KING AND TANNER CRAB RESEARCH IN ALASKA:

ANNUAL REPORT FOR

JULY 1, 1993 THROUGH JUNE 3O, 1994

Submitted Under Cooperative Agreement NA37FL0333 To

National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Alaska Fisheries Science Center
Resource Ecology and Fisheries Management Division
7600 Sand Point Say N.E., Building 4
Bin C15700
Seattle, Washington 98115

By

Gordon H. Kruse
ADF&G Project Coordinator

Regional Information Report No. 5J94-18
Alaska Department of Fish & Game
Commercial Fisheries Management and Development Division
P.O. Box 25526
Juneau, Alaska 99802-5526

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FORWARD

A federal budget initiative for crab research was funded by the United States Congress in 1992 to address pivotal biological and fishery research questions associated with the determination of optimal management strategies for the king *(Paralithodes, Lithodes)*, Tanner *(Chionoecetes bairdi)* and snow crab *(Chionoecetes opilio)* fisheries off Alaska. This initiative, funded within the National Marine Fisheries Service (NMFS), was developed by staffs of the Alaska Department of Fish and Game (ADF&G) and NMFS. It reflects the shared responsibilities for crab research and fishery management by the state and federal governments. It funds cooperative investigations conducted by crab researchers with both agencies and universities. ADF&G was awarded a cooperative agreement for $299,000 for the period July 1, 1993 through June 30, 1994.

PURPOSE OF DOCUMENT

This document reports on work performed under Cooperative Agreement NA37FL033 during July 1, 1993 through June 30, 1994. The following are addressed: (1) a synopsis of long-term research strategy for king, Tanner, and snow crabs; (2) brief description of goals for first-year research that includes five projects; and (3) a project summary for July 1, 1993 to June 30, 1994. Sections of this report were authored by individual project leaders as noted below.

OVERALL LONG-TERM RESEARCH STRATEGY

The Gulf of Alaska (GOA), Aleutian Islands area (AI), and Bering Sea (BS) support large commercial fisheries that harvest king, Tanner and snow crabs. Many crab stocks crashed in the 1980s, and 12 fisheries remain closed due to low abundance. Poor success in maintaining productive fisheries over the long-term prompted a re-evaluation of management strategies (Kruse 1993a). This cooperative agreement funds research studies to support the development of optimal fishery management strategies for crab stocks in Alaska.

Kruse (1993b) proposed a long-term crab research strategy. In sum, it was proposed that wise management of any fishery can only be accomplished by providing answers to four fundamental questions: (1) what are the stocks?, (2) how abundant are they?, (3) what features drive their productivity?, and (4) how should this productivity be best harvested? Although previous crab research provided insights, serious uncertainties exist that prevent a critical and thorough evaluation of alternative management strategies. Investigations into four broad areas will provide answers to these pivotal questions.

1. Stock Structure

Fisheries cannot be managed successfully without understanding the underlying stock structure. Although we have made some good progress (e.g., Seeb et al. 1990a,b) into genetic stock identification of red king crabs *(Paralithodes camtschaticus)*, key questions remain about the structure of BS/AI crab stocks. Some of the most important questions concern the Tanner and snow crab species complex and golden king crabs *(Lithodes aequispinus)*. Answers to these questions will be used to improve the alignment of fishery management units with genetic stocks.

2. Stock Assessment

Good stock assessment programs exist for many stocks in the BS and GOA, and for some stocks in the AI. Yet, for some other stocks, such as BS blue king crabs *(Paralithodes platypus)*, precision is low; for yet others (e.g., Adak red king crabs) assessments are too costly to conduct annually; and for still others (e.g., all golden king crab stocks) no assessments are conducted due to fiscal constraints. Thus, assessment models are needed that integrate multiple years of survey and fishery data into more precise estimates of abundance. Progress was made to develop stock estimation models that incorporate multiple years of survey data for red king crabs (e.g., Kruse and Collie 1991). However, because of our inability to determine crab ages, more advanced length-based population estimation methods are needed that can provide for objective evaluation of diverse and sometimes conflicting information collected from fisheries and surveys. The goal is to better distinguish population changes from survey measurement errors.

3. Stock Productivity

Unlike most groundfish, herring and salmonids, we lack critical biological information about parameters that regulate productivity of many crab stocks and species. For example, good natural mortality estimates are lacking for most stocks. Growth of Tanner and snow crabs (including terminal molt of males) is poorly understood. Serious questions exist about size of maturity of snow crabs. Finally, little is known about most life history traits of golden king crabs. Knowledge of these parameters that drive stock productivity is imperative so that harvest rates can be specified to reflect the underlying biological productivity of each species and stock.

4. Harvest Strategy

Crab harvest strategies may be seriously flawed. Unwittingly, size limits, sex restrictions, and current exploitation rates may adversely affect fishery productivity. In some instances, size limits are based on size of morphological maturity (i.e., males with a large claw) rather than functional maturity (i.e., males that actually participate in reproduction). Thus, high harvest rates may have eliminated breeding males from stocks managed by size-sex-season regulations. Further, gear designs may promote handling mortality that may exacerbate stock declines. Management strategies should be matched with stock- and species-specific biological characteristics such as growth, terminal molt phenomena, mortality, size of maturity, and recruitment dynamics. Statistical and simulation studies are needed to evaluate implications of biological traits on harvest strategies.

OVERALL PLAN FOR FIRST YEAR

For the first year, the following five studies were conducted: (1) relative roles of fishing, predation and environment on long-term dynamics of Alaskan crab stocks; (2) effects of handling mortality on red king crabs; (3) functional maturity of Tanner crabs; (4) alternative crab harvest strategies; and (5) nearshore crab studies. Projects (1), (2) and (3) were conducted by the University of Alaska Fairbanks (UAF) through Reimbursable Services Agreements with ADF&G. Cooperating university faculty are located at the School of Fisheries and Ocean Sciences (SFOC) in Fairbanks, the Institute of Marine Science (IMS) in Seward, and the Juneau Center, School of Fisheries and Ocean Sciences (JC-SFOS). Project descriptions, annual milestones, and plans for fiscal year 1995 (FY 95) follow. Manuscripts resulting from these projects appear as appendices.

PROJECT 1: LONG-TERM DYNAMICS OF ALASKAN CRAB STOCKS

Dr. Albert V. Tyler, UAF, SFOS

Background and Need

Three decades of catch histories and one to two decades of stock assessments reveal a wide range of crab population trends. To date, most stocks have crashed and not improved (e.g., Kodiak red king crabs), some others have crashed and recovered (e.g., Eastern Bering Sea (EBS) Tanner crabs), and still a few others remain rather healthy despite huge fisheries (e.g., Bering Sea snow crabs). A number of possible causes of these dynamics have been proposed, including anthropogenic and natural causes. Despite wide speculation about the relative roles of various factors on crab populations, the supporting evidence for the alternatives has never been objectively evaluated.

Project Description

The purpose of this multi-year project is to investigate the relative effects of fishing and natural changes on the long-term dynamics of crab populations in Alaskan waters. This will be accomplished through five phases of research: (1) data bases will be compiled relevant to variables that would be implicated in possible causes of change, including: crab spawning stock abundance and recruitment, oceanographic variables, and predator abundance; (2) workshops will be conducted with biologists and fishery oceanographers to develop a conceptual model of causal mechanisms by which fishing, predation, and oceanography could act on the long-term dynamics of Alaskan crab populations; (3) analyses will be conducted to characterize intrinsic features of the data sets, such as time intervals between successful crab year classes, periods of increased predator abundance, and years of favorable ocean conditions during crab larval stages; (4) the causal mechanisms will be stated in terms of alternative hypotheses and tested with available data sets by a range of statistical methods; and (5) based on the results the most likely mechanisms will be selected for inclusion in a computer simulation model to fully explore the relative roles of these competing factors on crab populations. The simulation model will be used to identify possible confounding effects of several mechanisms that may interact in sequential and non-linear ways not amenable to standard statistical methods.

Project Progress

Data bases for red king and Tanner crabs belonging to ADF&G were reviewed for population trends and recruitment survey trends that would lend themselves to analysis of changes in recruitment productivity for several stocks. King crab stocks of Bristol Bay, Adak, and Kodiak show promise. The limiting factor in the analyses will be the availability of surveys for juveniles over sufficient time periods. A 15 year time period of recruitment records will be necessary for interpretation of trends with oceanographic variables in view of recent published research on decadal-scale changes in productivity in the ocean. Also, records of juvenile abundance cannot be compared to resulting catches from the adult component of the population without a lag of 5 to 8 years, because these large crabs don't enter the fishery until they are 5 to 8 years of age. Thus, juvenile surveys cannot be interpreted against catch-age analysis in the year of the survey, but only after a suitable period has lapsed. To date only the Bristol Bay red king crab stock has been identified as having data of sufficient length of time period, and also year by year consistency of juvenile survey data. In 1993 a new method of catch age analysis was developed by Dr. Jie Zheng of ADF&G. He showed that a length-based, catch-age analysis is possible for the Bristol Bay king crab stock. He used it to estimate a 14 year relationship between spawning stock size and recruitment.

This data series was used in the Crab Population Dynamics Project to examine decadal changes in productivity for this stock. It was noticed that a sequence of 10 years (1966 through 1975) had very high recruitment levels, with annual recruitment of greater than 47 million age-7 crabs added to the population. Since that time, however, annual recruitment has been less than 21 million age-7 crabs with the exception of an intermediate level of recruitment from the 1977 year class (43 million). Dr. Zheng fit a Ricker stock-recruitment function to the data from 1972 to 1985, a period wherein both spawning stock size and resulting recruitment could be estimated. He noted that the model would not fit the data well because recruitment in the early period (1972 to 1975) was too high. To explain this lack of fit and simultaneously the two periods of productivity, new recruitment hypotheses have been developed based on changes in physical oceanography. It is possible that the earlier high productivity period (1966 to 1975) was related to physical conditions: (1) retention of larvae due to favorable advection; and (2) increased opportunities for high rations due to high primary and secondary productivity. The subsequent low productivity period (1976 to 1985) should show a change in the physical variables that influence these responses. The key years for major physical change appear to be 1976 and 1977.

Time-series data that relate to advection and other physical changes in Bristol Bay and the EBS were examined. Large scale changes in barometric pressure seems to drive aspects of ocean physics in the North Pacific. The Aleutian low barometric pressure field is a major feature. Two data series for the Aleutian Low system show similar decadal scale changes that are in turn related to changes in advection in the Alaska Coastal Current, as well as to currents in the EBS. These changes are also closely linked to changes in sea temperature at depth off Seward, Alaska, in the northern Gulf of Alaska. A major shift in barometric pressure occurred in 1977 and 1978, coincident with lowered year-class strength in both the Bristol Bay and Kodiak red king crab stocks. Next, attention will be focused on the identification of mechanisms responsive to ocean physics that could influence year-class success.

A modeling workshop on recruitment of king crabs was held at the Juneau Center, May 18 and 19, 1994, and attended by 14 people from ADF&G, NMFS, and SFOS. The modeling was organized by Gordon Kruse and Al Tyler. Presentations were made on several subjects related to recruitment, including:

Management concerns for king crab (Kruse)

New length based modeling of trends in year-class formation in Bristol Bay red king crab (Zheng)

Decadal scale changes in king crab recruitment, other biota, and physical factors (Tyler)

Decadal scale changes in ocean physics in the Bering Sea and Alaska Gyre (Niebauer)

King crab larval survival and factors of influence (Shirley)

Changes in red king crab and associated species in Bristol Bay (Otto).

A conceptual structure for modeling was developed by Tyler, followed by a discussion of recruitment hypotheses within the model structure. The result was an intensive review of knowledge on mortality, growth and development of king crabs. In addition, a recent video was shown by Donaldson made while SCUBA diving on a king crab pod in the Kodiak area. Also, Zhou demonstrated mating of crabs in the laboratory. The session is being written up by Tyler and Kruse, with the help of workshop participants. The report will be published in an ADF&G report series.

Plans for FY 95

During the second year, the following milestones will be accomplished:

(1) The proceedings of the king crab workshop will be published in the ADF&G report series.

(2) Additional relevant biological and oceanographic data will be procured from ADF&G, NMFS, and NOAA. Tanner and snow crab *(Chionoecetes opilio)* data will be added to the king crab data already in hand. Data will be compiled into an electronic data base suitable for analyses.

(3) A workshop will be conducted with biologists and oceanographers to identify possible mechanisms responsible for the observed Tanner crab population dynamics.

(4) Analyses will be conducted to gain insights into the nature of the historic variability in both king and Tanner crab populations, their predators, and the environment.

Benefits of Project

Results from this multi-year project will help plan future long-term research into areas of greatest consequence to crab stocks. In particular, we hope to attain a better understanding of the relative roles of fishing, predators, and environmental change on the dynamics of crab stocks. A cognizance of the magnitude of the effects of fishing and reduced spawning biomass on stock productivity will help us later evaluate the merits of alternative crab management strategies within the context of natural variability. Likewise, understanding the strength of relationships among populations of crabs and their predators would help reveal the merits of potential future multi-species or ecosystem management approaches.

PROJECT 2: HANDLING MORTALITY OF RED KING CRABS

Dr. Thomas C. Shirley, UAF, JC-SFOS

Background and Need

Pots capture male and female crabs of a range of sizes and carapace conditions. Yet, all Alaskan crab fisheries are regulated by size and sex restrictions. As a result, females and small males are discarded. Several lethal and sublethal effects may result from catching, handling and discarding processes. An understanding of these effects will help to estimate total fishing mortality and to determine appropriate remedial action to reduce handling mortality of the discards.

