at levels of 3 times and .3 times the constant recruitment level to assess the effect on the estimate of age 5 males. These effects are shown in figure 5 where strong and weak recruitment is compared to the constant R case for

age 5. When the strong year class is age 4, age 5 recruits are overestimated; the next year age 5 recruits are underestimated; and in the following year when the strong year class is age 6, recruitment is again overestimated. Slight overestimation occurs the next year but the bias goes to zero thereafter. This pattern is caused by contamination of the estimation interval when the year class is at ages 4 and 6, and exclusion from the interval of significant numbers of age 5 recruits in the intervening year. The pattern is reversed during years of a weak year class. When it is age 5, adjacent age groups are over-represented. The age 6 individuals provide less compensation for the excluded tails of the actual age 5 distribution, causing underestimation. This occurs to a lesser degree with the age 4 year class because its size distribution overlaps less with the estimation interval.

The effect of increased mortality on the estimates of age 5 recruits under variable recruitment is depicted in figure 6. The effect of a strong year class on the estimate is dampened considerably when survival is reduced to 0.5. Conversely, the effect of a weak year class is increased substantially by increased mortality. Weak recruitment combined with increasing mortality approaches the missing year class situation. The performance of the age 5 recruitment estimate based on the growth curve is probably approaching a "worst case" under these conditions.

In order to examine the effect of biased recruit estimates on the spawner-recruit relationship, corrections to the time series were made based on the foregoing analysis of bias. The largest departures from average recruitment occurred in 1977 (+2.7x) and in 1985 (~.35x). The values for the years 1976-78 were divided by the ratios 1.12,.84 and 1.45, respectively (figure 5). Values for 1984-86 were corrected using the ratios .99,3.70 and .82 of figure 6b, since mortality was relatively high during those years. The corrected series is given in table 1. Results of fitting the Ricker model to the corrected scatterplot are shown in figure 7. While variance is increased somewhat, parameter estimates remain essentially unchanged (table 2). Further, a non-parametric classification of both data sets according to the methodology of Rothschild and Mullen (1985) gives quite similar results (figure 8). Both sets exhibit a prepoderance of states two (S2,low stock/high recruitment) and four (S4,high stock/low recruitment), leading to classification as a type III stock which suggests the presence of compensatory mechanisms.

EFFECTS OF TEMPERATURE-DEPENDENT GROWTH VARIABLITY

Stevens (1989) has proposed that temperature is a fundamental determinate of the rate of growth of juvenile red king crabs in Bristol Bay. Under this condition, the time required for a given cohort to reach a given recruit interval will vary according to variation in the temperature regime to which the cohort is exposed. In order to relate progeny to spawning

stock in this situation, either the estimated recruit interval specified for a particular age must vary, or the lag time for a given recruitment to reached a fixed interval must vary. The latter approach has been adopted here to re-estimate the spawner-recruit relationship under the hypothesis of temperature-dependent growth. New recruit values which can be related to a given spawning year were estimated by allocating the original values (95-109mm) to year classes based on the Stevens' growth model. A Ricker fit to the new data points was computed, as well as a non-parametric classification. Results were then compared to the original data set.

Table 5 of Stevens gives the number of each estimated year class recruiting to the 95-109mm interval by year. Summing over year classes by year, proportions were calculated to allocate the value of the recruit interval to year classes for each survey year. Then for each year class, allocated values were summed over years to give the total recruitment contribution. These calculations were done for each of the five recruitment scenarios examined by Stevens and each data set was fit by the Ricker model. Parameter estimates were similar for each scenario so an average of all was computed to simplify comparisons. The average values are given in table 1, associated with the appropriate spawning stock. The time lags implicit in this data set vary from 8-10 years from mating year to recruitment to the 95-109mm interval, compared to a 6-year lag for the original data set.

A fit of the Ricker model to the data is shown in figure 9a, where years of spawning stock estimates are indicated. The associated parameter estimates are given in the last column of table 2. These data indicate a higher S(max), although the approximate 95% confidence interval includes the estimates for the other data sets. The value of R-squared is somewhat improved over the other fits. It should be noted that the points for 1978 and 1979 are underestimated due to incomplete recruitment to the survey, but were included because they are associated with high spawning stocks. Their actual values should not change the parameter estimates substantially in subsequent years, based on the pattern of recruitment in earlier years. Non-parametric classification of the data (figure 9b) indicates a more uniform distribution of points among states, which suggest a Type I stock where no particular form of stock-recruitment control is evident. This is at odds with the parametric analysis, which indicates a better fit to the temperature-dependent data, and suggests that at higher spawner levels recruitment is not related to stock.

DISCUSSION

This study indicates that bias caused by an indirect method of age determination for recruits has not materially affected parameter estimates for the Ricker model, or substantially changed the distribution of data points according to the non-parametric classification of Rothschild and Mullen

(1985). Only the largest departures from average recruitment have been corrected, and the correction factors used are approximate. The need for a more accurate method of dealing with future annual fluctuations in recruitment is apparent. The interaction involved in indirectly estimating recruitment and age-specific mortality from survey abundance estimates suggests that some iterative scheme might be developed, whereby recruits and mortality are estimated alternately in successive iterations until some predetermined level of stability is achieved. Iterative solutions of this type would probably be required for adjacent age groups, as well as the recruit age group. A starting point for such computations might come from a matrix of correction factors relating R to Z, estimated by simulations similar to those described in this study.

Growth parameter inputs to simulations of king crab growth may be out of date, since the last complete analysis was carried out on data from the 1950's and 1960's (Balsiger 1974). Cursory examination of more recent tagging data suggests that growth increments and molting probabilities have not changed. However, a more thorough review of the data is required in order to confirm that conclusion.

Stevens' hypothesis of temperature-dependent growth appears to have more impact on the the spawner-recruit relationship. Results from this model, which estimates a slower rate of growth for immature male crabs, lead to a higher estimate of S(max). This in turn would presumably lead to a somewhat more conservative mode of management in terms of setting exploitation rates. The results of the non-parametric analysis of these data, suggesting that compensatory mechanisms may be lacking, has further implications for management. The depressive effect of high stock sizes on recruitment may not be occurring, making management decisions less critical when stocks are at high levels.

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Alternative Spawner-Recruit Specifications for Alaska Red King Crab: An Empirical Comparison

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INTRODUCTION

The purpose of this paper is to compare and contrast the conceptual basis and empirical results of 5 different spawner-recruit relationships, as they apply to predicting the National Marine Fisheries Service (NMFS) size/age distribution of 5- to 8-year-old male king crab stock categories in Bristol Bay.[1] All 5 model specifications are variants of a basic Ricker framework. Relative merits and deficiencies of each specification are discussed.

The paper is organized in a sequential fashion to help illustrate the conceptual evolution of model development and to enhance the comparative analysis. The presentation begins with a "Simple-Ricker" functional form following that postulated by Reeves (1982); it is truest to the specification most commonly attributed to Ricker (1954). The presentation proceeds to a "Modified-Ricker" framework which explicitly recognizes the potential role of adult male crab. A "Trajectory Adjusted Intrinsic Recruitment Model" (TAIR) then is reviewed. Critical examination of its component parts motivated the "Flexible-Modified-Ricker" specification. The final model framework, "SUR-FMR," embraces a systems approach or cohort analysis in which a seemingly unrelated regressions estimation is applied to a variation of the Flexible-Modified-Ricker. This last model is most defensible biologically and statistically.

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[1]Age and size categories are used interchangeably throughout this paper. Following NMFS age/carapace length composition data, male5 = 95-109mm, male6 = 110-119mm, male 7 = 120-129mm, male 8 = 130-139mm, and male 9-14 ≥ 140mm.

The analysis is based on the 1968-87 NMFS annual trawl survey data for the Bristol Bay portion of the Southeastern Bering Sea. Model results reported here pertain to biomass estimates, measured in millions of pounds.

Care was taken to internalize a variety of suggestions raised by NMFS concerning the earlier Matulich, Hanson, and Mittelhammer (1988) research. In particular, excessive use of indicator variables, lack of concavity in the adult male direction and the need for weighted least squares are addressed throughout this analysis.

SIMPLE-RICKER

The general form of the Simple-Ricker model is presented in equation (1).

$$\text{(1)} \qquad \text{Male } a_t = \beta_0 F_{t-(a+1)} \exp(\beta_1 F_{t-(a+1)})$$

Age-specific male recruitment (Male a_t) is a function of adult female parental stock ($F_{t-(a+1)}$) where male recruitment and adult female stocks are measured in millions of pounds of biomass. Adult female biomass is defined as all females 5 years old and older. Male recruitment into the ath age class in period t is a function of lagged (t-(a+1)) adult female stock, reflecting the approximate time period required for gestation and growth of progeny into the given age/size class. The principal merits of this specification are two-fold: 1) it is simple, and 2) it allows for concavity or density dependent recruitment, providing $\beta_1 < 0$.

A shortcoming of this Simple-Ricker model is that it ignores the explicit contribution of adult male breeding stock. This omission establishes it as a significant departure from the Ricker's original work in which total broodstock biomass was the explanatory variable--not just adult females. Absence of adult males as an explanatory variable forecloses any policy feedback between harvest and future stock formation.

Individual recruitment models were estimated for male 5-, 6-, 7-, and 8-year-old recruitment. The 1977 male 5- and 6-year-old observations are regarded outliers and are dropped from the estimation, as suggested by Terry (personal communication, 1988). Parameter estimates for each of the age classes considered are presented in Table 1 along with the associated t-statistics (in parentheses). The t-statistics associated with the leading term (β_0) test the hypothesis that the coefficient is 1.0. All other t-statistics refer to tests that the parameter equals zero.

All parameters in the age-specific Simple-Ricker models are correctly signed and statistically significant at the 0.05 level. The simulated R^2 values range from a low of only 26.0% in the male 5-year-old model, to a high of 65.6% in the male 6-year-old model. Mean Square Error (MSE) varied from a low of 83.0 in the 6-year-old model to a high of 805.2 in the 8-year-old equation.

MODIFIED-RICKER

A variation of the Simple-Ricker functional form is considered in the Modified-Ricker framework presented in equation (2).

$$\text{(2)} \qquad \text{Male } a_t = \beta_0 F_{t-(a+1)} \exp(\beta_1 F_{t-(a+1)} + \beta_2 FM_{t-(a+1)} + \beta_3 M_{t-(a+1)})$$

TABLE 1. Simple-Ricker Recruitment Model Parameter Estimates for 5-, 6-, 7-, and 8-Year-Old Male Alaskan Red King Crab (millions of pounds, 1968-1987)

Model	Parameter Values		Goodness-of-Fit Statistics					
	β_0	β_1	R^2	U1	M%E	MAE	MSE	DF
MALE5	2.55580 (2.10)	-0.02298 (-6.10)	0.260	0.4166	-3.416	-7.177	159.520	11
MALE6	2.92421 (3.17)	-0.02561 (-8.42)	0.629	0.3178	-2.395	-10.746	82.987	10
MALE7	4.87036 (3.97)	-0.02732 (-7.71)	0.656	0.3415	6.392	12.142	250.180	10
MALE8	5.55020 (2.58)	-0.02749 (-4.84)	0.465	0.4799	64.120	23.330	805.170	9

t-statistics on β_0 coefficient tests the null hypothesis that the coefficient = 1.0.

Goodness-of-fit statistics were simulated over the estimated model.

1977 is omitted from the 5- and 6-year-old equations as an outlier observation.

Male recruitment into the ath age class in period t is a function of adult female stock, adult male stock and the product of adult females and adult males (FM), all lagged (t-(a+1)) years. This specification is consistent with Matulich, Hanson, and Mittelhammer (1988). As in the Simple-Ricker model, all variables are in millions of pounds of biomass.

Inclusion of adult male stock as an explanatory variable is an explicit recognition of the contribution of males to stock formation. It also provides a feedback linkage between current period harvests and future recruitment. As before, parameter sign specification was not restricted a priori, but had to meet minimal "reasonableness" criteria. In particular, concavity (density dependence), at least in the female direction, is essential. This requires the following parameter signs: $\beta_1<0$, $\beta_2>0$, and $\beta_3<0$.

There are two principal deficiencies with the Modified-Ricker approach. First, each age-specific Modified-Ricker model has two fewer degrees of freedom than its Simple-Ricker counterpart. The degree of freedom loss is most critical in the 8-year-old recruitment model, which also requires a 9-year parental stock lag.

The second cost associated with incorporating adult male breeders concerns the asymptotic properties of this specification. The Modified-Ricker model is concave only in the female direction. It permits large male recruitment in the absence of a male parental stock. This implication clearly is untenable. Like the Simple-Ricker model, the Modified-Ricker model should be viewed as representative of recruitment behavior only over the relevant range of data. A zero or near-zero male parental stock has never been observed. Thus, the asymptotic character of this function has no practical policy significance so long as regulatory constraints prevent dropping below some threshold or minimal stock of breeding males. Attempts to impose concavity in both the male and female directions is discussed in a later section of this paper.

The statistical results for the 4 estimated age-specific Modified-Ricker recruitment functions are reported in Table 2. The age-specific Modified-Ricker recruitment function out performed its Simple-Ricker counterpart. For example, all R^2 are higher, ranging from a 32.4% increase for the 6-year-old equation to a 145.0% increase in the 5-year-old equation. Furthermore, the average MSE for the 4 Modified-Ricker equations (167.93) is almost half the average MSE of the 4 Simple-Ricker equations (324.46). Unfortunately, significance and a priori sign expectations are lost on several parameters in the 7- and 8-year-old equations.

Why this model specification failed to perform well in the 7- and 8-year-old equations is unclear. Build-up of cumulative predictive error was posited as a contributing factor. The Modified-Ricker approach ignores a variety of potential sources of predictive error that impacts the intrinsic spawner-recruitment trajectory. Potential sources of error include the effects of: cyclic variations, environmental perturbations, structural changes in survival or mortality, measurement errors of parental stock that is used to predict abundance of some subsequent age class, and even errors inherent in using a 1-year lag structure between carapace size categories to estimate king crab age classes. The further a particular age class is removed from parental spawning stock estimates, the greater the potential for cumulative predictive error. This reasoning motivated development of the Trajectory Adjusted Intrinsic Recruitment Framework (TAIR).

TABLE 2. Modified-Ricker Recruitment Model Parameter Estimates for 5-, 6-, 7-, and 8-Year-Old Male Alaskan Red King Crab (millions of pounds, 1968-1987)

Model	Parameter Values				Goodness-of-Fit Statistics					
	β_0	β_1	β_2	β_3	R^2	U1	MXE	MAE	MSE	DF
MALE5	4.75524 (3.81)	-0.03419 (-7.67)	0.000052 (5.54)	-0.00369 (-2.49)	0.637	0.2275	6.997	5.483	58.150	9
MALE6	4.63435 (4.46)	-0.02508 (-8.02)	0.000043 (5.06)	-0.00670 (-4.46)	0.841	0.1748	4.895	3.709	31.381	8
MALE7	3.09976 (1.82)	-0.00960 (-1.22)	-0.000104 (-1.35)	0.00273 (0.39)	0.869	0.2571	-24.146	9.428	177.280	8
MALE8	1.59543 (0.47)	0.00683 (0.53)	-0.000254 (-1.84)	0.01130 (1.16)	0.821	0.3001	-14.201	11.980	404.910	7

t-statistics on β_0 coefficient tests the null hypothesis that the coefficient = 1.0.

Goodness-of-fit statistics were simulated over the estimated model.

1977 is omitted from the 5- and 6-year-old equations as an outlier observation.

TRAJECTORY ADJUSTED INTRINSIC RECRUITMENT MODEL (TAIR)

An adjustment framework was developed to proxy the cumulative deviations from intrinsic recruitment tendencies. Specifically an intermediate observation of age-class abundance is used to adjust the intrinsic recruitment trajectory and improve the estimate of actual age-class development. The TAIR specification is illustrated in equation (3) for 7-year-old male king crab recruits.

$$(3) \qquad \text{Male7}_t = (\text{Male7}_t^*)^{\beta_4} (c_7\text{Male6}_{t-1})^{\beta_5}$$

Recruitment of 7-year-old male king crab is formulated as a geometric weighted average of 2 expectations. The intrinsic spawner-recruit trajectory, (Male7_t^*), is specified as a Modified-Ricker.

$$(4) \qquad \text{Male7}_t^* = \beta_0 F_{t-8} \exp(\beta_1 F_{t-8} + \beta_2 FM_{t-8} + \beta_3 M_{t-8})$$

That trajectory is formed 8 years earlier, based solely upon spawning stock biomass.

Adjustment to the intrinsic recruitment trajectory involves 2 components: 1) the second expectation $c_7\text{Male6}_{t-1}$, formed as the growth/survival of an intermediate observation of prerecruit biomass, and 2) geometric weights (β_4 and β_5) that measure the relative importance of each expectation. These components adjust the intrinsic recruitment trajectory to more accurately reflect actual spawning, growth and survival. Accordingly, this weighted adjustment process proxies cumulative effects of predictive error that cannot be modelled at the time of spawning. The parameter c_7 is an age-specific growth/survival rate. The adjustment term is incorporated multiplicatively because Ricker (1954, pg. 573) argued that inclusion of ". . . environmentally caused deviations from the reproductive norm must be multiplicative rather than additive."

The TAIR specification is empirically flexible, permitting the data to determine the tendency toward intrinsic recruitment. If $\beta_5 = 0$ and $\beta_4 = 1.0$, then the Modified-Ricker specification given in (4) predicts observed recruitment. If $\beta_5 = 1.0$ and $\beta_4 = 0$, growth/survival of observed prerecruit biomass is sufficient to explain age class recruitment. When neither of these parameters is zero, then the TAIR specification predicts recruitment through an adjustment to the intrinsic recruitment rate.

Two parameters (β_0 and c_7) in equations (3) and (4) cannot be identified statistically as separate parameters. An estimable but more aggregate form of (2) that combines the influence of these parameters is given by

$$(5) \qquad \text{Male7}_t = \overset{*}{\beta}_0 F_{t-8}^{\beta_4} \exp(\overset{*}{\beta}_1 F_{t-8} + \overset{*}{\beta}_2 FM_{t-8} + \overset{*}{\beta}_3 M_{t-8})\text{Male6}_{t-1}^{\beta_5}$$

where $\beta_0^* = \beta_0^{\beta_4} c_7^{\beta_5}$

$\beta_i^* = \beta_i \beta_4$, i = 1, 2, 3

$\beta_1^*, \beta_3^* < 0 \quad \beta_2^*, \beta_4, \beta_5 \geq 0$.

There are 2 main conceptual deficiencies to the TAIR specification, First, it retains the same general asymptotic property of recruitment at low male parental stocks that characterizes the Modified-Ricker specification. The geometric weight parameters also cost two additional degrees of freedom.

Prior TAIR modelling (Matulich, Hanson, and Mittelhammer, 1988) assumed prima facie heteroscedasticity in the male 7- and 8-year-old models due to the extreme range in data. Accordingly, the estimation technique was weighted non-linear least squares. A Park-Glejer test for heteroscedasticity failed to detect heteroscadasticity in any current TAIR model; weighting was dropped.

As before, a 5-year-old TAIR recruitment model was not estimated. The 4-year-old prerecruit biomass estimates needed to specify the 5-year-old TAIR model is believed to be substantially flawed due to sampling error. Four-year-old king crab escape full recruitment into the survey gear. The Modified-Ricker model is retained as the male 5-year-old prediction equation.

The 3 estimated TAIR recruitment models are reported in Table 3. The goodness of fit statistics for each age-specific TAIR model are clearly superior to their respective Modified-Ricker counterparts. The most notable improvement occurs in the 7- and 8-year-old TAIR models. MSE of the 7-year-old TAIR model is one-third as large as that of Modified-Ricker and one-quarter that of the Simple-Ricker. The 8-year-old TAIR MSE is one-sixth as large as its Modified-Ricker counterpart--one-thirteenth as large as the corresponding Simple-Ricker model. The Mean Percent Error (M%E) and Mean Absolute Error (MAE) are both much smaller for the 7- and 8-year-old TAIR models relative to their respective Simple- and Modified-Ricker models. The incorrect parameter signs obtained in the 7- and 8-year-old Modified-Ricker models now are both correct and statistically significant at the .05 level or lower in the TAIR specification.

Ironically, the adjustment parameter (β_5) is insignificant in all 3 age-specific TAIR models. This result raised the question as to whether the improved fits are a consequence of the weighted adjustment term $(c_7 \text{Male}6_{t-1})^{\beta_5}$ in equation (3).

FLEXIBLE-MODIFIED-RICKER (FMR)

Truncating the TAIR specification in equation (5) results in the flexible-Modified-Ricker (FMR) recruitment function given in equation (6):

$$(6) \quad \text{Male } a_t = \beta_0^* F_{t-(a+1)}^{\beta_4} \exp(\beta_1^* F_{t-(a+1)} + \beta_2^* FM_{t-(a+1)} + \beta_3^* M_{t-(a+1)})$$

TABLE 3. Trajectory Adjusted Intrinsic Recruitment Model (TAIR) Parameter Estimates for 6-, 7-, and 8-Year-Old Male Alaskan Red King Crab (millions of pounds, 1968-1987)

Model	Parameter Values						Goodness-of-Fit Statistics					
	B_0	B_1	B_2	B_3	B_4	B_5	R^2	U1	M%E	MAE	MSE	DF
MALE6	0.52776 (-0.53)	-0.03198 (-2.44)	0.000052 (2.42)	-0.00749 (-3.37)	1.43185 (2.72)	0.261685 (1.24)	0.883	0.1486	2.497	3.302	30.251	6
MALE7	0.04875 (-12.76)	-0.07023 (-3.26)	0.000125 (3.15)	-0.01501 (-3.76)	2.97938 (3.78)	0.07684 (0.28)	0.943	0.1391	1.183	5.173	69.160	6
MALE8	0.00087 (-421.61)	-0.09697 (-1.94)	0.000171 (2.16)	-0.02041 (-2.17)	4.04625 (1.98)	0.49153 (0.86)	0.978	0.1003	-2.010	4.549	63.367	5

t-statistics on B_0 coefficient tests the null hypothesis that the coefficient = 1.0.

Goodness-of-fit statistics were simulated over the estimated model.

1977 is omitted from the 6-year-old equation as an outlier observation.

where all parameters are defined as in equation (5). Dropping the * notation for expository simplicity, this FMR specification is identical to that of the Modified-Ricker model, with the exception of the β_4 exponent on the leading female term.

The significance of the flexibility parameter (β_4) becomes apparent by viewing the Ricker framework in a somewhat unconventional, albeit, conceptually simple context. Cushing (1973) describes the basic Ricker model, such as equation (1), as a product of density independent and density dependent components. The leading linear term, $\beta_0 F_{t-(a+1)}$, is purported to be the density independent component, whereas the exponential term, $\exp(\beta_1 F_{t-(a+1)})$, is the density dependent term.

This view serves to obfuscate the simple elegance of the Ricker framework and its inherent weakness. When viewed in a classical production function context, a Ricker model is directly interpretable as a yield per adult female relationship. This is first shown for the Simple-Ricker and then for the Flexible-Modified-Ricker.

Equation (1) is identical algebraically to

$$(7) \qquad \text{MALE } a_t/F_{t-(a+1)} = \beta_0 \exp(\beta_1 F_{t-(a+1)})$$

where $\beta_0 > 0$ and $\beta_1 < 0$, as before. This average product relation has the tenuous property of declining average productivity over any level of female breeding stock. That is, the Simple-Ricker model requires that each additional adult female is less productive than the preceding one--regardless of parental stock levels. This conclusion is easily verified by evaluating the partial derivative of the female average product relation in equation (7) with respect to females.

$$(8) \qquad \frac{\partial [\cdot]}{\partial F_{t-(a+1)}} = \beta_0 \exp(\beta_1 F_{t-(a+1)}) \beta_1 < 0$$

given $\quad \beta_0 > 0$ and $\beta_1 < 0$.

The Flexible-Simple-Ricker approach allows for both increasing and decreasing yield per female (average product). Incorporating the flexibility parameter, β_4, into equation (1) yields

$$(9) \qquad \text{Male } a_t = \beta_0 F_{t-(a+1)}^{\beta_4} \exp(\beta_1 F_{t-(a+1)})$$

with the corresponding average product given in equation (10).

$$(10) \qquad \frac{\text{Male } a_{t-(a+1)}}{F_{t-(a+1)}} = \beta_0 F_{t-(a+1)}^{\beta_4 - 1} \exp(\beta_1 F_{t-(a+1)})$$

Given the signing convention that $\beta_0 > 0$, $\beta_4 > 1$, and $\beta_1 < 0$, the average product relation in equation (10) exhibits first increasing yield per female and then decreasing yield per female--a more believable theoretical construct.[2]

Extension to the FMR specification adds an additional signing requirement to maintain biological integrity. The yield per female relation corresponding to the FMR model given in equation (6) is

$$\text{(11)} \qquad \text{Male } a_t/F_{t-(a+1)} = \beta_0 F_{t-(a+1)}^{\beta_4 - 1} \exp(\beta_1 F_{t-(a+1)} + \beta_2 FM_{t-(a+1)} + \beta_3 M_{t-(a+1)})$$

This relation exhibits rising then falling average productivity when,

$$\frac{\partial[\cdot]}{\partial F_{t-(a+1)}} \gtreqless 0 \text{ as } F \gtreqless \frac{\beta_4 - 1}{-(\beta_1 + \beta_2 M)} \text{ and } -\beta_1 > \beta_2 M$$

where $\beta_1 < 0$, $\beta_2 > 0$, $\beta_3 < 0$, and $\beta_4 > 1$.

The additional term in the denominator is a consequence of direct recognition of males in the Modified-Ricker specification. The additional signing convention requiring $-\beta_1 > \beta_2 M$ is essential to assure that average product eventually declines.

The parameter estimates for the 4 age-specific FMR models are reported in Table 4 along with their t-statistics (in parentheses) and goodness of fit statistics. The t-statistics refer to tests that the parameters equal zero, except for β_0 and β_4, which are tested against 1.0.

---

[2] $$\frac{\partial[\cdot]}{\partial F_{t-(a+1)}} = \beta_0(\beta_4 - 1) F_{t-(a+1)}^{\beta_4 - 2} \exp(\beta_1 F_{t-(a+1)}) \beta_1 + \beta_0 F_{t-(a+1)} \exp(\beta_1 F_{t-(a+1)})$$

Collecting terms yields

$$= \beta_0(\beta_4 - 1) \exp(\beta_1 F_{t-(a+1)}) \left(\frac{\beta_4 - 1}{F_{t-(a+1)}}\right) + \beta_1 \ .$$

Therefore,

$$\frac{\partial[\cdot]}{\partial F_{t-(a+1)}} \gtreqless 0 \text{ as } F_{t-(a+1)} \gtreqless \frac{\beta_4 - 1}{-\beta_1}$$

The signing convention $\beta_1 < 0$ and $\beta_4 > 1$, assures rising then falling average product.

TABLE 4. Flexible-Modified-Ricker Recruitment Model Parameter Estimates for 5-, 6-, 7-, and 8-Year-Old Male Alaskan Red King Crab (millions of pounds, 1968-1987)

Model	Parameter Values					Goodness-of-Fit Statistics					
	β_0	β_1	β_2	β_3	β_4	R^2	U1	MXE	MAE	MSE	DF
MALE5	13.51090 (0.54)	-0.02429 (-1.48)	0.000037 (1.42)	-0.00228 (-0.82)	0.56802 (-0.61)	0.651	0.2219	8.927	5.325	62.265	8
MALE6	1.70427 (0.32)	-0.03560 (-2.67)	0.000059 (2.70)	-0.00805 (-3.52)	1.42313 (0.80)	0.852	0.1679	3.379	3.806	33.079	7
MALE7	0.04674 (-14.19)	-0.07490 (-4.78)	0.000123 (4.53)	-0.01578 (-5.25)	3.13769 (3.54)	0.941	0.1400	0.724	5.269	60.050	7
MALE8	0.00009 (-5689)	-0.14270 (-6.83)	0.000243 (6.29)	-0.02897 (-6.30)	5.91340 (6.05)	0.976	0.1066	-4.463	4.681	59.577	6

t-statistics on β_0 and β_4 coefficients test the null hypothesis that the coefficient = 1.0.

Goodness-of-fit statistics were simulated over the estimated model.

1977 is omitted from the 5- and 6-year-old equations as an outlier observation.

All parameters are statistically significant and correctly signed in the 7- and 8-year-old FMR model. Insignificance of the flexibility parameter, β_4, in the 5- and 6-year-old equations may be due to less accurate measurements of observed Male5 and Male6 stocks.

The additional flexibility of the FMR specification corrects for both the lack of significance and/or incorrect parameter signs reported for the β_1, β_2, and β_3 parameters in the 7- and 8-year-old Modified-Ricker equations. Moreover, even though they have one more degree of freedom, the 7- and 8-year-old FMR models have a smaller MSE than their TAIR counterparts.

Each age-specific FMR model has a larger R^2 and smaller MSE relative to the Simple-Ricker counterpart. The improvement in statistical fit is most notable in the 8-year-old equation. The R^2 is nearly twice as large as the Simple-Ricker specification (91.0% versus 46.5%) and its MSE is less than one-thirteenth as large (59.6 versus 805.2).

SEEMINGLY UNRELATED REGRESSION--FLEXIBLE-MODIFIED-RICKER (SUR-FMR)

Each of the preceding age-class models suffers from a major conceptual deficiency; they fail to recognize that all age classes within a single cohort share a common parental stock. For example, male 5-year-olds in year t, male 6-year-olds in year t+1, male 7-year-olds in year t+2, and male 8-year-olds in year t+3 derive from an identical parental stock. The practical implication of this commonalty is that each member of the cohort shares a common spawner-recruit trajectory from year t-6 (the time period in which the cohort was spawned) to year t (the time period in which the cohort was 5 years old). The cohort's biomass trajectory then may be extended to 6-year-olds in year t+1 by adjusting the underlying trajectory for mortality and growth. Similarly, the population trajectory may be adjusted for 6- and 7-year-old mortality and growth, yielding the beginning of year populations of male 7- and 8-year-olds in year t+2, and t+3, respectively.

Accounting for the commonalty between individual age classes within a cohort requires adjustment to the previous modelling procedure. Rather than specifying age-specific, and thus, independent spawner-recruit functions, the approach taken here is to share a single spawner-recruit function among the prediction equations for male 5- to 8-year-olds. The system of prediction equations is provided in (12).

$$
\begin{aligned}
&\text{Male5}_t = f(\text{Adult}_{t-6}) \\
&\text{Male6}_{t+1} = f(\text{Adult}_{t-7})(\text{Wt}_6/\text{Wt}_5)\exp(z_5) \\
(12)\quad &\text{Male7}_{t+2} = f(\text{Adult}_{t-8})(\text{Wt}_7/\text{Wt}_5)\exp(z_5+z_6) \\
&\text{Male8}_{t+3} = f(\text{Adult}_{t-9})(\text{Wt}_8/\text{Wt}_5)\exp(z_5+z_6+z_7) \\
&\text{Male 9-14}_{t+4} = (\text{male 8-14}_{t-1} - \text{Harvest}_{t-1})\exp(z_{814})
\end{aligned}
$$

where $f(\text{Adult}_{t-6})$ represents a common spawner-recruit function; Wt_5, Wt_6, Wt_7, and Wt_8 are the constant biomass weights of male 5-, 6-, and 7-year-olds, respectively; z_a, a=5,6,7,814, are the 5-, 6-, 7-, 8 to 14-year-old survivability coefficients.

The system of equations specified in (12) portrays male 5-year-olds as a function of the parental stock 6 years previously. Male 6-year-olds are a function of the common spawner-recruit function, and the male 5-year-old growth and mortality rates. Male 7-year-olds is modelled as a function of all the factors in the 6-year-old equation, and the 6-year-old growth and mortality rates. Male 8-year-olds similarly are expressed as a function of all the factors in the 7-year-old equation, and the 7-year-old growth and mortality rates.

An aggregate age class (male 9-14$_t$) is specified for 9 to 14-year-old males for several reasons. First, the age class is managed as a composite class of legal crabs; management does not, nor is it expected to, discriminate among these larger size categories. Second, individual age/size class models similar to male 5$_t$ to male 8$_t$ would exhaust too many degrees of freedom. Third, isolating the transition from 8- to 9-year-olds would require a tenuous assumption concerning the age/size distribution of harvest, for which there is no data. Accordingly, male 9-14$_t$ is specified as a simple function of unharvested 8 to 14-year-old crab in the previous period, and a composite growth/mortality rate. A common error term is shared across all equations.

The proposed cohort analysis offers other conceptual advantages over the single equation approach previously discussed. For one, it bases spawner-recruit function estimation on several successive observations of a cohort, as opposed to a single observation per year. This operational feature of a systems approach is more advantageous than it might first seem. The NMFS trawl survey data suffer from a variety of inconsistencies, probably due to a combination of survey error and problems inherent in using carapace size to estimate crab age. However, use of several observations on a cohort that was spawned by the same parental stock lessens the influence of any single anomalous observation on the underlying spawner-recruit function.

A related benefit of the systems approach to cohort analysis is the pooling of cross sectional and time series data. The resultant increase in observations and decrease in equation-specific parameters gains degrees of freedom. This benefit is especially important to this research since few degrees of freedom plagued the preceding spawner-recruit models.

An additional attraction of the systems approach specified in (12) is that the passforward framework provides mortality rate estimates for 5-, 6-, 7-, and 8 to 14-year-old age classes. A final benefit is that a consistent model form is used for population estimates of all sublegal age classes.

The system of equations was estimated in the form presented in (13). The spawner-recruit function is modelled as a FMR. The results from this specification were superior to all other spawner-recruit specifications modelled. The SUR-FMR retains the undesirable asymptotic properties at low male stocks discussed previously.

$$\text{Male5}_t = \beta_0 F_{t-6}^{\beta_4} \exp(\beta_1 F_{t-6} + \beta_2 FM_{t-6} + \beta_3 M_t\text{-}6)$$

$$\text{Male6}_t = \beta_0 F_{t-7}^{\beta_4} \exp(\beta_1 F_{t-7} + \beta_2 FM_{t-7} + \beta_3 M_{t-7})(2.52/1.77)\exp(z_5)$$

(13)
$$\text{Male7}_t = \beta_0 F_{t-8}^{\beta_4} \exp(\beta_1 F_{t-8} + \beta_2 FM_{t-8} + \beta_3 M_{t-8})(3.31/1.77)\exp(z_5 + z_6)$$

$$\text{Male8}_t = \beta_0 F_{t-9}^{\beta_4} \exp(\beta_1 F_{t-9} + \beta_2 FM_{t-9}$$

$$+ \beta_3 M_{t-9})(4.27/1.77)\exp(z_5 + z_6 + z_7)$$

$$\text{Male9-14}_t = (\text{Male8-14}_{t-1} - \text{Harvest}_{t-1})\exp(z_{814})$$

where all variables are as previously defined. The parameters β_0-β_4 are shared across equations. A priori expectations were that β_1, β_3, z_5, z_6, and z_7 would be negative, z_{814} would be indeterminate since it is a net mortality/growth parameter, β_0 and β_2 would be positive, and $\beta_4 > 1$. A separate growth/mortality rate was hypothesized for the period beginning in 1981. Variations on this hypothesis were evaluated with an indicator variable on z_a.

The SAS nonlinear SUR (seemingly unrelated regression) procedure, SYSNLIN, was used in model estimation. SUR was used because cross equation restrictions require identical parameter estimates (β_0-β_4) within the spawner-recruit function; the individual mortality parameters (z_a) varied freely across equations. The 9 year lag defining 8-year-old parental stock dictated 1977 as the first year for which a complete data set could be specified. The 1977 observations on 5- and 6-year-olds were regarded as outliers. Rather than eliminating all 1977 observations by marking them with an indicator variable, a cubic spline was fit to the data.[3] Replacement biomass values of 50.25 and 51.48 for male 5- and 6-year-olds, respectively, were inserted into the data set.

The model estimates are presented in Table 5 with t-ratios presented parenthetically. The t-ratios report whether a particular parameter was significantly different than zero, except for β_0 and β_4 which test whether they differ significantly from 1.0. The results are for the only model in which a statistically significant structural change in mortality was found, i.e., a change in male 8 to 14-year-old mortality. This structural break is evident only for the period 1981 through 1985. The reported composite age class model was specified as

[3]Marking any one annual observation requires marking all observations for that year. Otherwise, the SUR variance-covariance estimates are biased. Use of the cubic spline avoided loss of information.

TABLE 5. Seemingly Unrelated Regression - Flexible-Modified-Ricker (SUR-FMR) Recruitment Model Parameter Estimates for 5-, 6-. 7-, and 8- and 9- to 14-Year-Old Male Alaskan Red King Crab (millions of pounds, 1968-1987)

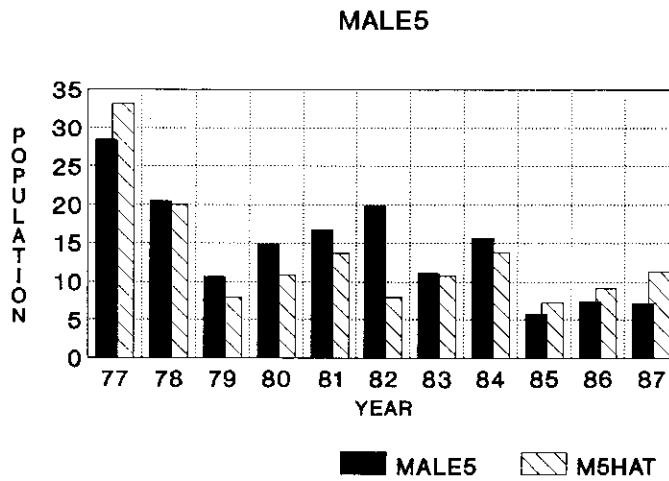
Age Class	Parameter Values										Goodness-of-Fit Statistics				
	B_0	B_1	B_2	B_3	B_4	Z_5	Z_6	Z_7	Z_{814}	Z_{814A}	R^2	U1	MXE	MAE	MSE
MALE5	0.00448 (-295.98)	-0.0990 (-12.07)	0.00175 (11.79)	-0.02161 (-13.52)	4.21270 (12.75)						0.638	0.287	-1.89	5.88	64.26
MALE6	0.00448 (-295.98)	-0.0990 (-12.07)	0.00175 (11.79)	-0.02161 (-13.52)	4.21270 (12.75)	-0.66290 (-8.43)					0.880	0.212	-10.23	4.26	30.95
MALE7	0.00448 (-295.98)	-0.0990 (-12.07)	0.00175 (11.79)	-0.02161 (-13.52)	4.21270 (12.75)	-0.66290 (-8.43)	-0.12389 (-1.86)				0.943	0.144	-0.96	4.77	31.53
MALE8	0.00448 (-295.98)	-0.0990 (-12.07)	0.00175 (11.79)	-0.02161 (-13.52)	4.21270 (12.75)	-0.66290 (-8.43)	-0.12389 (-1.86)	-0.10678 (-1.69)			0.962	0.151	30.33	6.72	65.60
MALE914									0.01997 (0.90)	-0.65354 (-5.06)	0.988	0.081	28.85	7.54	96.03

t-statistics on B_0 and B_4 coefficients test the null hypothesis that the coefficient = 1.0.

Goodness-of-fit statistics were simulated over the estimated model.

The 1977 observation of 5- and 6-year-olds were replaced with a cubic spline estimate.