Handling mortality occurs during fisheries when crabs are killed due to crushing, desiccation, exposure to extreme temperatures, and other factors. Handling mortality has been well documented in crustaceans (Brown and Caputi 1983, 1985; Lyons and Kennedy 1981). Death may be immediate or delayed (Tegelberg 1972; Carls and O'Clair 1990; Stevens 1990). For example, when exposed to cold air, half of the Tanner crab deaths occurred within 24 h and nearly all occurred within 8 days, whereas most red king crab deaths occurred during molting 47-120 days later (Carls and O'Clair 1990). Stress from handling may reduce vigor and predator defenses. King and Tanner crabs that survived exposure to cold air showed reduced vigor (Carls and O'Clair 1990). Lobsters such as *Panulirus marginatus* (Gooding 1985), *P. argus* (Vermeer 1987), and *P. cygnus* (Brown and Caputi 1983) showed reduced tail flipping and drifted limply to the bottom with prolonged air exposure. Experiments revealed that octopi and most fishes only attacked lobsters that did not assume defensive postures (Brown and Caputi 1983).

Sublethal effects of handling include injuries. Appendage loss increases during the fishing season (Shirley and Shirley 1988), and may be a function of air temperature during severe weather (Carls and O'Clair 1990). Although some crabs survive amputation and regenerate lost limbs (e.g., Edwards 1972; MacKay 1942), severely injured crabs may experience reduced growth and initial molt inhibition, followed by shortened intermolt period (Bennett 1973). Likewise, exposure to extreme temperatures inhibits molting of Dungeness crabs, *Cancer magister* (Kondzela and Shirley 1993), depresses feeding rates in Tanner crabs, and reduces growth rates of red king crabs (Carls and O'Clair 1990).

Project Description

This study addresses the effects of sorting and handling by commercial red king crab fishing practices on sublethal stress and survival of sublegal and female red king crabs. Specifically, this study addresses:

1. The effects of handling by commercial red king crab fishing practices on limb damage and loss, and subsequent effects on survival;

2. Whether deck and water impacts result in decreased crab survival;

3. If repeated capture and handling results in additive damage;

4. The causative mechanisms or agents which result in mortality (specifically, can bacterial or protozoan infections be implicated); and

5. Whether damage can be ameliorated by alteration of handling techniques.

Project Progress

Sublegal male and female red king crabs were collected in Barlow Cove and Auke Bay with commercial and sport crab pots, and handled gently and in a manner to reduce thermal and salinity shock during transport to the laboratory. Within the laboratory, crabs were kept in tanks with flowing seawater from a -30 m intake. Crabs were fed a mixed diet of fish, squid and mussels *ad libitum*. All crabs were acclimated to laboratory conditions for at least two weeks prior to experimentation. All laboratory experiments were completed and a manuscript (Appendix 1) describes the results. The authorship and title of this manuscript is as follows:

Zhou, S., and T.C. Shirley. MS. Effects of handling on feeding, activity and survival of red king crabs. Manuscript to be submitted to the *Journal of Shellfish Research*.

Plans for FY 95

This project approaches the handling problem in two ways. The first approach, taken during FY 94, investigated the lethal and sublethal effects of handling by simulating the catching and discard processes in the laboratory. The second approach, proposed for FY 95, examines ways to minimize handling of king crabs by the commercial fishery. Specifically, the FY 95 research will examine the behavior of red king crabs with respect to commercial crab pots, with the intent of formulating gear and/or deployment techniques which will decrease the catch of females and sublegal-sized males in the fishery. The reactions of king crabs to commercial pots will be recorded and analyzed by means of video cameras and computer-assisted quantitative techniques. An improved fishing method, which considers optimal soak time, bait composition, and modified crab pots, may limit the catch of female and sublegal male red king crabs. Such a method will be proposed and tested in a laboratory situation and *in situ*. These efforts may increase the catch efficiency of legal males with concomitant decreased catches of females and sublegal male king crabs.

Also, in FY 95 field observations will be made from a variety of sizes of commercial fishing boats to quantify the average impact distance for crabs from the pots onto the vessel deck and the average distance that crabs fall before impacting the water surface when they are returned to the sea. Measurements of crab vessel deck heights above the water line (rail height to deck, rail to water line, false deck to water line, overflow line to water line) are available for commercial crab vessels; measurements were made while the vessels were assembled for crab holding tank inspections (L. Watson, ADF&G, personal communication). We hope to obtain these measurements from vessels participating in the red king crab fishery in the BS, GOA, and Southeast Alaska. Because many crab vessels fished in multiple fisheries (e.g., Tanner, snow, and Dungeness crab fisheries), the data could be collected at the time of holding tank inspections prior to the opening of other fisheries by cross-referencing fishery registration information.

Benefits of Project

This project will help us understand the potential magnitude of handling mortality on king crab stocks. Because such a large fraction of the crab stocks are handled and returned to the sea, this project will contribute to critical decisions about new crab management strategies. For example, if handling mortalities are low, then gear modifications may be all that is required to minimize adverse effects on crab populations. On the other hand, if handling mortalities are very high, this would enable us reevaluate the effects of fishing on historic stock trends and it could lead us to substantially different management strategies (e.g., fixed harvest rate, both sexes, no size limit) to maintain healthy stocks and sustainable fisheries over the long term. Results from the study of crab behavior in relation to fishing gear may lead to alternative pot configurations that provide for greater escape and therefore lower handling mortality of female and sublegal male crabs.

PROJECT 3: REPRODUCTION OF TANNER CRABS

Dr. A.J. Paul, UAF, IMS

Background and Need

Effects of crab shell condition on reproductive success have not been studied. Crabs that molted within the year have clean carapaces and are called "new shells," whereas those that molted more than a year prior have worn shells often with barnacle growth and are called "old shells." Limited submersible observations suggest that only old shell Tanner crabs participate in breeding (W. Donaldson, ADF&G, Kodiak, personal communication). It is conceivable that male crabs tend to make growth and reproductive tradeoffs. Those that grow tend not to reproduce, whereas those that mate tend not to grow. Studies are required to test this hypothesis. A more detailed background for this study was provided by Kruse (1993b).

Project Description

This study addresses important, management-related questions about the reproductive biology of Tanner crabs. An ongoing study by Dr. A.J. Paul funded by Alaska Sea Grant is addressing the concept of terminal molt and its relationship to maturity state. The additional work, reported here, complements this ongoing study by also addressing questions concerning effects of shell condition on reproductive success. Specifically, this new research addresses the following hypotheses:

H_{01}: Similar-sized new shell and old shell Tanner crab males are equally likely to mate with multiparous females; and

H_{02}: Similar-sized new shell and old shell Tanner crab males are capable of mating with an equal number of females.

Project Progress

Experiments have been completed and a manuscript of the results has been submitted to the *Journal of Crustacean Biology.* This manuscript, attached as Appendix 2, provides details about this project. In summary, when pairs of similar sized old shell and new shell male *Chionoecetes bairdi* were presented with multiparous mates the old shell males dominated 70% of the copulations. In 39% of all copulations possession of the female was contested. Old shell males won 69% of those contested matings. Recently molted males did not copulate with either primiparous or multiparous females. The authorship and title of this manuscript is as follows:

Paul, A.J., J.M. Paul, and W.E. Donaldson. MS. Shell condition and breeding success in Tanner crabs. Submitted to the *Journal of Crustacean Biology.*

Plans for FY 95

There are no plans for FY 95, as this project has been completed.

Benefits of Project

This project helps define the requisite attributes of functionally mature male Tanner crabs. The finding that old shell males dominate matings with females has significant implications to studies of population dynamics and fishery management. With regards to population dynamics, historical crab data should be analyzed to determine whether population egg production and recruitment are related to the abundance of old shell spawning males. With regards to fishery management, the effects of size limits and harvest rates on proportions of old shell males in the spawning stock should be examined.

PROJECT 4: CRAB MANAGEMENT STRATEGIES

Dr. Jie Zheng, ADF&G

Background

Biological production parameters are needed to determine optimal management strategies and to develop fishery yield models for the king and Tanner crab fisheries off the coast of Alaska. Although analyzed for inseason management decisions, comprehensive analyses have not been conducted on relative abundance, shell condition, sex ratios, and commercial catch data. For most stocks, the common biological and reference points, such as $F_{0.1}$, yield per recruit, optimum yield, and stock-recruit relationships have not been computed. Utility of fishery thresholds and alternative harvest rates have not been thoroughly evaluated either. Given historic vulnerability of crab stocks to collapse, uncertainties in crab stock productivity jeopardize the long-term viability of fisheries.

Project Description

ADF&G will conduct quantitative analyses of existing abundance, biological, and fisheries data and will conduct simulation modelling to develop optimal harvest policies for king and Tanner crab fisheries. Data analyses will focus on information germane to harvest policy: optimal thresholds, biological reference points, natural and handling mortality, size limits, stock and recruitment relationships, effects of fishing on growth and reproductive success, sustainable yields, and molting seasonality (fishing seasons).

Project Progress

During the past year, this crab research project focused on a literature review, data gathering, a feasibility study, construction of length-based population models and parameter estimations, and simulation studies to evaluate the current crab harvest strategies and optimal strategies. Literature on biology, population dynamics, stock assessment, and fisheries management for red king and Tanner crabs have been reviewed, and some important results from the past studies have been summarized. A literature review for blue king crabs is being conducted and expected to be finished by the end of 1994.

The historical NMFS trawl survey data for Bristol Bay red king crabs, EBS Tanner crabs and blue king crabs have been obtained from NMFS. The simple "area-swept" method was used to estimate the crab abundances for these crab stocks, and the estimated abundances were compared to that estimated by NMFS each year. The catch data for Bristol Bay red king crabs, EBS Tanner crabs, Kodiak red king crabs, and Kodiak Tanner crabs were obtained from the Alaska Department of Fish and Game and literature. The growth and mortality data were calculated from literature.

Length-based population models have been constructed for Bristol Bay red king crabs and EBS Tanner crabs. Population parameters have been estimated for Bristol Bay red king crabs, and preliminary parameter estimation has been conducted for EBS Tanner crabs. Preliminary catch-at-length analyses were conducted on Bristol Bay red king crabs to examine feasibility of fitting length-based population models without survey information. A feasibility study of length-based population modelling was also done for Norton Sound red king crabs. Simulations were conducted to evaluate the current threshold levels and harvest rates for Bristol Bay red king crabs.

Two manuscripts have been prepared. One describes the length-based population model and stock-recruitment relationships for Bristol Bay red king crabs (Appendix 3). This manuscript has been submitted to the *Canadian Journal of Fisheries and Aquatic Sciences*. The second manuscript describes analyses of optimal thresholds and harvest rates for Bristol Bay red king crabs. This latter manuscript is currently undergoing internal agency review and is not yet ready for public distribution. Authorship and titles of these two manuscripts are as follows:

Zheng, J., P. Murphy and G. H. Kruse. MS. A length-based population model for red king crab, *Paralithodes camtschaticus*, in Bristol Bay, Alaska. Submitted to the *Canadian Journal of Fisheries and Aquatic Sciences*.

Zheng, J., P. Murphy and G. H. Kruse. MS. Analysis of harvest strategies for the red king crab, *Paralithodes camtschaticus*, fishery in Bristol Bay, Alaska. Manuscript in review.

Plans for FY 95

Second year work will continue progress made in the first year. For Bristol Bay red king crabs, work in FY 95 will focus on:

(1) A paper on the length-based population estimation model, written during the first year, will be published in a fisheries journal. Model results will be used to set guideline harvest levels in the Bristol Bay red king crab fishery.

(2) After undergoing review, final revisions will be made to a manuscript that describes a modeling study of management strategies based on threshold and exploitation rate. The manuscript will be submitted to a fisheries journal.

(3) Stock rebuilding strategies will be analyzed.

(4) Additional catch-at-length analyses will be conducted on Bristol Bay red king crabs to examine feasibility of fitting length-based population models to crab stocks that lack survey information. Because good survey data exist for Bristol Bay red king crabs, this stock provides an excellent case study to validate the new approach.

Once these objectives for Bristol Bay red king crabs are completed, new work will address:

(5) Completion of a length-based population model for Bering Sea Tanner crabs and submission of a manuscript for review.

(6) Initiation of work on a population model for another red king crab stock such as Adak Island or Kodiak Island. Both of these stocks once supported large commercial fisheries.

Benefits of Project

This project relates to the overall long-term research strategy in at least two ways. First, for all major crab stocks we intend to develop population estimation models -- models that provide estimates of crab abundance that are relatively insensitive to survey measurement errors in any single year. Second, because these models embody critical biological parameters specific to a species and stock, they provide a framework within which to evaluate optimal harvest strategies.

PROJECT 5: NEARSHORE CRAB STUDIES

S. Forrest Blau, ADF&G

Background

Although computer simulation modelling and laboratory studies are effective methods for answering an array of management-related questions, there remains a vital role for field studies. For example, field studies collect the data on growth, mortality, and recruitment used in fishery production models. Also, because of potential for laboratory effects, field studies are important to ground-truth laboratory findings on, for example, size of functional maturity. Unfortunately, high costs of vessel charters are often prohibitive to conducting field studies in Alaska.

Project Description

This nearshore crab research project addresses three primary objectives, namely to: (1) gather new information on mating pairs of Tanner crabs in the shallow subtidal areas to complement laboratory studies by Dr. Paul (project 3) and ongoing submersible studies in depths of 500 feet in Chiniak Bay, Alaska (Stevens et al. 1993); (2) study settling dates and density dependent mortality among post-larval red king crabs that recruit to artificial collectors; and (3) deploy, maintain, and retrieve underwater thermographs for use in studies of crab behavior, abundance, and movements.

Project Progress

The major task accomplished this year was the planning and manufacturing of a 26' aluminum skiff and the associated equipment purchases. The total cost of the skiff was $53,039 of which federal funds paid 78% or $41,439. ADF&G covered the remaining costs. Of the total cost, major expenditures were $20,000 for the skiff, $12,300 for salaries, $8,061 for a 150 hp outboard engine, $3,398 for a trailer and $1,780 for radar. A detailed list of expenditures is available on request.

The skiff features a small cabin just aft of the bow and a 4' x 4' hold, level with the deck, for storing/studying live crab in seawater, or for storing gear. Safety and operational features include: radar, video sounder, 150 hp outboard with hydraulic steering, global positioning system receiver, 11 hp engine and a pump to run a crab block for pulling pots. The skiff was launched in late June.

Plans for FY 95

Whereas federal funds provided for the purchase of the skiff, state funds will be used to cover all future operational costs of this project. In FY 95 the skiff will be used to conduct several research projects in Chiniak Bay on Kodiak Island. First, it will be used to retrieve 55 strings of artificial collectors (5 collectors per string) that are used to provide an index of year class strength of 0-age red king crabs. Young-of-year red king crabs collected from these collectors are assessed in an ongoing attempt to relate the number of settling crabs to subsequent recruitment to the fishery five or more years later. Also, attempts will be made to relate numbers of age-0 crabs to environmental and parent population parameters. In addition, 12 strings of the same gear were set in shallower waters to investigate the catch rates of the 0-age crabs compared to those found at index stations. This information will help to better determine the depth distribution of settling young-of-the-year crabs. The skiff will also provide a diving platform to set and retrieve underwater thermographs, and to collect mating pairs of Tanner crabs in shallow waters. An agency report on the historical thermograph data will be published in FY 95.

Benefits of Project

This project represents a low cost alternative to expensive at-sea crab studies by making use of an existing ADF&G program and the proximity of king and Tanner crab populations to the Kodiak regional office.

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APPENDIX 1

Effects of Handling on Feeding, Activity and Survival of Red King Crabs

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Short title: **Handling effects on red king crab**

Key words: king crab, handling effects, mortality, feeding, handling

INTRODUCTION

Both male and female red king crabs, Paralithodes camtschaticus (Tilesius, 1815), are caught in pots in the commercial fishery in Alaska, but only legal-sized males may be retained. During the harvest and sorting operations, a large number of female and sublegal-sized males are exposed to air (and the resulting desiccation and large temperature gradients), are crushed by the catch or gear, damage each other by pinching, and receive impacts when dropped on deck and when returned to the sea.

Handling of king crabs during sorting and deck operations often results in limb loss and autotomy. Juveniles are particularly vulnerable to limb loss, which decreases their growth rate (Edwards, 1972; Kurata, 1963; Niva and Kurata, 1964). Little quantification exists for limb loss and mortality of red king crabs resulting from pot capture and commercial crabbing activities. However, the immediate mortality (47%) of red king crabs captured by bottom trawls was high, and increased (52%) after two days (Stevens, 1990). Similarly, trawl-caught Norway lobster (Nephrops norvegicus) had high (40%) short-term mortality (Chapman, 1981).

Other potentially serious consequences of sorting and handling are impact wounds, contusions, limb loss, and secondary infections of these wounds. The amount of physical trauma received from impact with the vessel deck, and that crabs later endure when dropped from commercial vessels at 2-3 meters above the water surface, is unknown. Likewise, the number of times that immature and female king crabs are recaptured by the commercial fishery is poorly known.

Ship design, pot structure and handling protocol vary greatly among commercial crabbers in Alaska. Crabs captured in cone-shaped pots may receive a greater impact if crabs are released onto the deck from a drawstring on the underside of the pot. Crabs caught in standard rectangular pots are usually dumped out of a top door onto the deck or into sorting bins, with the pot being tipped over by a hydraulic arm (pot launcher). Variation in handling stress also occurs on the same vessel. Full pots routinely have their catch dropped onto the deck or into sorting containers. A pot with only a few crabs may instead have its crabs individually retrieved from the pot and returned to the sea. Crabs caught in pots containing many crabs may be exposed to more crushing weight and longer sorting times. The height that sublegal and female crabs are dropped from the ship's deck when returned to the sea varies with ship design, how laden the ship is, and sea conditions. Most commercial vessels have a drop distance of at least 2 m.

Prior investigations of handling effects on Dungeness crabs in southeastern Alaska demonstrated that increased handling resulted in higher mortality, resulting in 100% mortality after being handled four times simulating techniques used in the commercial fishery (unpublished data, T. Shirley). The mortalities were not acute, but rather occurred over the four month period following the handling. The average number of missing limbs and percentage of the population with missing limbs increased as the Dungeness crab season progressed (Shirley and Shirley, 1987). Because red king crabs are larger and heavier than Dungeness crabs, and would be expected to have fewer adaptations to aerial exposure and impacts because of their subtidal life style, the effects of handling may be more deleterious. Recapture rates of sublegal and female king crabs are unknown, but should vary with the density of pots, the length of the season, and the number of times that pots are redeployed.

This study examined the effects of sorting and handling by the commercial fishery on sublethal stress and survival of sublegal and female red king crabs. We examined: 1) the effects of handling on limb damage and loss, and subsequent effects on survival; 2) whether deck and water impacts result in decreased crab survival; 3) if repeated capture and handling results in additive damage; 4) the causative mechanisms or agents which result in mortality (specifically, whether bacterial or protozoan infections can be implicated); and, 5) whether damage can be ameliorated by alteration of handling techniques.

METHODS

Sublegal male and female red king crabs were collected near the laboratory in Auke Bay and Barlow Cove, Alaska, with commercial and sport pots, handled gently, and maintained in sea water during transport to the laboratory. Within the laboratory, crabs were kept in tanks with flowing seawater from a -30 m intake and fed a mixed diet of fish, squid and mussels *ad libitum* All crabs were acclimated to laboratory conditions for at least two weeks prior to experimentation.

Each crab was individually numbered with a numbered cinch tag attached to the basis of a walking leg. Sex, wet weight, carapace length and morphological condition was recorded for each crab. Twenty-seven crabs were used in each experiment: 9 ovigerous females, 9 non-ovigerous females and 9 sublegal males. Crab sizes were selected so as to have similar-sized crabs within each treatment, however the placement of crabs into each treatment was determined by random selection. A total of 135 individual crabs of the appropriate sex and size were used for the experiments.

Deck impacts were studied by treating crabs in a manner similar to that experienced onboard commercial vessels. Crabs were placed in a simulated commercial pot (approximately one-half size but of similar shape) and the pot dropped onto the deck and subsequently tilted at a 45° angle prior to crab removal, in a manner similar to that used in the fishery by pot launchers/retrievers.

Crabs were then dropped from 3 m heights into seawater. The crabs were subdivided into three groups, with one group being dropped only once, another group being dropped a second time two days later, and a third group being dropped three times at two day intervals. To standardize impact, crabs dropped once were dropped onto their dorsal surface. Crabs dropped twice were dropped onto their dorsal surface and on their second drop onto their ventral surface. Crabs dropped three times were dropped initially onto their dorsal surface, then their ventral surface, and the final time onto their dorsal surface.

One group of crabs receiving a modified handling treatment was dropped from the pot into a container filled with seawater rather than onto the deck. The crabs were returned to the water by means of a slide tilted at a 45 degree angle rather than by dropping from 3 m into seawater.

A control group received no handling or aerial exposure after the initiation of experiments, other than that used for determining weights and measurements. Crabs from all treatments were returned to laboratory holding tanks for examination. Crabs used for feeding measurements and crabs undergoing molting were kept in individual compartments.

Mortality was recorded daily. Limb loss, wounds and other treatment effects were recorded for each crab immediately after experimental treatment and weekly thereafter until termination of the experiment.

One day after treatment, the time required to turn over (righting time) was recorded for each crab. Righting time has been found to a sensitive indicator of general well-being of many marine invertebrates, as an integrated coordination of muscles and sensory perception is required for rapid righting (Shirley and Stickle, 1982). Righting time was measured weekly until the experiments were terminated.

Feeding rates were measured by placing known weights of food into each crab container and weighing all food remaining in the chamber 24 hours later. Feeding rates were measured weekly for a subset of 9 crabs in each treatment (3 of each of the subgroups: sublegal males, non-ovigerous females and ovigerous females) until the experiments were terminated.

At the termination of the experiments (four months after experimental treatments), wet weights and anatomical condition were recorded for all crabs.

Blood samples were collected from crabs used in feeding determinations (9 crabs in each treatment) at the end of the experiment to examine the incidence and intensity of bacterial infection. Hemolymph samples were obtained by puncture of the periarthrodial membrane at the base of the third walking leg with a sterile 1-ml syringe fitted with a 20G1 1/2 needle. A protocol developed by the Alaska Department of Fish and Game was used (Dr. T. Meyers, personal communication). Blood smears were made by expressing a drop or two of hemolymph onto a glass slide and pushing a second slide to drag the blood by capillary action and produce a uniform thickness smear. Slides were air-dried, stained with Diff-Quik, and examined with phase contrast optics. Bacterial rods were counted in 50 randomly selected fields on each slide.

A Chi-square test for differences in probabilities (a five populations and four categories contingency table) was used to test for differences in mortality and injury among treatments (Conover, 1980). A similar Chi-square analysis was used to test for differences in incidence and intensity of bacterial infection among treatments. Two-way ANOVA with equal cell numbers was used to test for differences in feeding rates (Kleinbaum et al., 1988). Before testing, the data were standardized to grams of food consumed per 100 grams of crab (wet weight) for 24 hours. Similarly, two-way ANOVA was used to test crab righting time among treatments and groups.

RESULTS

Mortality was uniformly low in all experimental groups. A total of 18 crabs of the 135 crabs used in the experiment died over the four month study; six of the mortalities were due to experimental error (Table 1). There were only two mortalities of unknown causes in each of the handling treatments and the control group, except for the treatment group which was handled twice, which had four mortalities. No were no significant differences in mortality among the treatments (Table 1).

Damage induced by handling increased with an increase in handling; a significant difference in combined damage existed among the treatments (Table 2). A significant difference in damage among the treatments did not occur for all body parts, but only for the rostrum and spines. Carapace spines were damaged more commonly than the legs, rostrum or carapace; 70% of the crabs handled three times had damaged spines, while only 11% of the crabs handled once had damaged spines. Crabs in the modified handling treatment (without deck impact and returned to water by means of a slide) had the least damage.

Feeding rates did not differ significantly among the treatments or by sex group, after feeding rates were standardized to grams of food consumed per 100 grams of crab wet weight per 24 hours (Figure 1). Average feeding rates of the different treatments varied between 4.80 and 5.07 $g \cdot 100\ g\ crab \cdot d^{-1}$. No significant differences in average feeding rates occurred among the treatments over time (Figure 2).

Righting time did not differ significantly among the treatments or by sex groups (Figure 3). The average righting time increased slightly for all treatments over three months (Figure 4), but the slight increase (approximately one second) probably has little biological significance.

Bacterial counts were low and unrelated to treatment (Table 3). Only one out of the nine crabs sampled contained bacteria in each of the experimental treatments.

DISCUSSION

In Alaska crab pots are the standard commercial fishing gear for red king crab. In comparison to other fishing gear (e.g., trawls) pots have many advantages: they are inexpensive, fish unattended, have minimal bycatch, and are suitable for most bottom types and depth ranges. In addition, their requirements for engine power and deck equipment are modest. However, a large number of female and sublegal-sized male (<178 mm or 7 inches in carapace width, or <165 mm or 6.5 in CL, depending on the management area, Otto and Dyson 1985; Otto 1985; Blau 1988; Byersdorfer and Watson 1992) are incidentally caught in this male-only fishery.

A field survey using king crab pots in Kodiak, Alaska reported that 75% of king crabs caught were female, and, of the males captured, 26% were sublegal size (Blau 1988). This means that 81.5% of the king crab captured had to be returned to the sea. The sex ratio in the catch in Bristol Bay varied from year to year. The male:female ratio in a 1991 survey was 47:53. In the 1992 survey, although the male:female ratio was high (70:30), and 62% of males caught were legal-sized (>165 mm CL) (Byersdorfer and Watson 1992), as high as 57% of the red king crabs caught had to be returned to the sea.

Before they are released, these discarded female and sublegal-sized male red king crabs are inevitably exposed to desiccation when in air and large temperature gradients between sea water and air, crush each other, and sustain damage when dropped on the deck and into the sea from 2-3 meters above the water surface during sorting and release operations. These procedures have been suspected of increasing mortality and perhaps playing a role in depleting the red king crab populations.

Red king crabs, especially juveniles, are vulnerable to limb loss which decreases the growth rate (Edwards 1972, Kurata 1963, Niva and Kurata 1964). The 1991 red king crab survey conducted by the National Marine Fisheries Service (NMFS) in Bristol Bay with trawls (Byersdorfer and Watson 1992) reported that 2% of crabs were injured and 0.1% died immediately after handling. There was no report on the incidence of handling-induced injury or mortality during commercial fishing with pots. The immediate mortality (47.3%) of king crabs captured by commercial sole trawls was high (Stevens 1990). Moreover, the delayed mortality after two days was higher (52.1%). Exposure to cold air reduced vigor, feeding rates and growth, and also caused limb autotomy and mortality in ovigerous red king crabs and tanner crab (Carls and O'Clair 1990). Severely exposed king crabs often died during ecdysis.

Crabs and lobsters returned to the sea by fishermen had increased injury, reduced growth, and increased mortality (Brown and Caputi 1985, Simonson and Hochberg 1986). When the time that rock lobster were exposed to sunlight and air increased, the percentage of inactive animals and loss to predators increased, and the descent rate through the water column and the recapture rate decreased (Brown and Caputi, 1983). Sixty to seventy percent of discarded spanner crabs (<u>Ranina ranina</u>) with one or more dactyls broken off by handling during commercial fishing died within 50 days (Kennelly et al. 1990). Instantaneous crab mortality estimated from measuring declawing wounds of crabs harvested by four commercial fishermen ranged from 23% to 51% (Davis et al. 1978).

After their first year of life, king crabs are exclusively subtidal inhabitants; consequently, they would be expected to have few adaptations to the greater impacts, abrasion and crushing associated with aerial exposure. The greater size and heavier weight of red king crabs should tend to exacerbate the potential effects of handling incurred during sorting activities.

In our study ovigerous and non-ovigerous females and sublegal-sized male red king crabs displayed few acute or chronic responses to laboratory handling treatments designed to mimic handling occurring during sorting operations in the commercial fishery. No handling effects were evident in acute mortality or mortality four months after experimental treatments. Similarly, no significant differences were found in feeding rates, righting times or the incidence and intensity of bacterial infections, between unhandled crabs and crabs handled once, twice and three times.