System degrees of freedom = 36



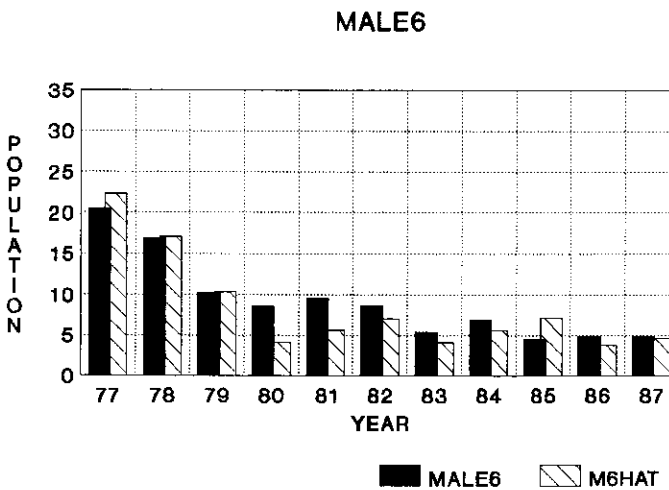
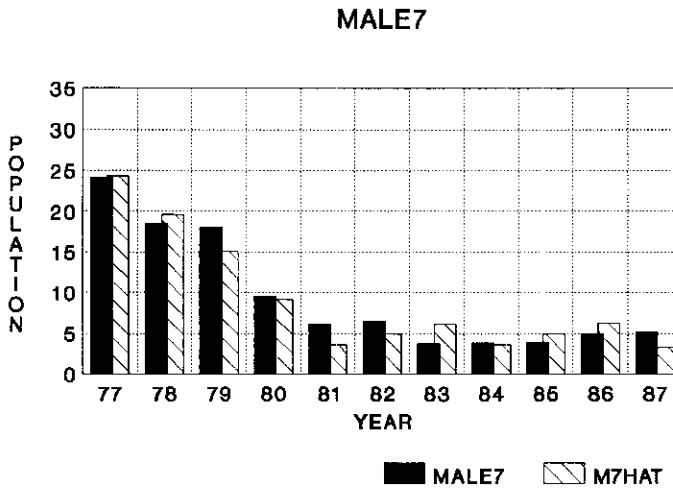


Figure 1. SUR-FMR predicted vs. observed population estimates--males 5-8 years old, in millions.



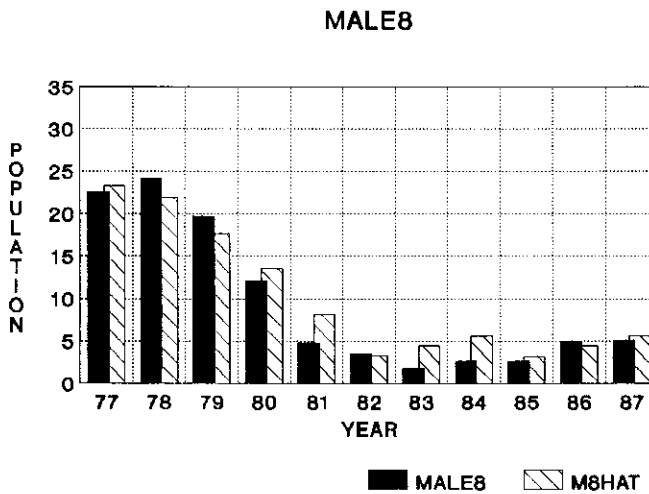


Figure 1. continued.

$$\text{Male } 9\text{-}14_t = (\text{Male } 8\text{-}14_{t-1} - \text{Harvest}_{t-1})\exp(z_{814} + I_{8185} z_{814A})$$

where: I_{8185} is an indicator variable marking 1981 to 1985, z_{814} is the growth mortality parameter for the years 1977-80 and 1986-87, z_{814A} is the growth mortality parameter for 1981-85.

All parameters are significant at the 0.001 level with the exception of z_6, z_7, z_{814}, z_6, and z_7 are significant at the 0.13 level, while z_{814} is not statistically different from zero over the two periods 1977-80 and 1986-87. In other words, growth offsets mortality. The signs on all parameters conformed to a priori expectations. The goodness of fit statistic indicate that the predictive accuracy of each age class is quite good. The R^2 ranges from 0.64 for the 5-year-old equation to 0.96 for the 9- to 14-year-old equation, while MSE ranges from 30 for the 6-year-old equation to 66 for the 9- to 14-year-old equation. Note, also, that the system degrees of freedom are 36. This represents a significant improvement over the single-equation confidence intervals.

Figures 1 and 2 further illustrate the overall excellent system-wide fit. They also bring attention to the principal strength of this type of cohort analysis. The single-equation approach taken in previous sections imposes a single-minded standard of predictive accuracy--closeness of fit relative to individual observations. That criterion is inherently flawed when the underlying trawl survey data is known to contain two types of inconsistencies: over or under reporting of the actual population, and the appearance of increasing population within a cohort. The systems approach to stock estimation imposes a second criterion on parameter estimation and model performance. Closeness of fit relative to an individual observation within any age class is tempered by the influence of that prediction on prior and/or subsequent age classes.

Consider Figure 3. The prediction of the 1982 population of 5-year-olds overestimates the observed population by 12 million crab. However, examination of the cohort reveals that the 1983-85 estimates of male 6-, 7-, and 8-year-olds, respectively, are close to the observed populations. The survey data suggest an extremely high, probably unrealistic (73%) mortality rate affecting male 5-year-olds in 1982. A strength of the cohort framework is that it smooths these types of extremes. Consistency across a cohort may necessitate substantial deviations between predicted and observed population for a single age class.

The SUR-FMR approach avoids the second problem of increasing cohort population over time provided that the survivability coefficients (z_a) are negative. The results in Table 5 indicate this is the case. Converting the estimated survivability coefficients to mortality rates, m_a, as below,

$$(14) \quad m_a = 1 - \exp(z_a), \quad a = 5, 6, 7, 8\text{-}14$$

reveals that 5-year-old crab face the highest annual mortality rate (49%), 6- , and 7-year-old crab die off at about 10% per year. See Table 6.

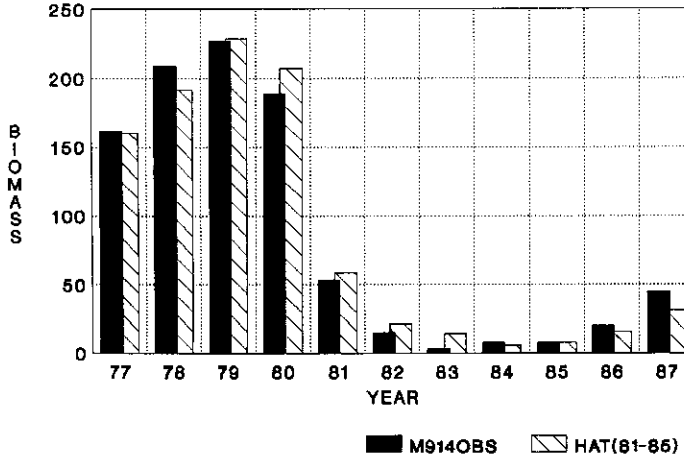


Figure 2. SUR-FMR predicted vs. observed biomass estimates--males 9-14 years old, in million lbs.

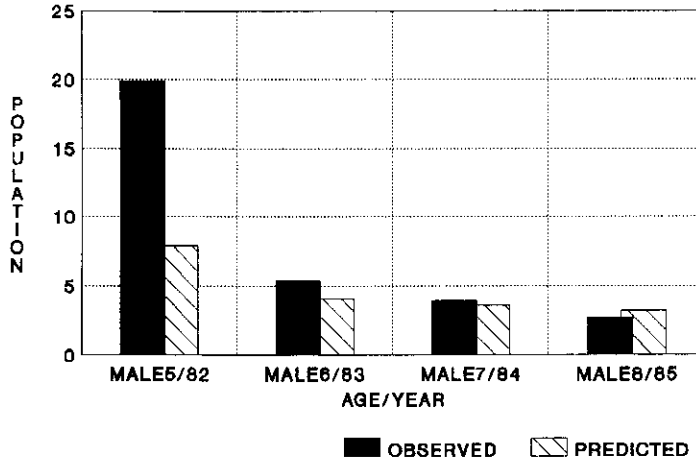


Figure 3. SUR-FMR predicted vs. observed populations estimates-- cohort 1982, in millions.

TABLE 6. Estimated Male Mortality Rates[1]

Age	Mortality Rate
5	0.485
6	0.117
7	0.101
8-14	-0.020 (0.480)[2]

[1]Mortality rate for the 8-14 age class is not a pure mortality rate, as with 5, 6, and 7. Rather, it is a net growth/mortality rate.

[2]The parenthetical rate pertains to the 1981-85 time period.

DENSITY DEPENDENCE

As previously noted, all variants of the modified Ricker, including SUR-FMR, maintain concavity only in the female direction. Each was modified to include an interactive leading term (the product of adult male and females) thereby assuring concavity in both directions and also assuring zero progeny if either adult stock dropped to zero. Convergence was obtained only in the single equation models. Unfortunately, the leading parameter (β_0) declined toward zero in the 8-year-old equations. Model convergence could not be obtained in the systems approach. The problems encountered stem primarily from no observations at low parental stocks. The single-equation concave functions consistently peaked at parental stock levels which were less than half of the lowest adult female and male observations.

CONCLUSIONS

This paper presents a series of spawner-recruit models for population estimation of male adult, sublegal king crab. The models are presented sequentially, with each subsequent model outperforming the prior models. The paper culminates with the presentation of the SUR-FMR model. Unlike all other models presented, each of which estimated age-class populations independently, this model takes a systems approach to population estimation by utilizing cohort analysis. It includes legal 9 to 14-year-old crab as part of the cohort framework. The SUR-FMR model is viewed as being superior to the other models, both statistically and biologically. Statistical improvement is gained in this model by its increase in degrees of freedom (36 degrees of freedom as opposed to less than 11 degrees of freedom for the single equation models). This provides greater confidence in the test statistics. The predictive capability of the model is considered excellent.

The systems approach estimates a single shared spawner-recruit function which explicitly recognizes the commonalty between all members of a cohort and their parental stock. Thus, all observations on a cohort are simultaneously used in

estimation of the spawner-recruit function. This feature is considered particularly desirable due to the inconsistencies which exist within the NMFS population estimates. Additionally, the model explicitly estimates 5-, 6-, and 7-year-old mortality rates, as well as a composite 8 to 14-year-old mortality rate. The results suggest that the 1981-85 period faced unusually high mortality only in the 8 to 14-year-old age class. However, it would appear that this period of high mortality returned to the lower rate experienced in 1977 to 1980 by 1986.

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Genetic Structure of Red King Crab Populations in Alaska Facilitates Enforcement of Fishing Regulations

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ABSTRACT

Horizontal starch-gel electrophoresis of proteins has proven to be a powerful tool for the management of many marine species. This technique provides data on the genetic relationships of reproductively isolated populations, thereby helping scientists to optimally manage these self-recruiting stocks. Additionally, when large genetic differences are found between populations, collections from unknown origin may be genetically screened and unambiguously classified.

We examined collections of red king crab from thirteen localities in Southeast Alaska, the Aleutian Islands, and the eastern Bering Sea for genetic variation at 42 protein coding loci. Two highly polymorphic loci, *Pgdh* (Phosphogluconate dehydrogenase) and *Alp* (Alkaline phosphatase), were useful for discriminating population differences between major geographic areas. The eastern Bering Sea collections from Bristol Bay and Norton Sound were very different from all other collections. Further, Southeast Alaska collections appear to form a population unit discrete from the Kenai, Alaska Peninsula, and Aleutian collections. Additional polymorphic loci appear to be useful in further differentiating populations, and we are continuing our study.

In January, 1989, we analyzed 89 red king crab samples of unknown origin. These samples were from a boatload of crabs allegedly caught near Adak Island in the Aleutian Islands. Enforcement personnel from Alaska Department of Public Safety and biologists from Alaska Department of Fish and Game believed that the crabs were actually caught in Bristol Bay during an area closure. Our data clearly showed that the crabs could not have come from Adak Island and that they probably originated from the Norton Sound/Bristol Bay population. Based on these findings the vessel owner and the skipper agreed to pay the state $565,000 in penalties for fishing violations.

We believe that these genetic data should be of considerable use in the harvest management of Alaskan red king crab. Additionally, the knowledge by fishermen that unknown samples may be identified to population of origin may deter illegal fishing and improve the quality of catch statistics used to manage crab fisheries.

INTRODUCTION

The red king crab, *Paralithodes camtschatica* (Tilesius), is a large anomuran decapod of the family Lithodidae which is distributed from the Chukchi Sea south along the western side of the North Pacific Ocean to the Sea of Japan (Sato, 1958) and along the eastern side to British Columbia (Butler and Hart, 1962). Since the mid-1950s major Alaskan fisheries for this species have occurred primarily in Bristol Bay, around Kodiak Island, around the Aleutian Islands, and along the southern coast of the Alaska Peninsula (Blau, 1985). Red king crab stocks have experienced an extreme decline in abundance in the last decade. To conserve this dwindling resource, commercial fisheries for red king crab were open only in limited areas during recent years.

The poor condition of red king crab stocks prompted attempts to evaluate causes of the declines (Blau, 1986; Otto, 1986) and to reexamine present methods of stock assessment and management (Otto, 1986). The delineation of genetic stock structure is an important concern in crustacean management (e.g., Davidson et al., 1985) and may provide critical insight into optimal harvest strategies for non-interbreeding populations. In 1987 we began biochemical genetic investigations of Alaska red king crab to determine (1) the amount of variation within populations, (2) the amount of divergence between populations, and (3) optimal sampling strategies to maximize allozyme activity and resolution (Seeb et al., 1990).

We previously surveyed three populations and found overall genetic variability to be low. However, two highly polymorphic loci distinguished geographically isolated collections of crabs (Seeb et al., 1990). As a result, we additionally examined 13 crab collections throughout Alaska to further ascertain the amount of genetic population subdivision and to evaluate how these genetic data could aid in defining self-recruiting management units.

In this study we demonstrated the enforcement potential of these data as illustrated by the analysis of confiscated crabs of unknown origin allegedly caught near Adak Island in the Aleutian Island chain. Enforcement personnel from Alaska Department of Public Safety and biologists from Alaska Department of Fish and Game believed that the crabs were actually caught in Bristol Bay during an area closure. Our data showed that the confiscated crabs did not belong to the same genetic stock as our known Adak Island samples, and they most likely originated from an eastern Bering Sea population.

MATERIALS AND METHODS

Red king crab were collected by personnel of the Alaska Department of Fish and Game from 13 sites ranging from Southeast Alaska to the eastern Bering Sea (Figure 1). Sampling included two separate locations from the Adak Island vicinity. Sample sizes ranged from 50-100 individuals from all populations with the exception of Excursion Inlet (N=26) and a very small sampling from Bristol Bay (N=6). Tissues (muscle, gill, hepatopancreas, and heart) were dissected from each individual, labeled, placed in a capped tube, and frozen as soon as possible at -15°C. Within a few weeks, all tissues were transported to the laboratory on dry ice and stored at -80°C until analysis.

Red king crab of unknown origin, allegedly caught near Adak Island in the Aleutian Islands, were confiscated by the Alaska Department of Public Safety. Tissues from these confiscated individuals were dissected and handled as above.

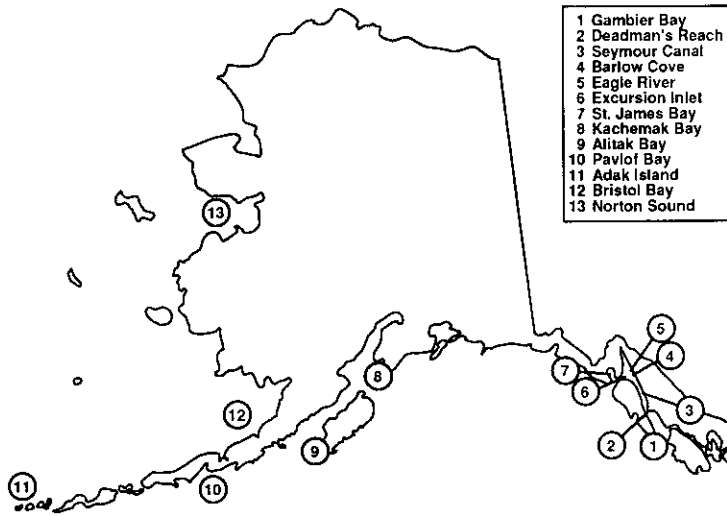

Figure 1. Sampling localities of red king crab.

Procedures for horizontal starch gel electrophoresis followed those of Harris and Hopkinson (1976), Allendorf et al. (1977), May et al. (1979), and Seeb et al. (1990). A total of 42 loci were resolved using the following buffers (see Table 1): (1) N-(3-aminopropyl)-morpholine, citrate (**AC**, pH 6.9; Clayton and Tretiak, 1972); (2) Tris, borate, citrate, lithium hydroxide (**TBCL**, pH 8.7; Ridgway et al., 1970); (3) Tris, citrate (**TC**, pH 7.0; Shaw and Prasad, 1970); (4) Tris, citrate (**TC**, pH 8.0; Selander et al., 1971); (5) Tris, borate, EDTA (**TBE**, pH 8.5; Boyer et al., 1963); (6) Tris-citrate (0.005 M), MgCl (0.02 M) gel buffer adjusted with NaOH to pH 7.5 and a borate (0.03 M) tray buffer adjusted with NaOH to pH 8.6 (**TCM**).

Allele frequency estimates were calculated for each population, including the unknowns, and used to generate a distance matrix of Cavalli-Sforza and Edwards chord distances (Cavalli-Sforza and Edwards, 1967). These distance values were in turn used to construct a phenogram (UPGMA) using the computer program BIOSYS-1 (Swofford and Selander, 1981).

Two separate statistical analyses were used to test whether the unknown samples originated from Adak Island, as claimed by the owner of the confiscated crabs, or from some other eastern Bering Sea population, as suspected by enforcement personnel. First, heterogeneity chi-square tests were performed to test the null hypothesis of panmixia between the two Adak Island collections and among the Adak and confiscated samples. Degrees of freedom for an M by N contingency table, where M is the number of populations and N the number of alleles, were calculated as $(M\text{-}1)(N\text{-}1)$.

Second, a discriminant analysis was performed using SPSS^{x} (Nie, 1983) to describe the linear function that maximized separation between eastern Bering Sea (represented by the Norton Sound population because the Bristol Bay sample size was too small to accurately characterize the population) and the pooled Adak Island populations and to identify the loci contributing significantly to their separation. At each polymorphic locus, the number of discriminating variables was equivalent to N-1 where N is the number of alleles, and the most common allele was the one eliminated. Each individual was scored according to number of doses of particular alleles. Seven polymorphic loci were included in the analysis (*Ah*, *Alp*, *Gpi*, *Mdh1*, *Pgdh*, *Ldh3*, *Peplt2*), producing eight discriminating variables

Table 1. Forty-two allozyme loci examined in this study. Included are Enzyme Commission number, locus abbreviation, tissue studied, and electrophoresis buffer. Tissue abbreviations are: (M) muscle, (H) heart, (GL) gill, and (HP) hepatopancreas. Buffers are as described in the text.

Enzyme	E.C. Number	Locus	Tissue	Buffer
Acid phosphatase	3.1.3.2	*Acp1*	HP	TCM
Aconitate hydratase	4.2.1.3	*Ah*	HP	TBCL
Adenosine deaminase	3.5.4.4	*Ada2*	HP	TCM
Alanine amino-transferase	2.6.1.2	*Alat*	M	TBCL
Alkaline phosphatase	3.1.3.1	*Alp*	HP	TCM
Aspartate amino-transferase	2.6.1.1	*Aat*	M	TBE
Creatine kinase	2.7.3.2	*Ck2*	H	TC8.0
Cytochrome-b_5 reductase	1.8.1.4	*Cybr2*	H	TBCL
Esterase	3.1.1.1	*Est1*	GL	TBE
		Est2	GL	TBE
		Est3	GL	TBE
		Est4	GL	TBE
Fructose-biphosphate aldolase	4.1.2.13	*Fb1*	M	AC6.9
		Fb2	M	AC6.9
Fumarate hydratase	4.2.1.2	*Fh1*	M	TBE
b-N-acetylgalactos-aminidase	3.2.1.53	*bGala2*	GL	TBCL
		bGala3	GL	TBCL
N-acetyl-b-glucos-aminidase	3.2.1.30	*bGa1*	GL	TBCL
		bGa2	GL	TBCL
Glucose-6-phosphate isomerase	5.3.1.9	*Gpi*	M	TBCL
b-Glucuronidase	3.2.1.31	*bGus*	HP	TBCL
Glyceraldehyde-3-phosphate dehydro-genase	1.2.1.12	*Gapdh*	M	TC7.0

Table 1. Continued.

Enzyme	E.C. Number	Locus	Tissue	Buffer
Glycerol-3-phosphate dehydrogenase	1.1.1.8	*Gpdh1*	M	AC6.9
		Gpdh2	M	AC6.9
Isocitrate dehydrogenase	1.1.1.42	*Idh1*	M	TC7.0
		Idh2	M	TC7.0
Lactate dehydrogenase	1.1.1.27	*Ldh2*	M	TBCL
		Ldh3	M	TBCL
Malate dehydrogenase	1.1.1.37	*Mdh1*	M	AC6.9
		Mdh2	M	AC6.9
Malic enzyme	1.1.1.40	*Me*	H	TC8.0
Mannose-6-phosphate isomerase	5.3.1.8	*Mpi*	M	TBE
Peptidase-Lt[1]	3.4._._	*Peplt1*	M	TBCL
		Peplt2	M	TBCL
Phosphoglucomutase	5.4.2.2	*Pgm1*	M	TC7.0
		Pgm2	M	TC7.0
Phosphogluconate dehydrogenase	1.1.1.44	*Pgdh*	M	TC7.0
Superoxide dismutase	1.15.1.1	*Sod1*	H	TBCL
		Sod2	GL	TBCL
		Sod3	M	TBCL
Triose-phosphate isomerase	5.3.1.1	*Tpi*	M	TCM
Tripeptide amino-peptidase[2]	3.4.11.4	*Tpep*	M	TBCL

[1] Resolved with DL-leucyl-DL-tyrosine

[2] Resolved with DL-leucylglycylglycine

(two variables described *Pgdh*). Discriminant function coefficients were standardized by dividing each by the largest coefficient. The absolute value of each standardized value was interpreted as the relative contribution of each variable to discrimination.

Next, the resultant function was used to test the integrity of the discrimination procedure. We classified individual specimens from the eastern Bering Sea and Adak Island populations using the discriminant function and compared these to theoretical group membership. Last we used the discriminant function to classify confiscated crab specimens of unknown origin.

RESULTS

Of the 42 loci resolved, 14 were polymorphic in at least one population of crabs. Of these 14 loci, 11 (*Ada2*, *Ah*, *Est3*, *Gapdh*, *Gpi*, *Gpdh2*, *Ldh2*, *Mdh1*, *Peplt2*, *Pgm2*, *Sod3*) had only low frequency variants (< 0.05), while the remainder were variable at a frequency ≥ 0.05 (*Alp*, *Pgdh*, *Ldh3*). Accordingly, average heterozygosity was low, ranging from 0.013 to 0.025. Pertinent to this project, eight loci were polymorphic in the Adak, eastern Bering Sea, and unknown collections (Table 2).

The overall similarity among populations across all loci is depicted in the phenogram (Figure 2). A central cluster composed of all Southeast Alaska (sites. 1-7) is formed at a genetic distance of approximately 0.032. This cluster is connected to two subgroups including sites in the central and western Gulf of

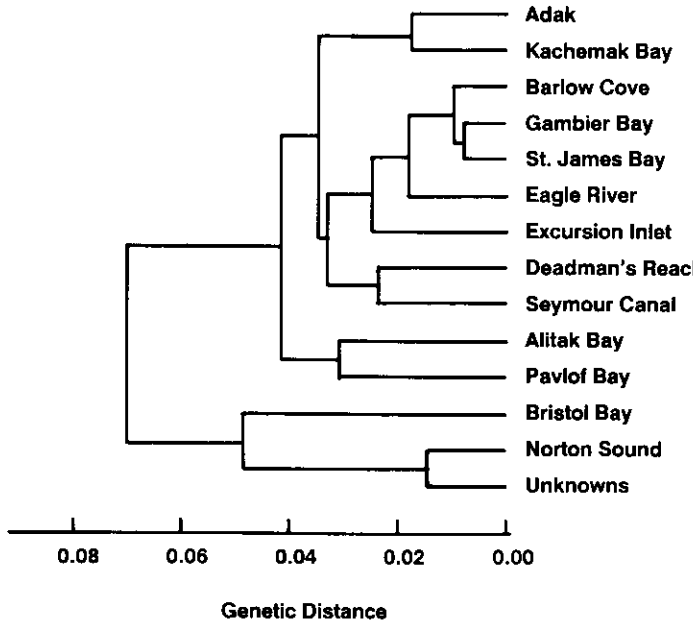

Figure 2. Phenogram based on Cavalli-Sforza and Edwards chord distance (Cavalli-Sforza and Edwards, 1967) depicting overall similarity among red king crab collections in Alaska.

Table 2. Allele frequency estimates and sample sizes (in parentheses) for Alaska red king crab populations. Alleles are identified by their mobility relative to the most common allele in Adak Island which is assigned a mobility of 100.

Locus and Alleles	Population			
	Adak Island	Bristol Bay	Norton Sound	Unknowns
Ah				
	(82)	(4)	(92)	(95)
100	1.00	1.00	0.97	0.96
90	0.00	0.00	0.03	0.04
Alp				
	(69)	(6)	(77)	(69)
100	0.76	0.25	0.23	0.20
129	0.24	0.75	0.77	0.80
Est3				
	(89)	(4)	(90)	(98)
100	1.00	0.75	0.99	0.98
102	0.00	0.25	0.01	0.02
Gpi				
	(86)	(6)	(90)	(98)
100	1.00	1.00	0.97	0.99
169	0.00	0.00	0.03	0.01
Ldh3				
	(89)	(6)	(94)	(98)
100	0.97	1.00	1.00	1.00
95	0.03	0.00	0.00	0.00
Mdh1				
	(88)	(6)	(93)	(98)
100	1.00	1.00	0.99	0.99
30	0.00	0.00	0.01	0.01
Peplt2				
	(85)	(6)	(92)	(98)
100	0.99	1.00	1.00	1.00
121	0.01	0.00	0.00	0.00
Pgdh				
	(81)	(6)	(85)	(96)
100	0.70	0.50	0.52	0.48
104	0.29	0.50	0.45	0.51
90	0.01	0.00	0.02	0.01
94	0.00	0.00	0.01	0.00

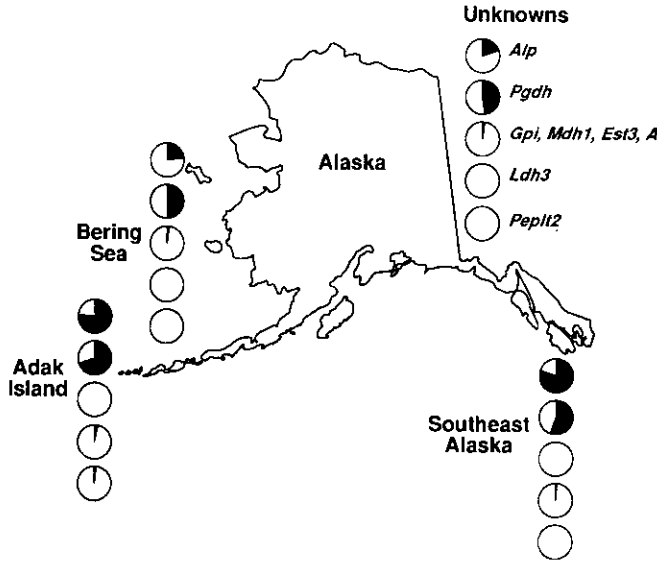

Figure 3. Pie diagrams showing allele frequencies at eight polymorphic loci in representative collections from the eastern Bering Sea and Adak Island. Also shown are pooled frequencies from seven Southeast Alaska collections and the frequencies observed in the unknown samples.

Alaska: (1) Adak Island and Kachemak Bay and (2) Alitak Bay and Pavlof Bay. A separate main branch, including the Bristol Bay (site 12), Norton Sound (site 13), and the unknown population joins the Gulf of Alaska branch at a genetic distance of approximately 0.07. The unknown samples cluster with the Norton Sound and Bristol Bay populations and not with those from Adak Island. The genetic similarity value between Norton Sound and the unknowns was 0.015; genetic similarity between Adak Island and the unknowns was 0.069.

The genetic similarity between the eastern Bering Sea collection and the unknowns can also be seen on a locus-by-locus basis. Figure 3 depicts the frequencies of the Adak Island, eastern Bering Sea, unknowns, and pooled Southeast Alaska populations for six polymorphic loci. For example, Adak Island has a frequency of 0.761 for the common allele at *Alp*. The eastern Bering Sea and unknowns have frequencies of 0.227 and 0.203, respectively. Similarly, the common allele at *Pgdh* occurs at a frequency of 0.698 in Adak Island; but is consistently lower in the eastern Bering Sea and unknown populations with frequencies of 0.500 and 0.479.

Two tests of heterogeneity were performed. In the first we tested for heterogeneity between the two Adak Island collections at the four loci for which they were polymorphic (*Alp*, *Pgdh*, *Peplt2*, or *Ldh3*; Table 2). No evidence of heterogeneity ($P < 0.01$) was found. Significant heterogeneity was detected between pooled Adak and unknown collections, and the null hypothesis of panmixia was rejected ($P < 0.01$) at *Pgdh* and *Alp* (Table 3).

Table 3. Results from chi-square heterogeneity analysis of Adak Island and confiscated crabs of unknown origin.

	Pgdh			*Alp*		
	X^2	df	*P*	X^2	df	*P*
Adak1 - Adak2	1.5	2	0.47	1.2	1	0.28
Adak1 - Adak2 - Unknowns	21.6	4	<0.001	88.5	2	<0.001

One significant function was derived (X^2 = 96.67, 3 df, $P < 0.001$) in the discriminant analysis. *Alp* and *Pgdh* provided the greatest discriminating power based on the values of standardized discriminant function coefficients. Discriminant function scores for each individual from the two base populations (eastern Bering Sea and Adak Island) were plotted on a frequency histogram with the collection of unknown origin (Figure 4). The distribution of the eastern Bering Sea and unknown individuals overlap considerably with the most frequent value being 1.6. In contrast, the most frequent value of the individuals known to be from Adak Island was -1.6. The classification procedure of the discriminant analysis was able to classify approximately 85-88% of the known individuals into their correct population (Table 4). The predicted membership of the unknown group was 87% eastern Bering Sea and 12% Adak Island. The percent of known individuals misclassified (13-15%) was indistinguishable from the percent of unknown individuals classified as Adak Island (13%).

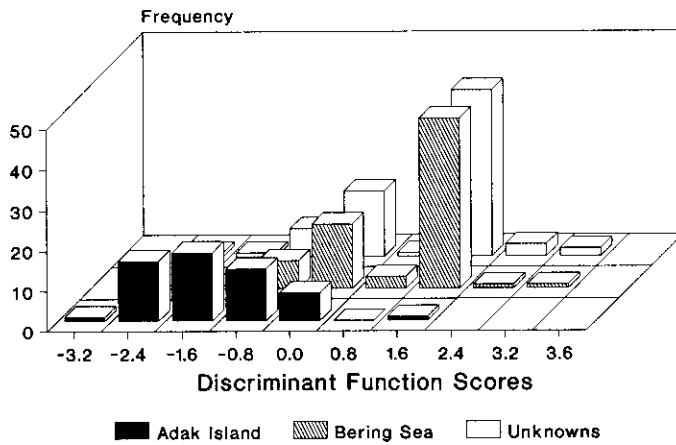

Figure 4. Discriminant function scores for individuals from the Adak Island and eastern Bering Sea populations and for unknown individuals.

Table 4. Classification results from the discriminant analysis of red king crab populations.

Actual Group Membership	*N*	Predicted Group Membership: Adak Island	Predicted Group Membership: Bering Sea
Adak Island	54	46 85.2%	8 14.8%
Bering Sea	72	9 12.5%	63 87.5%
Unknowns	71	9 12.7%	62 87.3%

DISCUSSION

Red king crab from major geographic regions have genetically differentiated despite the fact that the average amount of genetic variability within populations is low. There is also evidence of subdivision within each region. These data should be particularly useful in defining management units of self-recruiting populations.

The data also have considerable potential to aid in enforcement of crab fishing regulations. At least three separate lines of genetic evidence argue that the confiscated crabs analyzed in this study did not originate from the Adak Island population represented by our known Adak samples. The null hypothesis of panmixia among known Adak and the unknown samples was rejected based on heterogeneity chi-square tests at two loci ($P < 0.001$ for both tests). Secondly the distribution of discriminant function scores for the unknowns and eastern Bering Sea samples overlapped considerably, and individuals from the two groups had the identical most frequent score (1.6). A final line of evidence, the cluster analysis, based upon overall similarity, placed the unknowns on the same branch as the eastern Bering Sea samples.

These data clearly show that the crabs could not have come from Adak Island and that they probably originated from the eastern Bering Sea as represented by our Norton Sound samples. The sample from the Bristol Bay collection, the most likely source based on circumstantial evidence, was too small ($N = 6$) for accurate characterization on its own. However, these data suggest that both eastern Bering Sea collections are much more similar to each other than to collections in the Gulf of Alaska. Based partially on these findings, the vessel owner and skipper agreed to pay the state of Alaska $565,000 in penalties for the fishing violation.

Forensic application of genetic data in fisheries is not new, although it has not seen widespread use. In our laboratory we have identified confiscated fillets of rockfish (genus *Sebastes*) to species (Seeb, 1986), and we have assigned the continent of origin to confiscated chum salmon (*Oncorhynchus keta*; Seeb and

Seeb, 1986). With the advances in new genetic techniques such as DNA sequencing and DNA fingerprinting, forensic applications are destined to increase in importance. Additionally, the knowledge by fishermen that unknown samples may be identified to population of origin may deter illegal fishing and improved the quality of catch statistics used to manage crab fisheries in the future.

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Stock Assessment and Management

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Snow Crab Growth and Stock Size Estimations Obtained with Coded Wire Tags in the St. Lawrence Estuary

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ABSTRACT

In a preliminary tagging study on snow crab (Chionoecetes opilio), Bailey and Dufour (1987) demonstrated the usefulness of coded wire tags as a stock assessment tool. The method described was tested in the field and proved to be efficient in tagging large numbers of crabs at sea. Meaningful estimates of stock size were derived and potential for retention during ecdysis was discussed.

The present work was aimed at demonstrating the capabilities of coded wire tags to be recovered after more than a year, to be retained by crabs molting at sea and to provide useful data on stock size despite variations in the distribution of fishing activities.

Information on growth was obtained from 7 out of 11 crabs that were tagged in 1984 and recaptured in 1986. None of the molting crabs exhibited deformities of the tagged legs. Growth increment of the 7 crabs that molted varies between 22.8 % and 26.8 % with an average of 25.3 %. In some snow crab populations, size frequencies can be separated in modal components that seem related to molt classes. Increment between modes overlapping the 95 mm recruitment size ranged from 23.1 % to 33.3 %. Our results are more consistent and less variable than those cited in the litterature and perhaps reflect better the actual growth increment in nature.

The Petersen method was applied to the tagging results to estimate the initial biomass of the commercial size crabs present during the 1985 and 1986 fishing seasons. The biomass estimates obtained were more precise than the ones obtained with Leslie analysis used in 1984, 1987 and 1988 on the same area. More reliable fishery indices like the rates of exploitation were derived from them.

INTRODUCTION

In a preliminary tagging study on snow crab (Chionoecetes opilio), Bailey and Dufour (1987) demonstrated the usefulness of coded wire tags as a stock assessment tool. The method described was tested in the field and proved to be efficient in tagging large numbers of crabs at sea. Meaningful estimates of stock size were derived and the potentiel for retention during ecdysis was discussed.

The present work was aimed at demonstrating the capabilities of the coded wire tags to be recovered after more than a year, to be retained by crabs molting at sea and to provide useful data on stock size despite variations in the distribution of fishing activities.

The area under study is located along the north shore of the St. Lawrence estuary. The marginal fishing area on the south shore has been excluded from the study. This fishery exists since the late 1960's and is presently pursued by 22 fishermen on a seasonnal basis (summer). Fishermen normaly make daily fishing trips and land their catch in 4 main ports. Total landings from the north shore area reached a peak of 880 t in 1987 and average around 700 t since 1984.

MATERIAL AND METHODS

Tagging Methodology

The tagging material and method were the same as described in Bailey and Dufour (1987). The dactylus was selected, like in the first study, as the most suitable site for implantation, both for practical purposes and human health considerations. Size class of an individual crab at the time of tagging was identified by the leg selected for tagging. Each leg was assigned a different size class. Pre-selected alternative legs, combined with differently coded tags, were used in cases where the appropriate leg was missing.

Procedures at sea involved fishing crabs with traps, sorting them by size classes, implanting the tag in the appropriate dactylus, magnetizing the tag, testing the magnetization with a detector, and returning the crab at sea as close as possible to the capture site. Different codes on the tags were used each year. Recoveries were made in the commercial landings by a team of scientists. Crabs were examined on the wharves or in processing plants, with an effort to sample as many loads and sites as practical. Recovered crabs were measured to the nearest mm (CW) and their tag codes was deciphered under binocular microscope.

The Petersen single census method was used to estimate the commercial-size crab populations present at the beginning of 1985 and 1986 fishing seasons. These estimates were obtained from the modified Petersen estimator with probability better than 0.95 of being accurate within 25 % of the true population size (Robson and Regier, 1964).

Only crabs with size (CW) ≥ 95 mm and tagged in the year of recapture were used in the analysis. The numbers of tags recovered during 1985 and 1986 were corrected for possibilities of tag shedding. A value of 11 % of tags lost was found in a 1985 double tagging experiment and was applied to the 1985 and 1986 results. Crabs (N = 372) were double tagged with a vinyl bright orange spaghetti tag tied around their carapace. Fishermen were rewarded for the return of these crabs from their captures.

Discussion concerning the applicability of the method may be found in Ricker (1975) and Bailey and Dufour (1987). The following formulae were used:

$$N = (M+1)(C+1)/(R+1)$$

Confidence interval of $N = (M+1)(C+1) / ((R+1.92 \pm 1.960 \sqrt{R+1}) + 1)$
at $1-p=0.95$, if $R > 30$
(Ricker, 1975)

where N= Population estimate in number,
M= Number of crabs tagged and released (CW ≥95 mm),
C= Number of crabs checked for tags in the landings,
R= Number of tags recovered in the sample C.

The fishing and tagging areas are bordered on the eastern, southern and western sides by the Laurentian channel (depths greater than 200 meters), and by the coast on the northern side (Figure 1). Information on the fishery was obtained from fishermen's log books which provided data on fishing effort, catch and positions.

The snow crabs were tagged in three consecutive years (1984, 1985 and 1986) from mid-april to mid-june at the latest (Table 1). Rectangular traps (1.6 m X 1.6 m X 0.6 m) used for tagging were normally set for 24 hours and baited with frozen herring and mackerel. The recapture took place during the commercial fishing season from mid-april to the end of june at the latest, from the years 1985 to 1987.

In eastern Canada, Leslie analysis (Leslie and Davis, 1939; De Lury, 1947; Ricker, 1975; Mohn and Elner, 1987) is a common technique used to estimate the commercial biomass of crabs available to the fishery annually. The analysis is based on a least-squares regression of catch per unit of effort against cumulative catch at regular time intervals. When the requirements of the methodology are met, the Leslie analysis will provide a useful " a posteriori " stock size estimate. Leslie analysis was used in 1984, 1987 and 1988 on this same population.

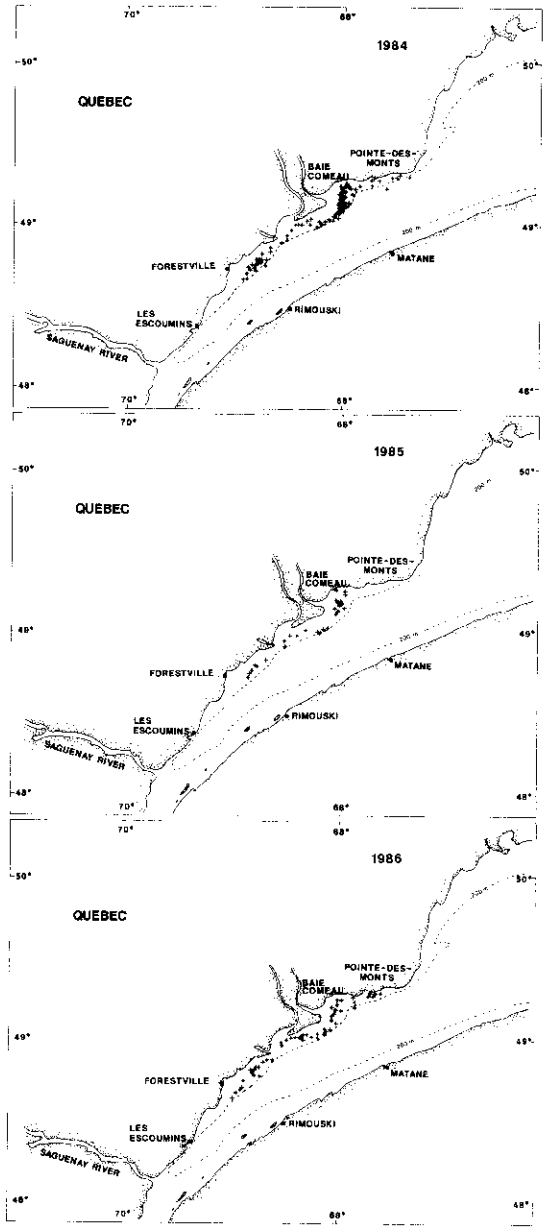

Figure 1. Tagging stations (+) and fishery effort pattern (contoured) from 1984 to 1986.