We hesitate to infer from the results of our experiments that handling during commercial crabbing activities causes little or no mortality to sublegal-sized and female red king crabs. The handling that crabs received in our experiments was probably conservative in comparison to that received during commercial crabbing activities. In our experiments, the crabs were not on the deck of a pitching and rolling crab vessel during winter weather conditions. Our experimental crabs received minimal aerial exposure, with the total time of exposure being only a few minutes. Little crushing was involved in our study, as only 27 sublegal-sized crabs were contained in each crab pot during dumping and sorting. No larger and heavier, legal-sized males were included in our treatments, which might have contributed to crushing effects; commercial crab pots often contain large numbers of heavier crabs.

The effects of commercial crabbing operations on mortality of non-targeted segments of crab populations have been examined for only a few crab species. Those species that have been examined generally had alarmingly high levels of mortality associated with handling received during commercial sorting activities. Additional study, particularly field studies involving the quantification of damage and mortality of red king crabs received during commercial crabbing operations, are warranted.

ACKNOWLEDGEMENTS

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Table 1. Mortality of red king crabs in handling experiment of four months duration (September 15 to January 15). There were only two mortalities of unknown cause in each of the treatment 1, 3, 4, and 5, and four unknown mortalities in treatment 2; non-molting edema was associated with all unknown mortalities.

Date	1 handling	2 handling	3 handling	Modified	Control
9-15	1				
9-28				1[a]	
10-17				1[b]	1[b]
10-17					1
10-23	1[c]				
10-27			1	1	
10-30					1
12-02	1				
12-15				1	
12-25		1			
12-28		1			
12-31			1		
1-04	1[d]				
1-05		1			
1-07		1			
1-10		1[e]			
Total	2(+2)	4(+1)	2	2(+2)	2(+1)

a. Crab fell out of tank
b. Water in the tank dried out
c. Crab injured by falling tank divider
d. Two legs of the crab severed, perhaps due to cannibalism
e. Water flow accidently stopped

Chi-square test:
Statistics T=1.46, degree of freedom df=4, α=0.05, $X_{0.95}$=9.488.
Accept H_o. There is no significant mortality difference among the five treatments.

Table 2. Number of crabs with damage induced from handling. The damage (broken parts) was examined immediately after handling.

Treatment	Any part	Leg	Rostrum	Carapace	Spines
1 handling	7	1	2	1	3
2 handling	12	0	3	0	11
3 handling	24	3	5	0	19
Modified	1				1
Control	0				
Total	44	4	10	1	34

Chi-square test of the effect of treatments excluding the control:

	df=3, α=0.05,	$X_{0.95}$=7.815
Any part damage:	T=43.88,	Significant difference
Leg damage :	T=6.23,	No significant difference
Rostrum damage :	T=9.53,	Significant difference
Carapace damage:	T=3.03,	No significant difference
Spine damage :	T=34.85,	Significant difference

Table 3. Bacteria counts at the end of red king crab handling experiment. Nine crabs were sampled from each treatment. Bacteria were counted within two random selected transection cross the slide, which is about 160 fields of observation. Only one crab was found with bacteria for each treatment sample; only one bacteria was observed in each of the three crabs, and two and five bacteria in the other two crabs.

Treatment	1 handling	2 handling	3 handling	Modified	Control
# of crab with bacteria	1	1	1	1	1
# of bacteria in this crab	1	1	1	5	2

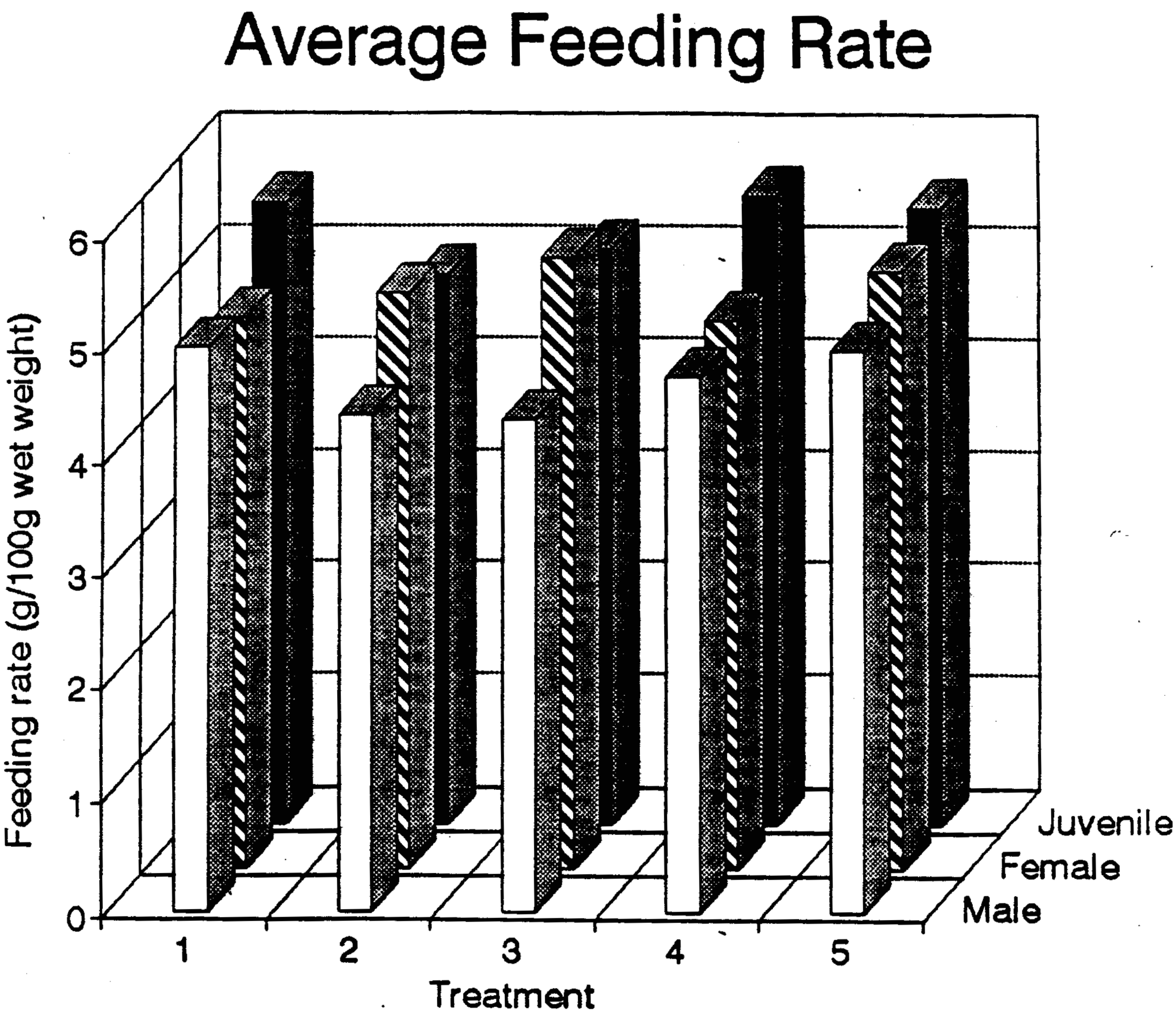
Legends for the figures

Figure 1. Average feeding rate of red king crabs in handling experiment. There was no significant difference of feeding rate among treatments and sex groups (ANOVA, $P>0.05$).

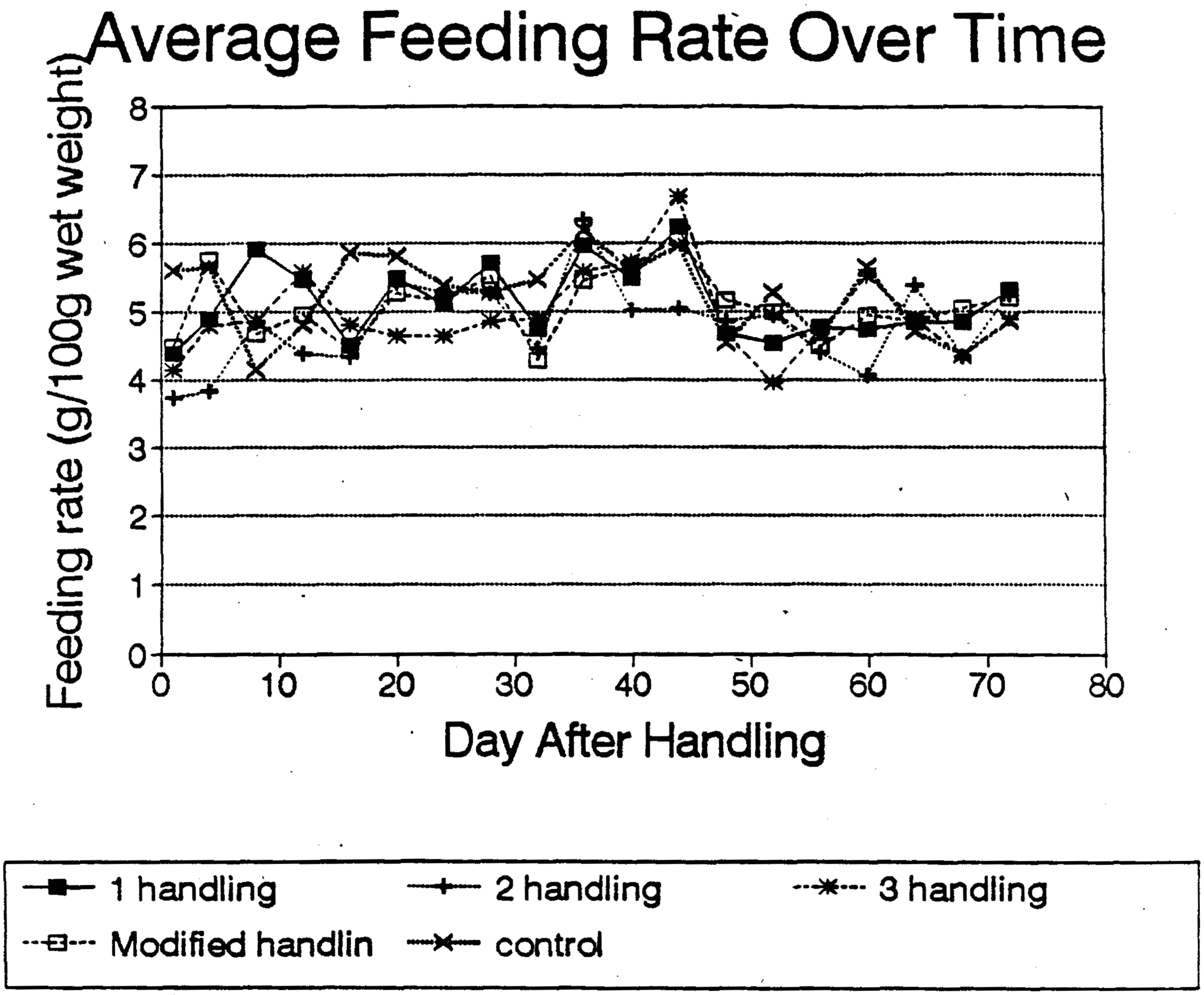
Figure 2. Feeding rate of red king crabs over time. The data were the average of nine crabs in each treatment, including sublegal males, ovigerous females, and juvenile females. No significant change of feeding rate over time was detected (ANOVA, $P>0.05$).

Figure 3. Average righting time of red king crabs. There was no significant difference among treatments and sex groups (ANOVA, $P>0.05$)

Figure 4. Righting time of red king crabs over time. The data were the average of twelve crabs for each treatment, including sublegal males, ovigerous females, and juvenile females.

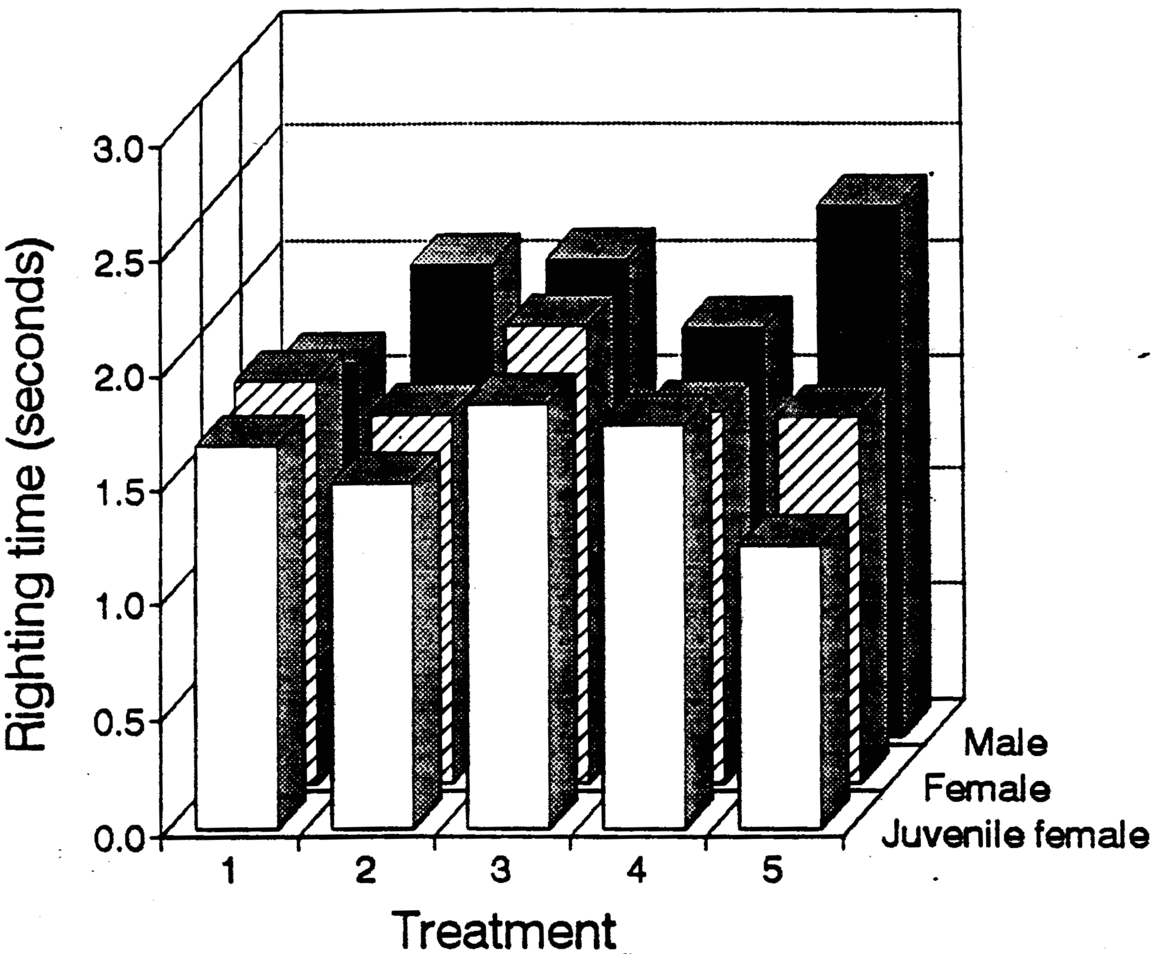


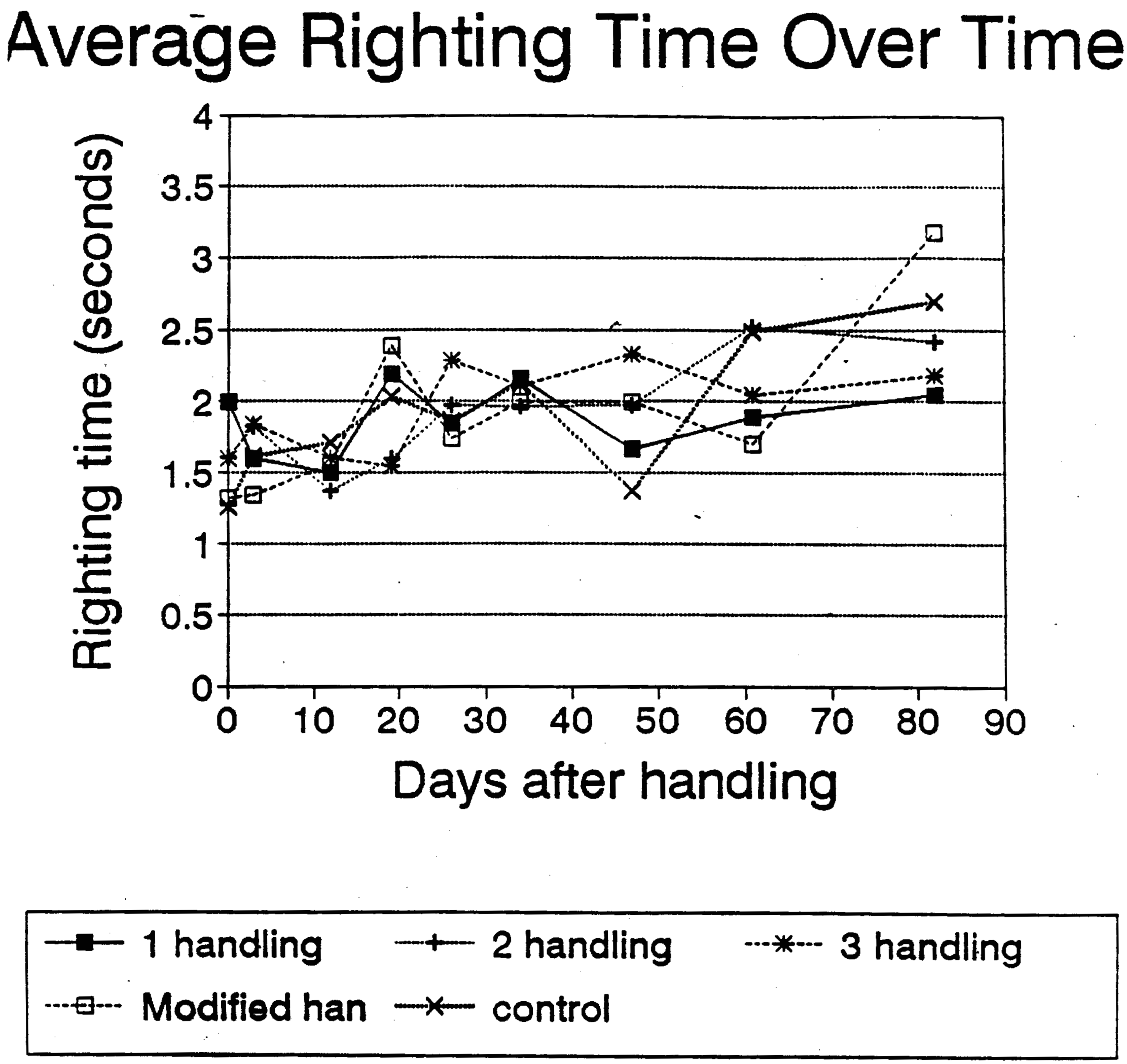
Average Feeding Rate
Feeding rate (g/100g wet weight)
0
1
2
3
4
5
6
1
2
3
4
5
Treatment
Juvenile
Female
Male



Average Feeding Rate Over Time
Feeding rate (g/100g wet weight)
0
1
2
3
4
5
6
7
8
0
10
20
30
40
50
60
70
80
Day After Handling
1 handling
2 handling
3 handling
Modified handlin
control

Average Righting Time




Average Righting Time Over Time
Righting time (seconds)
4
3.5
3
2.5
2
1.5
1
0.5
0
0
10
20
30
40
50
60
70
80
90
Days after handling
1 handling
2 handling
3 handling
Modified han
control

APPENDIX 2

SHELL CONDITION AND BREEDING SUCCESS IN TANNER CRABS

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Running head: Tanner Crab Reproduction

ABSTRACT When pairs of similar sized old shell and new shell male Chionoecetes bairdi were presented with multiparous mates the old shell males dominated during 70% of the copulations. In 39% of all copulations possession of the female was contested. Old shell males won 69% of those contested matings. Recently molted males did not copulate with either primiparous or multiparous females.

INTRODUCTION

Previously the effects of shell condition on reproductive success of male Chionoecetes bairdi have not been studied under controlled conditions. One criteria used to categorize male crabs in the fishery and population surveys is shell condition. Crabs that are thought to have molted within the year have clean carapaces and are called "new shells" (NS), whereas those that molted more than a year prior have worn shells often with epiphytic growth and are called "old shells" (OS). The relative proportion of OS and NS males in the fished population is monitored on a regular basis to better understand growth and recruitment to the fishery.

A predominance of grasping C. bairdi males observed in situ were OS crabs (Stevens et al., 1993). It is conceivable that male crabs tend to make growth and reproductive tradeoffs. Those that grow tend not to reproduce, whereas those that mate tend not to grow. This study addressed two questions concerning effects of shell condition on reproductive success: 1) Do similar-sized NS and OS Tanner crab males have an equal likelihood of inducing females to copulate; and 2) Are similar-sized NS and OS Tanner crab males capable of mating with multiple mates?

MATERIALS AND METHODS

MALE DOMINANCE EXPERIMENT

All specimens of both sexes for this experiment were captured at 135 to 155 m depth in Chiniak Bay, near Kodiak Alaska, on 6 January 1994 with trawls and delivered to the Seward Laboratory via air charter. Specimens were held in the Seward Marine Center Laboratory where seawater is pumped from a fjord at 80 m depth. Water temperature ranged from 4.2 to 4.5^{o}C and salinity ranged from 32 to 34 ppt during experiments reported here.

Between 19 April and 14 May 1994, 24 pairs of males, with similar carapace widths (CW), were placed in separate 800 l tanks. One male in the pair was OS and one NS in appearance. Males were considered NS if their spines were not worn, there was no epiphytic growth on the carapace, and the shell color was reddish. In contrast, OS carapaces had some combination of worn spines, epiphytic growth, and a darker color. Carapace width and chela heights (CH) were measured to the nearest mm for each male. In this experiment the males were 117-170 mm CW and 22-42 mm CH (Table 1). Pairs were selected to minimize the differences in the size of the males. In nine of the 24 competing pairs of males their CW was the same, in 14 pairs there was only a 1 mm difference, while one pair had a 2 mm difference in CW. Differences in chela sizes varied by 3 mm or less. Male Chionoecetes are thought to undergo a molt in which the size of the chela increases disproportionately compared to carapace growth (Conan and Comeau, 1986). In Chiniak Bay males observed grasping multiparous mates have CH/CW ratios >0.17 (Stevens et al., 1993). In our study all males were large claw morphotypes with the ratio of CH/CW > 0.19, so all these experimental males were big enough to be considered functionally mature.

Multiparous females (n = 72) were held communally in two 1,000 l tanks. Multiparous females are terminal molt hard shell individuals that produce their second or subsequent clutch. They were examined daily to find those whose eggs had hatched, and had cleaned the old egg shells from the pleopods, but had not extruded a new clutch. Females in this state are ready to copulate (Paul and Adams, 1984).

When a female was ready to mate, she was placed in a tank with a pair of males at 0800 h. In all cases the males were larger than the female with the minimum difference in CW between the sexes being 8 mm when male CW <120 mm and 18 mm when male CW >120 mm. The pair of males and their potential mate were observed continuously between 0800 and 1900 h. Observations included incidents of fighting between males over the female and which male copulated. Copulation was considered successful if the female and male assumed positions shown in Figure 3b of Donaldson and Adams (1989). At 1900 h the female was removed from the tank. Each pair of males was given an opportunity to breed on three separate successive days with a new female.

One week after the female ovulated, her clutch was examined to determine if the eggs were dividing which indicates fertilization. In this species females can store sperm for at least two years (Paul, 1984), but they do not always have enough sperm in storage to fertilize a clutch (Paul and Paul, 1992). Therefore, in these experiments it was not possible to be certain if the copulating male was the parent.

In each pair of competing males the one copulating with two or more of the three females available to them was termed the dominant male. The three variables CW, CH and shell age were examined for the probability that there were effects in allocating dominance due to these parameters (Devore, 1987).

RECENTLY MOLTED MALE EXPERIMENTS

In the second experiment, observations on shell condition and mating success involved seven males (130-159 CW and 26-40 mm CH) that molted in the laboratory between 1 March and 30 April, 1994 (Table 2). These crabs had been captured during July 1993 in lower Cook Inlet, near Homer, Alaska by trawling at 30 to 60 m depth. Each of these recently molted males was placed separately in a 350 l tank containing one multiparous female (90-110 mm CW) whose eggs had just started hatching. In all cases the female CW was at least 30 mm smaller than that of the male. Continuous daily observations of the pairs between 0800 h and 1900 h included notation of grasping behavior and copulation. Each evening the female was removed from the tank and the same female put back into the tank the following morning. This procedure was continued until the female produced a new clutch. Table 2 lists the chronology of male molting which preceded egg extrusion by their potential mates by 50 to 99 days.

The last experiment involved males that had successfully fertilized primiparous mates in 1993 in the laboratory and subsequently molted prior to the 1994 breeding season. These crabs had been captured at various times in 1992 in lower Cook Inlet, near Homer, Alaska by trawling at 30 to 60 m depth. These recently molted males were held individually in 350 l tanks and a newly molted virgin primiparous female put in the tank for one hour to see if grasping or copulation would occur. Five males (104-122 mm CW) were available for this experiment (Table 3). The males were all larger than their prospective mates; females were 85-103 mm CW (Table 3). If no copulation occurred the female was placed with a >140 mm OS male to see if copulation and egg production would occur.

RESULTS

MALE DOMINANCE EXPERIMENT

In the first experiment there were 74 copulations (Table 1). Old shell males accomplished 52 (70.3%) of the copulations vs. 22 (29.7%) for NS males. In 39% of the 74 copulations, possession of the female was contested. Old shell males won 69% of those contested matings. Old shell males bred all three females available to them in 16 of the 24 trials, whereas NS males bred all three females in only six trials. In two cases a female was bred by both males. In both incidents the OS male copulated first and then released the female. Afterwards the NS male copulated with her uncontested. In this experiment every female copulated prior to egg extrusion and had normal appearing clutches with >90% of the eggs initiating division.

In 15 pairs of competing males where CW was not identical the dominate male had a larger CW in seven cases (47%) and eight pairs (53%) a smaller CW, nearly a 50:50 ratio, suggesting no effects due to CW. In 20 cases where CH was not identical 10 (50%) dominant males had larger CH and ten (50%) smaller CH; a frequency which indicated no effects due to CH. In 70% of the copulations the OS male was dominant, an outcome different from that expected if the probability of OS dominance is only 0.5. Thus, the null hypotheses of no dominance effect related to shell age is rejected with p-value of 0.32, statistically significant at alpha 0.05 (Devore, 1987).

RECENTLY MOLTED MALE EXPERIMENTS

In the second experiment involving the recently molted males and multiparous females only one of seven males did any grasping of a female (Table 2). That male grasped the female on several days, including the ovulation day, but did not copulate. In all cases the females extruded a clutch and used stored sperm to fertilize the eggs. In all clutches > 90% of the eggs were dividing.

In the third experiment no grasping activity or copulation occurred in the tanks where functionally mature recently molted males had access to newly molted primiparous females (Table 3). All of the primiparous females subsequently placed with >140 mm CW males copulated and extruded fertilized eggs.