Table 1: Synopsis of the tagging.

Year	Tagging Dates	Numbers tagged CW≥75mm	Numbers tagged ≥95mm	Recapture Dates	Total number examined for tags CW≥75mm	Total number examined for tags ≥95mm	Number of tags found (for each year tagging) 1984	1985	1986	1987	Total
1984	May 30-June 13	11,024	5,314	----	----	----	----	----	----	----	----
1985	May 03-May 07	7,194	2,291	May 17-June 28	63,091	61,404	23	82	----	----	105
1986	April 17-April 28	1,498	1,498	May 02-June 11	89,834	93,094	11	1	62	----	74
1987	----	----	----	April 14-	21,973	----	0	0	0	0	0

RESULTS

Growth Results

Information on growth was obtained from 7 out of the 11 crabs that were tagged in 1984 and recaptured in 1986 (Table 1). The remaining 4 crabs were recaptured in the same size classes they were tagged in. None of the 23 crabs tagged in 1984 and recaptured in 1985 and the only crab recaptured in 1986 from the 1985 tagging did molt either. All the other crabs were recaptured the same year without molting. Growth increment of the 7 crabs that molted varies between 22.8 % and 26.8 % of the median pre-molt size class they were tagged in, with an average of 25.3 % (Table 2). An Hiatt diagram of these results reveals the linear relationship between premolt and postmolt sizes of the crabs (Figure 2).

Estimation of the Commercial Population Size

The fishing effort distribution shifted slightly during the three years of the tagging experiment (Figure 1). The fishery expansion to the north-east virtually overlapped our tagging distribution and thus each tagged crab had a chance to be recaptured. In 1985, 82 commercial-size (≥ 95 mm CW) crabs were recaptured from a total of 2291 crabs tagged, while in 1986, 62 commercial-size crabs were recaptured and 1498 were tagged initially. Tagging number was lower in 1986 but the recovery effort was increased to 89,834 crabs examined, as suggested by Robson and Regier (1964). Commercial landings in 1985 were high compared to 1986 and resulted in a high exploitation rate of 76 %. In 1986, the management restricted the fishing season to a 10-week period (april to july) which resulted in a low 400 t total catch compared to 769 t in 1985 when there was no time limit.

The population size and precision obtained from Leslie analysis varied considerably during the three years of the study (Table 3). With an almost equal amount of variation explained by the three years regression fitting (average of 69 %), the biomass confidence intervals obtained ranged from 754 t to infinity in 1988, leading to an unreliable stock size and exploitation rate estimates for the 1987 and 1988 years.

DISCUSSION

The growth results confirm that coded wire tags can be retained by snow crabs molting in nature. None of the recaptured crabs exhibited deformities of the tagged leg such as described by Hurley and al. (1989). Perhaps the laboratory stressful conditions are partly responsible for the abnormal ecdysis observed by these authors in crabs injected with the wire tags.

All 7 crabs that molted had an initial size smaller than 95 mm CW. Crabs larger than 95 mm CW are recruited to the fishery and have a

Table 2. Growth information on 7 crabs having molted at sea during the study. All were tagged between May 30 and June 13, 1984. Sizes represent carapace width.

DATE OF RECAPTURE	SIZE-CLASS (mm) AT RELEASE	SIZE (mm) AT RECAPTURE	GROWTH INCREMENT (%)	
			Median	Range
May 04, 1986	85 - 89	107	22.9	20.2 - 25.9
May 04, 1986	80 - 84	103	25.6	22.6 - 28.8
May 12, 1986	90 - 94	113	22.8	20.2 - 25.6
May 16, 1986	80 - 84	104	26.8	23.8 - 30.0
May 22, 1986	80 - 84	104	26.8	23.8 - 30.0
May 22, 1986	75 - 79	97	26.0	22.8 - 29.3
June 2, 1986	90 - 94	116	26.1	23.4 - 28.9

Table 3: Estimates of commercial biomass and rates of exploitation, using Petersen tag-recapture method and Leslie fishing-success method (see text for explanations).

Year	Numbers tagged (CW≥95mm) M	Numbers examined for tags in commercial landings C	Number of tags found in commercial landings [1] R	Estimation: Population Number N	Estimation: Biomass [2] (t)	Commercial landings (t)	Rate of exploitation (%) μ	Coefficient of determination (r^2)
1- Petersen method								
1985	2,291	61,404	92	1,513,336 [1,234,564-1,851,845] [3]	1,006 [849-1,196]	769	76 [64-91]	----
1986	1,498	83,094	70	1,754,358 [1,399,544-2,224,275]	1,036 [837-1,299]	400	39 [31-48]	----
2- Leslie method [4]								
1984	----	----	--	----	1,150 [863-2,220]	674	59 [30-78]	0.70
1987	----	----	--	----	1,153 [1,063-368,005]	880	57 [0.002-83]	0.66
1988	----	----	--	----	1,095 [754-?]	730	67 [?-97]	0.70

(1) R was adjusted for the tags lost at Sea (11%) from the 1985 double tagging experiment.
(2) Average individual weight = 561g in 1985-86.
(3) Confidence interval (0.95).
(4) Catch rates used were from the same and most frequent model of traps (top entry conical traps).

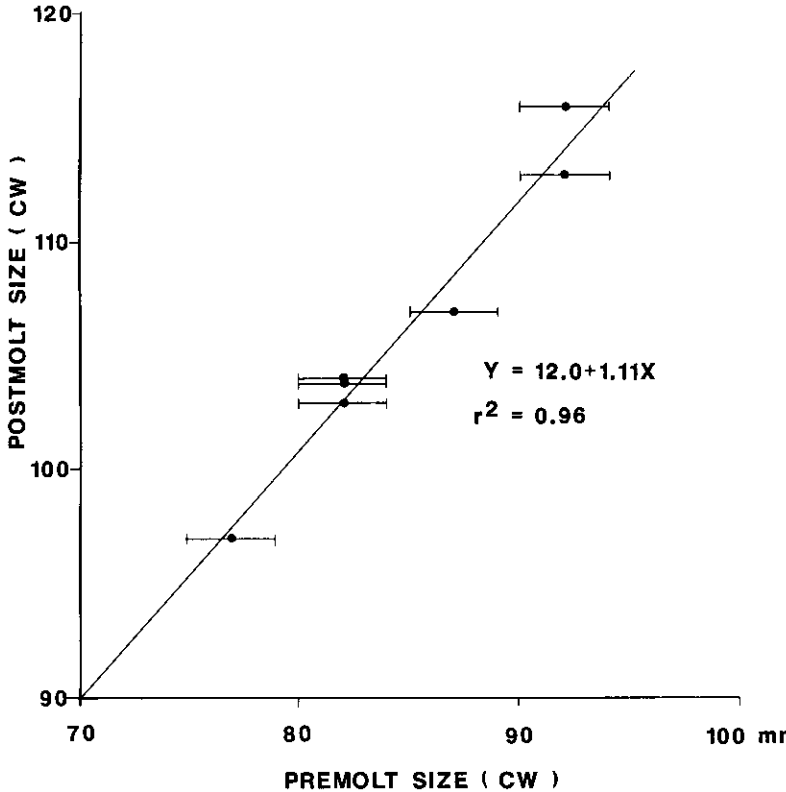

Figure 2: Hyatt diagram of growth increments from seven (7) crabs tagged in 1984 and recaptured in 1986 (Size at pre-molt is within a 5mm size-class). Regression is calculated on medians of pre-molt size-classes.

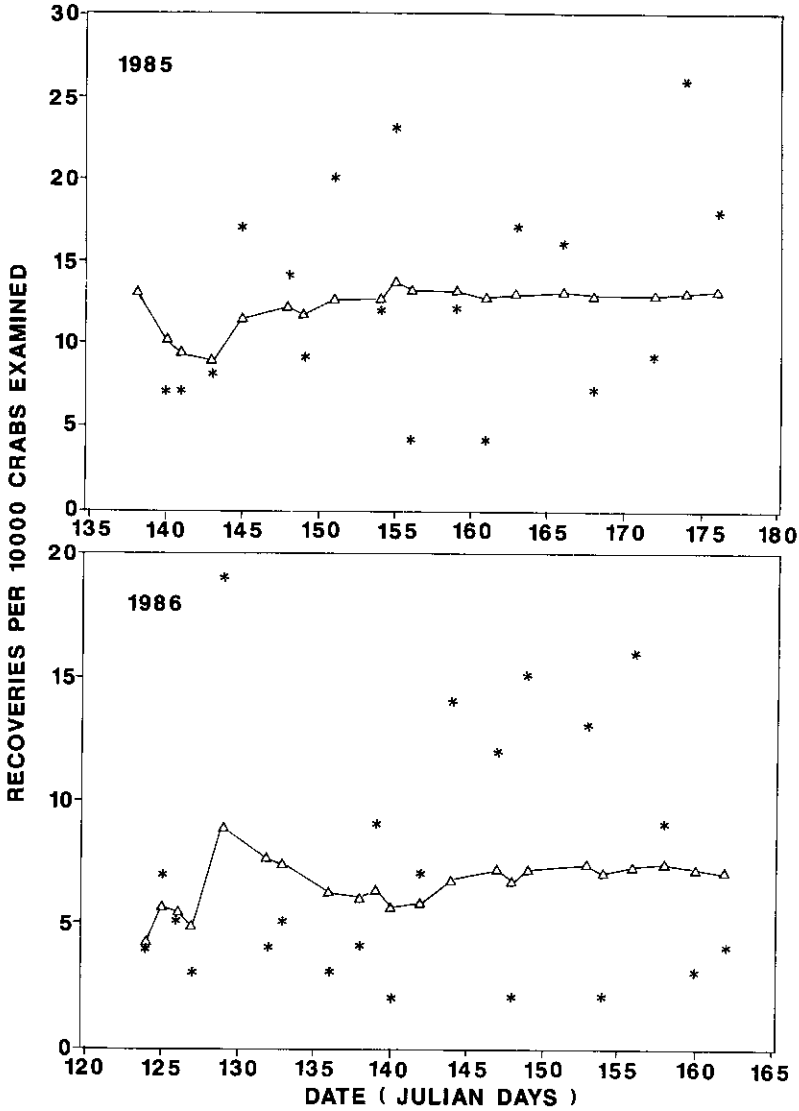

Figure 3. Rates of recovery in 1985 (from May 18) and 1986 (from May 04). Daily occurrences (stars) and cumulative averages (triangles) are represented.

smaller chance to molt before being captured. Moreover, larger crabs are more likely to have reached their terminal molt (Conan and Comeau, 1986).

None of the 23 crabs tagged in june, 1984, and recaptured between may 17 and june 28, 1985, had molted. Surprisingly, 7 out of 11 crabs tagged in 1984 but recaptured between may 2 and june 11, 1986, had molted. We suggest that crabs tagged in 1984 were either in terminal molt or had molted earlier in late winter of 1984. Although they had a chance to molt earlier in the year, the 23 crabs captured in the 1985 summer did not molted probably because they were in terminal molt. Unfortunately, no morphometric data, in regards to the terminal molt aspect, were taken at that time. We believe that those who molted in 1985 were not accessible yet to the fishery between may 17 and june 28 of the same year. Softshell crabs of commercial size are generally apparent in the summer, after or toward the end of the fishing season. Their molting would then be later than that postulated for smaller crabs, like those initially tagged in 1984. Crabs who molted in 1985 became recruited to the fishery in 1986 and showed up in proportion of 7 crabs out of 11 recaptured from the 1984 tagging. To validate this interpretation, we will study the seasonnal timing of the molt in relation to size and the terminal molt status of all recaptured crabs in the future tagging experiments.

Greendale and Bailey (1982) found clear modes in size frequency distributions of snow crabs from this area. They interpreted these modes as molt classes and calculated a molt increment between 25.0 % and 33.3 % for male snow crabs of size ≥ 50 mm. Our average growth increment (25.3 %) falls within this range. Although the tagging methodology can be improved by getting a better precision on the size of crabs when tagged, the range of the growth increments found is narrow (22.8 % to 26.8 %), with a clear linear relationship, suggesting that our results are not far from reality.

Snow crabs held in captivity tend to have a lower size increment than what we found in our study. For instance, Miller and Watson (1976) report a mean size increment of 18.4 % for crabs observed molting in captivity. This stresses the importance of getting growth information, for stock assessment purposes for instance, from individuals in nature, and of being cautious in using data obtained in captivity.

This study confirms the feasibility of large-scale tagging experiments on snow crab populations, using coded wire tags, such as reported by Bailey and Dufour (1987). According to Robson and Regier's (1964) tables, enough crabs were tagged and examined in this study to provide populations estimate with levels of accuracy and precision generally recommanded for management purposes.

The confidence intervals on the population estimates obtained in the tag-recapture experiment have a better precision than what generally obtained with the usual Leslie analysis. Other studies showed the weaknesses of the Leslie analysis when it is not used properly (Bailey, 1983; Mohn and Elner, 1987). Futhermore, Mohn and Elner's

study suggests that Leslies' analysis could easily be biased negatively and thus be less accurate than a tag-recapture study.

More discussion on the methodology and requirements of a tagging experiment, may be found in Ricker (1975) and Bailey and Dufour (1987). In the present study, effort was made to disperse the tagged individuals randomly over most of the fishing grounds. An examination of the trends in the recovery rate (Figure 3) indicates that in both 1985 and 1986, the average number of tags per 10,000 crabs examined stabilized, after a few days, at 12.21 and 6.60 respectively with no tendancy to change thereafter. This is generally a sign of good mixing between the tagged and untagged animals.

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A Comparison of Trawl and Pot Surveys of Red King Crab Populations (*Paralithodes camtschatica*) Near Kodiak, Alaska

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ABSTRACT

Male red king crab (*Paralithodes camtschatica*) length data from pot and trawl survey gear were analyzed to identify differences in length frequencies. Three separate areas around Kodiak Island, Alaska, were surveyed independently with trawl and pot gear between 1973 and 1986. The differences in the probability distributions of male crab lengths from the two gear types were analyzed by smoothing the distributions with the average shifted histogram method. When major differences occurred, patterns or trends were examined in more detail. Very few differences occurred, other than those accounted for by small sample sizes and the rare situation of one gear or the other capturing a higher proportion of a particular size of crab. We present the probability distributions for comparison and discuss their similarities and differences. Trawl and pot catch of crabs 100 mm or less in carapace length were also analyzed separately and shown not to be significantly different ($P=0.81$) in the areas and the period examined. Small crabs (100 mm or less) appear to be equally recruited to pot and trawl gear. The appearance of small crabs in either type of gear is irregular but their presence usually foretells strong future recruitment of the representative cohort.

INTRODUCTION

Surveys of crab populations prior to an annual fishing period are an integral part of the management process and have been conducted in the Kodiak region since the early 1970's. The primary purpose is to provide an estimate of crab abundance, which is then used to set harvest levels. The surveys also provide information on size composition of the catch, resource distribution, relative abundance of female crabs, and relative abundance of small male crabs that may recruit to the fishery in later years.

The Alaska Department of Fish and Game has used crab pots to survey crabs in the Gulf of Alaska and Aleutian Islands. The National Marine Fisheries Service has used trawls for crab surveys in the Bering Sea. The International Pacific

Halibut Commission has conducted trawl surveys in the Gulf of Alaska for examining juvenile halibut abundance.

Whether trawl or pot gear is the more appropriate sampling tool for crabs has been a subject of considerable interest. A criticism of pot surveys is the limited information they provide on the abundance of pre-recruit crabs, because of apparent size selection of the gear for larger animals. However, pots have been much more efficient than trawl gear in collecting crabs and providing a large sample of crabs for tagging studies and length measurements.

This study is a comparison of the size composition of male crabs caught in pots by the Alaska Department of Fish and Game and trawls by the International Pacific Halibut Commission in the Kodiak area. The data presented are unique because the two surveys were designed for sampling different target species, but occurred in the same years and general areas. In addition, the selection of sampling locations and measuring techniques were independent. The objective of this study is to analyze the sampling characteristics of the two gear types based on the size frequencies. The large number of trawls and pots over the 14-year period provide a unique opportunity for independent comparisons of the two gear types.

MATERIALS AND METHODS

Surveys

King crab population surveys in the Kodiak area were conducted with pot gear in a standard manner from 1973 through 1986. Data elements collected included latitude, longitude, depth, weather, date and time the pot was set and pulled, buoy number, bottom type (infrequently), species, sex, size (carapace length), shell condition, and descriptive data on female clutches. Large catches were usually sub-sampled at a ratio of 1:2, 1:3, and others up to 1:10. The sampling fraction was chosen so that 50 to 100 crabs were measured from each pot. Occasionally a sample was taken such that the ratio was not a fraction.

A grid of sample sites were designated throughout the area. Each year specific sample sites were selected and a series of pots were deployed at each. The number of sites in the survey varied among years because of budget constraints. In bays, three or four pots were fished at 0.54 km (1/3 mile) intervals and outside of bays (open ocean) up to 13 pots were fished at 0.40 km (1/4 mile) intervals at each sample site. The pots at each sample site were oriented from west to east, except in 1984 when additional stations were oriented north to south. A few pot sample sites that did not follow the normal sampling grid pattern were discarded. Pot gear used in the survey were commercial pots (2.13 m x 2.13 m x .76 m) covered with 9 cm stretch-mesh webbing.

Trawl surveys have been conducted using a 400 mesh eastern otter trawl in the Gulf of Alaska and the waters surrounding Kodiak Island from 1965 to the present. The data elements collected that were used in this analysis include location, depth, distance trawled, time trawled, number of king crabs, and samples of the carapace length of male king crabs. Trawls with king crab catch but no size information were excluded from the analysis.

Analysis

The pot and trawl surveys were conducted independently with juvenile halibut being the primary target species of the trawl survey and red king crab the primary target species of the pot survey. To obtain comparable data for each gear type from the complete data set, only pot sample sites and trawls within the same year

and located within four miles latitude and longitude of each other were included in this analysis.

The selected trawls and pot stations naturally grouped into three geographic areas: the area northeast of Kodiak from Marmot Bay to Ugak Bay, the area near the mouth of Alitak Bay, and the area around the Chirikof Island. An example of the sampling is provided in Figure 1.

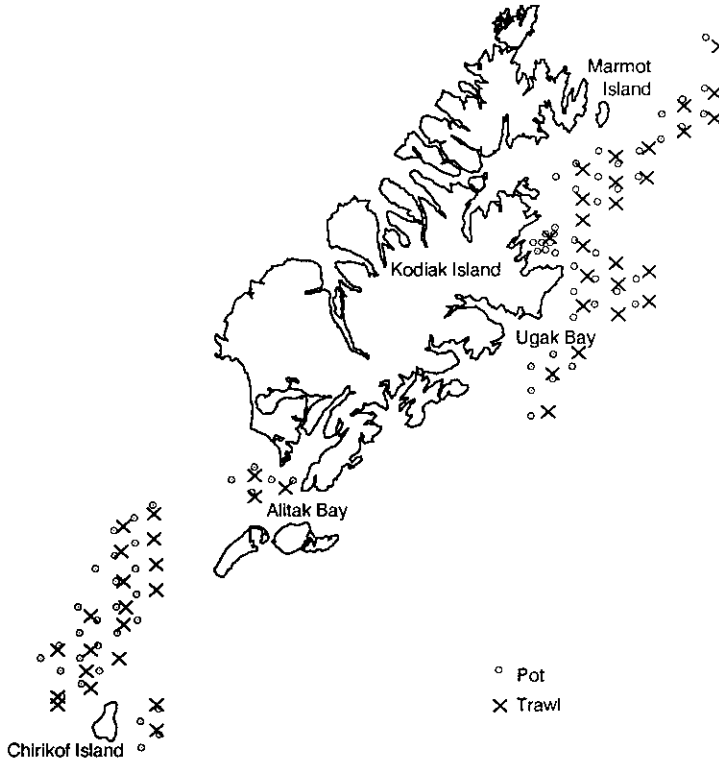

Figure 1. Sample areas around Kodiak Island in 1980.

A total of 7,296 pot-lifts and 560 trawls were included in the analysis (Table 1) with corresponding catches of 128,863 and 16,773 crabs in the respective gear (Table 2). In 1978, comparable pot and trawl samples were taken only in the Chirikof area (Table 1). When the total sample size was less than 10 crabs in either gear, no comparisons were made. This occurred in 1977 in the Alitak area, in 1985 in the northeast and Chirikof areas, and in all areas in 1986 (Table 2).

The number of crabs caught for each millimeter size was estimated by expansion of the counts proportional to the sampling fraction.

Table 1. Number of trawl hauls and pots by area and year.

Year	Northeast Pot	Northeast Trawl	Alitak Pot	Alitak Trawl	Chirikof Pot	Chirikof Trawl	Total Pot	Total Trawl
1973	231	53	30	3	298	15	559	71
1974	250	20	19	3	305	16	574	39
1975	150	10	69	3	335	15	554	28
1976	195	14	51	3	324	20	570	37
1977	115	12	10	1	266	19	391	32
1978	-	-	-	-	269	17	269	17
1979	159	12	25	3	131	14	315	29
1980	467	25	50	3	333	19	850	47
1981	307	27	39	3	383	20	729	50
1982	343	24	43	3	228	17	614	44
1983	179	13	55	3	239	19	473	35
1984	403	32	114	6	312	36	829	74
1985	38	3	53	2	269	21	360	26
1986	42	11	54	3	113	17	209	31
Total	2879	256	612	39	3805	265	7296	560

Table 2. Number of crabs in pots and trawls by area and year.

Year	Northeast Pot	Northeast Trawl	Alitak Pot	Alitak Trawl	Chirikof Pot	Chirikof Trawl	Total Pot	Total Trawl
1973	619	328	1395	337	10226	2094	12240	2759
1974	6197	239	477	555	24286	1915	30960	2709
1975	776	58	2704	318	12628	1972	16108	2348
1976	1077	169	1447	377	2802	1188	5326	1734
1977	2830	139	97	6	7938	2863	10865	3008
1978	-	-	-	-	8127	1298	8127	1298
1979	2379	173	1752	246	6328	257	10459	676
1980	3866	223	2913	126	10690	630	17469	979
1981	3305	280	1024	77	3264	265	7593	622
1982	1085	168	1361	32	785	96	3231	296
1983	18	11	1487	21	388	88	1893	120
1984	75	26	3000	54	372	93	3447	173
1985	0	1	957	31	4	7	961	39
1986	0	0	184	8	0	4	184	12
Total	22227	1815	18798	2188	87838	12770	128863	16773

Length frequency data for each year and geographic area were smoothed using the technique of average shifted histograms (Silverman 1986). This technique provides a probability density function (pdf) of catch at size. The parameters used in the smoothing procedure were H=5 (the bandwidth or window width), M=5 (the number of histograms smoothed for each point), and a triangular kernel. The sum of the absolute differences in the probability density functions of catch at size is presented as a statistic to enable comparison of crab length frequency distributions. Tests on equal probabilities of crab 100 mm or less in carapace length are based on the Wilcoxon rank sum test (Conover 1980).

RESULTS

Size Distribution Analysis

Smoothing the size distributions by the average shifted histogram method (Silverman 1986) helped identify true peaks and valleys of the size distributions. A qualitative examination of the size distributions shows a wide array of situations (Figures 2, 3, and 4). Most of the size distributions are remarkably similar for the two gear types. In later years, small sample sizes cause greater divergence in the size distributions between pot and trawl gear. However, consistent differences are not apparent when size distributions are compared among areas.

To provide a quantitative comparison of the size distributions, we computed the sum of the absolute differences between the trawl and pot distributions (Table 3). We have limited our consideration of the absolute differences to those years and areas with a sum of absolute differences of at least 0.4. The area with the least effort, Alitak, had more values exceeding the median absolute differences (0.446) than did the northeast or Chirikof areas. After 1982, less than 174 crabs were measured from all the trawl catches in any single year and all but one of the absolute differences in size distributions were above the median.

Table 3. Sum of the absolute differences in the pot and trawl size distributions by area and year.

Year	Northeast	Alitak	Chirikof
1973	.197	.287	.276
1974	.359	.693	.317
1975	.343	.564	1.033
1976	.400	.910	.449
1977	1.512		.380
1978			.418
1979	.478	.797	.350
1980	.518	.472	.381
1981	.227	.446	.318
1982	.365	.686	.392
1983	.770	.522	1.226
1984	.564	.362	.815
1985		.545	

To further illustrate the similarities and differences, we plotted the differences between pot and trawl gear probability density functions of catch at size by year and area (Figures 5, 6, and 7). This provides another qualitative comparison between the two sampling gears. Many of the size distributions were quite similar, as illustrated by the minimum deviations of the absolute differences around the zero axis, although a few diverge widely. Once again, no consistent pattern in dissimilar size distributions is apparent.

Small Crabs

One hypothesized difference between trawls and pots is greater catchability of small crabs in trawls. To address the catchability of small king crabs, we compared the tail probabilities for crab 100 mm or less. In 21 of 32 sample pairs, the trawl had a larger tail probability than the pots; that is, the number of sample pairs in which the probability of a crab being 100 mm or less was higher in trawl catches.

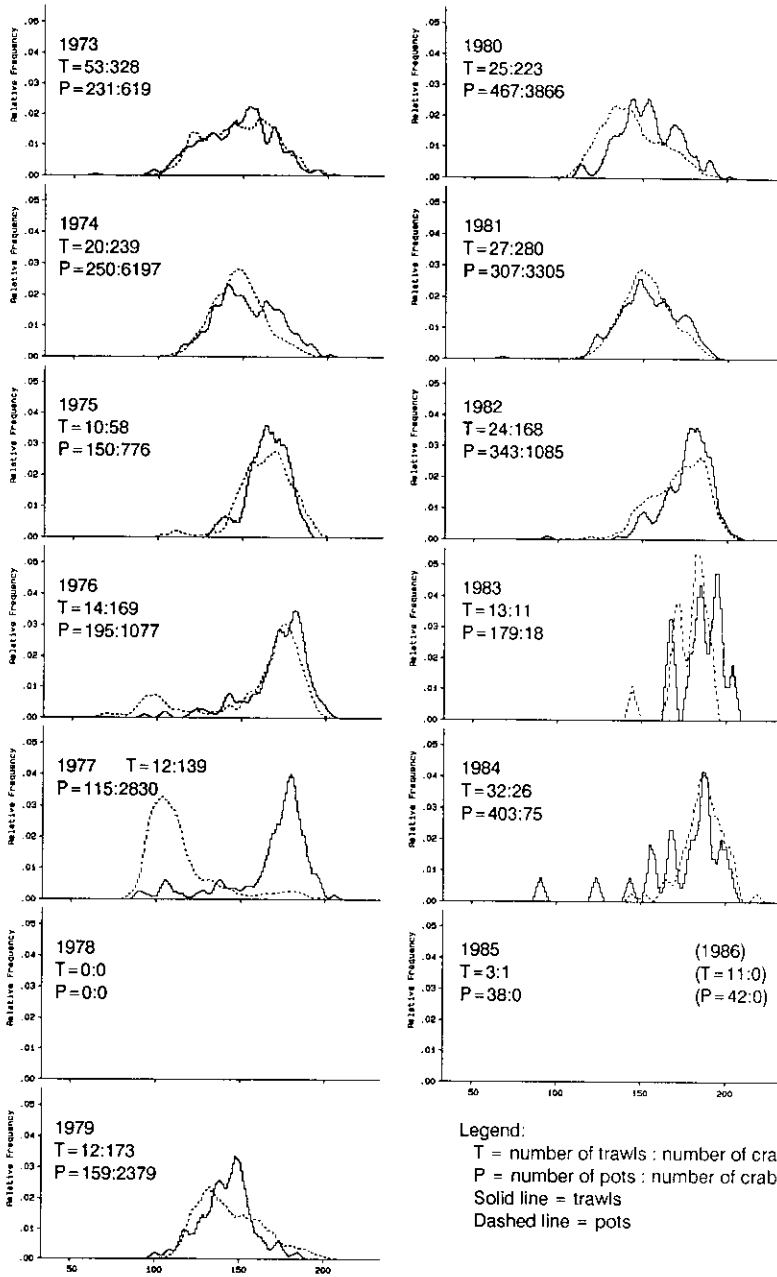

Figure 2. Size frequency by year for the Northeast District.

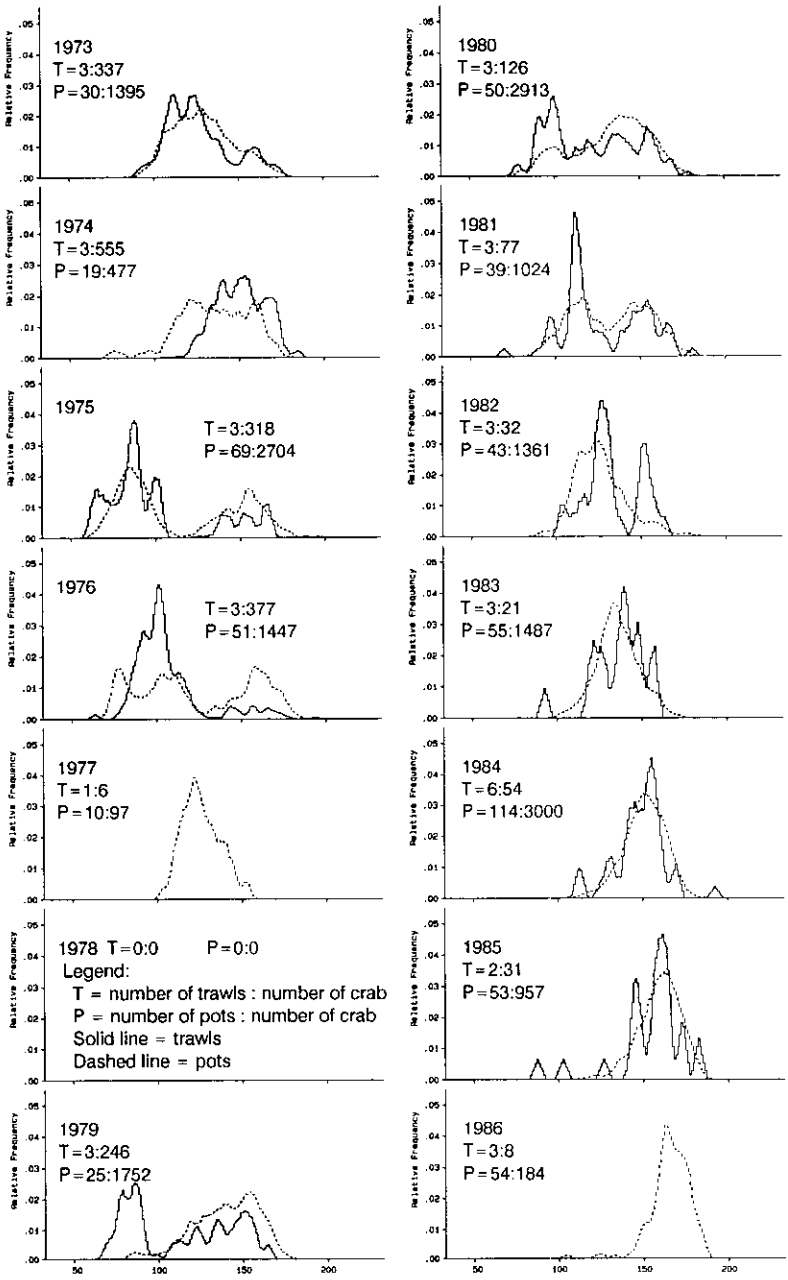

Figure 3. Size frequency by year for the Alitak area.

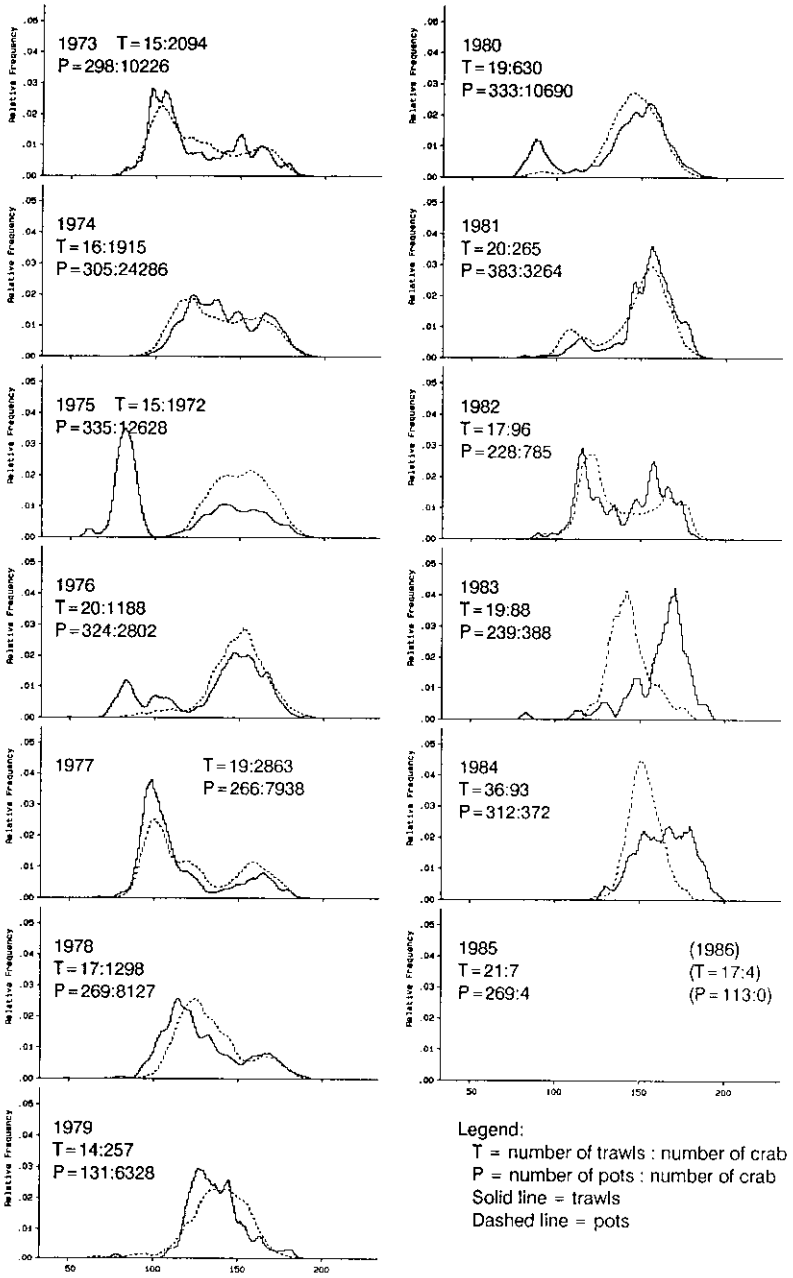

Figure 4. Size frequency by year for the Chirikof area.

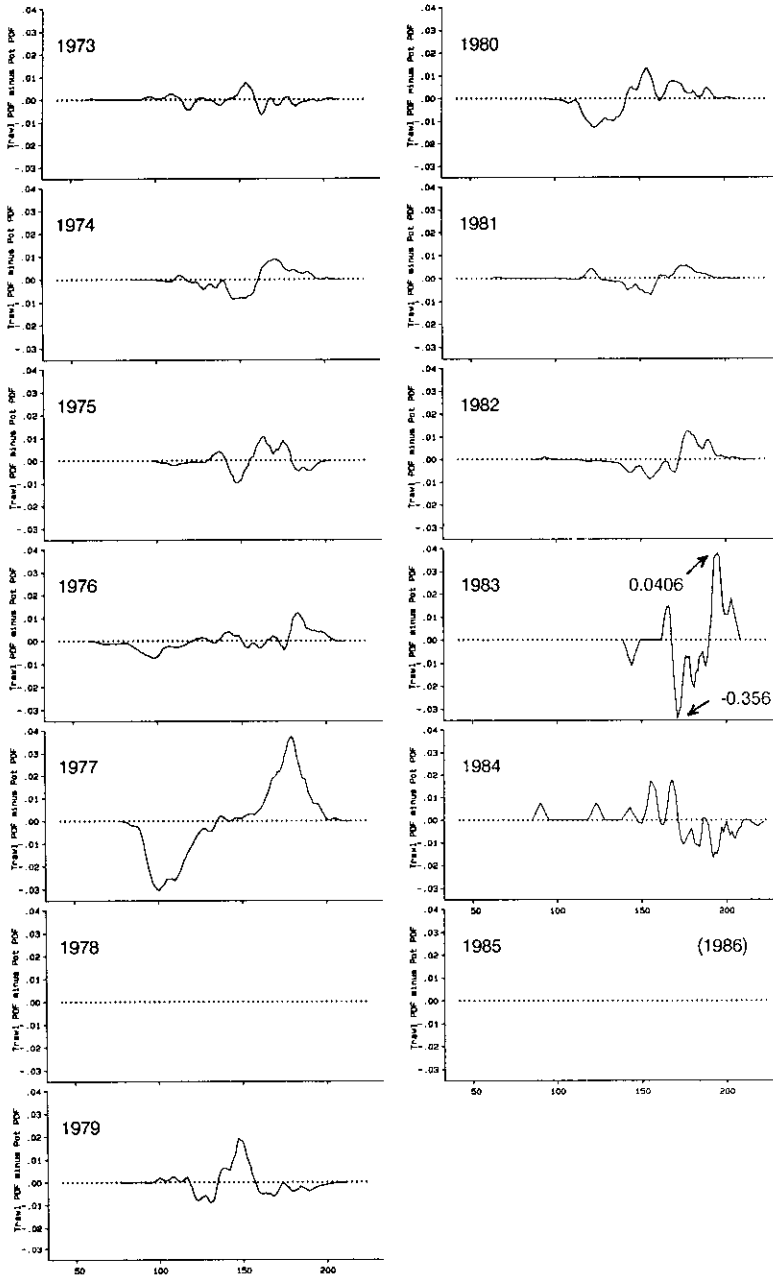

Figure 5. Difference between densities by year for the Northeast District.