DISCUSSION

Previous speculations and observations concerning *Chionoecetes* male functional maturity have primarily focused on body size (see Stevens *et al*., 1993 for a review) and chela measurements (Conan and Comeau, 1986; Conan *et al*., 1988; Donaldson and Johnson, 1988). In *C. bairdi* males begin to produce sperm at CW of 55 to 65 mm (Adams and Paul, 1983; Paul, 1992), but these small mature males have not been observed mating in nature (Stevens *et al*., 1993). *In situ* males grasping multiparous mates range in size from 100 to 170 mm CW, and averaged 120 to 131 mm CW (Stevens *et al*., 1993). Thus, in our male competition observations (Table 1) all males were big enough to produce sperm and mate with multiparous females. Given that each competition was between males virtually identical in size, the primary variable was male shell condition. These experiments demonstrate that OS males typically dominate NS males in competition for mates. During *in situ* observations of pairs of *C. bairdi* in Chiniak Bay near Kodiak, Alaska, proportions of soft-shell, NS and OS males grasping multiparous mates were 0, 32 and 68%, respectively, whereas the analogous proportions for unpaired males in trawl samples were 5, 84 and

11% (Stevens *et al.*, 1993). Those observations are consistent with the results of this controlled experiment in which 70% of the males copulating were OS.

The visual shell aging methods used in this study to differentiate OS and NS crabs are subjective. It is unlikely that crabs classifed as OS had actually molted within the past year, but some of the crabs classified as NS in these experiments might not have molted within the past year. Such shell age misclassification would cause overestimation of the frequency of copulations by NS males.

Due to the size limit of 140 mm CW, fishing removes the larger, older crabs. Thus, compared to unfished populations, fished stocks are dominated by NS recruits (Donaldson, unpublished). Our results, along with those of Stevens *et al.* (1993), show that multiparous females are preferentially bred by OS males. Studies of *C. opilio* in Canada show that NS males can successfully breed with multiparous mates (Ennis *et al.*, 1988; Sainte-Marie, 1993), and our experiments verify the *in situ* observations (Stevens *et al.*, 1993) that some NS *C. bairdi* do likewise (Table 1).

The results of these experiments suggest that males do not breed for at least 99 days after molting even when no other male competitors are present (Table 2). This is consistent with field studies of Tanner crab pairs in which no soft-shell males participated in mating despite their presence in trawl samples (Stevens *et al.*, 1993). These results coupled to previous field observations show that shell age is an important criteria in determining whether a male is likely to participate in breeding. Thus, the shell age composition of the male population needs to be considered in management strategies for C. bairdi to minimize the impact of fishing on the resource.

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Table 1. Mating success of competing old shell and new shell *Chionoecetes bairdi* with access to three multiparous females.

OLD SHELL MALES			NEW SHELL MALES			
CARAPACE WIDTH (mm)	CHELA HEIGHT (mm)	NUMBER BRED	CARAPACE WIDTH (mm)	CHELA HEIGHT (mm)	NUMBER BRED	NUMBER OF CONTESTED COPULATIONS
118	25	3	117	22	0	0
119	24	0	119	24	3	2
127	25	3	126	27	0	2
130	28	3	130	28	0	2
131	28	3	132	31	0	2
133	28	3	132	29	0	2
133	31	1	134	30	2	3
134	31	3	135	28	0	2
138	33	0	138	32	3	2
138	32	3	137	30	0	0
140	29	3	141	33	0	0
142	34	3	141	33	0	2
143	33	0	143	31	3	0
147	34	3	147	35	0	1
151	35	2	151	33	1	0
152	34	3	151	34	0	1
155	38	3	156	39	0	0
158	38	3	158	37	1*	3
160	39	3	160	39	0	0
164	41	1	164	39	3*	1
164	42	3	165	40	0	2
165	40	0	166	42	3	0
168	41	3	167	39	0	1
170	39	0	168	41	3	1

* Female bred by both males

Table 2. Mating activity of recently molted male <u>*Chionoecetes bairdi*</u> with exclusive access to a multiparous female during spring 1994.

MALE MOLT DATE 1994 (mo/d)	MALE CARAPACE WIDTH (mm)	MALE CHELA HEIGHT (mm)	DATE PUT FEMALE IN TANK (mo/d)	GRASPING ACTIVITY (yes/no)	COPULATION (yes/no)	DAYS AFTER MALE MOLT NEW CLUTCH	FEMALE CARAPACE WIDTH (mm)
3/01	143	31	4/19	n	n	99	110
3/18	149	31	4/19	n	n	59	101
3/25	130	26	4/19	n	n	55	95
3/31	159	35	4/19	n	n	66	104
4/02	159	40	5/02	y	n	72	98
4/03	152	33	5/03	n	n	71	90
4/30	128	27	5/16	n	n	50	91

Table 3. Mating activity of recently molted male *Chionoecetes bairdi* with exclusive access to a primiparous female during spring 1994.

MALE MOLT DATE 1994 (mo/d/)	MALE CARAPACE WIDTH (mm)	MALE CHELA HEIGHT (mm)	DAYS AFTER MALE MOLT FEMALE ADDED	GRASPING (yes/no)	COPULATION (yes/no)	FEMALE CARAPACE WIDTH (mm)
2/02	116	21	72	n	n	98
2/18	104	20	60	n	n	85
3/31	122	23	49	n	n	101
4/05	112	23	44	n	n	99
4/05	121	23	44	n	n	103

APPENDIX 3

A length-based Population Model and Stock-recruitment Relationships for Red King Crab, *Paralithodes camtschaticus*, in Bristol Bay, Alaska[1]

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Abstract

A length-based population model was constructed for red king crab, *Paralithodes camtschaticus*, in Bristol Bay, Alaska. The model incorporates stochastic growth, gradual recruitment over length, and a bowl-shaped pattern for instantaneous natural mortality as a function of length. A non-linear least squares approach was used to estimate abundance, recruitment, and natural mortality. The model was applied to abundance and catch data from 1968 to 1993. The observed population abundances were fitted well with a length-based model. Natural mortality was estimated to be 3 to 6 times higher in the early 1980s than during other periods. High natural mortality

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coupled with high harvest rates and followed by low spawning biomass may have contributed to the collapse of the population in the early 1980s and its continued lack of recovery. The stock-recruitment data estimated from the length-based model provided a good fit to both general and autocorrelated Ricker stock-recruitment models. The general Ricker model is supported by strong recruitment associated with intermediate levels of spawning biomass and extremely low recruitment related to low spawning stock, while the autocorrelated Ricker model fitted the data slightly better and is supported by the fact that extremely strong and weak recruitment occurred successively over two separate periods.

Introduction

The red king crab (RKC), *Paralithodes camtschaticus*, stock in Bristol Bay, Alaska, was one of the largest RKC populations in the world and still supports one of the most valuable fisheries in the United States (Otto 1990). The fishery began in the early 1930s and peaked in 1980 with a catch of 59,000 t, worth an estimated $115.3 million ex-vessel (Otto 1986, 1990). The catch declined dramatically in the early 1980s and has stayed at low levels during recent years. Despite a low catch of 6,441 t, the 1993 fishery was valued at $54.7 million. The Bristol Bay RKC fishery currently takes place during a short period in the fall, and the catch quota is based on abundance estimated from the National Marine Fisheries Service (NMFS) trawl survey in the previous summer (Otto 1986).

Over 20 years of trawl survey and catch data are available for

Bristol Bay RKC, yet no comprehensive length-based population models have been developed. The purpose of this paper is to incorporate available trawl survey, fishery, and tagging data into a length-based population model for Bristol Bay RKC. Such a comprehensive population model would provide the basis for subsequent analyses of harvest strategies.

Many traditional population models are not applicable to RKC because of biological features. First, like other crustacean species, aging of RKC is difficult, precluding the use of age-based population models. Secondly, growth of RKC occurs during a brief period when crabs molt. A crab that has molted during the past year has a clean carapace and is considered a new-shell crab, while one that has not molted exhibits a worn and encrusted carapace and is called an old-shell crab. Therefore, shell condition can be used to identify whether a male crab molted during the past year. Juvenile RKC molt multiple times per year, but molt frequency decreases with age (Weber 1967). After reaching maturity, male RKC molt once per year or less (Balsiger 1974; McCaughran and Powell 1977) and female RKC molt once per year (Fukuhara 1985). Because of this punctuated growth, conventional length-frequency analyses are not applicable. Tagging studies have shown that length-specific growth of RKC is highly variable (Weber and Miyahara 1962; Balsiger 1974); thus, the assumption of a one-to-one relationship of length-at-age is invalid.

Since development of length-cohort analysis in the late 1970s (Jones 1979, 1981), much progress has been made on length-based stock-assessment methods. The effects of parameter variation on length-cohort analysis were investigated by Lai and Gallucci (1987, 1988), a length-based production model was developed by Fournier and Doonan (1987), and a general size-structured fish population model was derived by Schnute (1987). The dynamics of age and length for a stochastic population model was investigated by Deriso and Parma (1988) and Parma and Deriso (1990). Sullivan et al. (1990) advanced length-based population modeling by incorporating growth variation into the models and separating recruitment into year and length components. They relaxed three common assumptions of length-based methods: (1) a one-to-one relationship of length-at-age, (2) knife-edged and constant recruitment, and (3) steady state distribution of lengths over time. This enhances the applicability of length-based methods to crustaceans.

In this paper, we modified the length-based population model proposed by Sullivan et al. (1990) for application to Bristol Bay RKC. The model incorporates stochastic growth in which individual crabs molt from one length-class to another with a probability, gradual recruitment over length, and a bowl-shaped curve of natural mortality over length. General and autocorrelated Ricker stock-recruitment (S-R) models were fitted to the S-R data derived from the length-based model.

Methods

Data

Catches of Bristol Bay RKC by length and year were obtained from annual reports of the International North Pacific Fisheries Commission from 1968 to 1973 (Jackson 1974; Phinney 1975) and from the Alaska Department of Fish and Game (ADF&G) from 1974 to 1992 (Griffin and Ward 1992). Tow-by-tow trawl survey data for Bristol Bay RKC during 1975-1993 were provided by NMFS.

We estimated abundances by sex, carapace length (CL), and shell condition using the "area-swept" method (Alverson and Pereyra 1969) without post-stratification. Fourteen and eleven length-classes were defined for males and females, respectively, with a length-class interval of 5 mm. Because juvenile crabs are not fully recruited to the survey gear, we set the minimum length at 95 mm for males and 90 mm for females. The last length-class included all crabs with length equal to or greater than 160 mm for males and 140 mm for females. The catch from one station (F06) in 1991 was discarded because it was considered an outlier (Stevens et al. 1991).

For 1968-1970 and 1972-1974, abundance estimates were obtained from NMFS directly because these survey data by tow were not currently available (J. Reeves, NMFS, 7600 Sand Point Way NE, Seattle, WA 99115, personal communication). There were spring and fall surveys in 1968 and 1969. The average of estimated abundances from spring and fall surveys was used for these two years. The abundance in 1971 was derived as the average of those in 1970 and 1972 because a complete survey was not conducted in 1971. We considered abundance estimates from the 1973-1993 data to be estimates of absolute abundance; pre-1973 estimates were considered as relative abundance because of an apparent change in catchability. A footrope chain was added to the trawl gear starting in 1973, and the crab abundances in all length-classes in 1973 and beyond were much greater than those estimated prior to 1973 (Reeves et al. 1977).

The length-based population model was fitted to the abundance data from 1972 to 1993 because shell condition data were limited to this time series. The catchability for the 1972 survey gear was estimated by the model. We simply assumed that the catchability for the survey gears in 1968-1971 was the same as in 1972 because the survey gears and methods were identical during these years. Thus, the relative abundances from 1968 to 1971 were divided by the estimated catchability in 1972 to obtain the absolute abundances. The absolute abundances from 1968-1993 were used to construct S-R relationships.

Length-based Population Models

The NMFS trawl survey has been conducted from late May to August and covers the majority of Bristol Bay during June (Otto et al. 1990). Bristol Bay RKC generally complete molting and mating before June each year. Therefore, we modeled population abundances each year during June. The following model was developed for male crabs. For female crabs the model was the same except that catch equalled zero and molting probability equalled 1.0 to reflect annual molting.

The growth of an individual crab is characterized by a change in size, or, growth increment, during molting. At a population level, growth is a function of the size distribution, the probability distribution of growth increments, and the molting probability at each specific length. For simplicity, we assumed that crabs within the same length-class have the same probability distribution for growth and molting probability. Mean growth increment per molt for length-class l, G_l, is assumed to be a linear function of mean CL ι of the length-class just before molting (Weber and Miyahara 1962):

$$G_l = a + b\iota, \tag{1}$$

where a and b are the intercept and slope.

The variation in growth increment per molt is described by a gamma distribution because of its versatility and flexibility in approximating several functional forms (Sullivan at al. 1990):

$$g(x|\alpha_l, \beta) = x^{\alpha_l - 1} e^{-x/\beta} / (\beta^{\alpha_l} \Gamma(\alpha_l)), \tag{2}$$

where x is growth increment per molt, and α_l and β are parameters. The mean of x is given by $\alpha_l\beta$ and is equal to G_l for a given length-class l. Thus $\alpha_l = G_l/\beta$, and the growth is represented by two parameters G_l and β. The expected proportion of crabs molting from length-class l to length-class l' is equal to the integral of the gamma function over the length interval $[l_1, l_2)$ of the receiving length-class l':

$$P_{l,l'} = \int_{l_1}^{l_2} g(x|\alpha_l, \beta)\, dx. \tag{3}$$

For the last length-class L, $P_{L,t} = 1$.

The molting probability for a given length-class and time t is modeled by a logistic function (Balsiger 1974):

$$m_{l,t} = \frac{1}{1+\alpha_t e^{-\beta_t \iota}}, \tag{4}$$

where α_t and β_t are parameters, and ι is the mean length of length-class l. Three logistic functions were used to describe the molting probability during three periods: a high abundance period (1972-1979), a dramatically declining period (1980-1984), and a low abundance period (1985-1992), with parameters α_1 and β_1, α_2 and β_2, and α_3 and β_3, respectively.