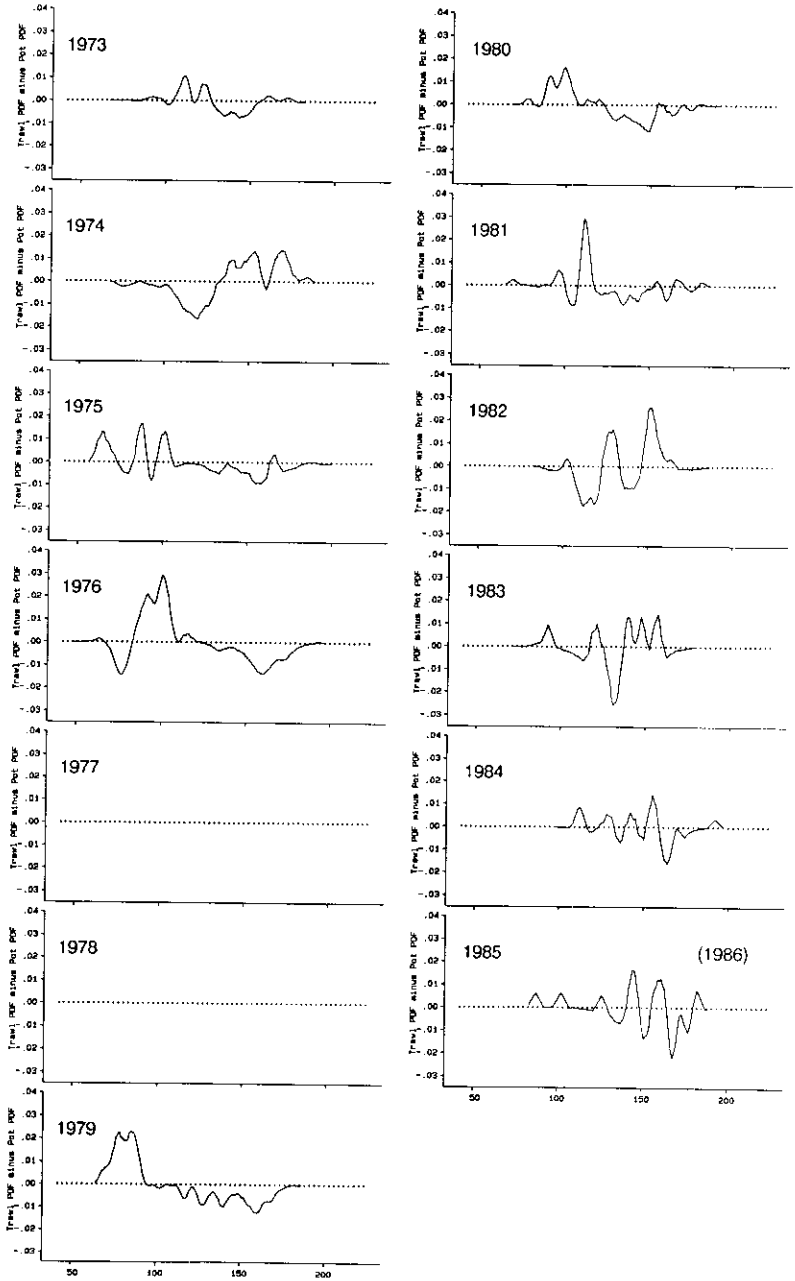

Figure 6. Difference between densities by year for the Alitak area.

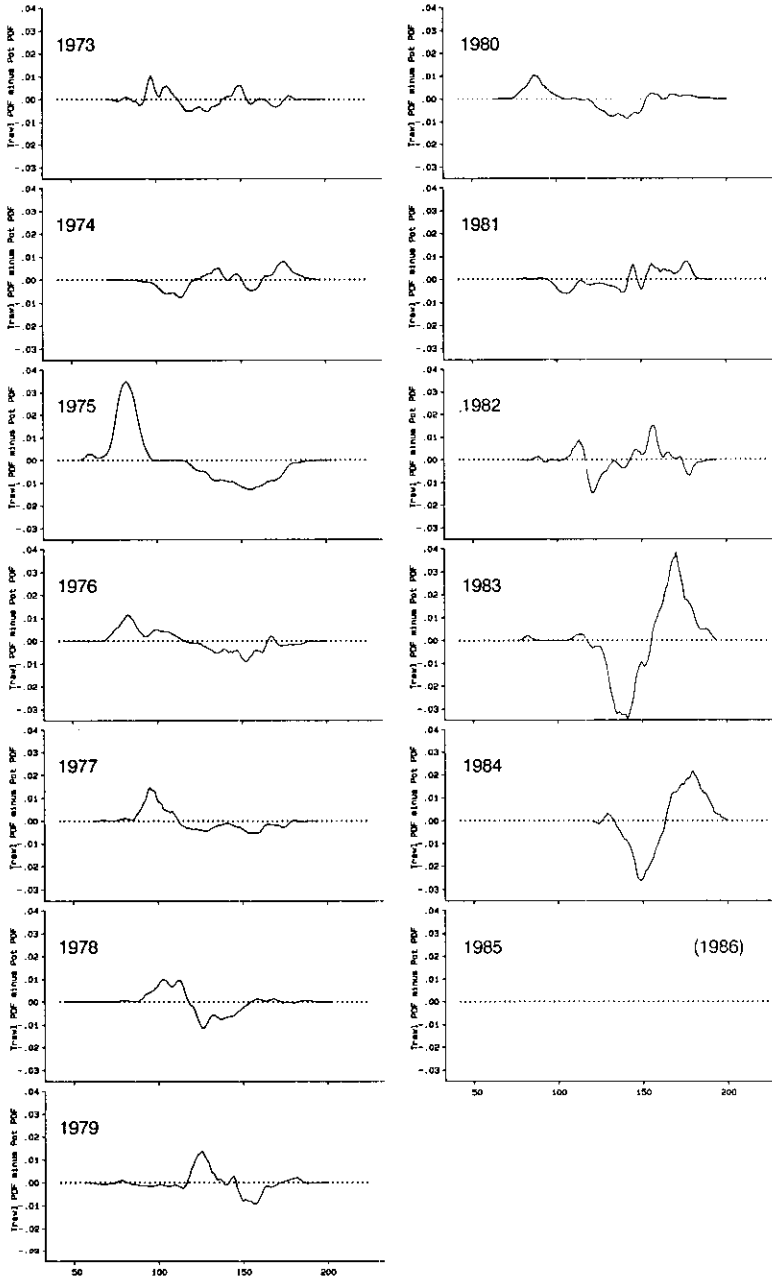

Figure 7. Diference between densities by year for the Chirikof area.

This suggests that trawls were better at catching small sized crabs. However, if we consider the probabilities to be a random variable, the distribution of probabilities show a high degree of right-skewness. The trawl median (0.0226) probability and pot median (0.0219) probability are similar. The trawl tail probabilities are not significantly greater ($T_1 = .875$, $P = 0.81$) than the pot tail probabilities. If the trawl was consistently better at catching smaller crabs, a difference would result.

Within Area Analysis

In the northeast area the size distributions were similar in both range and shape for many of the years. In 1977 the pots captured a mode of crabs near the 100 mm size which was not present in trawl catch (Figure 2). A similar but much smaller difference was also present in 1976 (Figure 2).

In the Alitak area, the size distributions were similar in 1973 and 1984. For most years the ranges were the same for pots and trawls but the shapes of the curves were different. In 1975 and 1976 both trawls and pots caught small crabs, approximately 60 to 100 mm in size. In 1979 and 1980 the trawl captured a mode of crabs at approximately 80-100 mm which was not well represented in the pot catch (Figure 3).

In the Chirikof area, the size distributions were similar in both range and shape for 1973 and 1974. A mode of crabs approximately 70 to 80 mm in size appeared in the trawl data in 1975, persisted in following years, was more abundant in trawl than in pot data but the greater abundance in trawl data appears to decrease through 1979 (Figure 4). In 1980 another mode appeared at approximately 90 mm in the trawl data but the following year the pots caught this group as a greater proportion of the total than did the trawl.

Among Area Analysis

Several metrics of size composition suggest differences among areas. If we consider the average size of all crabs caught in each area, several differences are clear. The average size of crabs caught by pots (145 mm) was less than those caught by trawls (156 mm) in the northeast area, and the average for trawls in Alitak (124 mm) and Chirikof (126 mm) is less than the average for pots (134 mm and 138 mm).

When crabs 100 mm or less are considered, trawls had larger tail probabilities in 50% of the cases in the northeast, and 73% in both the Alitak and Chirikof areas. Comparing the total catch of crabs for all years, it appears that pots caught more small crabs (100 mm or less) in the northeast (4.2% in pots versus 0.8% in trawls) and trawls caught more small crabs in the Alitak and Chirikof areas (26.6% in trawls versus 13.3% in pots and 24.1% in trawls versus 6.2% in pots, respectively).

Recruitment

We defined recruitment for our analysis as the first appearance of juvenile crabs in either of the gear types, rather than recruitment to legal size crabs captured in the commercial fishery. In the entire data set there are two periods of strong recruitment. In 1975 the trawls in the Chirikof area revealed a strong mode of crabs at approximately 70 to 90 mm. From 1975 through 1977 modes of crabs between approximately 70 to 100 mm appeared in all areas and can be followed in later years. Powell (1967) and McCaughran and Powell (1977) show growth of small crabs (70 to 100 mm) ranged from 14 to 18 mm per year.

The second recruitment event appeared in 1979, in Alitak, as a mode of approximately 75 mm to 90 mm in the trawl catch and was evident for several

years. A peak at approximately 85 to 90 mm also appeared in 1980 in the Chirikof samples and was evident for several years.

The 1975 recruitment event was seen in the pots and trawls in Alitak, but only in the trawls in the Chirikof area. The 1979 recruitment appeared first in trawls. In these two areas crabs recruited to the gear at approximately 70 to 90 mm. In the northeast area in 1977, the pots captured many small crabs although the trawls did not. The smallest size mode of crabs, 100 mm, occurred in many of the pots, but did not occur in trawls in the immediate vicinity.

Single Sample Effects

The effects of removing a single sample are examined for the highly different size distributions. Examination of Figures 2, 3, and 4 reveal that the trawl and pot length frequencies show very similar size distributions. The considerable difference in size frequencies of crabs in the Chirikof area in 1975 is due to the presence of one trawl haul with 1000 small crabs. When this one sample is removed, the size distributions are very similar (Figure 8). The smaller crabs were not homogeneously distributed over the sample area. When the influential trawl is removed, the sum of the absolute differences equals 0.15 versus 1.033, indicating similar size distributions.

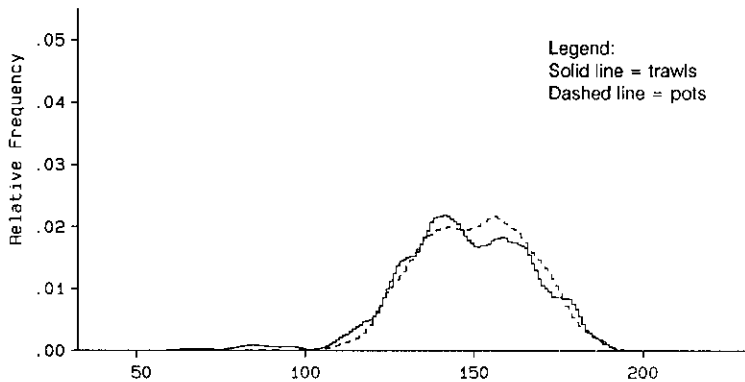

Figure 8. Size frequency by year for the Chirikof area with an influential trawl removed.

Close examination of the Alitak area illustrates the effect of a small number of sample points. There were less than four trawls each year in the Alitak area, except 1984, and the number of pot locations surveyed each year were less than seven. The trawl and pot length frequencies track quite well, except for the larger catch of small crabs by trawls in 1979 and 1980. The effect of an influential sample can be illustrated by reanalyzing the data. In 1979 a single trawl accounted for the large magnitude of smaller crabs. Figure 9 shows that the size frequencies of pot and trawl catch are essentially the same (sum of absolute differences, 0.37) when the influential trawl is removed. For 1980, removal of a single trawl did not result in similar size frequencies.

DISCUSSION

Before this study, small red king crabs were assumed to have a greater catchability in trawl gear than in survey pot gear. The most striking conclusion from this

analysis is the similarity between the gear types in length frequencies of all sizes of crabs. The occurrence of small crabs in either type of gear was irregular and not consistent. In general, the appearance of small crabs in either gear type accurately predicted future recruitment of the represented cohort.

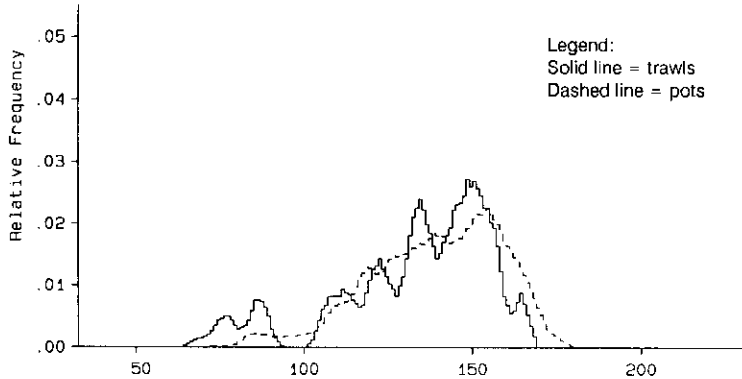

Figure 9. Size frequency by year for the Alitak area with an influential trawl removed.

The possible differences among areas suggests that location, and perhaps habitat, may affect the relative catchability of crabs in the two sampling gears. The northeast area has a hard rocky bottom but the Alitak and Chirikof areas have a sandy bottom. The possibility that bottom type, habitat, or location may affect catchability of small crabs should be considered in sampling design and the selection of the types of gear used as a sampling tool.

The effects of influential samples on length frequencies portrays part of the problem associated with sampling smaller crabs. Red king crab aggregate by size (and perhaps age) groups and tend to be more aggregated at smaller sizes. The well known podding behavior of red king crabs as juveniles reflects this sampling problem. A typical stratified grid pattern used in survey sampling will need many stations and samples to provide a representative relative abundance of small crabs, when compared with the less aggregated large crabs. We do not advocate removal of sample data, but the assumption of a homogeneous group of size frequencies can be violated by a single sample. If previous years do not show a particular size class, and the size class has not moved into the next year, the gear may have sampled a single group of small crabs. However, small crabs often may be relatively abundant and still not occur in representative numbers with normal survey efforts and design. This usually is reflected in their sudden and abundant appearance in later years. Analyzing the data with and without influential samples and comparing to adjacent survey years is a necessity.

Contrary to expectations, trawls do not consistently reveal recruitment sooner than pots. Of the two occurrences of recruitment illustrated, one recruitment was first detected in trawls and the other was seen in both types of gear. The selectivity for crabs 100 mm and less tended to be greater in trawls, but was not significant. Whatever selectivity may exist, it is not great in the Kodiak region and is probably confounded with bottom type or habitat. The trawl data will be invaluable in reanalyzing population models based on pot data.

ACKNOWLEDGEMENTS

We are particularly indebted to the International Pacific Halibut Commission and their staff who have provided us with their raw data, without which this paper would not have been possible. The many years of data collection and analysis of the Kodiak crab pot survey was made possible through the assistance of many Alaska Department of Fish and Game staff members. Guy Powell, Bill Donaldson, Forrest Blau, Bill Nippes, Al Spalinger, and Dave Jackson are only a few of the current and former employees who contributed to the information base used in this study. Peggy Murphy reviewed and assisted with final preparation of this report. Contribution PP-015 of the Alaska Department of Fish and Game, Division of Commercial Fisheries, Juneau.

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Proc. Int. Symp. King & Tanner Crabs
Nov. 1989, Anchorage, Alaska

An Industry Perspective on Problems Facing the Rebuilding of King and Tanner (Bairdi) Crab Stocks of the Eastern Bering Sea

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ABSTRACT

The Alaska Crab Coalition started in 1985 to protect and rebuild Bering Sea crab resources (king and bairdi species). The founders and leaders of the ACC are essentially the survivors of the king crab resource collapse of 1981 who did not diversify into trawling for philosophical and other reasons. In summary, they have a strong commitment to conservation of crab and fishery resources of the Bering Sea.

Due to the notorious reputation of the Bering Sea fleet of the 1970s and the collapse of the resource in 1981, the ACC has encountered considerable difficulty in convincing fisheries managers, both the Alaska Department of Fish and Game and the North Pacific Fishery Management Council of its sincerity in terms of conservation, despite written comments requesting conservative fishing quotas and premature fishery closures. This is only one of the problems facing the ACC in its attempts to rebuild the "Sick Man of the Bering Sea," red king crab (Paralithodes camtschatica).

Given the necessary time constraints of this information transfer forum, I will merely identify some of the major problem areas that the ACC views as impediments to a comprehensive program for rebuilding one of the most valuable renewable resources of the Bering Sea.

1. An ongoing 12-year jurisdictional dispute between state and federal management agencies (aided and abetted by resident and nonresident fishery participants), impedes the planning and development of cohesive research programs and establishment of protectionist management policies needed to rebuild crab fisheries. At the January meeting of the

NPFMC, a management plan with federal oversight and State of Alaska management was approved at the regional level. The ACC hopes that this plan recently approved in Washington, D.C, will foster cooperative research and management efforts between industry, scientists, and managers alike. The ACC is also actively pursuing advanced research and management techniques with Soviet and Canadian experts as they might pertain to east Bering Sea crab fisheries.

2. The ACC recognizes that an undefined combination of factors caused the collapse of king and bairdi crab resources in the North Aleutian Basin. These factors include: environmental change (water temperature), fishing/handling mortality to discards, and predation on weakened discards. The ACC sees the need for revitalizing crab research efforts and the need for improved cooperation between state and federal agencies, universities and the industry. The ACC has offered vessel platform time to NOAA/OCSEAP as a contribution to encourage habitat and early life history research.

3. Bycatch in trawl fisheries is presently recognized by the NPFMC and the National Marine Fisheries Service as an "allocation" issue, not a "conservation" issue despite record low harvests in king and bairdi crab fisheries. The ACC views trawl bycatch as a conservation issue and a major factor impeding the rebuilding of king and bairdi crab fisheries. The associated research and management emphasis of the NPFMC has focused on the development of groundfish trawl fisheries in the North Aleutian Basin, to the detriment of crab, halibut and herring resources in the same area. The extent of the problem is illustrated in statistical charts.

4. The ACC is also concerned about oil spill impacts to crab and finfish in the North Aleutian Basin (OCS Sales 92 and 117). After the March 1989 disaster in Prince William Sound, the ACC has moved to support a permanent moratorium on drilling in the Basin and it also supports a State of Alaska lease buyback program. At this time it appears the oil industry is unable to demonstrate the ability to provide adequate safeguards and containment in the Southeastern Bering Sea in the event of an oil spill.

INTRODUCTION

The Alaska Crab Coalition (ACC) was formed in 1985 with organizational goals to protect and rebuild Bering Sea king and tanner crab resources and fisheries. The founders and leaders of the ACC are essentially the survivors of the collapse of the red king crab (Paralithodes camtchatica) fishery in 1981. They are crab fishermen who did not diversify into regional groundfisheries but rather have redirected their effort to the harvest of the opilio crabs (Chionoecetes opilio). Recent harvests of this species of Tanner crab (100-140 million lb. annually) rival the pre-1981 commercial catches of red king crab. The ACC actively participates in the management process of Alaskan crab fisheries and as a group, maintains a strong commitment to the conservation of fishery resources.

Due to the time constraints of the International King and Tanner Crab Symposium, I would like to identify, but only

briefly describe, several serious issues impeding the recovery of Bering Sea crab populations.

LACK OF CONFIDENCE

Perhaps due to the notorious reputation of the Bering Sea fleet of the 1970s and the collapse of the resource in 1981, the ACC has experienced considerable difficulty until this year, in convincing fisheries managers, within both the Alaska Department of Fish and Game (ADFG) and the North Pacific Fishery Management Council (NPFMC), of its sincerity. This perception is being overcome due in part to the ACC's recommendations to the NPFMC and ADFG for conservative fishery measures for the trawl fisheries and crab fisheries, including restricted quotas and closures for crab fisheries. The lack of confidence by management authorities is viewed as a major hurdle facing the ACC in its attempts to help rebuild the "Sick man of the Bering Sea," red king crab. It is also part of the reason ADFG has declined several ACC offers of cost effective inseason data reporting to improve on the information available from the very limited resource assessment program. This would also help optimize harvests in pulse nature king crab fisheries.

STATE AND FEDERAL FISHERY JURISDICTION

An ongoing 12-year jurisdictional dispute between state and federal management agencies (aided and abetted by resident and nonresident fishery participants arguing for, or against one or the other agency), continues to impede the planning and development of cohesive research programs and establishment of protectionist management policies needed to rebuild crab fisheries. In January of 1989, the NPFMC approved a management plan calling for federal oversight and State of Alaska management. The ACC hopes that this plan, recently approved in Washington, D.C. will help foster cooperative research and management efforts between industry, scientists and managers .

COOPERATIVE RESEARCH

The ACC recognizes a combination of undefined factors caused the collapse of king and bairdi crab resources in the North Aleutian Basin. These factors include: environmental change (increase in water temperature), fishing/handling mortality to discards and predation on weakened discards. Today's Bering Sea crab fleet rivals that of 1980 in terms of fishing power and effort expended in fishing. This is important, considering that in 1980 there was 10 times the volume of king crab resource available to be harvested. Bering Sea crab fishermen now rely on the high volume opilio crab fishery for their livelihoods, not king and bairdi crab.

The ACC realizes that research dollars within governmental agencies are declining and that certain information needs pertaining to the management and conservation of stocks might best be addressed through cooperative research. Throughout 1989, the ACC has reviewed options with universities, State of Alaska and federal agencies to participate in cooperative research involving tagging, handling mortality, habitat and early life history. The ACC encourages ap-

plied research in vital areas such as juvenile habitat relationships and early life history in the nearshore North Aleutian Basin. Such approaches are viewed by our group as necessary to fully understand the effects of fishery and other sources of mortality on crab productivity, as well as to identify critical habitats.

The ACC has recently begun scoping the industry, State of Alaska, NOAA/NMFS agency scientists and university scientists to determine if there is a need for developing a king and tanner crab information consortium for the Bering Sea and Gulf of Alaska. Possible functions of the consortium would be three fold: (1) to act as a resource data base to collect and track regional, national and international research activities relative to king and tanner crab resources; (2) to develop research priorities in conjunction with industry; (3) to seek multi-year research funding from public and industry sources. A computerized bulletin board could initiate centralization of research information.

FISHERIES BYCATCH

Bycatch in trawl fisheries is presently recognized by the NPFMC and the National Marine Fisheries Service (NMFS) as an "allocation" rather than a "conservation" issue. This is so despite record low harvests of king and bairdi crab fisheries. The ACC disagrees with the NPFMC on this issue and maintains that bycatch is a conservation issue and a major impediment to the recovery of king and bairdi crab stocks. Bycatch, defined as the incidental catch of prohibited species in fisheries for cod, pollock and flounders, is discarded by the trawl industry as waste. Bycatch species have been shown to sustain high levels of mortality, 50 to 100 per cent in the discard process. Prohibited species comprising the bycatch include king and bairdi crabs, Pacific halibut, Pacific salmon, and Pacific herring.

The associated research and management emphasis of the NPFMC for the past eight years, appears to have been focused on the development of groundfish/trawl fisheries in the Bering Sea. As an example of the rapid growth in this industry, Dr. Lee Alverson, a former administrator for the NMFS and a fisheries consultant, is quoted in the Seattle Post Intelligencer (2 May 1988) as comparing the growth of domestic Bering Sea groundfisheries to "one new Columbia Center (a Seattle skyscraper) every year." And more recently, Walter Pereyra, another former administrator for the NMFS and now CEO for Profish International Inc., a Seattle groundfish firm, as quoted in the Puget Sound Business Journal (30 October 1989), predicts near a "50 per cent increase in processing capacity" in 1990 or shortly after, with all the new shipyard and shorebased plant construction in progress.

During the late 1960s and the early 1970s, bilateral agreements between the U.S. and Japan and the U.S. and the USSR to protect traditional halibut, crab, salmon and herring fisheries resulted in restrictions on foreign fishing fleets operating within the U.S. Exclusive Economic Zone that continue today (Fig. 1). Current regulations, requiring trained U.S. observers onboard foreign processing ships, prohibit foreign fishing in much of Bristol Bay in the so-called "Pot

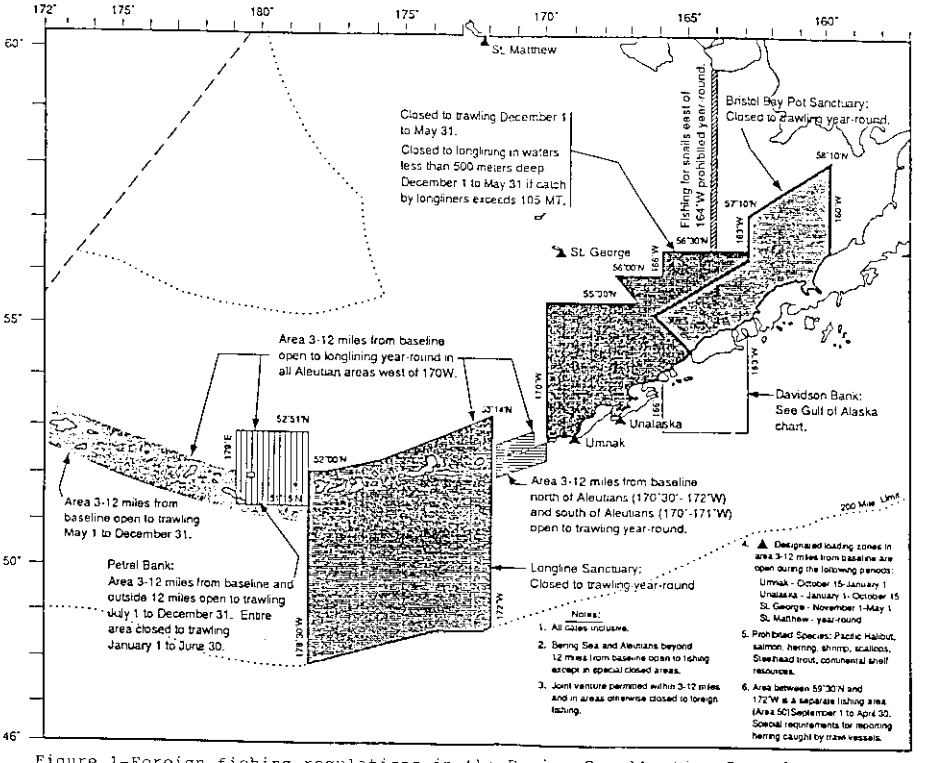

Figure 1-Foreign fishing regulations in the Bering Sea-Aleutian Islands Management Area (NMFS, Juneau, Alaska)

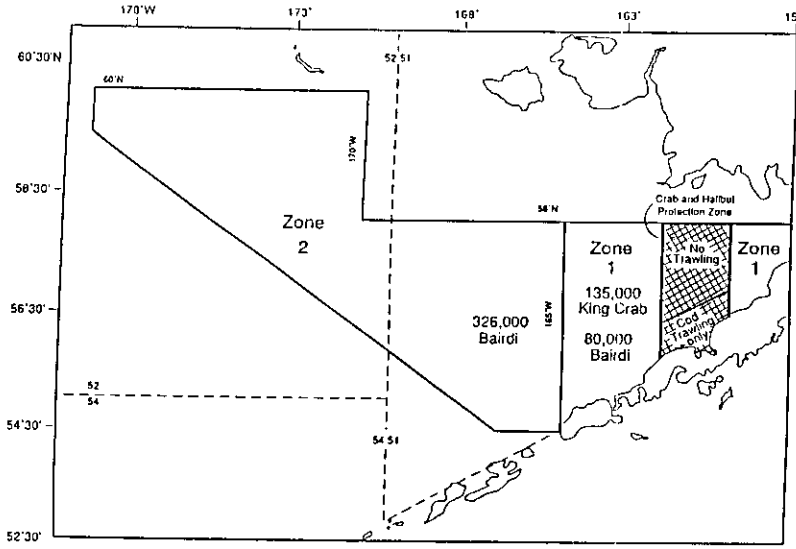

Figure 2-Eastern Bering Sea trawl bycatch restrictions on king and Tanner crabs as established by Amendment 10 to the Bering Sea Aleutian Islands Fishery Management Plan (April 1986)

Sanctuary", an area that until recently was historically "off limits" to bottomfishing because of its importance to king crabs and juvenile halibut. In 1981, however, the NPFMC relaxed trawl restrictions in the shallow waters of the North Aleutian Basin, and thereby encouraged the development of a nearshore flatfish and cod fishery. It is the bycatch and habitat changes associated with the extensive trawling in this area (by 120 flatfish catcher boats and and a fleet of more than 50 pollock/cod factory trawlers) that are of concern to the ACC and other fishermen groups. These waters provide important habitat for crab, herring, halibut, and salmon resources of Bristol Bay. The ACC is concerned that current management decisions do not adequately safeguard these resources from trawl-induced changes in populations and habitats.

In 1981, the coastal waters along the north side of the Alaska Peninsula were opened to a joint venture yellowfin sole fishery. By 1984 it was widely recognized that the high incidental catches of prohibited species, chiefly red king crab, bairdi Tanner crab, and juvenile halibut, posed a serious management problem. Marine Resources Company International, the American-Soviet joint venture company operating in the area, voluntarily imposed bycatch reduction measures on itself in 1985. However, this action resulted in little change in bycatch harvests and in 1986 the NPFMC issued an emergency rule establishing bycatch quotas, or caps, on this industry in several fishery districts in the Bering Sea (Fig. 2). A third district (not shown in Fig. 2), Zone 3, lies north of the Pribilof Islands. In 1986, the Bering Sea Fishery Management Plan was amended (Amendment #10) to also close a portion of

Table 1-Joint venture harvestor performance in Zone 1 flounder fisheries prior to and after Amendment 10 to the Bering-Sea Aleutian Islands Fishery Management Plan (1986-88). Statistics from NMFS, NWAFC, Seattle, WA.

		Red king crab		Tanner crab, *C. bairdi*	
Year	Groundfish (mt)	Bycatch (number)	Rate (per ton)	Bycatch (number)	Rate (per ton)
1983	34,233	497,285	14.5	361,152	10.5
1984	45,924	230,050	5.0	149,786	3.2
1985	207,000	813,000	4.0	669,000	3.2
1986	75,942	127,571	1.6	117,000	1.5
1987	74,269	64,398	0.9	98,161	1.3
1988	100,768	50,722	0.5	92,492	0.9

Zone 1 to trawl fisheries.

The performance of joint venture harvestors in Zone 1 for the period 1983-1988 is shown in Table 1. In 1983 there was a high bycatch of red king and bairdi crabs. The greatly reduced bycatches (greater than 50%) of red king and bairdi demonstrate the effectiveness of bycatch quotas and existing time and area closures (during softshell periods of crab reproduction and molting). Gear experiments have also been conducted within the trawl industry to alleviate the bycatch problem and some of the observed decreases in catch may be attributed to these efforts.

Crab resource assessment surveys of the NMFS in 1987 and 1988 have indicated a general improvement in the status of bairdi crabs, but not red king crabs during this period (pers. commun. R. Otto, NMFS, Kodiak, Alaska). In fact, the abundance data suggest a doubling in population size of the bairdi crab population each year. This strengthening of bairdi numbers is seen by the ACC as evidence that fixed bycatch caps and fishery closures provide simple and effective incentives for "clean" fishing. However, the Northwest and Alaska Fisheries Center (NWAFC) has proposed new bycatch allocations for 1989 (Fig. 3) that greatly exceed those of previous years. These caps reflect the current philosophy within the NWAFC that a "floating 1% of biomass dedicated to bycatch", is a biologically acceptable formula. The ACC has serious reservations about this strategy and strongly opposes the "liberal" 1989 bycatch levels (Fig. 3). A 15 March-15 June closure of fishing in the area south of 58 degrees N and 162 degrees W and 163 degrees W can be expected to provide some additional protection to regional crab and halibut populations.

Another concern of our group pertains to enforcement of the established bycatch quotas in domestic fisheries. Without a defined data collection (observer) program of up to 100% coverage in place, this will be difficult. Even though significant reductions have been achieved, particularly in the joint venture segment of the industry, the problem of by-

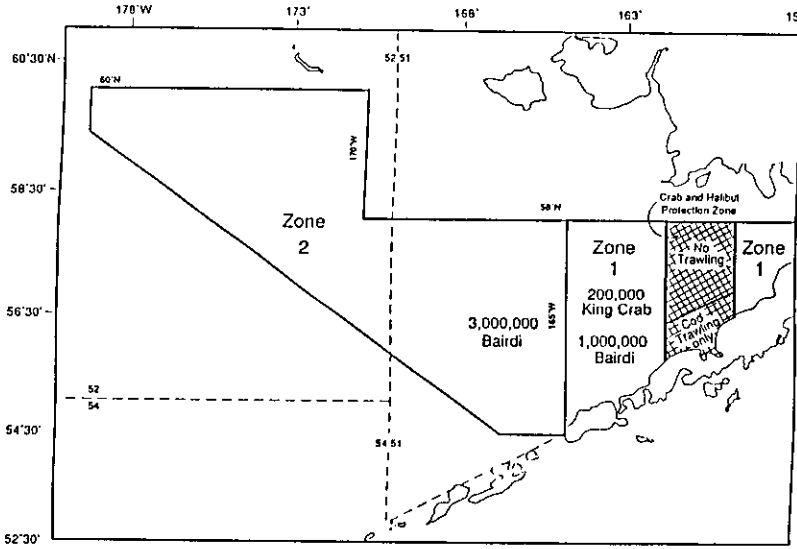

Figure 3-Eastern Bering Sea trawl bycatch restrictions on king and Tanner crabs in 1989.

catch remains controversial, and it will likely worsen with increased political pressures from an overcapitalized groundfishery in need of liberalized bycatch quotas.

A recently approved domestic observer program schedulled to start 1 January 1990, if implemented at the 100% level (as is the intent of the NPFMC) on factory catcher processors, could provide considerable relief for prohibited species.

A closer inspection of catch statistics reported for joint venture fisheries operating in Zones 1-3, during the period 1 January to 6 August 1988, reveals the magnitude of the bycatch problem with respect to halibut and crabs (Table 2). In 1988, during this fishing period (the last year with adequate observer data), nearly 1.5 million halibut were captured incidentally by joint venture fishermen. Most of these fish were taken in Zone 1 (20%) and Zone 2 (73%) of Bristol Bay. Similarly, almost 600,000 bairdi crabs and 73,000 red king crabs were taken (and incidentally released) by joint venture fishermen. In the case of red king crabs, 82% of the bycatch was reported from Zone 1.

Throughout 1989, a similar bycatch pattern has emerged for Zones 1 and 2. However, the unobserved domestic boats are harvesting 1,300,000 tons of groundfish, an amount similar to the joint venture harvest of 1988, under the MFCMA mandate of domestic preference. Joint venture harvests have been reduced to 600,000 tons, but these are still observed.

The bycatch of red king crabs has tripled over 1988 to 281,000 and the bycatch of bairdi crabs has doubled. With the domestic catches being largely unobserved (estimated

Table 2-Summary of 1988 Bering Sea joint venture prohibited species catches for the period 1 January through 6 August 1988. Statistics from NMFS, NWAFC, Seattle, WA.

Prohibited species	Target fishery	Zone	Groundfish catch (mt)	Prohibited species catch (numbers)	Prohibited species rate (numbers)
Pacific halibut	JV Flounder	1	100,768	147,241	1.46
		2	196,474	371,566	1.89
		3	94,484	49,172	0.52
		1-3	391,726	567,979	1.45
	JV Other	1	158,909	159,638	1.00
		2	421,076	717,869	1.70
		3	170,448	48,336	0.28
		1-3	750,432	925,843	1.23
	Total All JV	1	259,677	306,879	1.18
		2	612,550	1,089,435	1.78
		3	264,931	97,508	0.37
		1-3	1,142,158	1,493,822	1.31
Bairdi Tanner crab	JV Flounder	1	100,768	92,492	0.92
		2	196,474	285,903	1.46
		3	94,484	28,318	0.30
		1-3	391,726	406,713	1.04
	JV Other	1	158,909	90,987	0.57
		2	421,076	97,351	0.23
		3	170,448	1,119	0.01
		1-3	750,432	189,457	0.25
	Total All JV	1	259,677	183,479	0.71
		2	612,550	383,254	0.63
		3	264,931	29,437	0.11
		1-3	1,142,158	596,170	0.52
Red king crab	JV Flounder	1	100,768	50,722	0.50
		2	196,474	2,645	0.01
		3	94,484	9,559	0.10
		1-3	391,726	62,926	0.16
	JV Other	1	158,909	8,924	0.06
		2	421,076	957	0.00
		3	170,448	19	0.00
		1-3	750,432	9,900	0.01
	Total All JV	1	259,677	59,646	0.23
		2	612,550	3,602	0.01
		3	264,931	9,578	0.04
		1-3	1,142,158	72,826	0.06

10% level of coverage, which NMFS considers insufficient for data extrapolation), NMFS has been using mathmematical formulae "estimators" to arrive at bycatch levels to institute closure notices. The bycatch of halibut is now being measured in tons, not numbers of fish, but it appears to be at a level similar to 1988. (Prohibited Species Status Report, NMFS, 17 November 1989). Managers and the indust- pect the new observer program, if implemented at the 100% level, will provide the data necessary upon which to base management decisions on bycatch and other issues.

QUESTIONS OF SCIENCE AND MANAGEMENT

If nothing else, the bycatch statistics indicate the importance of Zones 1 and 2 to juvenile crab and halibut resources of Bristol Bay. OCSEAP and other research in the North

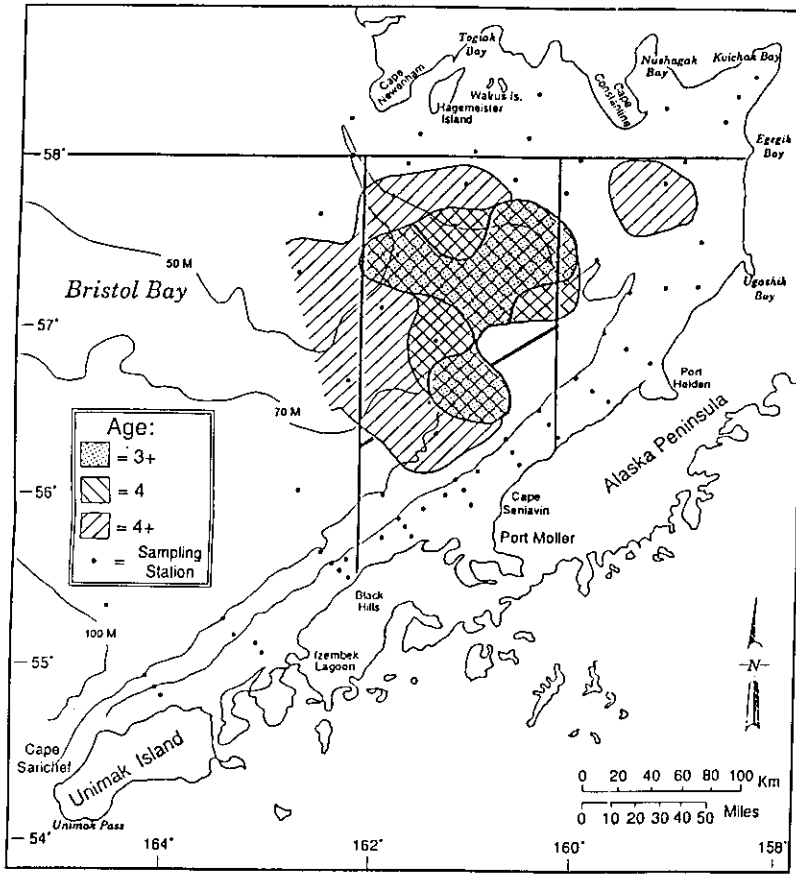

Figure 4-Distribution of juvenile red king crabs older than 3 years in June 1983 (McMurray et al. 1984).

Aleutian Basin has indicated that the coastal waters of the lease area (corresponding to Zone 1) are of prime habitat importance to larval and juvenile king crab. McMurray et al. (1984) reported on the distribution and abundance of juveniles near Port Moller and in other parts of Bristol Bay (Fig. 4). NMFS surveys and ADFG historic catch records support these findings. However, the recommendations of these OCSEAP investigators with regard to fishery resources and habitats have been summarily ignored by NPFMC and NMFS research leadership in the course of conducting the "business" of fisheries management. Of course, this attitude is not representative of all NPFMC members or NMFS personnel. The ACC believes that this information must be carefully evaluated before fishery boundaries or bycatch caps are altered by the NPFMC to accommodate further growth in the now overcapitalized groundfishery.

A technical paper developed by trawl gear specialist, Wes Johnsen (Seattle, WA 1985) estimates that actual trawl gear

Table 3-Summary of the species composition and incidence of prohibited species in the 1989 domestic Port Moller Pacific cod fishery in the cod trawl exemption area of Zone 1, inside 25 fathoms, Catch Statistics from NMFS, NWAFC, Seattle, WA.

Summary of 1989 Port Moller Fishery
(62.4 days on the ground; target = Pacific cod/pollock)

A. Preliminary estimate of groundfish catch (area 512):

	Metric tons	Percent of catch
Yellowfin sole	728.80	13.0
Rock sole	831.78	14.8
Other flatfish	78.21	1.4
Arrowtooth flounder	16.42	0.3
Walleye pollock	651.38	11.6
Pacific cod	2,854.29	50.9
Sablefish	0.01	<0.1
Other fish	120.87	2.2
Nonallocated species	322.43	5.8
Total	5,604.20	100.0

B. Preliminary estimate of prohibited species catch (area 512):

	Estimated numbers	Number per metric ton
Red king crab	13,940	2.487
Bairdi Tanner crab	5,225	0.932
Other Tanner crab	34	0.006
Chinook salmon	9	0.002
Other salmon	14	0.002
Pacific halibut	44,914	8.014

C.

	Estimated weight (kg)	Kg per metric ton	Percent of catch
Pacific halibut	56,016	9.995	1.00
Pacific herring	102,870	18.358	1.84

mortality to king crabs from crushing of the gear on the ocean floor, is 10 to 15 times the number of crabs that are caught in the net (and estimated by NMFS observers). Trawl groups are joined by certain scientists, the Director of the NAFC and the previous Chairman of the NPFMC in challenging the Johnsen paper. They also dismiss any consideration of "unobserved trawl gear mortality " in bycatch estimates and the NPFMC makes no allowance for the extent of this mortality when setting bycatch quotas. In so doing, they point to a controversial Trawl Bycatch study (NRC 1988) coordinated by the NAFC in conjunction with major industry trawl associations as disproving the Johnsen hypothesis. However, serious questions have been raised about the scientific credibility of the project. Legal issues relating to conflict of interest have also arisen about the government funded study.

"Therapeutic bottom trawling" has almost been prescription in the NPFMC forum of the 1980s, since the prevailing scientific attitude is there is "no conclusive evidence" to

prove bottom trawling is detrimental to crabs, halibut or the benthic environment. The bottom trawling experiment of 1981 (the opening of the "Pot Sanctuary" to joint venture sole fisheries) has been liberalized to encourage the growth of the domestic groundfishery and the concommitent bycatch needs of the 50 factory trawlers who operate routinely without observers. There is great concern among Bering Sea crab fishermen about the effects of bottom trawling on benthic habitats and crab productivity and they feel it is time the NMFS and the NPFMC initiate a "conservation experiment" in Zones 1 & 2 in an attempt to rebuild crab resources and to protect declining halibut stocks.

In the future, the NPFMC should also direct attention to the problem of factory bottom trawling for cod in the nearshore Port Moller area. Although this area has been identified in OCSEAP reports as the primary nursery area for juvenile king crabs, domestic trawlers have had a special exemption for cod trawling in the area for four years. The 1989 fishery was closed this year after the boats exceeded the red king crab cap of 12,000 crabs. Almost 9000 of these crabs were caught in two tows, when the nets hit two "pods" of uniform size juveniles. The fishery which took only 3,400 tons of retained groundfish, also took almost 45,000 halibut (see Table 3). Figures in Table 3 are not estimated, they are one of the few examples of 100 per cent observer coverage in the Bering Sea domestic groundfishery.

A concluding note refers to a comparative trawl bycatch control program for king crab in the USSR. Members of the ACC have learned in personal communications with Soviet crab biologist, Alexei Slizkin, that the Soviets have a very productive king crab fishery off the west coast of the Kamchatka Peninsula, in the Okhotsk Sea. Harvests have increased from 18,800 tons in 1980, to over 35,000 tons in 1986. Production has apparently been stable at this level the past two years.

Of particular interest to the ACC, relative to its goal of rebuilding king and bairdi crab, is that the entire west coast of Kamchatka, is closed to on-bottom trawling, out to 400 meters (Slizkin, TINRO, pers. comm. September, 1988). The central part of the coast has three degrees of latitude closed to all types of trawling, from 54 - 57 degrees N latitude. Adjoining zones on the north and south are open to mid-water trawling only. In addition, there is a 40 mile wide strip on the 57 degree line closed to groundfish trawling and crab fishing. This is the known habitat for female king crabs. Other than to say that they have been in place for almost 20 years, the Soviets did not elaborate on the specific role and functions these extensive trawl restrictions serve.

OCS OIL AND GAS DEVELOPMENT

The ACC has two major concerns regarding offshore development in the North Aleutian Basin (OCS Sales 92 and 117). A major issue we see relates to the impacts of potential oil spills on Bering Sea crab populations. Since the March 1989 disaster in Prince William Sound, the ACC has moved to support a permanent moratorium on drilling in the Basin and

it also supports a State of Alaska lease buyback program. The oil industry has been unable to demonstrate the ability to provide adequate safeguards and containment in the Southeastern Bering Sea in the event of an oil spill. A second concern relates to increased vessel traffic in Unimak Pass and the high potential for collisions involving tankers and fishing vessels.

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Standardized Effort for the Kodiak King Crab Fishing Fleet

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ABSTRACT

The relative efficiency of vessels fishing Kodiak king crab from 1969 through 1982 is being analyzed using Coast Guard documentation of vessel traits, fish ticket data on mean catch per pot, area fished, and date for each delivery, and pre–season abundance indices from annual research surveys.

The use of catch per unit effort (CPUE) as an index of absolute abundance relies on CPUE being directly proportional to abundance, or $C/E = qN$, where the catchability and efficiency q is the fishing mortality produced per unit of effort (C/EN). For C/E to be proportional to abundance, efficiency must be constant, but the fleets of some fisheries become more and more efficient through learning, experience, and the development of specialized techniques and vessels. If efficiency is assumed constant when it really is increasing, abundance will be overestimated, so it is desirable to standardize effort for any major changes in efficiency.

This is typically done by first fitting a log–linear model, with log CPUE as the response, factors for area–time strata, and log transformed covariates for available vessel characteristics such as gross tonnage and horsepower. Parameter estimates are then used for standardization. Kimura (1981) gives an excellent explanation of parameterizing such a model, and Allen and Punsly (1984) is also a good case study. Since Beverton and Holt (1957) fit a multiplicative model with gross tonnage proportional to efficiency, the equivalent use of log transformation and linear models (Robson, 1966) have worked well to normalize CPUE and stabilize variances in models for vessels using mobile fishing gear. Although studies have been performed to standardize individual hauls of stationary gear for factors such as soak time and bait, I found no references to standardizing effort for vessels using stationary gear such as king crab pots. For pot gear it is assumed that knowing either the number of pots used and time fished or the number of potlifts makes standardization of effort between vessels unnecessary. This study tests

that assumption.

To choose between the many vessel characteristics available (length, breadth, depth, gross tonnage, net tonnage, year built, age, horsepower and their log transforms), I initially modeled them directly against $\ln C/EN$, where N is the preseason abundance estimate minus cumulative catch to date of landing. $\ln C/EN$ is thus a measure of both catchability and efficiency, and includes both the vessel's ability to fish in areas and times of high density and differences between vessels fishing similar densities. Technically, each observation needs to be weighted by the variance associated with each corresponding preseason abundance estimate, but the variances are not yet available, so the results are preliminary.

Log gross tonnage and log length were highly correlated ($r = .96$) and either one explained about 10% of the variation in $\ln C/EN$. Additional vessel characteristic variables explained very little. In comparison, strata for vessels explained from 32–26%, depending on whether all vessels were included or just those for which there were 15 or more observations. About 2/3 of the between vessel differences are therefore unexplained by measured vessel traits, and perhaps reflect unmeasured traits such as skill and luck (Hilborn and Ledbetter, 1985). The indication that 1/3 of the variation can be explained by a vessel trait indicates that standardization of effort may be useful.

Next, log linear models were fitted using log gross tonnage or log length to represent differences in efficiency. Factors were included to stratify for year, 4 large areas (corresponding to stocks I, II, III, and IV–VII, see Blau, 1988), and area–year interactions. These factors help account for differences in the densities of crab fished. In the same sequence as they were entered, year explained 29%, area 6%, and area–year interactions 5%. In addition, log gross tonnage explained 5% or log length explained 4%. The pooled interactions between vessel trait and area, year, and area–year factors were 1.5% for tonnage and 1.6% for length. As pointed out by Allen and Punsly (1984), such interactions should be minimal for standardized CPUE to be accurate and the parameters corresponding to the interactions are not used in standardization. In this respect, the interaction terms for these models are dissapointingly large in comparison with the term for vessel trait. A total of 44–45% of the variation in log CPUE is therefore explained by year, area, and log gross tonnage or log length.

However, residual analysis suggests neither model is an adequate fit to the data. Nearly all outliers, many of them extreme, have large negative residuals. For the untransformed data, area–year cell variances increase dramatically with cell means. Instead of stabilizing the variances, the log transform over corrects and results in decreasing variances with increased cell mean. Normal probability plots reveal that for all years but 1982 and for all years together, the log transform does not normalize CPUE. Instead, the cubic root transform seems to do a much better job, although its use will produce a model without the clear multiplicative interpretation of the log linear model. Because the cubic root transform is intermediate between no transform and log transform, it should also better stabilize the variances. The lack of the log transform to normalize CPUE may reflect some basic difference between CPUE's for mobile vs. stationary gears, or merely indicate an unusual data set.

Therefore, the model will be fit again using the cube root transform of CPUE, and residual analysis done again, before the parameter estimates are to be trusted

for use in standardizing effort. Models using $\ln C/EN$ will also be recalculated using the appropriate weighting factors.

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Alternative Red King Crab Fishery Management Practices: Modelling the Effects of Varying Size-Sex Restrictions and Harvest Rates

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ABSTRACT

The red king crab (Paralithodes camtschatica) harvest strategy that is presently used in Alaska applies varying harvest rates to legal crabs depending on the size and age structure of the population. That strategy, however, suffers from ambiguity in application and is apparently less effective in stabilizing annual landings in the face of variable recruitment than is a fixed harvest rate on legal crabs. We present an alternative harvest strategy that is intended to help stabilize landings under variable recruitment while providing a low fixed rate of exploitation on breeding males. The properties and utility of the proposed harvest strategy are studied using computer simulations applied to a growth and mortality model developed for Kodiak Area red king crabs. Our results indicate that, compared to fixed harvest rates on legal crabs, the proposed strategy offers more protection to breeding males and, under highly variable recruitment, greater stability in yearly landings while producing the same average yield per recruit.

INTRODUCTION

The Alaska Board of Fisheries (ABOF) identified three goals of red king crab (Paralithodes camtschatica) management that apply to commercial harvest strategies (ADF&G, 1988; Otto, 1985). These goals are as follows: (1) to establish stability in landings, (2) to produce long-term optimum yield, and (3) to the protect reproductive potential of the stocks. Otto (1985) reviewed these management goals relative to the history of instability and dependence upon fluctuating annual recruitment that has characterized the Alaska king crab fishery. In its policy statement, the ABOF acknowledges that "maximum physical yield will not necessarily produce the long-term optimum yield" (ADF&G, 1988). Thus, optimum yield is a compromise between maximum yield and stability in landings. Overall, the ABOF red king crab management policy indicates that a conservative harvest strategy should be applied to Alaska's red

king crab stocks -- a strategy that emphasizes stability more than maximum yield and insures adequate protection of breeding males.

The harvest strategy that is presently applied to Alaska's red king crab stocks is given in Table 1. This harvest strategy prescribes a harvest rate on legal crabs which varies with population size, the status of sublegal-sized males, and the relative abundance of males that have previously recruited to the fishery. The maximum harvest rate allowed in this strategy is 60% while, in some circumstances, the harvest rate prescribed may be 20% or less.

Table 1. Current harvest strategy for red king crab in Alaska (from ADF&G, 1986). Approximate harvest rates of legal crab at given levels of postrecruits.

Population Size	Prerecruit Abundance	Low*	Moderate**	High***
Depressed	Declining	Less than 20	Less than 25	Less than 25
	Stable	30	30	35
	Increasing	30	30	35
Average	Declining	40	40	40
	Stable	40	45	45
	Increasing	40	50	50
Peak	Declining	40	45	50
	Stable	50	55	60
	Increasing	60	60	60

*Low=less than 1/3 of total population (lbs).
**Moderate=1/3 - 2/3 of total population.
***High=2/3 of total population.
Prerecruits - those crab which will not reach legal size for one to two molts.
Recruits - those crab which have attached legal size for the first time.
Postrecruits - those crab which have been legal size for one or more years.

This current harvest strategy presents two problems to managers of Alaska's red king crab stocks. The first is that it cannot be operationally applied because the terms used to describe most of the stock conditions which set the harvest rate ("depressed," "average," "peak," "declining," "stable," and "increasing") are ambiguous and are not defined in either relative or absolute terms. Differences in interpretation of these terms as they are applied to a given stock of crabs can lead to enormous differences in the exploitation of that stock.

The other problem with the current harvest strategy is that it may be ineffective in establishing stability in landings over time. Otto (1985) used computer simulation studies to compare the performance of the current harvest strategy table with that of a harvest strategy which prescribed a fixed harvest rate of 40% on legal crabs. His results indicate that the two strategies would show little difference in average yearly landings, but that the current strategy would produce more variability in yearly landings than the constant 40% harvest rate. This result is not surprising since the current harvest strategy prescribes the highest harvest rates when stock size is high and the lowest harvest rates when stocks are depressed. In terms of landings, such a strategy would serve to amplify the effects of variable recruitment into the fishery.

We present here a revision to the current harvest strategy for red king crabs in Alaska. The revision was designed to accommodate the goals of the ABOF red king crab management policy statement without the ambiguity of the current harvest strategy

table. That is, this proposed alternative to the current harvest strategy attempts to (1) provide stability in landings in the face of variable recruitment into the fishery, (2) provide adequate protection to breeding male crabs, and (3) provide a reasonable balance between yield-per-recruit and the goals of stability and protection of breeding males.

In this paper, we investigate the properties and utility of the proposed harvest strategy as it would apply to red king crabs in the Kodiak area by using a growth model and an operational definition for breeding males that were both developed from data on Kodiak area red king crabs. Preliminary to the investigation of the proposed harvest strategy, we assess the effects that changing the current minimum legal size of 7 inches in carapace width for Kodiak area red king crabs and changing the current maximum harvest rate of 60% would have on yield per recruit.

RESULTS AND DISCUSSION

An Alternative Harvest Strategy

The following proposed harvest strategy is the basic component of our analysis. Note that we use the term "exploitation rate" when referring to the percentage of breeding males that are to be harvested, while we use "harvest rate" when referring to the percentage of legal crabs that are to be harvested. The proposed harvest strategy sets a constant exploitation rate, E, on breeding males. The number of crabs removed by the harvest will be applied to the legal component of the population as currently set by minimum size limits. That is, the harvest rate applied to legal crabs is,

$$H = \min\{E(N_b/N_l), 0.6\}, \tag{1}$$

where min{x,y} denotes the minimum of x and y, H is the harvest rate applied to legal crabs, N_b is the number of breeding males, and N_l is the number of legal-sized males. Note that, like the current harvest strategy, the maximum harvest rate that would be applied to legals is 60%. Because legal-sized males are a subset of the breeding males, equation (1) becomes,

$$H = \min\{E + E(N_b - N_l)/N_l, 0.6\}, \tag{2}$$

noting that $N_b - N_l$ is the number of nonlegal (i.e., sublegal-sized) breeding males. From equation (2) it is seen that E is both a constant exploitation rate on breeding males and a minimum harvest rate on legal crabs, a minimum that is attained only when all breeding males are legal-sized. We tentatively apply exploitation rates of E = 20% and E = 25%; these are at the low end of the harvest rates in the current harvest strategy.

To explore the behavior and utility of this revised harvest strategy, we required a growth and survivorship model for male red king crabs and an estimate of the minimum size of breeding males. A description of the growth model and the development of an estimate of minimum size for breeding males follow.

Growth and Survivorship Model for Male King Crabs

Our growth and survivorship model for Kodiak male red king crabs is summarized in Table 2. The model is designed to produce shell age and size distributions of male red king crabs in an unharvested population. The shell age and size distributions are intended to reflect those of the summer months that follow the spring breeding and molting period and precede the commercial fishery season of fall and winter. Shell condition identifies whether a crab has molted in the preceding spring: "newshell" crabs molted and grew, while "oldshell" (or, "skipmolt") crabs did not. The yearly changes in size distribution and relative abundance for an unharvested cohort resulting from this model are illustrated in Figure 1. Removal from the population due to harvest can be applied to the growth and survivorship model to model the effects of harvest strategies.

Our approach differs from that of the growth model of McCaughran and Powell (1977). While McCaughran and Powell (1977) modelled the growth in carapace length of individual crabs, we modelled the carapace length frequency distribution of a population of crabs. Our approach allows us to study the effects of harvest strategies applied to a population represented by a model size distribution; McCaughran and Powell's (1977) approach, which provides no model for a size distribution beyond the mean and variance of carapace length at age, does not.

Our model is based largely on an analysis of carapace length frequency data obtained from the Alaska Department of Fish and Game (ADF&G) Kodiak area pot surveys conducted from 1972 through 1986 (Peterson et al., 1986). Yearly length frequencies of over 140,000 newshell male red king crabs from southwest Kodiak Island were fit as mixtures of individual normally distributed components representing age-classes by using the EM algorithm to obtain maximum-likelihood estimates of the mixture parameters (Titterington et al., 1985). The multi-year length frequency data were fit simultaneously to mixture densities under the assumption that component means and variances did not vary among years. Parameter estimation for the growth model was supplemented by data from the extensive tagging studies on red king crabs performed by ADF&G in the Kodiak area in 1961 and from 1974 through 1982. The tagging data gave information on growth per molt, differential growth per molt due to shell age, molting probabilities dependent upon carapace length and shell age, and differential survivorship between newshell and oldshell male crabs.

"Recruits" to this model are a group of newshell crabs having a normally distributed carapace length frequency with a mean of 116.3 mm and a variance of 81.2. We believe that the model recruits are 6 years old. Individuals can remain in the model for up to 8 years after recruiting to the model. Age-classes following the recruit class in the model are denoted as + 1, + 2, up to + 8. Yearly growth decreases markedly after the + 2 age-class is attained. This is due to a higher incidence of skip-molting by larger crabs and a reduction in growth per molt in individuals that have skip molted. In terms of recruitment to the fishery, the Kodiak area minimum legal size limit of 7 inches in carapace width corresponds to a carapace length of roughly 147 mm (B. A. Johnson, ADF&G, Kodiak, personal communication). Thus, the + 2 age class is the first age-class to be largely exposed to the commercial harvest (Figure 1).

We assume that annual survivorship for the model recruit class is 75%. This value is not inconsistent with year-to-year trends in catch per unit effort observed in the pot

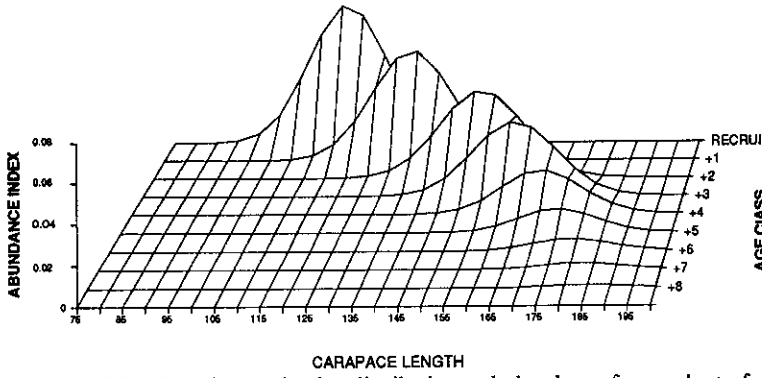

Figure 1. Modelled changes in size distribution and abundance for a cohort of male red king crab in the Kodiak area.

Table 2. Kodiak area male red king crab growth and survivorship model. Recruits to the model are probably six years old. Carapace lengths in the recruit age-class are normally distributed. Carapace length growth increments are normally distributed. Relative abundance is the probability that an individual in an unexploited population survives to an age class, given that it has attained the recruit age-class.

age-class	shell condition	carapace length (mm) mean (variance)	growth (mm) to next age-class mean (variance)	annual survivorship	relative abundance
recruit	all*	116.3 (81.18)	17.3 (6.52)	0.75	1.000
+1	all*	133.6 (87.70)	18.2 (7.85)	0.75	0.750
+2	all*	151.8 (95.55)	16.4 (8.00)**	0.75	0.563
+3	new	164.2 (82.52)	16.4 (8.00)**	0.75	0.245
	old	157.3 (72.51)	12.6 (8.00)***	0.45	0.177
	all	161.3 (90.00)		0.62	0.422
+4	new	171.2 (81.56)	12.6 (8.00)**	0.45	0.120
	old	166.5 (67.58)	12.6 (8.00)***	0.45	0.143
	all	168.6 (79.47)		0.45	0.263
+5	new	176.8 (66.75)	12.6 (8.00)**	0.45	0.054
	old	172.2 (67.54)	12.6 (8.00)***	0.45	0.065
	all	174.3 (72.39)		0.45	0.118
+6	new	181.8 (63.14)	12.6 (8.00)**	0.45	0.019
	old	177.0 (60.72)	12.6 (8.00)***	0.45	0.035
	all	178.7 (66.89)		0.45	0.053
+7	new	186.1 (57.86)	12.6 (8.00)**	0.45	0.007
	old	180.9 (57.63)	12.6 (8.00)***	0.45	0.017
	all	182.5 (63.41)		0.45	0.024
+8	new	189.6 (54.76)	12.6 (8.00)**	0.00	0.003
	old	184.3 (55.79)	12.6 (8.00)***	0.00	0.008
	all	185.6 (60.79)		0.00	0.011

* Age class is composed entirely of newshells.

** Probability of molting given length (l) is,

$$\exp(20.156-.130(l))/[1+\exp(20.156-.130(l))].$$

*** Probability of molting given length (l) is,

$$\exp(21.840-.125(l))/[1+\exp(21.840-.125(l))].$$

survey data. Because tagging studies have indicated an increased natural mortality in skip-molt males, the annual survivorship of oldshell males in the +3 age-class and all individuals in age-classes from +4 and above is reduced by a factor of 60% to an annual survivorship of 45%. This differential survivorship between younger and older age classes results in a survivorship at length relationship which is similar to that modelled by Balsiger (1974) for Bering Sea red king crabs.

To obtain the available yield in weight from carapace length, we applied the following weight at length equation from Blau (1986):

$$W = 4.45174(L^{3.11937})(10^{-7}), \tag{3}$$

where W is weight in kilograms (kg) and L is length in millimeters(mm).

Determination of Breeding Males

Powell et al. (1973) indicated that male red king crabs from the Kodiak area are sexually mature at sizes as small as 85 mm in carapace length. Our interest is not, however, with the size at which males attain physiological sexual maturity, but rather with the size at which males become important components of breeding pairs under natural conditions. That minimum size could then be applied to length frequency and abundance data from preseason surveys to estimate the abundance of breeding males in a population. To our knowledge there is only one data set that would allow an estimation of this size for any stock of Alaska red king crabs. This is the carapace length frequency data collected from mating pairs of red king crabs by Guy Powell in the east side of Kodiak I. during the springs of 1964 through 1971 (Powell et al., 1972; Eldridge, 1975). Although Powell et al. (1973, 1974) and Eldridge (1975) have referred to or presented some of these data, a graphical summary of the size frequencies within this data is presented for the first time in this paper. These data were collected by SCUBA divers and, hence, are probably not a random sample from the population of king crabs in the area. However, the data do reflect certain trends that are not obvious in experimental breeding studies conducted with caged animals (e.g., Powell et al., 1973).

The entire data set is composed of over 3400 mating pairs. Because the data were collected during the molting period for both male and female crabs, inclusion of all shell ages would forgo any comparison with survey length frequency data collected during the summer after the molting period. Consequently, the data set was reduced to include only those 1800 pairs in which the crabs had shell ages of approximately 12-months. Newly molted males grasping females with 12-month old shells comprised most of the mating pairs not included from the larger data set.

Length frequencies for the subset of grasping males and females with 12-month old shells are plotted in Figure 2. A plot for the full data set of all grasping pairs is similar (Figure 3). The exclusion or inclusion of the animals of different shell age had little effect on the conclusions drawn from this data set. Further subdividing the data by year or area did not change the major features depicted in Figure 2. These length frequency data from grasping pairs allow a comparison of the size at which females enter into mating pairs with the minimum size at which females extrude eggs. From data collected in population surveys, the minimum size for egg extrusion in the Kodiak area is known to be approximately 100 mm in carapace length (ADF&G unpublished data; Powell et al., 1973). In support of using the grasping pair data to determine minimum size for

breeding, the lower size bound for females in the mating pair data (Figure 2) agrees well with the minimum size for egg extrusion.

The length frequency distribution for males in this data indicates that males with carapace lengths less than 130 mm play an insignificant role in breeding under natural conditions. Note that the nature of the commercial fishery during the period that these

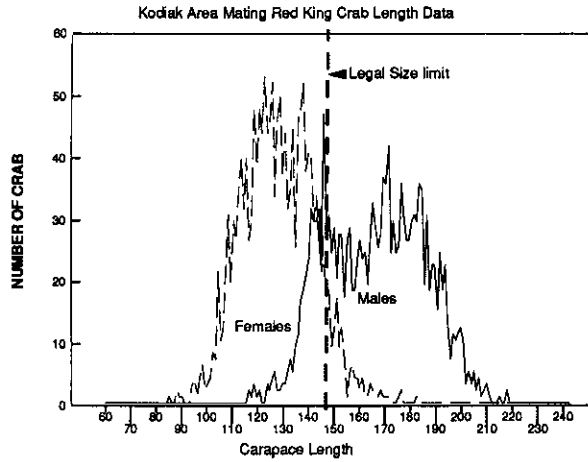

Figure 2. Length frequencies of male and female red king crab collected from the Kodiak area, 1964 through 1971. Only pairs in which both the male and female had shell ages of approximately 12-months are included.

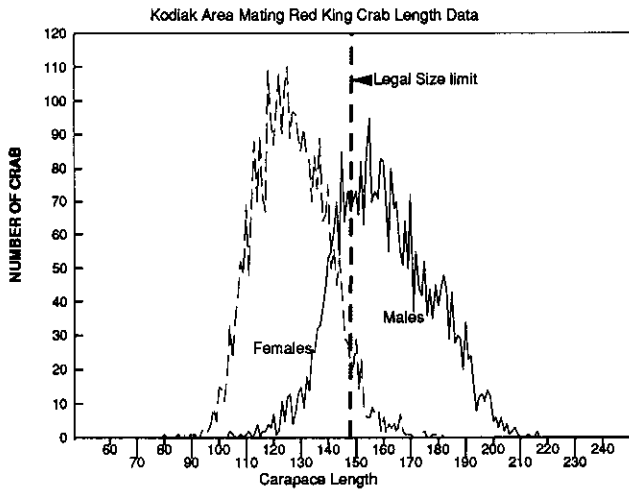

Figure 3. Length frequencies of male and fimale red king crab mating pairs collected from the Kodiak area, 1964 through 1971. Pairs of all shell ages are included.

data were collected -- largely unregulated except for size and sex restrictions -- should have tended to remove larger males from the stocks and, consequently, increase the proportional representation of smaller males in mating pairs. Males with carapace lengths greater than 163 mm are well represented in the mating pair data; growth per molt data from tagging studies in the Kodiak area indicate that males in that size range have been legal-sized for at least one fishery season. Overall, these data strongly suggest that the breeding population of males is dominated by legal-sized crabs, including those that have been legal-sized for over a year.

The grasping pair data indicate that breeding males are substantially larger than the minimum size to maturity cited in earlier publications (Powell et al., 1973) and we concluded that a carapace length of 130 mm is a generously low minimum size to delineate breeding males in length frequency data. We shall consider all males with carapace lengths greater than or equal to 130 mm as breeding males in our application of equations (1) and (2).

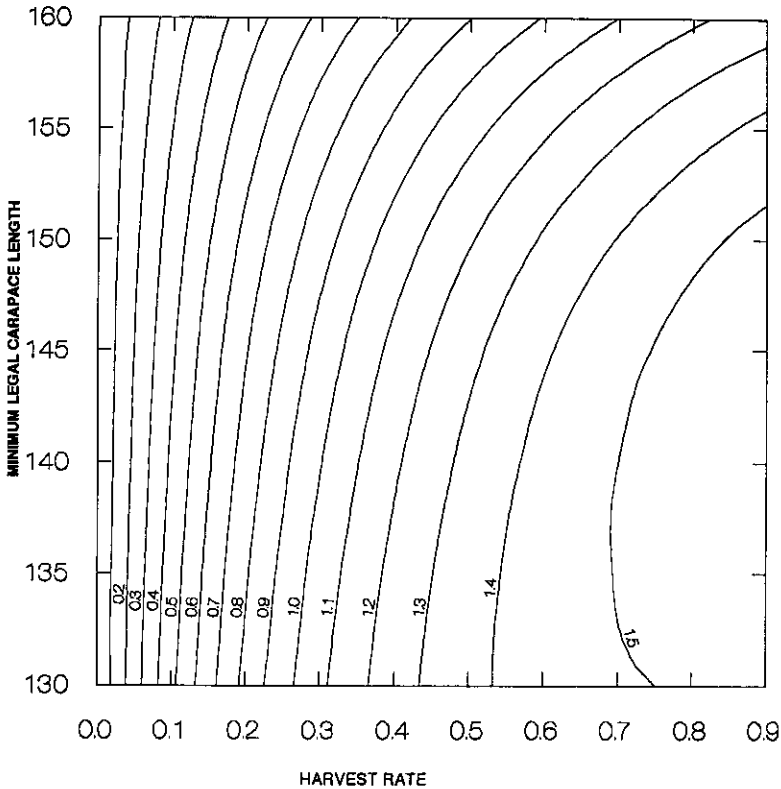

Figure 4. Yield per recruit contours based on the growth and survivorship model for Kodiak area male red king crab. Yield is in kilograms.

Effects of Size Limits and Harvest Rate on Yield per Recruit

Under the assumptions of the growth model outlined above, we can assess the effects of varying minimum legal size limits and harvest rates on yield per recruit. A "recruit" in this instance is, again, the first age class to recruit to the growth model. Yield is measured in weight (kg) and there is no attempt to attach an economic value to our yield per recruit analyses. Our results are for yield per recruit under the conditions of a fixed annual natural mortality function and a fixed harvest rate applied to legal-sized males. We assume that the period of exploitation is of short duration and that natural mortality is negligible during the harvest season. We also assume that all legal-sized crabs have an equal chance of being harvested.

Yield per recruit contours for minimum size limits ranging from 130 mm to 160 mm in carapace length and harvest rates of up to 90% are shown in Figure 4. Under the assumptions of our model there is little indication that a gain in yield would result by changing the current minimum size limit of 7 inches in carapace width (roughly 147 mm in carapace length). For fixed harvest rates of 60% or less, reducing the minimum size to 130 mm in carapace length, the minimum size of breeding males, will give only slight gains in yield; for higher harvest rates, reducing the minimum size would produce no gain or a slight loss in yield. Increasing the minimum size limit would reduce yield under all rates of harvest, with the reduction becoming more pronounced under the higher rates. Eldridge's (1975) yield per recruit analysis, which used an early form of the McCaughran and Powell (1977) red king crab growth model, also supported the 7 inch carapace width minimum size limit.

Our model for growth and mortality also indicates that there would be little to be gained from harvest rates greater than the current maximum rate of 60%. Under the assumptions of our model and the current minimum size of 7 inches in carapace width, a fixed yearly harvest rate of 60% would secure approximately 1.4 kg per recruit (Figure 4). This is more than 85% of the maximum yield (approximately 1.6 kg) that could possibly be derived from a cohort under any fixed harvest rate applied to legal-sized crabs with the current minimum legal size of 7 inches in carapace width.

Investigations on the Proposed Harvest Strategy

We investigated the behavior and utility of the proposed harvest strategy using the assumptions on growth, mortality, and size at maturity that have been stated or developed above. The values of E applied to equations (1) and (2) were 20% and 25%. Using a 130 mm carapace length as minimum size for breeding males and 147 mm as a minimum size for a legal crabs, we can restate the equation (2) representation of the proposed harvest strategy as,

$$H = \min\{E + E(N_p/N_l), 0.6\}, \qquad (4)$$

where E is the exploitation rate applied to breeding males, H is the harvest rate applied to legal-sized crabs, N_l is the number of legal males, and N_p is the number of sublegal males with carapace lengths greater than or equal to 130 mm. Notationally, we use N_p in equation (4) rather than (N_b - N_l) as in equation (2) because sublegal males greater than or equal to 130 mm in carapace length correspond well with "prerecruit-ones" -- males one year from recruiting to the fishery. The notation N_p here indicates that this is roughly the number of prerecruit-ones. Using the proposed harvest strategy the

harvest rate applied to legal crabs is linearly dependent on the ratio of prerecruit-one abundance to legal crab abundance and may range from a minimum of E to a maximum of 60%.

We will investigate this proposed harvest strategy by considering the following: (1) the steady state harvest rate on legals that would be attained under constant recruitment, (2) the behavior of the harvest strategy in the situation of a single recruitment event, and (3) the long-term behavior of the strategy through simulation studies of random recruitment. We use "recruitment" to mean recruitment to the recruit age-class in the growth model. All results reported here are from computer simulations of the proposed harvest strategy applied to the growth and survivorship model described earlier.

Steady state harvest rates on legal crabs. Under conditions of constant annual recruitment, the harvest rate applied to legal crabs prescribed by the proposed harvest strategy will converge to a fixed annual harvest rate. In the case when the minimum harvest rate, E, is set at 20%, the steady state harvest rate on legal crabs converges to 36%. Yield per recruit at a fixed annual harvest rate of 36% on legals is 1.05 kg, or 77% of that attained by a fixed harvest rate of 60%. If E is increased to 25%, the steady state harvest rate on legals converges to 47%. At a fixed harvest rate of 47%, yield per recruit is 1.23 kg, or 89% of that attained by a harvest rate fixed at 60%. The 36% steady state harvest rate is at the high end of the rates prescribed by the current harvest strategy when population sizes are "depressed"; the 47% steady state harvest rate is at the center of the rates prescribed by the current harvest strategy when population size is "average" (Table 1).

We used these steady state harvest rates and the 60% harvest rate as benchmarks for comparison in our studies of the behavior of the proposed harvest strategy.

Table 3. Simulation results for yearly harvest rate on legal crab in a population composed of a single cohort of males. Year 1 is year that the cohort recruits to the growth model. "Breeding" denotes the number per recruit of males with carapace lengths greater than or equal to 130 mm. "Legal" denotes the number per recruit of legal-sized crab. "Rate" is the harvest rate applied to legal crab.

EXPLOITATION RATE, E, ON BREEDING MALES = 20%									
Year	1	2	3	4	5	6	7	8	9
Breeding	0.07	0.50	0.53	0.32	0.13	0.05	0.02	0.01	0.00
Legal	0.00	0.06	0.37	0.30	0.13	0.05	0.02	0.01	0.00
Rate	-	60%	29%	22%	20%	20%	20%	20%	20%
EXPLOITATION RATE, E, ON BREEDING MALES = 25%									
Year	1	2	3	4	5	6	7	8	9
Breeding	0.07	0.50	0.53	0.30	0.12	0.04	0.01	0.00	0.00
Legal	0.00	0.06	0.37	0.28	0.12	0.04	0.01	0.00	0.00
Rate	-	60%	36%	27%	25%	25%	25%	25%	25%

Behavior of the proposed harvest strategy when applied to a single recruitment event. Here we consider the behavior of the proposed harvest strategy when it is applied through the life span of a single cohort recruited to the growth model. This allows for a detailed examination of the responses of the proposed harvest strategy to changes in the size distribution and abundance of a stock. This should also give an idea of how the proposed harvest strategy will respond through time when a stock is dominated by a single cohort.

In the first year of recruitment, the number of breeding males will be small and the number of legal crabs will be negligible relative to the size of the recruiting cohort (Table 3). In the second year, breeding males will be dominated by sublegals and the harvest rate on legals will be at the maximum value of 60%. Two years after recruitment, the harvest rate decreases to a value below the corresponding steady state harvest rate. In that year, the breeding males are dominated by legal crabs and the reduction in harvest rate is in response to the relatively low abundance of sublegal breeding males. By the third and following years after recruitment, the harvest rate is near or at the minimum.

Table 4. Simulation results for yield (kg) per recruit from stock composed of a single cohort of males. Year 1 is the year that the cohort recruits to the growth model.

Year	Proposed Harvest Strategy with:		Fixed Exploitation Rate on Legal Crab of :		
	E=20%	E=25%	36%	47%	60%
1	0.00	0.00	0.00	0.00	0.00
2	0.10	0.10	0.06	0.08	0.10
3	0.33	0.41	0.42	0.54	0.68
4	0.22	0.26	0.35	0.40	0.43
5	0.10	0.11	0.15	0.14	0.13
6	0.04	0.04	0.05	0.04	0.03
7	0.02	0.02	0.01	0.01	0.01
8	0.01	0.01	0.00	0.00	0.00
9	0.00	0.00	0.00	0.00	0.00
Total	0.82	0.95	1.05	1.23	1.37

The yearly and total yield per recruit obtained using the proposed harvest strategy is compared to those obtained using harvest rates fixed at the steady state values and at 60% in Table 4. Using the proposed harvest strategy, the yield from the cohort will be lower than those obtained using the fixed harvest rates. This relative reduction in yield is most apparent during the second and third years after recruitment, when the cohort is in the + 2 and + 3 age-classes. In those years and in the subsequent years of the cohort's lifetime, the proposed harvest strategy serves more to protect the breeding males than to maximize yield (Table 5).

Simulation studies on the long-term behavior of the proposed harvest strategy. We investigated the long-term behavior of the proposed harvest strategy through computer simulations of recruitment, growth, mortality, and exploitation. We modelled the yearly magnitude of recruitment into the growth model as being a lognormally distributed "white noise" process (i.e., the magnitude of recruitment to the growth model is random and uncorrelated among years). We investigated the behavior of the proposed harvest strategy under two random recruitment models. One is a "low

variability" model, in which the yearly magnitude of recruitment has a coefficient of variation equal to 25%; the other is a "high variability" model with a coefficient of variation of 100%. In both models, the median of the recruitment abundance index is 1. Simulation results reported here are all based on 1,000 simulated years of recruitment.

Table 5. Simulation results for number per recruit of crab with carapace lengths greater than or equal to 130 mm that escape harvest. Results are for a stock composed of a single cohort of males. Year 1 is year that the cohort recruits to the growth model.

	Sublegal	Legal					
		Proposed Harvest Strategy with:			Fixed Exploitation Rate on Legal Crab of:		
Year	No Harvest	No Harvest	E=20%	E=25%	36%	47%	60%
1	0.071	0.000	0.000	0.000	0.000	0.000	0.000
2	0.439	0.063	0.025	0.025	0.040	0.033	0.025
3	0.159	0.397	0.263	0.237	0.243	0.199	0.148
4	0.025	0.397	0.233	0.202	0.181	0.132	0.084
5	0.001	0.209	0.104	0.086	0.067	0.042	0.022
6	0.000	0.095	0.038	0.029	0.019	0.010	0.004
7	0.000	0.043	0.014	0.010	0.006	0.003	0.001
8	0.000	0.019	0.005	0.003	0.002	0.001	0.000
9	0.000	0.009	0.002	0.002	0.001	0.000	0.000

Table 6. Simulation results for yearly harvest rate on legal crab using the proposed harvest strategy in a randomly recruiting population. CV is the coefficient of variation of the yearly harvest rates. Q1 - Q3 are the first and third quartiles of the yearly harvest rates.

EXPLOITATION RATE, E, ON BREEDING MALES = 20%		
RECRUITMENT MODEL		HARVEST RATE ON LEGALS
Low Variability	Mean:	36.1%
	CV:	7.9%
	Median:	35.7%
	Q1 - Q3:	34.2% - 37.7%
High Variability	Mean:	37.1%
	CV:	25.2%
	Median:	34.2%
	Q1 - Q3:	30.3% - 41.2%
EXPLOITATION RATE, E, ON BREEDING MALES = 25%		
RECRUITMENT MODEL		HARVEST RATE ON LEGALS
Low Variability	Mean:	47.1%
	CV:	8.2%
	Median:	46.7%
	Q1 - Q3:	44.5% - 49.4%
High Variability	Mean:	46.3%
	CV:	19.4%
	Median:	44.4%
	Q1 - Q3:	39.0% - 54.1%

Under random recruitment, the harvest rates applied to legal crabs prescribed by the proposed harvest strategy will be centered about the steady state harvest rates of 36% for E = 20% and 47% for E = 25% (Table 6). Not surprisingly, yearly variability in the harvest rates on legal-sized crabs increases with variability in recruitment. Lower values of E will also tend to give lower yearly variability in harvest rates for a fixed level of variability in annual recruitment. Due to the maximum harvest rate cap of 60%, however, there is a point where variability in harvest rates will decrease with increasing values of E or variability in recruitment. Variability in harvest rate will decrease as a higher proportion of the yearly harvest rates attain the 60% maximum (e.g., compare the results for E = 20% with that of E = 25% in the "high variability" recruitment model simulations).