Instantaneous natural mortality, $M_{l,t}$, is separated into a time-dependent factor, MY_t, and a length factor, ML_l:

$$M_{l,t} = MY_t \, ML_l, \tag{5}$$

where ML_l is assumed to be a bowl-shaped curve, described by two exponential functions:

$$\begin{aligned} ML_l &= e^{n2\,(n1-\iota)} \qquad if\ \iota < n1, \\ ML_l &= e^{n3\,(\iota-n1)} \qquad if\ \iota \geq n1, \end{aligned} \tag{6}$$

where $n1$, $n2$, and $n3$ are parameters greater than or equal to 0, and ι is the mean length of length-class l. Constant natural mortality over length is a special case with $n2$ and $n3$ equal to 0. Large values of $n2$ describe high natural mortalities for small, young crabs and $n3$ for large, old crabs. A bowl-shaped curve of natural mortality over length is intuitive: small individuals suffer high mortality due to predation, and large individuals have high mortality caused by senescence.

Recruitment into the modeled population is a function of two parameters: (1) the number of recruits entering the modeled population for year t, R_t, and (2) the proportion of recruits belonging to each length-class, U_l (Sullivan et al. 1990). This is expressed by

$$R_{l,t} = R_t \, U_l, \tag{7}$$

where U_l is described by a gamma distribution, such as in equations (2) and (3), with parameters α_r and β_r. The mean length of recruitment is $\alpha_r \beta_r$; thus, we needed to estimate only β_r if we knew the mean length of recruitment. We assumed that R_t consists of crabs at the recruiting age with different lengths and thus represents year-class strength for year t. This assumption was needed to study S-R relationships. Because most crabs with the same age probably enter the modeled population in the same year, this assumption is approximately valid.

We modeled the new- and old-shell male crabs separately and assumed that they have the same natural mortality and probability of molting the following year. The annual abundance of new-shell crabs is the combined result of growth, molting probability, mortality and recruitment:

$$\begin{bmatrix} N_{1,t+1} \\ N_{2,t+1} \\ \cdot \\ \cdot \\ N_{L,t+1} \end{bmatrix} = \begin{bmatrix} P_{1,1} & 0 & \cdot & \cdot & 0 \\ P_{1,2} & P_{2,2} & 0 & \cdot & 0 \\ \cdot & \cdot & \cdot & \cdot & 0 \\ \cdot & \cdot & \cdot & \cdot & 0 \\ P_{1,L} & P_{2,L} & \cdot & \cdot & P_{L,L} \end{bmatrix} \times \begin{bmatrix} m_{1,t} & & & & \\ & m_{2,t} & & & \\ & & \cdot & & \\ & & & \cdot & \\ & & & & m_{L,t} \end{bmatrix} \times \begin{bmatrix} A_{1,t} \\ A_{2,t} \\ \cdot \\ \cdot \\ A_{L,t} \end{bmatrix} + \begin{bmatrix} R_{1,t+1} \\ R_{2,t+1} \\ \cdot \\ \cdot \\ R_{L,t+1} \end{bmatrix}, \tag{8}$$

where $A_{l,t}$ is total crab abundance in length-class l in year t just before molting. That is,

$$A_{l,t} = (N_{l,t}+O_{l,t})\, e^{-M_{l,t}} - C_{l,t}\, e^{(y-1)M_{l,t}}, \tag{9}$$

where $N_{l,t}$ and $O_{l,t}$ are the respective abundances of new-shell and old-shell crabs in length-class l in year t, $C_{l,t}$ is the commercial catch in length-class l in year t, and y is the period between the survey and the fishery, i.e., about 0.1 to 0.4 years for the Bristol Bay RKC fishery. Note that recruitment was defined as year-class strength; thus $R_{l,t}$ is positive only for the first several length-classes and equals zero when l is large. All recruits are new-shell crabs. The old-shell crabs are the non-molting portion of crabs surviving from the previous year:

$$O_{l+1,t+1} = ((N_{l+1,t}+O_{l+1,t})\, e^{-M_{l+1,t}} - C_{l+1,t}\, e^{(y-1)M_{l+1,t}})\,(1-m_{l+1,t})\,. \tag{10}$$

Males larger than 160 mm CL (140 mm CL for females) were grouped together to form the last length-class. The new-shell and old-shell crabs in the last length-class were lumped together because it is not necessary to separate them.

Parameter Estimation

Mean growth increment per molt was estimated for male crabs by Weber and Miyahara (1962) and derived for female crabs from the data presented in Gray (1963). The intercept and slope parameters for the linear relationships between mean increment per molt and pre-molt CL (in mm) respectively are 13.14 and 0.018 for male crabs, and 16.49 and -0.097 for female crabs. Once mature, the growth increment per molt for male crabs increases slightly and annual molting probability decreases, while the growth increment for female crabs decreases dramatically but annual molting probability is 1.0.

Few red king crabs less than 50 mm CL are caught during the trawl surveys (Incze et al. 1986). Abundance estimates of small RKC are unreliable because these crabs are contagiously distributed and not easily captured by the survey gear. Therefore, we did not include small RKC in the population model but estimated crab abundance for females with CL greater than 90 mm and for males with CL greater than 95 mm. The starting lengths of male and female RKC may correspond to similar starting ages because male RKC grow faster than females. Mean lengths at recruitment to our modeled population were assumed to equal 97 mm for females and 105 mm for males.

Model parameters are usually estimated under the assumption of two types of error: process error and measurement or observation error (Walters 1986). Process error is caused by short-term fluctuations in the population abundance due to natural processes. Measurement error occurs from inaccurate estimation of population abundance. Because process and measurement errors are confounded in an estimation procedure, the ratio of these two errors has to be known to estimate both errors simultaneously. This ratio is rarely available. Consequently, either process or measurement error is usually assumed (Walters 1986). A measurement error estimation procedure is preferable to a process error procedure for an age-structure model (Collie 1991). Thus, we assumed that the population dynamics of Bristol Bay RKC basically follow a deterministic model, and erratic fluctuations in the abundance are due primarily to measurement errors from the trawl surveys, although we allowed for some change in process by the inclusion of time-dependent natural mortalities and molting probabilities.

Measurement errors were assumed to be log-normally distributed:

$$\tilde{N}_{l,t} = N_{l,t} e^{\eta_{l,t}}, \qquad \tilde{O}_{l,t} = O_{l,t} e^{\delta_{l,t}}, \tag{11}$$

where $\tilde{N}_{l,t}$ and $\tilde{O}_{l,t}$ are estimated abundances of new-shell and old-shell crabs in length-class l and year t from trawl survey data and $\eta_{l,t}$ and $\delta_{l,t}$ are normally-distributed measurement errors of abundances with zero mean, independent between years and between length-classes within a year.

Wanting to minimize measurement error, we estimated parameters of the model using a nonlinear least squares approach which minimized the residual sum of squares (RSS):

$$RSS = \sum_{l,t} [(\ln(N_{l,t}) - \ln(\tilde{N}_{l,t}))^2 + (\ln(O_{l,t}) - \ln(\tilde{O}_{l,t}))^2]. \tag{12}$$

The total data points were 374 for males and 232 for females.

The following model parameters were estimated separately for male and female crabs: recruits for each year (year-class strength R_t for t = 73 to 93), total abundance in the first year (1972), parameters β and β_r, and instantaneous natural mortality parameters

$n1$, $n2$, $n3$, and MY_t. Molting probability parameters α_1, α_2, α_3, β_1, β_2, and β_3 were also estimated for male crabs. Two scenarios were examined for the time-dependent factor of natural mortalities (MY_t): (1) constant MY_t over time, and (2) four levels of MY_t. The four levels were one for the period before the collapse of the population (1972-79 for males and 1972-78 for females), one for the period after the collapse (1985-92 for males and 1986-92 for females), and two for the period during the collapse (1980-84 for males and 1979-85 for females). The periods when male and female crab populations collapsed were determined interactively by searching for the best fit of observed abundances to the population model. An F statistic described by Schnute (1981) was used to compare these two scenarios of natural mortality.

Starting in the second year, the abundances by length, sex, and shell condition were computed recursively from (1) the abundances by length, sex, and shell condition in the first year, (2) annual recruitment, (3) catch, and (4) model parameters. To increase the efficiency of the parameter-estimation algorithm, we assumed that the relative frequencies of length/shell-classes from the first year (1972) survey data approximate the true relative frequencies within sexes. Thus, we had to estimate only total abundances of males and females for the first year; 3n unknown parameters for the abundances in the first year were reduced to 2 under this assumption, where n is the number of length-classes.

IMSL FORTRAN subroutine DBCLSF (IMSL 1989) was used to perform nonlinear least-squares parameter estimation on the models through a modified Levenberg-Marquardt algorithm and a finite-difference Jacobian. All parameters were bounded to be non-negative. Initial estimates of total abundance in the first year and annual recruits were derived from the survey data. Initial estimates of natural mortalities were obtained from the literature (Balsiger 1974; Reeves and Marasco 1980; Reeves 1988; Greenberg et al. 1991). The sensitivity of initial conditions was investigated interactively by randomly increasing (up to 200%) or decreasing (down to 30%) initial parameter estimates. In all cases, different initial parameter estimates, except β, β_r, and natural mortality, converged to similar final estimates after a series of iterations.

Parameters β and β_r are slightly confounded with natural mortality. So, either β and β_r have to be fixed to estimate natural mortality or vice versa. We assigned the possible ranges of initial values of β and β_r to rows and columns of a matrix. The estimation procedure was as follows for each row and column combination of initial values of β and β_r: (1) estimate all other parameters while keeping β and β_r fixed; (2) fix natural mortality and estimate β, β_r, and other parameters; (3) repeat steps 1 and 2 until estimated parameter are stable; (4) estimate all parameters simultaneously; and (5) repeat steps 1 to 4 until estimated parameters are stable. The final parameter values were those producing the minimum residual sum of squares.

S-R Relationship

After reconstructing the population abundances from the length-based model, our next step was to estimate an S-R relationship for Bristol Bay RKC. An S-R relationship for RKC has been notoriously difficult to develop because of aging problems and lack of conclusive evidence to support appropriate sex and size ratios for successful spawning. Reeves and Marasco (1980) and Reeves (1990) estimated that male RKC recruit in Bristol Bay at age 5 when they are 95 to 109 mm CL, assuming that juvenile RKC in Bristol Bay have the same growth rate as those described by Weber (1967) for Unalaska. On the contrary, assuming that growth rates per degree day are identical in Bristol Bay and Unalaska, Stevens (1990) suggested that male Bristol Bay RKC would take 7 to 10 years to grow to 95 to 109 mm CL because mean temperatures in Bristol Bay as a whole are much cooler than those in Unalaska. The Bristol Bay temperature data Stevens (1990) used were approximate. Stevens and Munk (1990), using more accurate temperature data, indicated that female Bristol Bay RKC grow to 90 mm CL when they turn age 6 at the end of March. The subsequent molt in May or June would add about 7 mm CL.

Thus, in our study, we defined recruits of Bristol Bay RKC to be age 6.2 corresponding to a mean female CL of 97 mm and a mean male CL of 105 mm, assuming that hatching occurs by the end of March (Stevens and Munk 1990). With an addition of 9 months from the time of egg fertilization to hatching the period between parent and recruitment of its offspring became 7 years.

To date, spawning stock of Bristol Bay RKC has been measured in two ways: (1) as the fertilized female abundance (Reeves and

Marasco 1980; Reeves 1990; NPFMC 1990), and (2) as that derived from three variables: mature male biomass, mature female biomass, and the product of mature male and female biomasses (Matulich et al. 1988, 1990; Greenberg et al. 1991). Fertilized female abundance was defined as the product of the number of mature female crabs and the mean percentage of full egg clutches (Reeves 1988). Clutch sizes and maturity depend on time of year when measurements were taken. Variability in the timing of surveys can impact the estimate of fertilized female abundance (Otto et al. 1990). Therefore, use of fertilized female abundance in crab fishery management is questionable. The disadvantage of using three variables to measure spawning stock is that male crabs are weighed too heavily for reproductive success because surplus male crabs don't have female mates. In addition, biologically spurious results can occur; e.g., a model population without male crabs can still produce a very strong year class.

We propose an alternative definition of spawning stock which incorporates additional biological features. As pointed out by Kruse (*in press*), mating of RKC is complex and its success depends on the distribution, sex ratio, and size difference between mature female and male crabs. In confined environments, large male crabs (>140 mm CL) in Kodiak are capable of mating with 7 to 9 female crabs successfully (Powell et al. 1974). Small males (120-139 mm CL) are generally successful at fully fertilizing egg clutches of only 2 to 3 females (Paul and Paul 1990). Male crabs in mating pairs observed in the natural environment are generally much larger in average CL than their female partners (Powell and Nickerson 1965). Male crabs less than 120 mm CL in Kodiak are rarely observed among mating pairs (Powell and Nickerson 1965; Schmidt and Pengilly 1990). About 50% of female RKC in Bristol Bay mature by 89 mm CL and about 80% by 95 mm CL (Otto et al. 1990). For our estimate of spawning stock, we assumed that mature female crabs are at least 95 mm CL and that mature males are 120 mm or larger.

The spawning season for the Bristol Bay RKC population lasts about 2-3 mo, and 80% of observed females produce eggs within about 20 d (FAJ 1964). Spawning activities include hatching, molting, mating and ovulating. A male crab's precopulatory embrace of a female lasts throughout the pre-molt and molt stages, about 3-7 d (Powell and Nickerson 1965). An individual female crab then molts, mates and ovulates usually within a 1-2 d interval (Weber 1967). However, ovulation is incomplete if the mating does not occur within 1 d following the female molt and no ovulation occurs if a female does not pair with a male within 9 d after molting (FAJ 1963). However, McMullen (1969) showed that all female Kodiak RKC mated within 9 d of molting successfully ovulated.

Under ideal conditions, when male crabs carry hard shells during the mating season and all female crabs molt at equal intervals, a large male can mate with up to four females within a 20-d mating period and average 5 d per mating. Under the worst scenario, when all females molt at the same time, a large male can mate with a maximum of two females. Because there are few females larger than 160 mm, we adopted a conservative approach where a male of 160 mm CL or larger can mate with an average of three females while a male of 120 mm CL can mate with only one female. The number of females that a male crab between 120 mm and 160 mm CL can serve is interpolated linearly according to male crab weight (Table 1).