Yield per recruit for random recruitment under the proposed harvest strategy also tends towards the steady state results for constant annual recruitment -- 1.06 kg for E = 20% and 1.23 kg for E = 25% (Table 7). These central values of yield per recruit compare with a yield per recruit value of 1.38 kg attained under a fixed annual harvest rate on legals of 60%. Variability in yield per recruit among the recruiting cohorts is low, with coefficients of variation from the simulation studies ranging from 2.6% to 6.1%. Variability in yield per recruit under this harvest strategy increases with variability in annual recruitment.

Finally, we consider stability in the weight (kg) of yearly landings under the proposed harvest strategy and compare it with that of fixed yearly harvest rates. We compare stability in yearly landings using two measures, the coefficient of variation of yearly landings and the correlation between landings in adjacent years (i.e., the autocorrela-

Table 7. Simulation results for yield (kg) per recruit using the proposed harvest strategy in a randomly recruiting population. CV is coefficient of variation. Q1-Q3 are the first and third quartiles.

EXPLOITATION RATE ON BREEDING MALES = 20%		
RECRUITMENT MODEL		YIELD PER RECRUIT
Low Variability	Mean:	1.055
	CV:	2.6%
	Median:	1.055
	Q1 - Q3:	1.035 - 1.073
High Variability	Mean:	1.072
	CV:	8.5%
	Median:	1.065
	Q1 - Q3:	1.003 - 1.134
EXPLOITATION RATE ON BREEDING MALES = 25%		
RECRUITMENT MODEL	YIELD PER RECRUIT	
Low Variability	Mean:	1.228
	CV:	2.4%
	Median:	1.228
	Q1 - Q3:	1.207 - 1.247
High Variability	Mean:	1.216
	CV:	6.1%
	Median:	1.225
	Q1 - Q3:	1.160 - 1.270

tion of yearly landings at a one year lag). The coefficient of variation measures the variability of yearly landings relative to the mean of annual landings. The adjacent year correlation measures the smoothness and year-to-year predictability of annual landings.

Table 8. Simulation results on stability of yearly landings (kg) from a randomly recruiting population. CV is coefficient of variation. r(1) is autocorrelation of yearly landings at one year lag.

RANDOM RECRUITMENT MODEL	Proposed Harvest Strategy with:		Fixed Exploitation Rate on Legal Crab of:		
	E=20%	E=25%	36%	47%	60%
Low Variability					
CV:	11.6%	11.8%	11.8%	14.5%	15.2%
r(1):	0.78	0.77	0.71	0.67	0.62
High Variability					
CV:	43.7%	45.0%	54.9%	57.1%	60.0%
r(1):	0.80	0.76	0.71	0.67	0.62

The results of our simulation studies on stability of landings are presented in Table 8. Variability in yearly landings under any harvest strategy will obviously be determined by the level of variability in recruitment. Our results indicate that the proposed harvest strategy will, under random recruitment, yield yearly landings that are at least as stable as, and probably more stable than, those produced by harvest rates fixed at the steady state values of 36% and 47%. Landings under the proposed harvest strategy would certainly be more stable than those under a fixed harvest rate of 60%.

SUMMARY AND CONCLUSIONS

The red king crab harvest strategy that we have proposed maintains harvest rates on legal crabs which fall within the range of those prescribed by the currently used harvest strategy. Compared to the current strategy, the proposed strategy has the desirable property of being unambiguous in application. This proposed strategy is conservative in that it sets a low fixed rate, E, of exploitation on breeding males. The harvest rate on legal crabs is adjusted from a minimum of E up to a maximum of 60% in response to the ratio of prerecruit breeding males to legal-sized males. Although our results are preliminary and dependent upon the assumptions of our growth and mortality model, the simulation studies indicate that the proposed harvest strategy is superior to a fixed harvest rate strategy in the degree of protection it affords to breeding males and in the relative stability of yearly landings it provides without forfeiting the long-term yield per recruit.

We have investigated the cases where E has values of 20% and 25%. The actual choice of E in the application of this harvest strategy would depend on how conservative management should be in protecting breeding males at the expense of reducing yearly landings. Determining the optimum balance between yield per recruit and protection of breeding males is presently impossible due to the poor understanding of the relationship between parental stock size and future recruitment to the fishery. On this point, however, we note that the grasping pair data presented in this paper, which indicate that breeding males are dominated by legal-sized crabs, suggests that protection of breeding males may require more conservative harvest strategies than was previously believed.

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Research Perspectives on Northwest Pacific Bathyal Crustacean Resources

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The data on distribution and biology of deep-water crustaceans (Decapoda) collected in 1969-1989 in the northwestern Pacific are analyzed. These are the most complete results obtained on golden crab *Lithodes aequispina*, using fishing and research data. The deep-water tanner crabs *Chionoecetes angulatus*, *Ch. tanneri*, and *Ch. japonicus* are distributed somewhat deeper and wider on the upper continental slope and are also quite interesting for fisheries purposes. In 1988, in the course of Soviet-American experimental procedures some stocks of *Lithodes couesi* at the Shirshov Ridge in the Bering Sea were discovered for the first time. Our investigations showed that those stocks appeared to be a local independent population. The deep-water shrimps of Pandalidae and Crangonidae families did not form dense concentrations but can be harvested by accumulative fishing gear (traps and/or pots). With respect to deep-water crab and shrimp fisheries one should note the dispersed character of their distribution and low ecological plasticity. It is necessary to develop international cooperation in the investigation and exploitation of those resources.

Analysis of scientific data on the trawl survey results in the slope areas of Far-Eastern seas at depths 200-1,500 m in 1969-1989 revealed the presence of the following commercial and potentially commercial species:

LITHODIDAE:	*Lithodes aequispina* Benedict
	L. couesi Benedict
	Paralomis verilli Benedict
	P. multispina Benedict
MAJIDAE:	*Chionoecetes angulatus* Rathbun
	Ch. tanneri Rathbun
	Ch. japonicus Rathbun

PANDALIDAE: *Pandalus borealis eous* Makarov
P. hypsinotus Brandt
Pandalopsis multidentatus Kobjakova
P. aleutica glabra Kobjakova

CRANGONIDAE: *Sclerocrangon derjugini* Kobjakova

Until recently, the information about particular deep-water crab and shrimp species has been mainly faunistic, providing only an overall idea of the systematics and zoogeography of those species in the North Pacific (Makarov, 1938; Vinogradov, 1950; Birnstern, Zarenkov, 1970). As a rule, the above species do not form dense concentrations, but they can be fished by means of accumulating fishing gear (traps).

The fishery for *L. aequispina* in the Central Sea of Okhotsk (Rodin, 1970) is an example of the above type of harvesting. In that area, specialized research had been carried out in summer of 1969, 1973 and 1975 near 52°- 55°30' N from the 600 m isobath (westward to 153° E). Those activities revealed an independent population of *L. aequispina* in the area. The catches of that species did not usually exceed 1-6 individuals per 30 minutes trawling. More dense concentrations were observed near 53°30' - 54°30'N at depths of 300-500 m, where catches amounted to 60 individuals per trawling. The distribution of males and females was similar. The juveniles were discovered more to the north (Rodin, 1970). Current maps of this area indicate that *L. aequispina* larvae are transported from the adult habitat northward, where they descend in an area of water mass downwelling. As they grow, the juveniles seem to move in the opposite direction of larval transport. The juveniles occur in dense epifauna, while the mature individuals inhabit soft sediments.

Mating, spawning and molting of *L. aequispina* take place in August-September. The fecundity of this species is 14 times lower than that of *Paralithodes camtschatica*. The size of *L. aequispina* males varied from 20 to 180 mm, females were 20 to 150 mm. Minimal size of females with eggs was 100 mm. *L. aequispina* probably matures much later than *P. camtschatica*, since the size of female *P. camtschatica* with eggs is 80 mm. Due to its low fecundity, parasital castration, observed in crabs of the central Sea of Okhotsk (Kurochkin, Rodin, 1970), can be extremely important.

The feeding rate of *L. aequispina* is much lower than that of *P. camtschatica*, but the food variance is much higher. *L. aequispina* is cannibalistic and necrophagous, as indicated by carapace remains and squid sucker hooks in its stomach (Tarverdieva, Zgurovsky, 1985). The population of *L. aequispina* in this area was last estimated in 1975. The abundance of commercial size males was not great; about 125,000, about 18% of the total population. *L. aequispina* abundance decreased during the commercial exploitation period; its average size also decreased and the sex ratio became unbalanced. In August 1989, joint Soviet-American investigations on *L. aequispina* were carried out during a fishing effort in the Sea of Okhotsk, and the results were 150 specimens/trap. At present, the

data obtained in the course of those studies is being analyzed.

Ch. angulatus, P. verilli and *P. multispina* are distributed somewhat deeper than *L. aequispina* and more to the south. *Ch. angulatus* and *P. verilli* were discovered by us at depths of 1,350 m off the Kuril Islands (Zgurovsky, 1979). Tanner crabs are distributed much wider and they are more abundant than lithodid crabs. Denser concentrations of the tanner crab were observed off the North Kuril Islands (Onekotan and Paramushir islands). Commercial males were caught on the Sea of Okhotsk side; females and juveniles were caught on the Pacific side of Onekotan Island. The fecundity of *Ch. angulatus* is much lower than that of the shelf tanner crabs. But the minimal size of females with eggs is 35 mm across the carapace, which can be explained by either earlier maturity or lower growth rates of females (Zgurovsky, 1979).

The abundance of deep-water tanner crab commercial males off Onekotan Island can reach 2.5 million, recruits - 3.4 to 9.4 million on the Sea of Okhotsk side, but only 0.8 million on the Pacific side. *P. verilli, P. multispina* and *L. couesi* do not form pods but are rather widely distributed along the lower Pacific side of the Kuril Islands and the Southern Sea of Okhotsk at bathyal depths of more than 500 - 800 m. The biology of those species is studied insufficiently.

From July to August 1989, data were obtained on the biology and distribution of the bathyal crab *L. couesi* near the Shirshov Ridge (Bering Sea). That information was obtained from American trap catches in 1989 and indicates that the species occurs in rather high abundance in the area. The distribution of *L. couesi* in other far-eastern seas is sporadic (Makarov, 1938; Zgurovsky, 1979), as indicated by trawl surveys done by the research vessels *Professor Levanidov* and *Darwin* in the Sea of Okhotsk. Catches of commercial size male *L. couesi* (>100 mm across the carapace) over the Shirshov Ridge amounted to 60 individuals; the total catch was 100 individuals. But the average catches are not great which is only natural, since the crabcatchers are doing exploratory fishing in a new area (Table 1).

L. couesi concentrations have been discovered on both the eastern and the western slopes of the Shirshov Ridge. Crabs of intermediate and older age groups were dominant in the trap catches, possibly due to trap selectivity (Figures 1, 2): the average size of males was 135.5 mm; 55.5% of the males were at the III stage of molting in July 1989. Spawning and emergence of larvae were observed on both July 5-7 and on August 20, 1988 (Figure 2), and in early July, 65% of the mature females had already spawned; in August, as much as 77%. By the end of August, the spawning seemed to be over, which is proven by the absence of prespawning females in the catches. The simultaneous presence of post-spawning females with weakly developed embryos (15-20%) and females which had already released larvae, testifies to the considerable duration of spawning and larval release. Therefore, spawning of this species starts in early spring. The rich epifauna discovered by us on the Shirshov Ridge (glass sponges, hydroids, bryozoans), creates favorable conditions for survival of *L. couesi* juveniles. This is also indicative of high current speeds in the area. We have discovered juveniles of this species with carapace widths of 15-20 mm there in the epifauna.

Table 1. Mean catches of L. couesi in the Shirshov Ridge area by depths (individuals; zero catches are not taken into consideration).

Depth, m	Males size, mm			Females
	<100	100-130	>130	
350-400	-	1	-	-
400-450	-	-	-	-
450-500	-	1	2	2.5
500-550	0.6	2.7	7.8	29.1
550-600	2.4	4.8	11.0	22.5
600-650	3.6	6.9	10.7	20.3
650-700	3.4	5.4	7.2	15.8
700-750	1	1	1	-

The favorable conditions for crab reproduction in the Shirshov Ridge area facilitate the formation of self-reproducing populations with rather high density. We attempted to approximate *L. couesi* stocks from trap catches, taking into consideration the bottom area at depths of 500-700 m having suitable habitat for this species (1,100 sq km). The average catch of males with the carapace >130 mm wide (including zero catches) amounted to 4-5 individuals/trap. The stocks of this species in the above area were therefore estimated at about 9,000 to 11,000 tons. *P. borealis, P. hypsinotus* and *S. derjugini* were discovered around Iturup, Urup and Hokkaido Islands at depths down to 650 m. *P. aleutica* glabra was discovered still deeper, down to 1,350 m.

Harvesting of deep-water shrimps in the Soviet zone has been developing exclusively in the Sea of Japan up to the present time, so their biology and distribution are studied somewhat more thoroughly in that area (Mikulich, Kozak, 1971; Tabunkov, 1982; Bukin, Zgurovsky, 1988; etc.). The data are more detailed on the biology of *P. hypsinotus*, it being the object of specialized trap fishing. *P. borealis* and *P. multidentatus* are also present in the catches. Recently, interesting data have been obtained on the density, distribution and behavior of *P. hypsinotus* and other shrimps using the *TINRO-2* manned submersible over the continental slope of the Sea of Japan (Bukin, Zgurovsky, 1988). A heterogeneous distribution of *P. hypsinotus* was revealed, within which the densities varied from 0.007 to 0.02 individuals/sq m in summer at depths 180 to 500 m. As the depth increased, *P. borealis* density increased to 0.2 individuals/ sq m; some *P. multidentatus* specimens were also observed.

By the beginning of fall, density of those species somewhat increased (up to 0.152 individuals/sq m). At the same time, the vertical range of *P. hypsinotus* became smaller, and in the fall that species occurred at depths of 150-300 m, while in spring, at depths 200 to 300 m. *P. hypsinotus* catches in summer were 1-20 individuals, in spring, 1-82 individuals per trap per day.

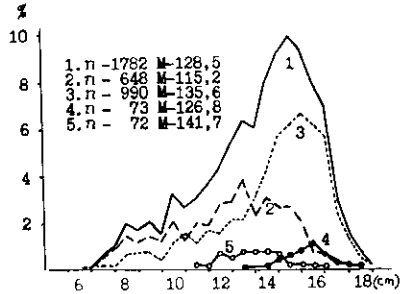

Figure 1. The size composition of the *L. couesi* males from trap catches at the Shirshov Ridge: 1. total; 2. II molting stage; 3. III stage; 4. IV stage; 5. pieces infested with *Briarosaccus sacculina*; n -number of specimens; L -carapace width, mm.

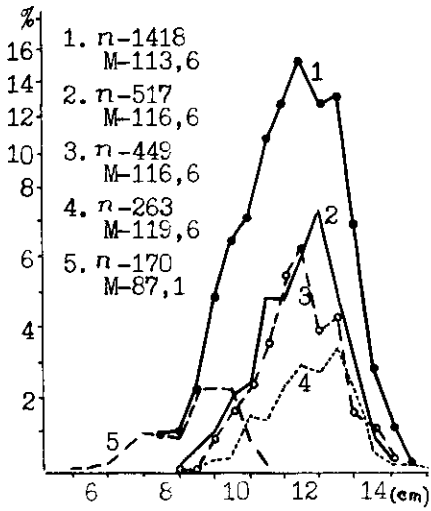

Figure 2. The size composition of *L. couesi* females from trap catches at the Shirshov Ridge: 1. total; 2. spawned females; 3. females with eyed embryos; 4. females without eggs; 5. subadult females; n - number of specimens; L - carapace width, mm.

Underwater observations on *P. hypsinotus* showed that this species is quite inactive; no vertical migrations were observed. Microconcentrations of the shrimp occurred in sheltered habitats. Spawning and larval releases take a long time. Fecundity varied from 3,666 to 10,900 eggs/female, which is higher than in other parts of this species range.

pHaving analyzed the available information, we can state that the abundance and biology data on deep-water shrimps and crabs (recently, in particular) is insufficient for rational exploitation of those resources. It is difficult to carry out specialized research on those species, due to their low density, the vast expanses of the northwestern Pacific continental slope, etc. Thus, it is considered worthwhile to carry out complex research and exploratory and experimental harvesting activities, employing all available means and methods. The organization of complex cruises of commercial and research vessels provided with traps, trawls and research equipment, including manned submersibles, will reduce the expenses considerably. With the same purpose, it is extremely important to develop international cooperation with Pacific Rim countries in deep-water bioresource development.

Due to their relatively low ecological plasticity and density, an equally distributed commercial effort is needed when developing commercial fisheries on deep-water shrimp and crabs. According to A. Arkhipov's observations (unpublished data), when trapfishing for *Ch. japonicus* at Yamato Shoal (the Sea of Japan), the crab juveniles suffer thermal shock and die in summer when the traps are being taken to the surface. This fact further proves the necessity for regulating not only catch volume, individual size and catch distribution, but temporal factors as well, so as not to destroy the reproductive potential of the populations.

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Proc. Int. Symp. King & Tanner Crabs
Nov. 1989, Anchorage, Alaska

Preserved Area To Effect Recovery of Overfished Zuwai Crab Stocks off Kyoto Prefecture

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ABSTRACT

The most useful fishing ground for capturing male Zuwai crab, *Chionoecetes opilio*, is limited between 250 m to 290 m depths (about 720 km^2) off Kyoto Prefecture. To allow the overfished stock of crab to recover, 2% of the entire male crab fishing ground was made into a preserve in 1983, to an average depth of 270 m. Male crab yield from the fishing grounds surrounding the preserved area has increased, compared with other areas fished by Danish seiners. The results of a series of monitoring surveys in the preserve and in the surrounding area suggested that prerecruit male crabs smaller than the legal minimum size of carapace width (9 cm) and soft-shelled crabs just molted before the fishing season could be protected from heavy exploitation by Danish seines. The findings of tag-recapture experiments indicate that male crabs in the preserved area seemed to conveniently disperse to the surrounding ground.

INTRODUCTION

Stocks of the Zuwai crab, *Chionoecetes opilio*, in the western Japan Sea have been overharvested by the Danish seine. Changes in size selectivity of fishing gear and reductions in fishing effort, fishing period in a year, and total amount of catch have been recommended; however, successful policies for rehabilitation of this stock have not yet been established. As a temporary or experimental measure to facilitate rehabilitation of a local stock off Kyoto Prefecture, a 13.7 km^2 area was preserved in 1983, around which illegal-sized male crabs less than 9 cm carapace width and rather large-sized male crabs occur with seasonal bathymetric movements.

Since Danish seiners cannot avoid capturing illegal sized crabs, a large number of the crabs regardless of sexes are discarded at sea in the hope that they will eventually recruit into the legal size. It is likely that a heavy juvenile mortality and continuous fishing pressure on the prerecruits caused a reduction in the average size of crab landed. It was considered that the preserve could contribute to preventing damage to commercially unacceptable crabs by Danish seine gear.

The purpose of this paper is to report on the effect of the preserved area on catches by the commercial Danish seiners and to describe the preserve as a mating ground for primiparous females in the area.

MATERIALS

Samples of *C. opilio* were collected monthly when possible, from 1983 to 1988, using pudding-shaped traps in the sea off Kyoto Prefecture. The traps used were 82 cm in diameter on the upper surface, approximately 130 cm on the lower surface, 48 cm in height, and had a 42 cm diameter opening on the top. Usually twelve traps (sometimes eight or sixteen) were attached at 50 m intervals to a ground line, and the traps were left in the sea for eight to ten hours. A total of 35 longline trap hauls were conducted at 272-275 m depths in the central part of the preserved area, and at 240-275 m depths in the surrounding grounds. Carapace width of crabs trapped was measured with calipers to the nearest 1 mm.

Catch and effort data of commercial Danish seines were obtained from 8 to 15 logbooks of the 24 master fishermen from 1983 to 1988, and one to four logbooks were available for the CPUE calculation in 1979 to 1982. Logbooks showed the catch for male crabs, in numbers classified into three categories of carapace width: larger crab (more than 13 cm carapace width, about 1.0 kg per crab), middle (11-12 cm, about 0.8 kg), and small (9-10 cm, 0.5 kg). The seining positions of net throwing by haul were recorded based on the Loran A and C with sea depth.

A total of 716 crabs were tagged and released in the preserved area during March, May and July 1985, of which 369 male crabs were larger than 9 cm carapace width (legal minimum size). During the fishing season from November 1985 to March 1986, 55 crabs having legal carapace width were recaptured by Danish seiners. The movements of crabs were estimated by drawing a straight line that connected released and recaptured sites. The tags used for recording short-term movements were (1) a 6-9 cm length of a narrow bar of bright-colored plastic (0.5 mm in diameter) fixed on the dorsal side of the carapace and (2) an Atkins disk tag (15 mm in diameter) tied around the third walking leg.

METHOD

In order to rehabilitate the overfished grounds of the Zuwai crab, a preserved area of 13.7 km^2 (3.7 km x 3.7 km) located in the sea off Kyoto Prefecture was

established in 1983 (Figure 1). A total of 83 concrete blocks (3 m^3, 12.5 tons per block on land) were sunk to the bottom to 266-274 m depths. The blocks were spaced to obstruct the Danish seine net and ground lines as shown in Figure 2. Since the 1985 fishing season, the preserved area has been completely closed to fishing, and the government of the Kyoto Prefecture has enforced the presentation of monthly logbooks to look for signs of recovering Zuwai crab stock. At the same time, a series of monitoring surveys both in the preserved area and the surrounding area was initiated by the Kyoto Institute of Oceanic and Fishery Science. The above-mentioned materials have been collected by the R/V *Heian-maru* belonging to the institute and by commercial Danish seines.

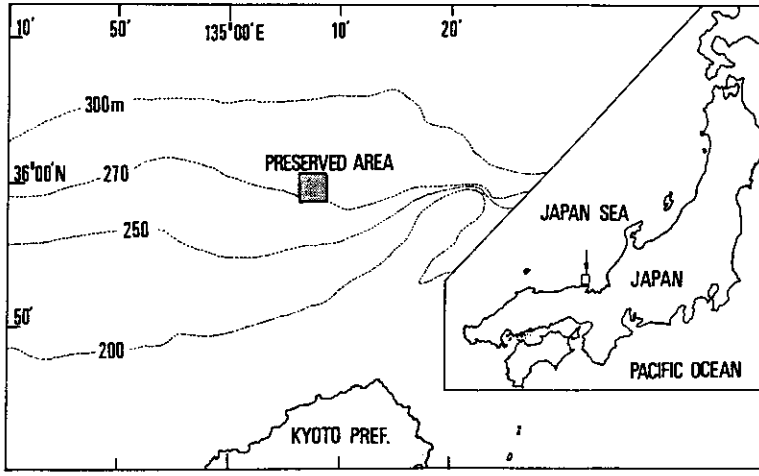

Figure 1. Location of the 13.7 km^2 preserved area in the sea off Kyoto Prefecture.

RESULTS AND DISCUSSION

CPUE Fluctuations in the Preserved Area

The CPUE of male crab fluctuated from 0.08 crabs to 9.58 crabs per trap between the first and sixth year after the establishment of the preserved area. The mean CPUE indicated an upward trend year by year from 3.04 crabs per trap in 1983 to 4.42 crabs per trap in 1988 in Figure 3. It was suggested that male crabs might move periodically into the preserved area during the period from the autumn (October to November) to the spring (March to April) and disappear during the period from July to September. Due to little movement at post-molting stage, the CPUE estimated by trap catch didn't reveal a density of crab. The periodical fluctuations of CPUE of male crab shown in Figure 3 did not agree well with monthly shell hardness data presented by Ito (1970).

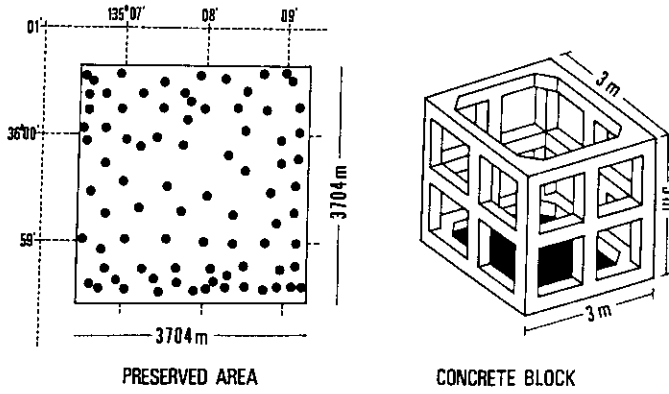

Figure 2. Distribution of concrete blocks in the preserved area and sketch of the block.

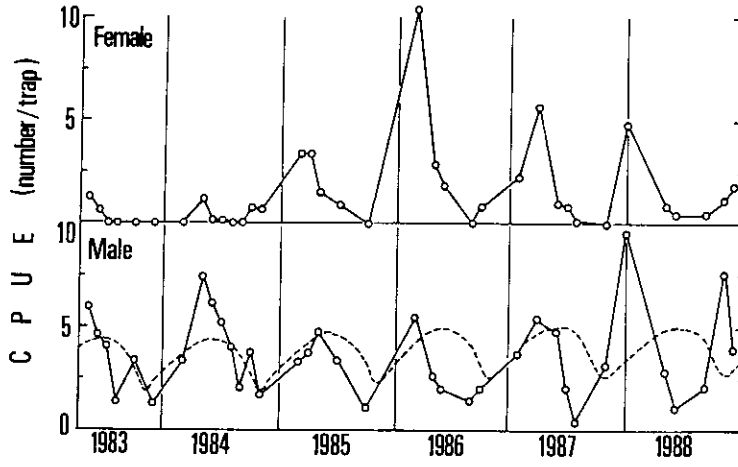

Figure 3. Fluctuations of the mean CPUE (number of crabs per trap) of female (upper) and male (lower) tanner crabs in the preserved area. Open circles: total CPUEs of male and female crabs. Approximate changes in shell hardness of male crab are shown by broken curve, modified from Ito (1970).

The proportion of large male crabs appearing in the preserved area, which were terminally molted crabs larger than 12 cm carapace width, increased from 10.0% in 1983 to 42% in 1987 with increase of the mean CPUE as indicated in Figure 4. For male crabs trapped from the surrounding grounds, legal-sized crabs larger than 9 cm carapace width have existed rather abundantly in the preserved area since 1986. In the surrounding grounds, the preterminal molt classes of male crab dominated in 1987 with considerable decrease in middle-sized crabs from 10 cm to 12 cm carapace widths. It is likely that during the period from September 1986 to May 1987, legal sized or terminally molted male crabs were heavily exploited or moved in abundance into the preserved area.

On the other hand, along the 270 m depth contour where the preserved area was established, primiparous females seemed to densely concentrate to mate every August to November (Yamasaki, unpublished). In addition, from the research submarine *Shinkai-2000* that went to 275 m depth in the central part of the preserved area in August 1989, one of the authors observed the pairing behavior of a primiparous female crab with a terminally molted crab (Yamasaki, unpublished). The female grabbed by the male's claws was going to molt; this molt in August was the terminal one to maturity.

The large CPUE values for female crabs shown in Figure 3 were due to catches of primiparous females carrying bright orange-colored eggs after terminally molting and mating. The mean CPUE has increased from April to June every year since 1985 with some annual fluctuations. Higher CPUE values for male crab in the preserved area corresponded most likely to increased incidence of primiparous females in the catch. However, this phenomenon was not evident in the early years after the establishment of the preserved area, probably because this area was used increasingly as the mating ground of primiparous females as time proceeded.

For a few weeks from the beginning of November when Danish seine fishing opened for males, the fishing effort showed one main fishing ground concentrated in the area surrounding the preserved area. A number of primiparous females with a soft-shelled carapace were damaged by the sweep line and the nets of Danish seiners, and by discarding the crabs from the deck. It therefore seems very worthwhile to restrict seining to protect the primiparous female crabs.

Dispersal of Male Crabs from the Preserved Area

Logbook records usable for CPUE calculations generally showed that more fishermen captured male crabs in the area surrounding the preserve. High CPUEs (more than 10 kg per seine haul) were recorded in the grids near the preserved area (Figure 5). Particularly every November, around 60% of the male catch of a whole were landed by heavy fishing activities.area (Figure 5). Particularly every November, around 60% of the male catch of a whole were landed by heavy fishing activities.

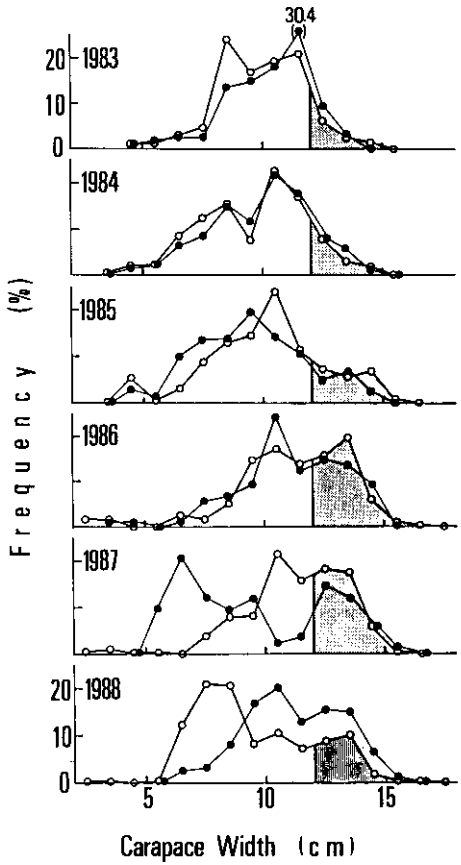

Figure 4. Comparative size distributions of male tanner crabs trapped from the preserved area (open circles) and the surrounding fishing ground (closed circles).

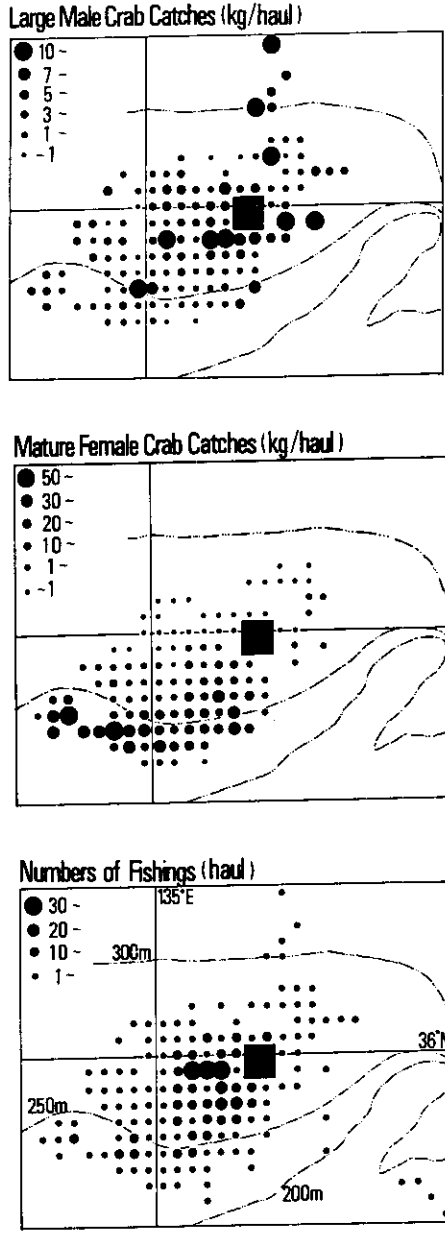

Figure 5. An example of distribution of Danish seining effort and mean relative abundances of male and female crabs (kg per seine haul) in one grid as indicated by fishermen's logbooks in November 1987.

The CPUEs of male crabs in the surrounding grounds (within 3 miles) were relatively higher than those beyond 3 miles, though there appeared to be annual fluctuations (Figure 6). Before establishing the preserved area, legal-sized crabs in this fishing ground were fully exploited, so no reason existed for fishing the area. The overall catch from the sea off the Kyoto Prefecture has not shown any trend.

Using the catch records by fishermen, which included fishing positions (Loran A and C), number of seining hauls, and catch by each seining haul, the CPUE distributions were established for four fishing years, 1984-1988. The mean CPUEs in the four subareas surrounding the preserved area, from 1 to 4 miles at 1 mile intervals, were plotted against the distance from the preserved area as shown in Figure 7. It appears that male crabs diverged from the preserved area with a variety of falling CPUE gradients, and that male crabs moved into waters 6 or 7 miles (11.1 km or 12.9 km) apart. The CPUEs based on intercepts on a longitudinal axis indicated relative stock richness of male crabs in the preserved area. That is, the CPUEs (kg per seine haul) from four intercepts fluctuated from 7 kg per seine haul to 23 kg per seine haul and corresponded closely to the mean CPUEs calculated from trap catches by monitoring surveys.

From tag-recapture data from fishermen, it was suggested that the majority of recaptures (80-90%) occurred within 6 to 8 miles (11.1 to 14.8 km) of the point of release in the preserved area as shown in Figure 8. Movement seemed to be random, but most male crabs apparently moved into waters shallower than 260 m depth where multiparous females were breeding with patchy structure.

Based on the two findings, (1) significant differences of CPUEs in the preserved and the surrounding areas (Figure 7) and (2) moving distance of tagged crabs (Figure 8), it was recognized that the preserved area male crabs had diverged largely into the surrounding grounds up to 3 to 4 miles (5.5 to 7.7 km) apart. Therefore, the Danish seine showed higher CPUEs for male crabs compared with those from other grounds. At present, however, many questions remain about the higher CPUE and its seasonal fluctuation in the preserved area. As pointed out by Sinoda et al., (1987), the selectivity due to the size of the Danish seine net is not precise and the net is able to catch various sizes of crab in front of the mouth. Since the Japanese Fishery Management Agency enforces a carapace size restriction which prevents landings of male crabs less than 9 cm carapace width, large numbers of crabs have to be discarded at sea as trash crab. Heavy juvenile mortality and continuous fishing pressure on the prerecruits are suspected. Moreover, even in the fishing season for demersal fishes *Arctoscopus japonicus, Hippoglossoides dubius, Argentinus semifasciata* and others, large numbers of juvenile and soft-shelled crabs are swept into the net and discarded as trash. However, all crabs in the 13.7 km^2 preserved area are protected from these unreasonable exploitations. The main reason the preserved area has higher CPUEs, or the highly patchy structure of the Zuwai crab, is largely due to the commercially unacceptable crabs protected from predation by the Danish seiners.

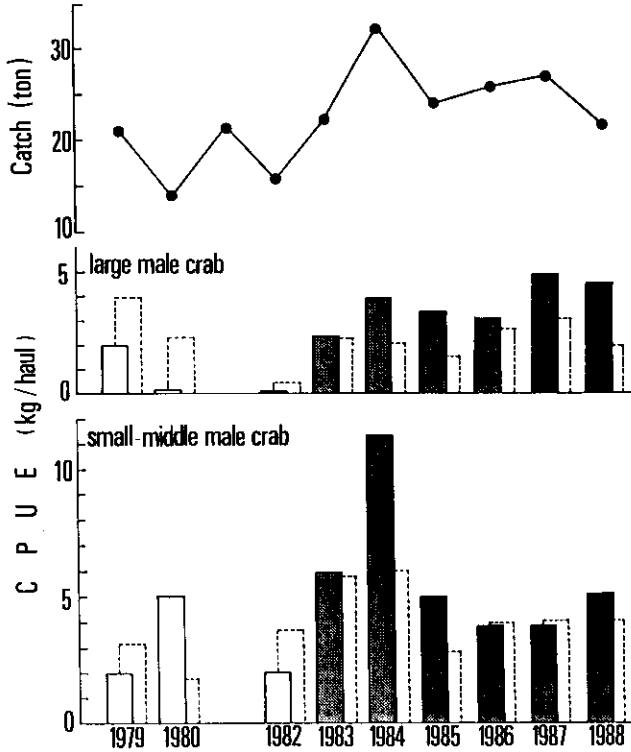

Figure 6. Annual mean CPUEs (kg per seine haul) of large male crab (more than 13 cm carapace width, CW) and small-to-middle-size crab (9-12 m CW) caught within 3 miles of the preserved area (closed bar) and other fishing grounds (broken bar). Up to 1982, the preserved area was used by Danish seiners with low CPUE (open bar).

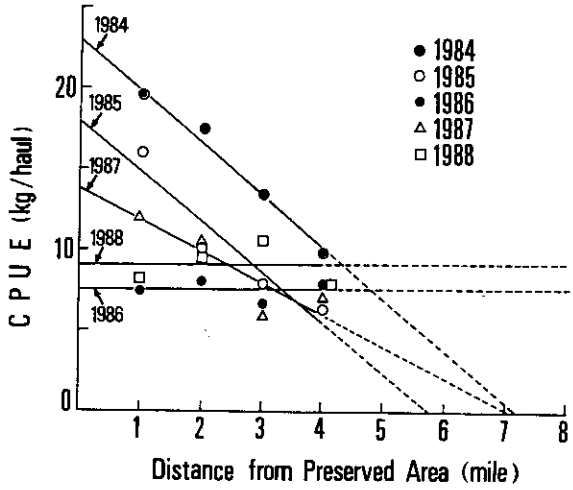

Figure 7. Relationship between mean CPUE in the subareas surrounding the preserved area and the distance from the delimitation of that area at 1-mile intervals.

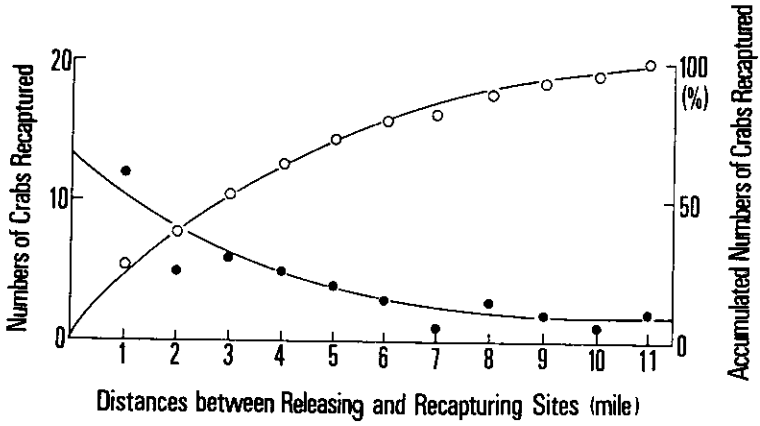

Figure 8. Dispersal of tagged crabs from the preserved area (closed circles) and the accumulated number of crabs recaptured with distance.

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Nov. 1989, Anchorage, Alaska

Development of a Fishery for *Chionoecetes tanneri* on the Continental Slope off British Columbia: Management Considerations

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ABSTRACT

In 1988, a modest trap fishery for male Chionoecetes tanneri was developed on the continental slope (580-670 m depth) off the west coast of Vancouver Island, British Columbia. This species has not previously been commercially exploited in Canada and because of both limited geographical distribution of the species, with a resultant presumed small population size, and an assumed terminal moult for the species, expansion of the fishery has been constrained until stock status can be determined.

The waters seaward of the surf line off British Columbia have been divided into 6 fishing zones, with only 2 scientific permits allowing fishing assigned to each zone. Permits valid for 3-month durations are renewable following review. Until a minimum size limit regulation is introduced, fishermen have voluntarily imposed their own size limit, based on market preference, and are only landing crab greater than 110 mm shell width. Fishing is primarily from the fall through to spring because of participation by fishermen in other seasonal fisheries.

INTRODUCTION

British Columbia currently has invertebrate fisheries for about 26 species and more are being developed each year. King and tanner crabs have been of particular interest to fishermen investigating the fisheries potential of under- or unexploited species both because of the large fisheries for snow crab (Chionoecetes opilio) in eastern Canada and for king (Paralithodes and Lithodes sp.) and tanner (Chionoecetes sp.) crabs in Alaska, and because these species are often bycatch species in other B.C. trap fisheries. Abundance and life history characteristics of both groups of crabs have been investigated in mainland inlets (Sloan, 1984a, 1984b, 1985a, 1985b; Jamieson and Sloan, 1985; Jamieson et al., 1986) but overall abundance was

generally low. While a limited fishery for Paralithodes camschatica, Lithodes aequispina and Chionoecetes bairdi occurred in the early 1980's (Jamieson and Sloan, 1985), no directed fishery for these crabs currently exists.

In 1984, a limited survey of tanner crab abundance in Queen Charlotte Sound was conducted in March (Jamieson, unpub. data) but again, few crabs were caught and fishery potential seemed low. However, in recent years, blackcod (Anoplopoma fimbria) fishermen, who fish with traps in deep water on the continental slope, noted Chionoecetes tanneri in abundance as a bycatch in certain areas (Fig. 1).

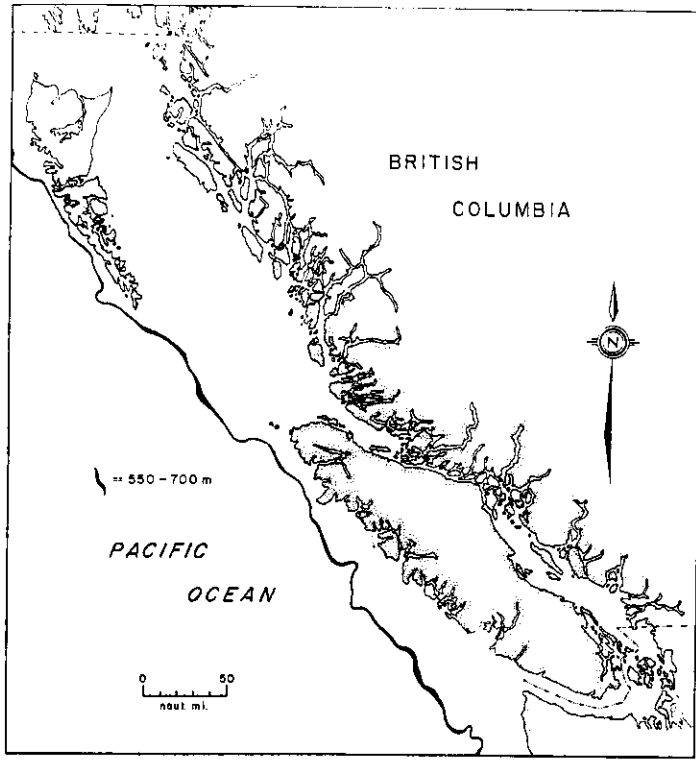

Fig. 1. The estimated occurrence (dark line: 550-700 m depth range) of C. tanneri along the continental slope of British Columbia.

This has led to recent development of a modest fishery (1988: 0.5 t; 1989: 35.5 t) for this species, and the present paper reports how managers and researchers are addressing this development.

Biology of Chionoecetes

Although there remains debate about the presence of a terminal moult in male Chionoecetes from the northeastern Pacific Ocean (Jamieson and

McKone, 1988), I believe that a terminal moult for majids should be assumed unless proven otherwise, rather than vice versa. Most majids studied in detail to date appear to have a terminal moult (Hartnoll, 1963). Published studies on Alaskan Chionoecetes have not utilized data bases collected to ascertain whether or not these crabs have terminal moults and so opinions may change as new data is obtained.

The assumption for C. tanneri in the present paper is that both male and female C. tanneri have a terminal moult and that the size, and presumably age, at which this may occur is variable. Being a previously unexploited population, terminal moult males would probably be relatively abundant since it has been suggested for Chionoecetes that terminal moult males may live for at least 3 y (Conan and Comeau, 1990; Yamasaki and Sinoda, 1990). Annual recruitment to the terminal moult cohort might then be only about 30% of this cohort's abundance. Terminal moult males are also assumed to be relatively large since although they probably can reach a terminal moult state over a considerable size range, the presence of other large males is hypothesized to encourage preterminal moult males to moult to the largest size possible before themselves moulting terminally. Only in heavily exploited Chionoecetes populations, where most of the large males have been removed by the fishery, would substantial numbers of males possibly have their terminal moults at relatively smaller sizes (Jamieson and McKone, 1988).

If the above hypotheses are true, a relatively small proportion recruiting annually to the terminal moult stage also implies a low percentage of soft-shell, or white, marketable crabs in a lightly exploited population, as most male crabs would not be moulting. Overfishing, where more crab are being harvested than are being recruited, would thus be indicated over time by both an increase in soft-shell proportion and by a decrease in average size of terminal moult males, both of which have been reported for C. opilio in the Gulf of St. Lawrence (Jamieson and McKone, 1988). In the Gulf, many male crabs may now reach their terminal moult size at a size smaller than the minimum legal size limit, and this combined with an increased soft-shell problem and depletion of the abundance of old, large terminal moult males is hypothesized to explain substantially reduced annual catches.

These presumed biological features of C. tanneri differ significantly from those shown to be evident for the Dungeness crab, Cancer magister, the major crab species currently exploited in British Columbia, and for king crabs. Males of these latter species have the potential to grow to a larger size after they become functionally mature and have mated successfully, although the extent to which they do this is perhaps variable.

Management

The primary management objective is conservation of the resource. Past experience with new developing fisheries has resulted in our current adoption of a cautious approach in allowing industry participation. Now, only a few fishermen are allowed to participate until sufficient biological information is obtained to allow biological concerns and alternate management options to be evaluated.

The tanner crab population off B.C., while probably relatively small (Jamieson et al., 1990), is nevertheless unique. Being only recently

discovered to have commercial potential and still in the early stages of being exploited, it may serve as a useful model to document the impact of exploitation in Chionoecetes in general, data which might be relevant in the exploitation of other Chionoecetes species as well. Consequently, particular attention is being devoted at this time to the collection of population size frequencies and other biological data for both preterminal and terminal moult individuals. This requires development of methodology to distinguish the two stages (Jamieson et al., 1990). Also, because both the Gulf of St. Lawrence and Bering Sea, locations of the major fisheries for Chionoecetes in North America, are ice-covered in late winter and early spring when much mating and egg-hatching apparently occurs, documentation of these phenomena for the genus has been relatively scarce. The relatively favourable weather conditions off British Columbia in the spring makes monitoring of these life history processes easier logistically. Consequently, managers have required those fishermen who would like to participate in development of the fishery potential of tanner crab fishing in British Columbia to work closely with research biologists and to provide them with required biological data.

For any crab species, population fecundity or recruitment of legal-size males have not measurably been negatively affected by past exploitation practices (Jamieson, 1986). Beyond restricting annual catch rates to reflect estimated average annual recruitment rates, which may require setting an annual catch quota, the presence of a terminal moult in an exploited population may not have any particular management consequences. Conceivably, the criterion for establishing a minimum legal size may be different but overall management practices should still otherwise apply.

The current policy for fishing tanner crab in British Columbia requires that fishermen have an experimental permit, that only a maximum of 2 valid permits be permitted in each of 6 designated areas (Fig. 2) at any one time, and that permits be granted based on the applicant's suitability with respect to vessel, gear, fishing and operational plans, experience, cooperation and reliability, and performance during prior experimental fishing operations. Permits are valid initially for three months, after which a new application must be made.

Fishing is permitted by trap gear only, and traps are required to have entry tunnels no less than 50 cm in diameter, an escape ring no less then 12.5 cm in diameter in the wall of the trap, and a self-destruct mechanism consisting of biodegradable twine not thicker than 2 mm in diameter which on degrading, creates an opening not less than 12.5 cm square. This may be achieved by attaching the fibreglass entrance tunnels to the trap with this twine. Only male crabs may be retained. Tanner crab samples and food and accommodation for a Departmental observer must be provided to the Department if requested, and fish log books must be maintained and submitted within 7 d after each landing.

Overall population abundance has not been estimated at this time since areal densities of crab abundance have not been determined. Quotas may be desirable in the long run but this will be evaluated at a later date. Limited survey resources, however, will probably necessitate a more passive management approach. Any recommended quotas will probably be based on estimates of long-term annual recruitment rates.

No minimum size limit has yet been established for C. tanneri,

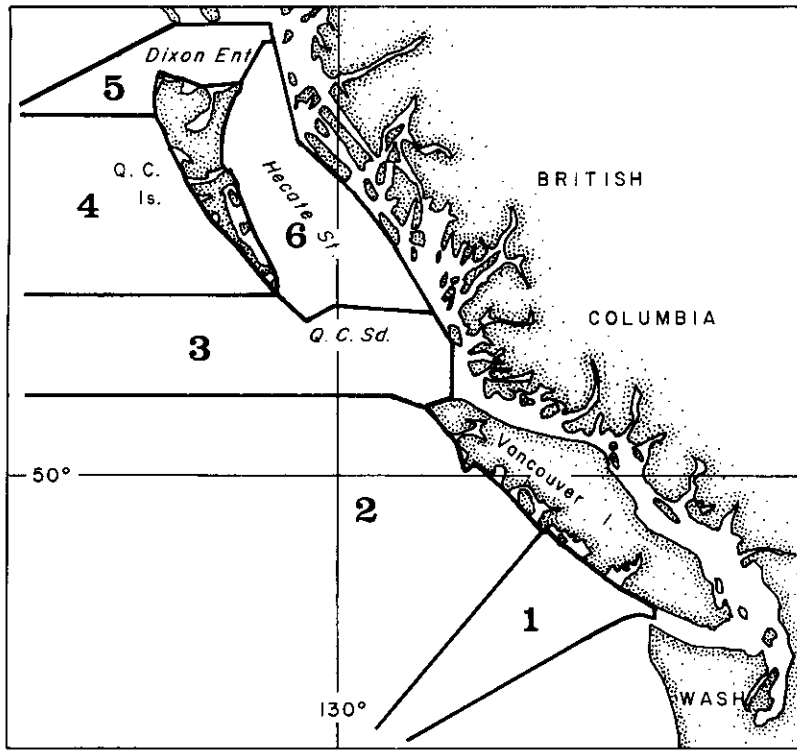

Fig. 2. Boundaries of the experimental permit fishing areas for Chionoecetes in southern British Columbia. To date, all C. tanneri fishing has occurred in Area 2 off northern Vancouver Island. Q.C. = Queen Charlotte.

although work to determine an appropriate size is currently in progress (Jamieson et al., 1990). However, since it may be desirable to focus fishing only on terminal moult crabs and since they occur over a variable size range, any size limit imposed may be on some aspect of claw morphometry rather than carapace dimension. Shape of claw changes most during a terminal moult and this is the most obvious secondary indicator of sexual maturity. A ring opening measurement through which any legal size claw should not be able to pass may be an acceptable criterion for defining a retainable crab. Currently, fishermen have imposed their own self-regulated acceptable size of 110 mm cw based on market preference. The fishing season is currently primarily from the fall through to late March because of participation by fishermen in other, more traditional seasonal fisheries.

To date, two permits have been utilized in Area 2 off the upper west coast of Vancouver Island and interest only has been expressed in other areas. The recent surplus of tanner crab on world markets has decreased prices sufficiently to curtail all fishing activity in late 1989. Being a minor fishery in terms of world production, fishery

development is influenced not only by sufficient resources but also by the market environment established by major crab fisheries. With relatively little commercial effort exploiting the resource in the short term, research emphasis is focused on describing population characteristics as the fishery develops.

ACKNOWLEDGEMENTS

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The Role of Japan in King Crab Price Determination

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ABSTRACT

In recent history exports of Alaskan king crab to Japan have accounted for a high market share of U.S. production, averaging 21% annually for the time period 1976-86. The prominent role of Japan has made it an important determinant of domestic market price and, thus, fishery management decisions. Therefore, it is crucial that the Japanese market be incorporated into marketing models of the U.S. king crab industry. In this paper a theoretical framework is developed for incorporating the Japanese market into a statistical supply and demand model of the domestic king crab industry. Empirical results from our initial attempts at incorporating this market are presented. Finally, the effect of the Japanese-U.S. exchange rate on exvessel price is examined.

INTRODUCTION

Japan is playing an increasingly prominent role in the Alaskan king crab industry. For example, in 1984, 17% of processed domestic king crab was shipped to Japan; 44% was shipped to Japan in 1988. The increased market share has established Japan as a primary determinant of world market price for king crab and thus, fishery management decisions. Therefore, it is crucial that the Japanese market be incorporated into market models of the U.S. king crab industry. This paper presents a theoretical framework of the world king crab market that facilitates a discussion of Japan's role in this market. A preliminary model of the Japanese demand for domestically produced king crab is presented. Finally, the influence of the exchange rate on exvessel price is investigated through an estimated exvessel price function for the Bristol Bay fishery.

WORLD MARKET PRICE

A simplified outline of the domestic king crab marketing channel will help facilitate the development of the Japanese market demand model. The Alaska Department of Fish and Game fixes the harvest of king crab by setting harvest guidelines and fishing season length. Fishermen deliver harvested crab to processors for some seasonal average price. Processors, in turn, take the raw king crab and produce processed king crab. The fixed quantity of harvested raw king crab translates to a fixed quantity of processed king crab. Processors allocate this product among three outlets: the domestic market, foreign markets, and inventory. The fixed nature of the supply of processed king crab requires that an increase (decrease) in shipments to any single outlet must be offset by an equivalent decrease (increase) in allocation to the other outlets.

Due, in part, to the fixed supply of domestic processed king crab, the foreign and domestic markets are interdependent, forming one world market for king crab, and a corresponding single world market price. The existence of a single world market price is easily motivated with a simple graphical aid. For illustrative purposes, assume the following: Japan represents the only foreign market; there are no inventories, tariffs and transportation costs; and processors are price takers at the wholesale level. These assumptions simplify the processors' allocation decision to choosing the allocation between domestic and Japanese markets.

Figure 1 provides a representation of the U.S. and Japanese markets for domestically produced king crab. Initially, let D^U and A_1^U , represent U.S. demand for and allocation of domestically produced king crab. Let D^J and A_1^J represent the corresponding Japanese demand and allocation. Price in each market is determined by the point of intersection of the demand and allocation curves. Initial prices in the U.S. and Japanese market are P_1^U , P_1^J , respectively. Note that given our initial assumptions, the sum of the quantities in each market, Q_1^U and Q_1^J , must equal the total supply of domestically produced product.

Figure 1 shows P_1^U to be less than P_1^J. This represents a disequilibrium in the world king crab market. The higher price in Japan provides an incentive for processors to increase the allocation of king crab to Japan, thus, a shift in the Japanese allocation curve to A_2^J. Since an increase in the allocation to Japan must be offset by an equivalent decrease in the allocation to the U.S., the U.S. allocation curve shifts leftward to A_2^U. The resultant equilibrium reflects an increase in quantity shipped to Japan ($Q_2^J > Q_1^J$) and a decrease in price ($P_2^J < P_1^J$). Quantity sold in the U.S. market declines by the amount reallocated to Japan, i.e., $Q_2^U < Q_1^U$. Notice, however, that the increase in domestic price (P_2^U - P_1^U) is not symmetrical with the decrease in Japan (P_1^J - P_2^J). This asymmetry in price is a consequence of the market specific factors that determine demand in the two countries. Accordingly, knowledge of the structure of Japanese demand vis-a-vis U.S. demand is central to determining world price.

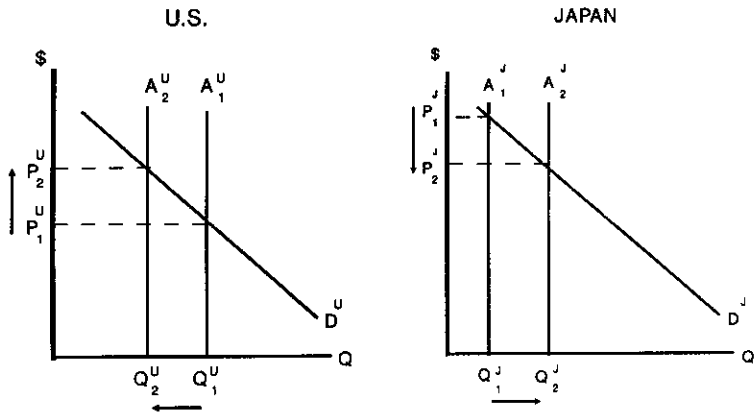

Figure 1. Hypothetical U.S. and Japanese Markets for domestically produced king crab.

JAPANESE DEMAND

Elementary demand theory suggests that price and quantity are inversely related -- the more one consumes, the less they are willing to pay for the product. In addition to price, the overall demand for a product depends on factors referred to as demand shifters. Demand shifters, in general, include income, price of substitutes, population, and tastes and preferences.

We have hypothesized the following Japanese demand relationship by tailoring this general theory.

(1) $Q_J^D = f(P_J^S, \text{EXCH, INC, POP, HARJ, IMPR, SUB})$

Q_J^D is quantity demanded by Japan for U.S. produced product (million pounds). P_J^S is the dockside price for domestic king crab sold to Japan ($/pound). EXCH is the 3rd quarter exchange rate (¥/$). INC is Japanese per capita income ($/person). POP is the Japanese population (thousands). HARJ represents the Japanese king crab harvest (million pounds). SUB represents other substitute seafood products which consumers may substitute for king crab (million pounds). All variables with the exception of EXCH are measured on a seasonal year, July 1 - June 30.

As previously noted, P_J^S and Q_J^D are inversely related. Income is positively related to quantity demanded, i.e., as income increases, the demand curve shifts outward to the right. The exchange rate (¥/$) is negatively related to Q . As the dollar weakens, (i.e., the exchange rate decreases) the price of Alaskan king

crab, in yen, decreases, thereby shifting the demand curve outward. Population is positively related to price. Population expansion in Japan leads to demand expansion, shifting the demand curve to the right. The other factors included in this demand function represent substitutes for U.S. processed king crab, where Q_J^D and prices of substitutes should be positively related. Japanese harvest and USSR imports of king crab represent near perfect substitutes for American produce product. The demand for U.S. product will decrease as the quantity of either of these supplies increase. Prices of a variety of substitute seafood products were also included in the initial demand specification.[1]

The conceptual Japanese demand model was specified in price dependent form for empirical estimation.

$$(2) \quad P^S_{J_t} = \beta_0 + \beta_1 IMPUS_t + \beta_2 EXCH_t + \beta_3 FEJ_t + \beta_4 POP_t + \beta_5 IMPR_t + \beta_6 HAR_t + \beta_7 SUB_t$$

IMPUS represents Japanese imports of Alaskan king crab (million pounds). FEJ represents Japanese per capita food expenditures (nominal $/person). This variable was used as the income measure. Other variables are as previously defined.

Ordinary Least Squares was used to estimate various specifications for the time period 1973-87. 1973 marked the beginning year of substantial U.S. exports to Japan. The specifications differed primarily in two aspects. Alternative substitute seafood products were tried and all prices and income were measured in both nominal and real values. Various Japanese consumer price indices were used to compute real values. A two-part criterion was used to determine which variables to retain in the model: satisfaction of a priori sign expectations and absolute t-values (a variable was deleted if $|t| < 1.0$). The equation of best fit that satisfied the above two criterion is presented in equation (3).

$$(3) \quad P^S_{J_t} = \underset{(-3.34)}{-0.044IMPUS_t} - \underset{(-1.86)}{0.004EXCH_t} + \underset{(1.09)}{1644.130FEJ_t} - \underset{(-1.25)}{0.349IMPR_t} + \underset{(2.41)}{1.002PTAIF}$$

$$R^2 = 0.908 \quad DF = 10$$

where PTAIF is Tokyo wholesale price ($/pound) of taisho ebi prawns. All other variables are as previously defined.

The statistical fit is quite good, with 91% of the variation in price explained by variation in the explanatory variables. The three t-statistics less than $|2.0|$ are reasonable considering the multicolinearity between income (food expenditures) and exchange rate, and also between income and USSR imports. Inclusion of

[1]These included prices of spiny lobster, kuruma ebi prawn, taisho ebi prawn, and aggregate categories of other lobsters, prawns, shrimps, and crabs.

both Japanese harvests and population resulted in low t-values. Japanese harvest has been under 500,000 pounds since 1976 and Japanese population has changed little over the 15 year time horizon.

Perhaps the most insightful way to examine the results of the estimated demand function is to measure the effect that changes in one determinant of demand has on the quantity of domestically produced Alaskan king crab demanded in Japan. Specifically, the elasticity of demand measures the percent change in quantity demanded given a 1% change in one of the other demand variables, ceteris paribus. For example, it would be useful to know how much additional crab would be exported to Japan if the dollar weakened or if income increased. Elasticities of demand computed from equation (3) are presented in Table 1. The elasticities were derived by setting all variables at their mean levels.

TABLE 1. Estimated Demand Elasticities

Variable	Elasticity
$P_J^{\$}$	-6.00
EXCH	-1.54
FEJ	3.21
IMPR	-0.80
PTAI	6.13

In general, Japanese consumers are very responsive to changes in the explanatory variables. Demand for domestically produced king crab is very elastic. For example, 1% change in the price of the U.S. produced product will result in a 6% change in the quantity demanded. The taisho ebi prawn elasticity of 6.1% is unexpectedly high. The appropriateness of taisho ebi as a substitute for king crab may be questionable. Although both taisho ebi prawn and king crab are high priced seafood products, the occasions at which they are consumed do not overlap. Given that most expensive seafood items prices tend to move together, it is possible that the taisho ebi price serves as a general proxy for this class of seafood products. Further research in the area of identifying possible substitutes is needed.

The USSR import elasticity of -0.8 is indicative of USSR imports being a close substitute for Alaskan king crab. The USSR import data used in this model was incomplete and represent the import quantities for only one major importer of Russian crab. However, it is important to recognize that future increases in USSR imports will depress market price.

Processors have indicated a belief that exchange rates are the single factor which has the greatest influence on market price of king crab. The results of the research presented here indicates that this belief is well founded. The exchange

rate is critically important to price formation and, thus, the allocation of processed product to Japan. A 1% change in the exchange rate results in a direct 1.4% change in the quantity of king crab demanded in Japan. In addition, the exchange rate has a second effect that is picked up by the income variable. As the exchange rate (¥/$) decreases, the purchasing power of the yen increases, thereby increasing per capita income. The food expenditure elasticity is 3.3%. This high elasticity reflects not only the growing Japanese wealth (measured in ¥), but also reflects the strengthening of the yen relative to the dollar. It can be expected, based on these preliminary results, that future changes in the exchange rate will have a significant impact on wholesale price for king crab.

EXVESSEL PRICE

The domestic exvessel price for king crab is based primarily on an expectation of wholesale price. The relationship between exvessel price and the exchange rate is examined through a single logistic exvessel price equation for the Bristol Bay king crab fishery, presented in equation (4). This function represents a reduced form equation which includes both the fishermen's price offer function and processors' demand function for raw king crab. It is hypothesized that exvessel price is equal to a percentage of wholesale price lagged one year. This percentage depends on a variety of factors including harvest guidelines, actual harvest levels, the cost of diesel fuel, the lagged margin between exvessel and wholesale prices, and the exchange rate. Inclusion of the exchange rate follows directly from its prominence in wholesale price formation.

$$(4) \quad EXVPT_t = \beta_0(1 + \exp(\beta_1 GUIDE_t + \beta_2(HART_t - GUIDE_t) - \beta_3 FUEL_t + \beta_4 EXCH_t + \beta_5(EXVPT_{t-1}/WTAVP_{t-1})))^{-1} WTAVP_{t-1} - \beta_6 IND83$$

EXVPT is the Bristol Bay (region T) exvessel price for king crab ($/pound). GUIDE is the mean of the upper and lower guidelines for Bristol bay (million pounds). HART is the Bristol Bay harvest of king crab (million pounds). FUEL is the Washington average diesel fuel price paid by farmers ($/gallon). WTAVP is the weighted average wholesale price for Alaskan king crab from all regions ($/pound). IND83 is an indicator variable marking the closure of the Bristol Bay fishery in 1983. EXCH is as previously defined. All variables with the exception of EXCH are measured on a seasonal year, July 1 - June 30.

Equation (4) was estimated for the period 1970-87 using nonlinear least squares. The parameter estimates, goodness-of-fit statistics, and degrees of freedom are reported in equation (4a), t-values are reported parenthetically. All t-statistics test whether a particular parameter was significantly different than zero, except β_0 which tests whether it was significantly different than one.

$$(4a)\quad EXVPT_t = 0.340(1 + \exp(\underset{(2.94)}{0.007GUIDE_t} + \underset{(3.23)}{0.026(HAR_t - GUIDE_t)} - \underset{(-2.90)}{}$$

$$\underset{(-1.85)}{0.480FUEL_t} + \underset{(5.22)}{0.008EXCH_t} + \underset{(2.21)}{2.225(EXVPT_{t-1}/WTAVP_{t-1})}))^{-1}$$

$$WTAVP_{t-1} - \underset{(-5.22)}{2.9006IND83}$$

$$R^2 = 0.9711 \quad DF = 11$$

The reported R^2 suggests that 97% of the variation in exvessel price is explained by variation in the explanatory variables.

Of specific interest is the exchange rate parameter value and its corresponding mean level elasticity. The positive coefficient in the logistic function implies that exchange rates (¥/$) and exvessel price have a negative relationship, i.e. as the exchange rate decreases, exvessel price increases. Following the previous reasoning, a decrease in the exchange rate shifts the Japanese demand curve out, resulting in a higher wholesale price. Processors and fishermen will adjust their wholesale price expectation upward. A higher wholesale price expectation translates into a higher exvessel price.

The estimated relation specified in (4a) suggests exvessel price is highly responsive to the exchange rate. Evaluated at mean levels, a 1% change in the exchange rate results in a 1.98% change in the exvessel price. This illustrates that exchange rates are a driving force in determining exvessel price as well as wholesale price.

CONCLUSION

In conclusion, the models presented here show Japanese demand to be highly responsive to a variety of factors. Exchange rates, through a direct affect and income affect, may be singled out as having the greatest impact (with the exception of price) on demand and thus, world market price. Exchange rates were also shown to have a significant impact on exvessel price. The recent strengthening of the yen relative to the dollar can be singled out as greatly contributing to the recent increases in both wholesale and exvessel prices for Alaskan king crab and the related increase in the share of domestic product exported to Japan. Future decreases in the exchange rate will provide a continuing upward pressure on wholesale and exvessel price, and result in an increasing proportion of domestic harvest being shipped to Japan.

There are several limitations to this paper. Data limitations are severe with regards to the Japanese market. Price and quantity data on processed king crab by product form and on several potential substitutes are not available. Inventory and complete USSR import data are also not available. A comprehensive understanding of Japanese consumption behavior with regards to king crab is lacking. In our discussions with individuals familiar with Japan, we received different and often conflicting descriptions of consumer consumption behavior.

It should be stressed that this study does not explicitly link the Japanese king crab market with the U.S. market. The interdependence of U.S. and Japanese markets requires this linkage for an accurate representation of the demand for domestically produced product. A simultaneous system of equations is essential to allow for this linkage. Thus, the results presented here must be regarded as preliminary.

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Importance of Bioeconomic Analysis in Managing the King Crab Industry

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INTRODUCTION

Conventional wisdom suggests that management and regulation of open access fisheries will lead to improved stock conditions and to enhanced economic returns for all participants. This is true only if management agencies have comprehensive methods/knowledge to forecast problems within the fishery and to analyze alternative policy remedies to those problems.

Few at this symposium would suggest our knowledge of the Alaskan king crab fishery is adequate for effective management, else we wouldn't be here. In fact, the ineffectiveness of management and regulatory policies is manifest in this boom-bust fishery. Returns to the industry plummeted more than half a billion dollars between 1980 and 1983, and remain depressed today. This collapse should be sufficient testimony to rethink the underlying management philosophy that annual sex, size and season length regulations can be set by considering only stock vitality. Effective management clearly requires a better understanding of fishery biology, especially population dynamics. However, effective management also needs to understand the various facets of industry behavior and market responses to management induced stock effects--neither of which have ever

played an important policy role in this once lucrative fishery.[1] The premise of this paper is that only when the linkages between biology and economics are well-understood can we reasonably expect management to be effective and in the public's interest.

The purpose of this paper is to outline a general bioeconomic framework for policy analysis. In so doing, I illustrate why a bioeconomic perspective is crucial to effective management of this complex fishery. The paper closes with some evidence that lowering the size limit may not be prudent at this time.

BIOECONOMIC INSIGHTS

The essence of a bioeconomic framework for policy analysis is captured in Figure 1. Figure 1 is a highly simplified illustration of the king crab industry. It shows the explicit interaction among management, biology, harvest and the market for king crab. These elements collectively account for feedback inherent in the industry. It shows, for example, that a management decision to lower the legal size of crab will have not only direct stock effects, but also a variety of price effects, from the exvessel market for raw crab, to the wholesale market for processed crab.

Virtually all research related to king crab has focused on the bottom two boxes in this figure.[2] **This focus is rational only if management induced stock effects are price neutral.** That is, if lowering the size limit has no effect on the price paid to fishermen or on the price received by processors, then it follows that a singular focus on stock vitality is prudent. Unfortunately, absence of price effects is unimaginable. An elementary tenet of economics is that price varies with the availability of product. Any management policy that significantly affects stocks and, thus, harvest, will ripple through the market place. An objective of bioeconomic modeling is to predict the various price effects and also to determine who is made better or worse off, and by how much. Only with this type of information can the Alaska Board of Fisheries anticipate the consequences of regulations on affected interest groups.

I am confident that many of you are disbelievers that bioeconomics is crucial to the policy process. So, perhaps I can convince you with a highly simplified, hypothetical policy problem. Consider the question of reducing the size limit given that there appears to be a higher than normal rate of mortality. The implications of this policy should be evaluated from several perspectives, but limit your concern to the impact on processors. The following scenario helps to make the problem more concrete. Suppose the projected king crab catch

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[1]The general management objectives of the Alaska Board of Fisheries have been almost exclusively biological in nature, emphasizing conservation. The twofold objectives are: "(1) to establish a stable fishery, insofar as possible, eliminating the extreme fluctuations in catch that have characterized this fishery, and (2) to develop and maintain a broad based age structure of legal size male king crab, insuring both breeding success and the availability of a wide spectrum of year classes to the fishery" (ADFG 1985).

[2]Notable exceptions include Queirolo et. al. (1978), Orth et. al. (1979) and Reeves and Morasco (1980). However, the only comprehensive bioeconomic analysis is by Matulich, Hanson and Mittelhammer (1988 a, b, c).

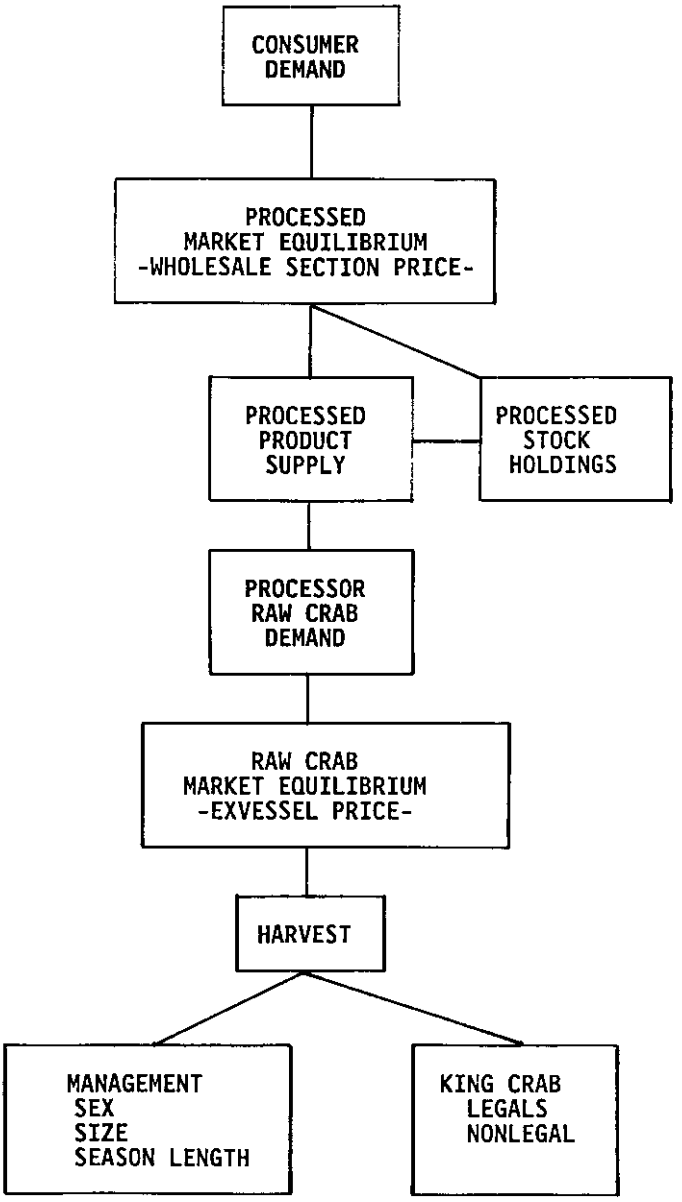


FIGURE 1. COMPONENTS OF A BIOECONOMIC ANALYSIS OF THE ALASKAN KING CRAB INDUSTRY

(processed weight) is 16 million pounds, and the average wholesale section price is $10.50 per pound. Further, suppose the reduced size-limit policy is expected to increase the supply of processed crab to 17 million pounds. Assume away any intertemporal effects, i.e., an increase in harvest this year has no effect on harvest in subsequent years. Should the reduced size-limit policy be adopted? Why or why not?

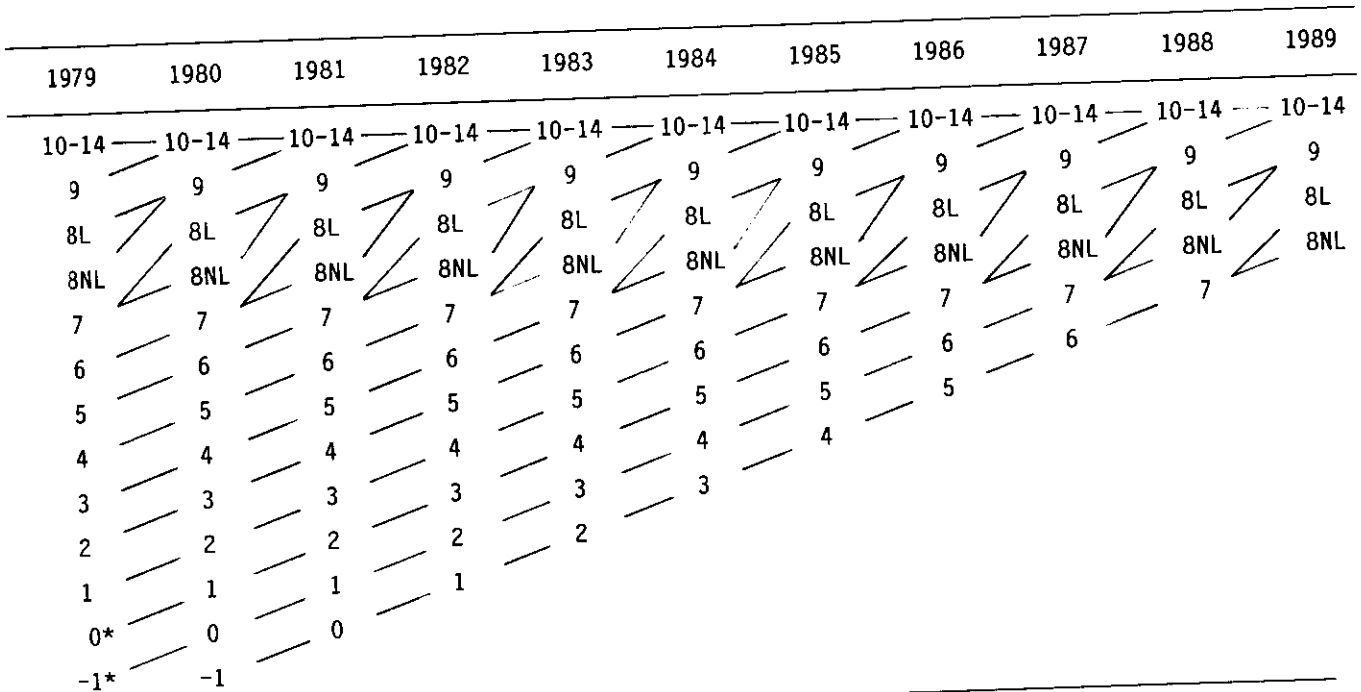
Your answer should be "It depends"---most notably on the anticipated price that processors will receive for their product. Specifically, processors will be better off from the more liberal harvest regulation if and only if average wholesale price remains above $9.31 per pound (assuming no change in per unit production costs). Processors will lose revenue, despite the fact that they can sell an additional million pounds of crab, if price drops below $9.31.

Whether the industry is better or worse off financially, depends on how much additional crab will be sold relative to the decline in price. If the percentage increase in quantity sold is greater than the percentage decrease in price, then processor revenues will increase. However, if price drops relatively more than catch increases, revenues will fall. This simple concept is known as elasticity of demand. It is critical to guiding effective regulatory policy. Unfortunately, there is no simple way to determine price elasticity, short of modeling industry behavior. Accordingly, there is no way to evaluate the prudence of changing regulations without a bioeconomic analysis.

Please keep in mind how simplistic this example was. First, it only considered the effect on processors. What about the fishermen? Figure 1 shows an entirely different market at exvessel level; exvessel price response will differ from the wholesale price response. Second, lowering the size limit will define an entirely new product. The smaller crab will probably grade out into 30+ count packs, that is, 30 sections per 10 pounds. The market for such a product is likely to compete directly with tanner crab, less so with traditional king crab markets. Prices in the tanner crab industry will soften, which, in turn, will depress the 30+ count king crab price. However, the most serious simplification concerns the myopic, one-year-ahead perspective that I imposed with the assumption of no intertemporal effects.

Current harvest policies certainly have an immediate impact on current biological stocks and current prices. But they also impact future harvestable stocks and future prices. The importance of formulating policies that consider the long and complicated lags that characterize king crab population dynamics, and thus, the long range biological and economic health of this industry, cannot be emphasized enough.

Consider Figure 2. The beginning stock of legal (harvestable) crab in 1989 is shown to consist of three age classes of male crab: 8-year old legals (8L), 9-year-olds (9) and 10 to 14-year-olds (10-14). The recursion illustrated in this figure shows the pass-through or pipeline of unharvested legal (L) and nonlegal (NL) crab in the previous year that comprise the beginning stock of current year age class. For example, both the current stock of $8L_t$ and of $8NL_t$ were formed from surviving 7_{t-1} the previous period. Likewise, 9_t was formed from $8L_{t-1}$ and $8NL_{t-1}$; $10\text{-}14_t$ was formed from 9_{t-1} and $10\text{-}14_{t-1}$. Carrying this recursion back to parental stocks, 8-year-old recruits in 1989 were created by sexually mature parent stock 9 years earlier (1980). Nine-year-old recruits in 1989 are the progeny of adult crab stocks in 1979 (10 years earlier). The



*The terms 0 and -1 refer to newly hatched larvae and breeding, respectively.

Figure 2.--Recursive age structured character of red king crab.

abundance of 10-year-olds in 1989 are a function of parental stock 11 years earlier, and so on.

This figure clearly illustrates that there are three dimensions to current period decisions concerning size limit policy that should determine the magnitude of 8L versus 8NL. Eight-year-old potential recruit class crab can have value as: 1) current harvestable stocks, 2) future harvestable stocks (up to 7 years into the future), and 3) parent stocks of progeny that can be harvested 9 to 15 or 16 years into the future. Evaluation of the implied biological and economic tradeoffs is precisely what is required by the Magnuson Fishery Conservation and Management Act (1976).

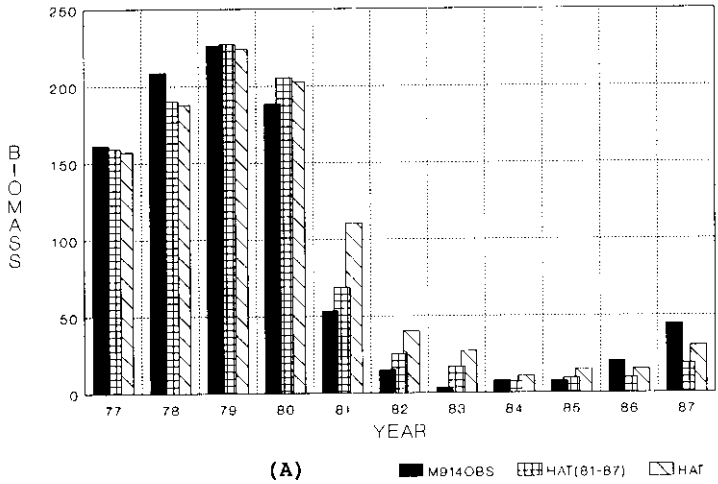
There is another advantage of a bioeconomic approach to policy analysis and crab management. It will help to mitigate the historic adversarial relationship between industry and the resource agencies (National Marine Fisheries Service and Alaska Department of Fish and Game). A singular focus on crab biology will continue to lose sight of the purpose of crab management. The goal of management is not to improve the well being of crab. It is to improve the well being of society. Long-term vigor of crab stocks obviously is essential to this. However, there is an important difference in management philosophies. One desires to maximize biological productivity; the other attempts to maximize societal well-being subject to maintaining long term stock vitality. The broader perspective will help to form a political coalition among interest groups, rather than leaving such important decisions to whim of narrowly defined political power.

MORE ON THE SIZE LIMIT QUESTION

Those of you still unconvinced of the merits of integrated bioeconomic analysis, let me make one last appeal to your scientific instincts. Once again, consider the policy question of lowering the size limit. The paper I presented earlier in this symposium identified preliminary evidence of a structural break in mortality between 1981-85. The break was found to affect male crab with carapace length longer than 130 mm. This conclusion was derived by estimating the SUR-FMR spawner recruit functions with different mortality parameters over time. Failure to find consistent statistical evidence of increased mortality across all size/age classes led to the empirical results compared in Figure 3.

Figure 3a compares observed population estimates for male crab larger than 140 mm carapace length (9 to 14-year-old males) with predicted population, assuming constant mortality from 1977-87, and a continuing structural break in mortality that began in 1981 (1981-87). Figure 3b compares the observed population with two alternative models that allow 8 to 14-year-old mortality to shift in 1981. The first shifts mortality over the entire period 1981-87. The second shifts mortality only during the 5-year period 1981-85. This latter model offers a clearly superior fit.

The evidence provided by the cohort analysis casts doubt on the advisability of a policy proposal to lower the size limit. Presuming the increase (48%) in mortality continues, when in fact it may have normalized, would be disastrous for the fishery. Obviously, the results should be viewed as tentative--only 2 years of data (1986-87) were included after the 1981-85 structural break period. Nonetheless, the goodness of fit statistics, consistency with a priori sign



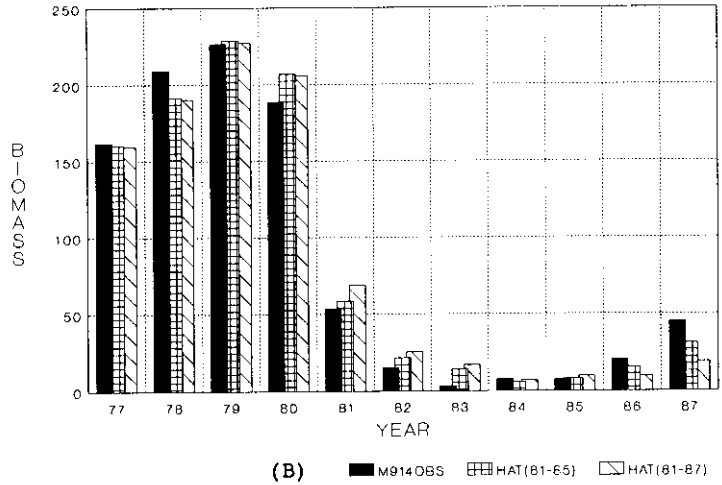


Figure 3. Comparison of Male 9-14 Biomass Estimates (in million lbs.), Different Mortality Assumptions: (a) Observed vs. Constant Mortality (HAT) vs. Mortality Shift in 1981 (HAT 81-87), (b) Observed vs. HAT 81-87 vs. Mortality Shift 1981-85 (HAT-81-85).

expectations and comparative model performance require, at the very least, careful reconsideration of any proposal to reduce the size limit.

Quite apart from any economic considerations (which have not been analyzed), one must weigh the consequences of making a type I statistical error versus a type II error. Let the null hypothesis be that crab mortality is abnormally high; the alternative hypothesis is that mortality has returned to normal. The costs of a type II error are the consequences of accepting the null hypothesis of abnormally high mortality when, in fact, mortality is low. The costs of a type I error are the consequences of rejecting the abnormal mortality null hypothesis when mortality actually is abnormal. Given our limited knowledge of crab biology, plus the conflicting statistical evidence presented at this symposium, the expected costs of a type II error are excessive.

If the proponents of a lower size limit are wrong (i.e., stock recovery started in 1986) the future of the fishery and the industry may be at stake. Any policy to increase harvests will threaten recovery at a time when stocks are critically low. On the other hand, if the proponents are correct, but choose not to lower the size limit, the only potential loss is near-term revenue. The surviving small crab next year will be larger and more valuable, they will add to the broodstock, and they will enhance recruitment 9-10 years later. Not all crab will die and the additional harvest can not select only those that would die. My recommendation, quite apart from bioeconomics, is to be conservative.

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Proc. Int. Symp. King & Tanner Crabs
Nov. 1989, Anchorage, Alaska

Workshop

Thomas Shirley and Scott Matulich, Moderators

THOMAS SHIRLEY, University of Alaska: The workshop will be an open forum so we can discuss virtually any issue that has come up during the symposium. However, there will be a bit of structure. I have asked Joe Donohue if he would make a presentation on bitter crab disease. Joe Donohue is a commercial fisherman and also is with the Alaska Seafood Marketing Institute. We will have a presentation by Scott Matulich, a resource economist from Washington State University. You will notice there are microphones on the tables. If you ask a question, we need for you to speak into a microphone. Let's start with Joe Donohue.

JOE DONOHUE, Commercial Fisherman: I appreciate this opportunity to speak at this symposium, and I appreciate the symposium itself. It's a wonderful gathering. I've learned quite a bit from it.

As a tanner crab fisherman who has been involved in the northern southeast Alaska plot fishery since its inception in the late 1960s, I am deeply concerned with the continued spread of bitter crab disease. We may well be facing the prospect of a total decimation of these tanner crab stocks if no steps are taken to reverse the present trend.

In review it should be pointed out that bitter crab are actually sick crab. Their blood system has been invaded by tiny dinoflagellates. Further, it is highly probable that this condition is extremely contagious to the health of tanner crab at some point, and probably could cause the death of the infected host. Coupled with the fact that infected crab will not survive is the additional problem of infertility. The drain on the crab's nourishment sources prevents the normal development of either egg or sperm. The crab will not contribute to the reproductive process, even if it goes through all the motions. A bitter crab is a drain on tanner crab resources.

There always have been a small number of infected tanner crab in the annual commercial catches, but these were largely ignored, or were separated from the remainder of the delivery if they were recognized. There has been a sharp increase in infection of more northerly stocks fished in southeast Alaska over the past four seasons.

The amount of bitter crab captured were of sufficient magnitude in 1987 to cause the local processors to assume selected stocks of tanners in northern Lynn Canal, and in the greater Icy Strait areas, should be visually hand sorted by knowledgeable people able to tell good from bad. This sorting step would take place both on processor's docks and on tender vessels sent out on the grounds to purchase tanner crab. Needless to say this development in general, and the sorting step in particular, was not popular either with the fishermen or the processors. Alaska Department of Fish and Game (ADF&G) shellfish biologists expressed alarm at the sorting of the crab on the grounds, or on the tenders, especially when it was observed the infected, rejected tanner crab could be spreading bitter crab disease into clean areas.

Auke Bay was cited as a prime example of the result of this concern following the 1987 practice of sorting and dumping thousands of pounds of infected tanner crab into the bay. During the fall and summer of 1987, tanner crab sampled from Auke Bay showed a large number of infected specimens where virtually none had been noted in prior years. During the annual ADF&G survey in the summer of 1987, infected tanner crab were recognized and documented in Lynn Canal, Icy Strait, lower Stephens Passage, and Peril Strait. Aside from the first two areas, little evidence of tanner crab infection was documented. However, Lynn Canal and Icy Strait catches indicated the amount of infected tanner crab was on the rise.

In 1988 the tanner season was managed in much the same way as the previous season with processors sorting once again and ADF&G expressing concern over the effect of these procedures. For economic reasons many fishermen began to sort their own crab on the grounds, at the site of capture, rather than take these bitter crab to the point of delivery. I did it because I did not have enough room in my tanks to take in crab I couldn't sell. All crab captured were separated on the deck and the bitter crab were thrown back over the side. In retrospect I can see where sorting created ever larger numbers of infected crab in relation to healthy specimens. The imbalance of unhealthy to healthy tanner crab created a higher probability the remaining healthy crab would have exposure to the bitter crab disease.

During the 1989 Southeast tanner crab season it was documented that larger percentages of bitter crab were being caught in more areas than had been the case during the previous season. I am certain the condition is spreading from the more heavily infected areas. Specific areas such as Berners Bay and Eagle River in Lynn Canal had greater evidence of bitter crab in the population fished by my vessel than in previous seasons. South of Eagle River between Amalga Harbor and Point Lena individual hauls yielded 10 percent to 35 percent infected tanner crab during the first days of the 1989 season. As a result of people sorting, ADF&G

field personnel suspect more than 150,000 pounds, and possibly as many as 200,000 pounds of crab were rejected or destroyed in 1989.

I take issue with the current passive form of management being used by ADF&G to control the spread of bitter crab disease. While I acknowledge there is little hard documented scientific knowledge of the life history of the bitter crab parasite, the present form of hands-off management used by ADF&G will eventually cause areas of northern Southeast to be entirely devoid of crab. A lack of definitive action such as off-season, non-commercial removal of infected crab from documented areas will only hasten the spread of the disease to surrounding areas. This blight on the population could spell economic disaster to fishermen and communities of northern Southeast during winter months.

Mechanisms must be put in place within the management and research divisions of ADF&G to react to the bitter crab disease problem. At present the only form of management ADF&G depends upon is the number of crab recorded on fish tickets—crab that are removed from the environment. The amount of crab left in the environment is unknown.

There are presently no management mechanisms in ADF&G to deal with bitter crab disease. Local and regional shellfish management biologists cannot authorize off-season fishing for diseased tanner crab. Money constraints further complicate the issue by making it necessary to prioritize all management research by dollars available and dollars spent, not according to value of catch or viability of the specific fishery.

Presently there is limited money available to ADF&G regional offices and the Fisheries Rehabilitation, Enhancement and Development Division (FRED) pathological research section to continue studies of blood samples taken from suspected bitter crab in a project related to seasonality of the bitter crab infection. Information important to this research on the spread of the parasite in the Sullivan Island area in northern Lynn Canal has been stalled due to the lack of appropriate funding.

It is my opinion that since the inception of this particular study in Sullivan Island, the area has ceased to be a viable commercial tanner crab fishing area due to the relatively small number of healthy crab remaining during 1989. My records show from zero to 10 percent healthy crab are in this area. By the 1990 tanner season, I doubt there will be any live crab in this study area.

Because of the lack of ADF&G research funding, the University of Alaska Fairbanks, Juneau School of Fisheries and Ocean Sciences and the National Marine Fisheries Service (NMFS) Auke Bay Laboratories entered into studies of the bitter crab disease. The university is asking for industry support of southeast Alaska processors, citing the fact that since 1985 southeast Alaskan processors have purchased hundreds of thousands of pounds of tanner crabs which had an aspirin-like bitter aftertaste, and were thus unmarketable.

A workshop called by principal biologists following the season in May included ADF&G, the University of Alaska, NMFS, and also area fishermen and processors. This group's first meeting was called the Bitter Crab Workshop. To date there have been two meetings, and both were enlightening. I believe the Southeast tanner crab fishing and processing industry must bring the scope of this problem to the attention of more participants. Both Southeast tanner crab fishermen and processors should consider an informational campaign to pre-sent their concerns to the Alaska Legislature. This campaign should identify the following major concerns.

1. We have a problem, and we do not know enough to positively control it.

2. The problem is spreading out of areas of major concentration into other tanner crab fishing areas.

3. The present passive form of tanner crab management is unsuitable to monitor or control the spread of the problem.

4. Southeast tanner fishermen are fearful their fishery may be decimated if the spread of the problem is not checked.

We should ask the Legislature to:

1. Support and fund a program to research bitter crab disease.

2. Fund a study of the economic impact of bitter crab disease on Southeast.

3. Explore alternative management measures to check the spread of bitter crab disease throughout Southeast.

We are presently attempting to do these things through the Bitter Crab Workshop. The Alaska Seafood Marketing Institute (ASMI), of which I'm a member of the quality committee, has designated $15,000 to help with bitter crab research through the University of Alaska and the NMFS Auke Bay Laboratory. The bitter crab study is ongoing, but the project needs support. As a commercial fisherman, and as a member of the processing sector, I feel greater attention must be given to the bitter crab disease issue, and other parasite issues in southeast Alaska. Thank you.

SHIRLEY: Let's open the microphone for questions.

FORREST BLAU, ADF&G in Kodiak: Have fisherman or processors ever considered a bounty type system in which they pay through a self-imposed tax, or some other process?

DONOHUE: Bounties have been considered, but it hasn't gone very far. We're

still in the developmental stage. The idea of going out and capturing sick crab during the off-season and then destroying them is the only idea so far.

ARMAND KURIS, University of California: I'd like to point out the release of undersized crab is risky from these areas because apparently the disease takes a long time to develop. Release of undersized crab may be spreading the disease.

DONOHUE: I didn't put it in here, but it's obviously not sex specific. Both sexes are infected.

MARIANNE JOHNSON, University of Washington: You expressed the feeling there wouldn't be any crab in a certain location next year. If you think they would all die out fast, might that be the fastest solution, to let them die and then re-introduce them?

DONOHUE: From a biological standpoint, it is probably an adequate idea. But as a fisherman, I don't think it is a good idea.

GORDON KRUSE, ADF&G in Juneau: Is there evidence to suggest infected crabs are the major source for infection of other crabs?

DONOHUE: I am not sure whether the studies have proven that so far. I think it's probably happening crab to crab, and I think the ones being thrown over the side are adding to the problem.

A.J. PAUL, University of Alaska: I'd just like to point out in the 1982 tanner crab symposium Dave Hicks gave a paper in which he showed about 30 percent of some populations around Kodiak had black mat disease, a fungus type disease. At that time Al Sparks, NMFS, was working on the descriptive biology of it. There was a plea for the University of Alaska and NMFS to get together and work on it. There was lots of lip service, but no funding ever arose. So here we are eight years later, and nothing was ever done about it.

DONOHUE: The bitter crab disease represents the same situation, but a different specific problem. We're thinking about putting together a non-profit research foundation so that much of the money can be garnered from the processing sector and put in a fund to help pay for vessel time, because vessel time is very expensive to ADF&G. In this way, we would be able to produce more information on the ADF&G vessels, and the fund would be used to not only pay the vessels for their time, but for the increase in their insurance, without which it is prohibitive to take small research crews out for short periods of time.

DAVID ARMSTRONG, University of Washington: A.J.'s comments reminded me of that disease. Has it subsided?
PAUL: I don't know. I think you should ask ADF&G.

ARMSTRONG: Anyone?

DANA SCHMIDT, ADF&G in Kodiak: The degree we monitor the disease is when it comes in on the fishery, and the occurrence of the disease on the survey. It doesn't stand out to me that we've seen any increase. I think it's still present in low levels, but I don't think it has increased more. I would defer to other members of my staff who might have a better knowledge of it. I do know one thing. Those crab have been more acceptable at market—more so in the last couple of years.

DONOHUE: I'm certainly not an expert on black mat. We do have it in Southeast though, and those crab are automatically rejected by the fishermen. Infected crabs seem to be concentrated in some areas.

DOUG MOLYNEAUX, ADF&G in Bethel: One of the methods proposed to deal with bitter crab has been to manage around it by having the seasons open earlier. During the course of this symposium, I've talked with at least two people who have encountered bitter crab disease much earlier in the year. Just so it's documented, I would like those people to speak up now.

DONOHUE: There is a proposal addressing this before the Board of Fisheries to consider this spring. ADF&G is asking for authority to open fisheries earlier, before the disease manifests itself to the degree where it actually turns crab meat bitter after cooking. I think it's a good idea.

MOLYNEAUX: I would like those people who have told me about fishing the bitter crabs earlier in the season, the summer and the fall, to speak up now so we can have it documented.

WAYNE DONALDSON, ADF&G in Cordova: I was on a pot shrimp survey a few weeks ago, and I visually saw bitter crab disease in Prince William Sound, perhaps 40 millimeter crab, about a three percent infection rate. That was mid-November.

ARNE AADLAND, Crab Fisherman: We have the bitter crab up in the Bering Sea, particularly west of St. Paul, and on up towards St. Matthew. We also have something similar to the black mat Dave was speaking about. This crab has been absolutely turned down on the market, and it looks like the whole section is getting affected more each year. We have a serious problem.

SHIRLEY: Thank you, gentlemen. Let's move on, and have Scott Matulich from Washington State University make a presentation.

[At this time, Matulich presented his paper, "Importance of Bioeconomic Analysis in Managing the King Crab Industry," which immediately precedes this workshop section.]

TIM KOENEMAN, ADF&G in Petersburg: The recommendations ADF&G makes basically have a biological basis. I think what you're saying is before the department makes its recommendations, it should try to integrate it with some of the other sciences.

MATULICH: Absolutely. That's what I'm saying.

KOENEMAN: That's been a very difficult thing to do. I want to point out that the Board of Fisheries does consider a lot of the political issues. Fishermen argue all the time for seasons. It's not just purely a biological season, even though that is what it looks like on the record books. I've advocated to Ken Parker (Director, ADF&G Division of Commercial Fisheries) we create a regulation book that says fishing seasons start such and such time. If it is purely biological, let's put a big "B" after it. If it's got some social or economic interaction, let's put a "B-E-S," or whatever else after it. We as biologists often end up trying to justify regulations biologically. In many cases, it's very difficult because there are a lot of influences that went into the development of those regulations.

MATULICH: I appreciate what you're saying. I'm trying to be devil's advocate today. I'm not trying to suggest there are grievous errors being made in biology. I don't know enough about biology to suggest any such thing. Fishermen don't have any great insight into economics. Nor do processors. I am now working under a grant from ADF&G and UniSea Corporation. I am working with the processors right now, and I have established many contacts here with catcher/processors who are going to participate in a pricing study. There's no data at all in the marketplace for us to use to know what happens with respect to price as the structure of the stock changes. What happens to prices in 9- to 12-count crab as opposed to 20- to 25-count crab? The reason those data don't exist, if you look at the structure of the processing associations, is because they're businessmen who have little background in economics. There are differences between business, economics, and biology. We all have something to contribute. What I think the economist contributes, or can contribute, is a marrying of the perspectives, bringing them together. Economics should not be the only discipline to guide the industry, but it's certainly no less important to management decisions than biology. Both are critical.

JOHN DOYLE, University of Alaska: One of the things you ignored in your economic model was that the value of crab is actually depreciating in the water at the rate of approximately 15 percent a year. This needs to be taken into consideration by an economic model. At the end of seven years the crab is essentially worthless in terms of a vessel owner who has to really depreciate his effort. Therefore, if I were going to strictly manage an economic model, I'd get out there and mine the stock to its economic limit, and then turn to another resource.

MATULICH: We have not ignored the time value of money. In fact, when you get into population dynamics modeling, you're ultimately moving towards an optimal control theoretic model. That's a type of a model where you're trying to look at the optimal levels of control that change from year to year based in part on present value income. We're not ignoring it. We just didn't discuss it.

ARMSTRONG: I am convinced economics are important. But my question is whether or not it is the mandate of state and federal regulatory agencies to maximize dollar return in their management practices, or rather to maximize the per-

petuation of the resource and access to the largest amount that won't jeopardize the resources. It seems to me in one sense your comments are a bit misdirected toward management agencies, rather than the industry itself. Georgia Pacific doesn't cut all its trees in one year, because it is a sophisticated company that understands the economics of that kind of action. But I don't know the extent to which the crab industry considers the subtleties of economics you just pointed out to us.

MATULICH: We have an open access fishery where there are no clearly defined property rights. Who owns the crab? The industry does not have it in its own interest to harvest the so called socially optimal amount of crab. That's why regulation is important; it's in part to keep them from over-harvesting. However, regarding the issue of what the objective function ought to be, or ought not to be, the Magnuson Act is very clear on this point. It's for the well-being of society. It's not for the well-being of the crab. That's federal law. If you look at the ADF&G charter, there's language that speaks to managing the resources for society.

KOENEMAN: What it really says is for the common good of the people of Alaska.

MATULICH: Actually I think that's right. In this case we probably ought not to have a fishery, since Seattle seems to own much of the fishery.

ARMSTRONG: In light of what you said, would you dispense with the quota system as an operational mode for these fisheries, and let it simply run at full tilt, and based on the assumption that biologically they have protected the resource?

MATULICH: No, I would not. First of all, we don't have a quota system, we have a harvest guideline system. What I would do is try to develop a population dynamics model that is more accurate in predicting what the stocks are going to be next year. I would use that as a target in the guideline harvest level plus or minus one. It serves not as a quota but as an acknowledgement of what the stock conditions are believed to be to the fisherman and to the processors. I would shut the season down if new information comes along that suggests the guideline harvest level was wrong.

ARMSTRONG: But now you're ranging into the biology of it all. When you evoke the 1983 crash as based possibly on the fact that management wasn't as effective as it could be, because of lack of biological information, it seems an alternative hypothesis is that management was superfluous to the course of population trends and abundance. So I guess I'm inclined to think you still would err in a very conservative mode by leaving out a high percentage of the resource to the fisherman that really isn't needed for perpetuation of the resource.

MATULICH: You're missing one fundamental point. In 1980, we had a record harvest of 180 million pounds of crab. One-hundred-thirty million pounds came out of Bristol Bay. A record harvest followed with a precipitous decline. If one could have predicted the decline, it would follow that you have expected prices for your crab to firm up (have higher prices in 1981, 1982, and 1983) because of a lower sup-

ply. Improved management does not mean the collapse was preventable. However, unless one argues that every crab caught during the peak harvest years of 1977 to 1980 would have died anyway, it follows that stock conditions in 1981 to present would have improved. Had industry foregone a little of the profit in 1978, 1979, and 1980, and pushed forward into 1981, 1982, and 1983, they could have made more money and faced more abundant breeding stocks.

GLEN JAMIESON, Department of Fisheries and Oceans, British Columbia: I am wondering where we are going in this conversation. I have the feeling it's becoming biologist against economist. It has not given me any direction I might take to address any biological issues, or how successful our management approaches are. I was just wondering if we could shift the conversation. I think we've got this aspect. I think it's a very relevant one, and I thank Scott for it. But I'm wondering if we can follow up some of the other points raised during the course of the meeting?

MATULICH: I was struck by the different approaches used by scientists and social scientists. Throughout the papers over the last several days, I didn't hear anybody ask the question, "So what's this good for in terms of management tomorrow?" What I would suggest in concluding my comment, is as you do more research, you have two reasons for doing it. One is to push back the frontiers of knowledge, and the second is to improve management. I'd like to see biologists define whether a research project is for management purposes. If it is, define exactly how the results are to be used, or speculate how they might be used upon conclusion of the research.

KURIS: I'd like to back up a moment. It's fairly sterile to pit biology against economics. In a certain sense, they are both just measuring different views of the same animal. I think, getting to your last point, Scott, if you could define your reasons for doing something, we'd all be a lot more knowledgeable than we actually are. When one does science you rarely know what the ultimate impact will be. So there's a need to do research for research's sake, every bit as much as more dedicated research.

BRAD STEVENS, NMFS in Kodiak: We're the ones largely responsible for doing stock assessment on king crab in the Bering Sea. I'd like to participate in broadening this discussion. I've saved up some comments through the day.

First, I find myself in the unusual and somewhat uncomfortable position of agreeing with something Scott Matulich said. We haven't maximized benefits to society with our current management scheme.

I'm going to back up and address some things Arni Thomson brought up earlier, and largely disagree with some of them. I've heard the word collapse said numerous times in this meeting, and it's a word I disagree with. To say king crab collapsed presupposes the levels they were at before were normal. When we look back over the history of king crab, we see that's not true. Red king crab stocks have gone through some fairly wide fluctuations, and the levels in the late 1970s

were among the highest levels ever reached, at least in the Bering Sea. I think we're asking the wrong question when we ask, "Why did it collapse?" The question we should be asking is, "Why was it so high in the late 1970s to begin with?"

If we look at the stock now, the current level is much more akin to something we would call normal. It's low, certainly, but it's been low for a longer time than it was high. The current level is statistically not significantly different from the long term average over the past 20 years.

I'd like to throw out a couple of opinions we share in the Kodiak shop, and that is over-fishing was not responsible for the decline, nor was by-catch responsible. By-catch is really a small proportion of the total population.

I'd like to agree with Glen Jamieson when he suggested the quota system, or the harvest guideline system, was not an effective way to manage invertebrate populations, particularly king crab. What I'd like to suggest is possibly some alternative mechanisms for managing this fishery. One would be to eliminate the harvest guidelines and go back to some other simpler management scheme like that used for most other crab populations in the United States. This would perhaps have several benefits.

We spend virtually our entire research budget on doing annual surveys on the Bering Sea to document current conditions for setting current harvest levels, which gives us very little information on why conditions are the way they are. We have no money left over to do any real research. We could probably get the same results by doing these surveys on an every-other-year basis, and in the between years, put the money to work trying to answer the questions. I would put the money into early life history and recruitment studies. We have no recruitment index whatsoever for red king crab because we don't see them until they're seven, eight, nine, who knows how many years old. We don't have any way to relate it to the year they were hatched, or the spawning stock abundance, or anything. Another benefit would be if we understood their life cycle better, we could perhaps predict good years much further in advance than we currently do.

One other way we could maximize the benefits to society—this is a radical idea in terms of the fishing industry—would be to impose user fees. Most other natural resources require user fees. You don't go into the forest and cut trees unless you've paid a fee to do it. You don't graze cattle on public land unless you pay the fee to do it. The fish in the ocean belong to all the citizens of the country, and not just those who happen to be there and catch them. And now, I'll quit and let people throw tomatoes at me.

ARMSTRONG: A point of clarification. The user fee would be redirected into supporting the research you spoke about?

STEVENS: That would be ideal.

ARMSTRONG: There are interesting examples of this in Australia. A phenom-

enal amount of revenue is generated where it is directed through competitive processes into an extraordinary amount of research. I guess because it's a tradition in that country, it is not controversial. It is seen as a very direct benefit of the rich catches they make. I think it's a good suggestion.

STEVENS: We're still asking the same questions about king crab biology we were asking 30 years ago. We haven't made any progress on answering them. What controls size, or age at maturity; what controls mortality rates? We haven't gotten any closer to answering these questions because we've just been doing the same thing over and over again.

KOENEMAN: A point of clarification. I'm not going to advocate one way or the other as far as guideline harvest level. You have to realize in many cases ADF&G goes to the board with the guideline harvest level recommendation. Proposals are altered based on social, biological, and other factors. I'm not an expert on Kodiak's fishery at all, but I know we had very high fish mortalities in some districts. It's fine to say, "Hey, guideline harvest levels didn't work." But you have to understand the constraints upon which it was developed, and then how it actually functioned. I don't think it's fair to say it didn't work. I think you say, "Where did those numbers come from? Were they appropriate?" As biologists I think we lost some of our basic perspectives on science because it wasn't that we were just doing surveys. We just failed to ask the questions, "Well, golly, maybe I should take disease samples? Maybe I should be necropsying 50 animals every time I go out in the boat? We just quit doing our job.

KURIS: I would like to follow up by urging management agencies be redirected to a significant extent from the increasingly routine procedures to a series of experiments that have a high probability of providing useful information. Experiments such as seeding areas with reproductive females, or fishing females, or an attempt to rid areas of parasites by fishing infected animals, or attempting to eliminate the worms that cause egg mortality. All of these are possible. Surveys provide the basis to do this on a large scale, with perhaps strong cooperation from the fishermen themselves. Most particularly there is a need to develop more work on the recruitment aspect. That is, as Brad mentioned, the biggest unknown in the system. There is a cascading system of events from the abundance of breeding females, their total fecundity, egg mortality, the number of first larval stages, the settlement process, and ultimately growth to fishable crabs, that needs study. A general way to approach this is to tackle it by linking the adjacent stages in a careful analysis, and not worry for the moment about the big picture.

JAMIESON: One of the things that struck me in talking to a number of people here at the meeting who are involved in the management of the resource was the general consensus of feeling frustrated. As biologists they recognize they don't know a lot about the biology of the animals, for example, the early recruitment issues Brad pointed out. The feeling I have is I'm not sure how to go about changing it. There seems to be a great deal of inertia in changing anything, any management approach. You've got an industry now tied into it. In the early stages opportunities to do anything are limited. Maybe in tiny, small steps you could initi-

ate something that would either free resources, or allow people to initiate other activities.

To change the subject slightly to tanner crabs, there is a need for research on terminal molt. It's not been a topic of discussion here, and yet in Canada it's generated a lot of discussion. I think there's a consensus of a few in the Gulf of St. Lawrence that terminal molt exists. The Japanese seem to feel there's something there. But what, from a management perspective, does this mean? Does it change our approach in any way? What are the views here? Is it a unique biological oddity? Should we just continue on? The final point I want to make is, do we want this many females breeding? We're just ignoring this. Yet crab fisheries are unique in that females in most cases are not harvested. What is the biological significance of this? We've ignored this in our studies.

JEAN-CLAUDE BRÊTHES, University of Quebec at Rimouski: I am glad to see we are far away from the matter between economists and biologists. I think when we manage a fishery, it's a system, and maybe the optimization of the system may be a subtle accumulation of every step of the system. As a biologist, our job is to assess the resource. As biologists, we have to think in terms of assessment, and keep in perspective that the changes over time are important. We know our data are not precise, and we have a lot of variance around the data because the fishes and the crabs never learned statistics. What is important are the trends.

ROBERT OTTO, NMFS in Kodiak: Let's quit beating around the bush. The fact of the matter is, the way most crab fisheries are managed precludes the possibility of a fishery being any sort of effective control on the population. The trends you see in a population, if anything, are as close to natural as we can possibly make them. We do this by avoiding any impact on the reproduction of the stock, if we possibly can. Frankly, I think king crab, or tanner crab, or Dungeness crab, or blue crab on the East Coast pretty much behave as they please. What we live with are the consequences of that behavior. I find myself agreeing with Scott, that the primary thing biology ought to do in fisheries management is lay out a few constraints. I'm afraid what we've done is laid these constraints out in such a manner as we've tried to preserve what might be called the natural character of a population. This reminds me of the kind of philosophy that was prevalent in game management 40 years ago. It was not successful, I might add. You have a lot of societal variables here that have nothing to do with dollars. They have to do with the ethos of agencies—who trained who. Who believed what happened when, and how. They have to do with paradigms that are not scientific. They have to do with interpersonal interactions, oral traditions which scientists frequently refer to as anecdotal. They might be anecdotal, but to turn around and say they have no influence is foolish. You have to realize also most of the agency people in this room, ADF&G managers in particular, don't formulate policy, they implement it. The forum where these things get put together in the history of shellfisheries has largely been the Alaska Board of Fisheries. Believe me, there is considerable debate of both economic and social issues in formulation of these decisions. I don't go so far as to say it's a scientific analysis, but the consequences certainly are considered.

I disagree with Brad that we don't know anything more about king crab than we did 30 years ago. That's pretty darn naive. We know considerably more about king crab than we did 30 years ago. You'd have to consider the state of knowledge of king crab in 1959. Probably the only person sitting here really able to do that is Koji Takeshita (Seikai Regional Fisheries Research Laboratory, Japan). But those of us who read history would recognize rather quickly we do know a great deal more. What one would also recognize in an objective sense is our increase in knowledge hasn't prevented anything from happening, or from recurring. We speak of the crash of king crabs in 1981. Well, it was spectacular all right in the Bering Sea. Bear in mind, there was an extremely spectacular crash of king crabs in Kodiak right about 1970. There was an extremely spectacular crash in king crabs in Adak in the late 1960s. What I'm saying is in each step along the way our policies have become more restrictive and more conservative without the adequate basis of knowledge to know what the crashes caused to begin with.

Now, I have to agree with Brad Stevens that we never really have been asked, or been able to ask exactly what happened. Now, from the social, economic, and biological perspective, you can talk about optimizing the benefits of a resource to the nation. Well, that's lovely. We have a hard time figuring out how to optimize the benefits of the resource to a single industry. Frankly there is no such thing as a king crab industry at this point. There is hardly anyone who derives his income from king crab who does not derive substantial portions of it from other fisheries, including tanner crabs, salmon, tendering, long lining, etc. Only a minute number of processors make their entire living processing king crabs. So what we deal with is a much more complex network than perhaps what we scientists or economists are accustomed to laying out in terms of our equations, our models, and our optimum functions. I would suggest all of us need to think about, as citizens as well as whatever our professional status may be, is you cannot please everyone all of the time. There probably is no way to manage a king crab resource, or a tanner resource, or any other resource in such a way as to optimize benefits for anything as complex as U.S. society. It behooves us to decide just how we are going to optimize the benefits. Thank you.

PAUL: I thought Brad's point was that scientists, in economics or biology, haven't asked questions, and then used the scientific method to answer them. I thought he was supporting Glen who was suggesting the *Chionoecetes* fishery is a large-scale experiment. We could harvest females, or harvest all of what we consider morphometrically mature males, and see what happens. As scientists we can provide some answers. I thought that was Brad's point about the level of knowledge.

OTTO: I was only kidding, Brad. The point being an increased biological knowledge of a resource is absolutely no guarantee whatsoever that the knowledge is going to be used, or that it is of interest to biologists. Suppose we did know what made successful king crab year classes. Would it really improve management of those resources? The other thing is—and here I'll kid Glen a little bit. I notice they're going to conduct an experimental fishery, and how do they start? Well, we limit the take of females. We'll specify what kind of gear we're going to use. We'll limit the number of licenses. It doesn't sound like a very experimental situation. It

sounds like adopting the status quo for North American crab fisheries and applying it to a brand new fishery.

JAMIESON: We are conducting a limited experimental fishery so we can get some biological data. The fishery itself is not experimental for the reasons you just suggested. That would have to come down the road. We just want to limit it because we don't have a lot of resources to put into it, even to monitor it.

From my experience looking at most invertebrate fisheries, we don't predict what's happening. What we sometimes do is explain to fishermen after the fact what happened, for example, why the resource collapsed in a few cases. But we don't predict what's happening. What we can do in fisheries, particularly king crab, where there's maybe eight years before they recruit to the fishery, is get two or three years lead time that something is happening. That perhaps there is a declined abundance, or an exceptional year class coming through. You aren't going to predict that ten years ahead, or twenty years ahead, with any accuracy. I agree with your earlier comments that the crabs are running it. In most cases, I don't think the fishery really has had much of an impact on future long-term recruitment. So I think the real role we play as scientists or biologists is the very short term benefits as to whether someone might gear up, or whether you should expect a great deal of effort in the fishery, or not. I think that's realistically all we can do. In the short term, scientifically, we'll enhance our own research opportunities by doing other work. We'll publish, and so on. But from a fishery point of view, that's about it.

OTTO: If you want to change policy, go to the policy makers.

DOYLE: I wanted to comment about something Bob brought up on the lethargy that sets in, in terms of changing regulations. From 1963 to 1965 there was some evidence the female red king crab reached sexual maturity at about the shell width of six and one-half inches, which was at the time a legal size for king crab in the Kodiak area. The first crash we saw in king crab was in 1965. It didn't manifest itself in the Kodiak area until 1967 because the boats were moving farther and farther afield at the time. The suggestion was made we should start harvesting what we were referring to as a senile female population. This met with shrieks of terror and shock. It was a violation of the sanctity of motherhood. The charge was led by industry. The industry was paying 10 cents a pound to the fishermen for these crab, and the recovery of meat, particularly in merus section, was much lower in females than it was in males. It was bad public policy to harvest the female even though she may not be contributing to reproduction. What I'm getting at is there were lots of things started really very early that had no relationship to the biological facts of life, but were related purely to the economics. I don't want somebody landing females because my return on females is going to be a lot less than it is on males.

ARMSTRONG: I have a slightly different theme, and that is to encourage state agencies to take advantage of opportunities that arise fortuitously as occasions to learn within the context of management. I think this bitter crab disease is an

excellent example. I know of so few examples in invertebrate fisheries, either molluscan or crustacean, where the epidemiology has been studied in a way that really gives some insight into diseases as a component of mortality in these populations. It seems, particularly in this case, there is a lot to be learned with application to the future, simply to know that perhaps even short of containment, it spreads, it runs its course, and then dies back. But I notice frequently in the state of Washington how the system simply is unable to respond in cases, be it an oil spill right off of an estuary or in gravel beaches, to issues that come up that require rapid response. I would support the gentleman who spoke, and his call for funding for this type of event. It seems like a very good opportunity, and it's not simply esoteric science.

SCHMIDT: One thing I would like to point out to everybody here, is that the Board of Fisheries is an open forum. Anyone here who has an idea, whether they're Alaskan, non-resident, anything, can write a proposal. It goes through the system of review. It gets in front of the Board. You can make your case, and you, too, can make policy changes in terms of how we manage king crab fisheries. A lot of people here have got good ideas, or different types of things they think should be instituted by ADF&G or by NMFS, or the Council process. All of these processes, or at least the Board of Fisheries process, aren't limited to fishermen writing proposals, or agency people writing proposals who work for the ADF&G. All of these can be brought up. You'll find it's a different experience. I have been involved with the Board process for four or five years, and it's an awakening. You see there's a lot of dissenting views that come out. The mechanism to implement a lot of the ideas people have had is there. It goes through a very rigorous hearing, and it is open to everybody.

AADLAND: I would also like to respond to John Doyle. Size on king crab, or any crab, was never set biologically. Size was set by the marketplace, as is very much the case today on the tanner crab. Biologically it's three inches. The marketplace requires a four inch crab. This goes back to the days when they extracted the meat, or smaller leg sizes for the ten pound box. When we first started in the Bering Sea, we fished five and three-quarter inch. I remember skippers hollering up and down, "We gotta get larger crab. They'll command a better price. We'll get a bigger merus section." That's what brought the size up. Biologically I'm sure we could go to a lot smaller crab, and we probably should. The Russians have been fishing a five and three-quarter. They've also been taking a female. They have a fishery over there. Look at our tanner crab. I mean, a few years ago, we used to harvest 50-60 million pounds of tanner crab. Now, what have we got today? Maybe a possibility of 185 million pounds if you took maximum out of Bering Sea today? I don't know. We're biologically on a three inch crab and we're taking four inch crab, and it's the only healthy one on the whole Pacific side.

KURIS: I wanted to make some generalizations about infectious disease in a wide range of invertebrates. I guess it's the pattern these catastrophic epidemic diseases tend to happen in a particular species in a particular geographic region. Perhaps no more than once in a lifetime, so they tend to be identified as very individualistic events, linked perhaps with management practices, or a particular cli-

matic event. And actually when you review the whole situation, they're rather wide spread, and there seems to be a wide range of possible causes. I'd like to list off the almost complete elimination of the dominant starfish in the Sea of Cortez (*Heliaster* sp.), by an unknown bacteria. The crash of sea urchin populations in various parts of the world including Caribbean-wide, of an urchin that has no fishery whatsoever, was caused by amoeba in some locations and bacteria in others. Also there are several protozoan diseases affecting numerous species of oysters around the world. In the last three years, on the Channel Islands in California, the abundant black abalone populations have crashed due to an unknown etiological agent, and the disease is spreading. So, these things happen.

SHIRLEY: Any more specific issues? Well, it is getting late in the day. I would like to thank everyone for their efforts resulting in a very interesting and informative meeting. There are far too many people to thank individually. We'd certainly like to thank Scott for getting us all excited, and getting the afternoon session rolling. And certainly all the participants, the speakers, chairmen, and especially Alaska Sea Grant.

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