We defined male reproductive potential as the mature male abundance by CL multiplied by the maximum number of females with which a male of a particular length can mate. If mature female abundance was less than male reproductive potential, then mature female abundance was used as female spawning abundance. Otherwise, female spawning abundance was set equal to the male reproductive potential. The female spawning abundance was converted to biomass, defined as the effective spawning biomass SP_t, using a length-weight relationship ($W = 0.02286\ L^{2.234}$) provided by Dr. B. Stevens of NMFS, where W is grams and L is millimeters.

The stock-recruitment relationships of Bristol Bay RKC were modeled using a general Ricker curve:

$$R_t = SP_{t-k}^{r1}\, e^{r2 - r3\, SP_{t-k} + v_t}, \tag{13}$$

and an autocorrelated Ricker curve:

$$R_t = SP_{t-k}\, e^{r2 - r3\, SP_{t-k} + \upsilon_t}, \tag{14}$$

where $\upsilon_t = \delta_t + a1\ \upsilon_{t-1}$, v_t and δ_t are environmental noises assumed to follow a normal distribution $N(0,\sigma)$, and $r1$, $r2$, $r3$, and $a1$ are constants. Equation (13) was linearized as

$$\ln(R_t) = r2 + r1 \ln(SP_{t-k}) - r3\, SP_{t-k} + v_t, \tag{15}$$

and equation (14) as

$$\ln(R_t/SP_{t-k}) = r2 - r3\,SP_{t-k} + \upsilon_t . \qquad (16)$$

An ordinary linear regression was applied to equation (15) to estimate model parameters *r1, r2* and *r3*, and an autocorrelation regression (procedure AUTOGRE, SAS Institute Inc. 1988) with a maximum likelihood method was used to estimate parameters *r2, r3* and *a1* for equation (16).

Results

Length-based Population Model

Observed and estimated length frequencies of male RKC under both scenarios of natural mortality are compared in Fig. 1. Corresponding parameter values for each scenario are summarized in Table 2. Under scenario 1 (constant instantaneous natural mortality rate), the minimum natural mortality equaled 0.27 and crabs ≥125.1 mm CL had relatively low natural mortality. For scenario 2 (four levels of natural mortality), the natural mortality was very low in the 1970s (0.19), dramatically increased in the early 1980s (0.71 and 1.26), and then returned to low levels in the mid-1980s (0.18). Abundances estimated with four levels of natural mortality (scenario 2) fitted closely to the observed abundance with RSS of 31.1. The model of constant natural mortality (scenario 1) did not fit the data well (RSS = 68.4); the abundance was overestimated before 1979, underestimated from 1979 to 1982, and then the abundance of large crabs was overestimated during the mid-1980s.

Common features of the two scenarios were strong recruitment in the 1970s, relatively weak recruitment in recent years and higher natural mortality in small crabs than large crabs (i.e., $n2$ is larger than $n3$, Table 2). However, recruitment was much higher in the 1970s and lower in the early 1980s for scenario 1 than for scenario 2.

For Bristol Bay, legal RKC are defined as males ≥135 mm CL (Schmidt and Pengilly 1990). Legal crab abundances estimated by the model are compared to the observed legal crab abundance and the NMFS estimate of legal crab abundance in Fig. 2. The NMFS estimate of legal crab abundance was similar to the observed abundance except during the late 1970s when multi-hauls were frequently conducted for a single survey station. The observed legal crab abundance was fitted very well in scenario 2 (Fig. 2). The legal crab abundance increased dramatically in the middle and late 1970s and decreased precipitously in the early 1980s. In scenario 1 legal crab abundance was underestimated in the late 1970s and overestimated in the early and middle 1980s (Fig. 2).

Molting probabilities were estimated for three periods: 1972-1979, 1980-1984 and 1985-1992. Molting probabilities were very high during 1972-1979, low during 1980-1984 and intermediate during 1985-92 (Fig. 3). Estimated molting probabilities during these three periods were consistent with that estimated from the 1966-1969 tagging data (Balsiger 1974) but lower than those estimated from the tagging data during 1954-1961 (Balsiger 1974) (Fig. 3). The variation in growth increment per molt (not shown here) was close to that estimated from the tagging data during 1966-1969 (Balsiger 1974).

Estimated length frequencies for female RKC are shown in Fig. 4, and parameter estimates are summarized in Table 3. Similar to the fit of male crab abundances, the model as formulated in scenario 2 fitted the female crab length frequency data quite well (RSS = 13.8), whereas the model of scenario 1 fitted poorly (RSS = 44.2). The observed female abundance was highly variable by year, but the overall time trend was similar to males.

Estimated natural mortality was much higher for females than males. As with male crabs, natural mortality tended to be low in the 1970s and after the mid-1980s, and very high in the early 1980s (Table 3). Both young and old crabs suffered higher natural mortality.

Female recruitment (year-class strength) over time for scenario 2 was quite different from scenario 1 (Table 3). Recruitment derived by scenario 1 was stronger in the 1970s and after the mid-1980s and weaker in the early 1980s than by scenario 2. Overall, for the two scenarios, recruitment was very high in the 1970s and low since the early 1980s.

As with legal males, large (>90 mm CL; Stevens et al. 1992) female abundance increased to a peak in the late 1970s, decreased dramatically in the early 1980s, and remained at low levels since the early 1980s (Fig. 5). The abundance obtained under scenario 2 was close to the observed abundance from the NMFS trawl survey. In scenario 1 the abundance of large females was overestimated in the early 1970s and underestimated in the late 1970s and early 1980s (Fig. 5).

In summary, male and female RKC abundances modeled with constant natural mortality fitted the observed data poorly while abundances modeled with variable natural mortality (scenario 2) fitted the data quite well. The F statistic test (Schnute 1981) was used to test the null hypothesis that scenario 1 is the same as scenario 2. The alternative hypothesis is that scenario 2 fits the data better than scenario 1. We calculated F = 134.6 with 3 and 337 degrees of freedom for males and F = 147.9 with 3 and 201 degrees of freedom for females. For both males and females, p-values were less than 0.001. Thus, the null hypothesis was rejected, and we concluded that scenario 2, with 4 levels of natural mortality, statistically fitted the data better than the constant natural mortality scenario. Therefore, we used only the results from scenario 2 to study the S-R relationship in the following section.

S-R Relationship

Recruitment and effective spawning biomass were estimated from the length-based model using variable natural mortality (Table 3). For 18 out of the 22 years of abundance data modeled, male reproductive potential exceeded the actual number of mature female crabs. Therefore, during these years the effective spawning biomass equaled the mature female biomass. However, a shortage of mature male crabs occurred in four years: 1972, 1973, 1981 and 1982 (Fig. 6). Thus, the effective spawning biomass during these four years was set equal to the biomass of the hypothesized maximum number of female crabs that can be fertilized by the males available. The most severe shortfall occurred in 1982 after several years of heavy fishing and high natural mortality. After the fishery was closed in 1983, the surplus of mature males increased and peaked in 1986 (Fig. 6).

To include the maximum range of available S-R data in the study of S-R relationships, we estimated the effective spawning biomass from 1968 to 1971. We divided the relative abundances estimated by NMFS from the trawl survey data from 1968 to 1971 by the catchabilities estimated for 1972 under scenario 2 (0.5208 for males and 0.2462 for females) to obtain absolute abundance. The estimated male abundances and effective spawning biomass were similar in 1968 and 1973 and low in 1970 and 1971, approximately reflecting the trend of catch per unit effort (CPUE) in the U.S., Japanese, and Russian crab fisheries (Table 4). The estimated mature female crabs in 1968 and 1969 were apparently too high due to the low female catchability for 1972, but the effective spawning biomasses in these 2 years were close to that in 1973 because the estimated mature males were insufficient to mate with females (Table 4).

S-R data derived from scenario 2 were fitted with a general (equation (13)) and an autocorrelated (equation (14)) Ricker curves. Effective spawning biomass was plotted against logarithm of total age 6.2 recruit crabs (i.e., 7-year time lag) in Fig. 7. Estimates of Ricker S-R model parameters are summarized in Table 5. Weak recruitment was associated with extremely small spawning biomass and strong recruitment was produced by intermediate spawning biomass, suggesting a dome-shaped curve. Other main features of S-R data were extremely strong year-classes in the late 1960s and early 1970s and very low recruitment in recent years. Effective spawning biomass increased from the early 1970s to the end of 1970s and then decreased dramatically during the early 1980s when all recruitment levels were below those estimated by the fitted S-R curves. The autocorrelated Ricker model (R^2 = 0.65, *df* = 16) fitted the data slightly better than the general Ricker model (R^2 = 0.62, *df* = 16).

Alternative spawning stock indices examined were total female spawning biomass and total male and female spawning biomass. The fit by the autocorrelated Ricker model was similar among the three spawning stock indices: effective spawning biomass (R^2 = 0.65), total female spawning biomass (R^2 = 0.63), and total male and female spawning biomass (R^2 = 0.63) (Fig. 8). The R^2 for the general Ricker model were different among the three spawning indices: 0.62 for effective spawning biomass, 0.46 for total female spawning biomass, and 0.66 for total male and female spawning biomass. The poor fit by the total female spawning biomass for the general Ricker model was mainly a result of extremely high estimated female biomass in 1968 and 1969. We feel that effective spawning biomass is the best representation of a spawning index for the S-R model because a spawning index based on total male and female spawning biomass overemphasizes the male crabs for reproductive success and total female spawning biomass alone completely ignores the role of males.

Discussion

Common population reconstruction methods like Virtual Population Analysis and catch-at-age analysis do not apply to most crustacean populations because of the difficulty in aging these animals. Length-based population models are necessary for reconstructing such populations and have at least two advantages over age-based methods: (1) length data are easy and inexpensive to obtain, and (2) lengths can be measured accurately and aging errors are thus avoided. We found that the observed population abundances of Bristol Bay RKC were fitted well with a length-based model.

Natural mortality is the most important parameter in population reconstruction. In most of population reconstruction studies, natural mortality is assumed to be known and constant over time and age or length. At least nine sets of natural mortalities have been used for male Bristol Bay RKC (Table 6). These natural mortalities were estimated either from tagging (Hirschhorn 1966; Balsiger 1974) or trawl survey data (Reeves and Marasco 1980; Reeves 1988; Greenberg et al. 1991). Two conclusions can be made from these estimates: natural mortality is bowl-shaped over length and varies over time. However, these published estimates are so variable that one can assume almost any positive value. Fortunately, length frequency data from annual trawl surveys provide information to directly estimate the natural mortality for Bristol Bay RKC in the length-based model. Compared with other estimates of natural mortality, ours are generally low for old crabs and high for 1981 and 1982 (Table 6). These differences may be attributed to the different data sets and methods. Few published estimates of natural mortality for female RKC exist.

One assumption needed to estimate natural mortality from the survey data is that trawl catchability is equal to 1 during 1973-1993. There are at least three reasons to accept this assumption: (1) the survey abundance is estimated by the "area-swept" method, for which catchability would be close to 1 if the trawling speed was fast enough to prevent mature crabs from escaping, (2) catchability and natural mortality are confounded, forcing us to assume that catchability is known to estimate natural mortality or vice versa, and (3) the survey abundances are regarded as absolute abundances for harvest management. Additionally, Kruse and Collie (1991) assumed two levels of natural mortality (0.3 and 0.5) and different error structures to estimate abundance of legal Bristol Bay RKC. Catchability for these models ranged from 0.9 to 1.27 for legal-size crabs, suggesting that the assumption of unity for catchability is not misguided. Until convincing data invalidate the catchability assumption of unity, the same measurement scale should be used to apply results from this study to management of future harvests.

Natural mortalities of the Bristol Bay RKC population were estimated to be 3 to 6 times higher in the early 1980s than during other periods. This trend probably contributed to the collapse of the population in the early 1980s. Recruitment defined in this study was not as high in the early 1980s as it was in the 1970s, but nor was it below average. The high mortality decreases the number of recruits before they reach legal size. Our results support the conclusions of Otto (1986) and Greenberg et al. (1991) that high natural mortality was an important factor in the population collapse. Factors causing the high natural mortality are not clear. Physical environmental conditions, predation, disease, and handling mortality or a combination of all these factors may have contributed to high natural mortality (Otto 1986; Blau 1986). Stevens' (1990) speculation that senescence may partially be responsible for the high mortality was not supported by our results which indicated that high mortality occurs for almost all sizes of crabs.

We used mean growth increment per molt estimated from tagging data collected in the 1950s and 1960s. Reeves (1990) indicated that growth increment patterns have not changed, based on cursory examination of more recent tagging data. New growth data can be used to update our length-based model as it becomes available. The mean growth increment per molt can also be estimated from length frequency and abundance data, although we chose not to estimate it in this manner because of confounding problems with other parameters and because of the existence of tagging data.

We took a new approach to define a spawning stock index based on reproductive biology of RKC. The index, or *effective spawning biomass*, is the biomass of spawning females converted from the smaller of either mature female abundance or male reproductive potential which equals the sum of the products of mature male abundance and the corresponding number of mates by length. The index is easy to compute, conservative and intermediate between the two extreme approaches: i.e., assuming a unit weight of male crabs is as important as that of female crabs versus assuming no role of male crabs in reproduction. By applying the new index to the data in the past 22 years, a shortage of mature males for mating females occurred only for 4 years. The most severe shortage occurred in 1982 and was accompanied by a substantial failure of mating and spawning by mature females (Otto et al. 1990).

Perhaps, the most important result from this study is the development of S-R relationships. The dome-shaped Ricker curve is supported by strong recruitment associated with intermediate levels of spawning biomass and extremely low recruitment related to low spawning stock. The results of our fit to a general Ricker curve is consistent with the notion of a weak depensatory effect on recruitment when effective spawning biomass is very low. Unfortunately, our data do not lend themselves to testing the existence of depensatory effects. The most likely mechanisms for depensation are increased predation mortality, difficulty in finding mates (the Allee effect), and breakdown in social structure and migration patterns (Walters 1986). Aggregate (podding) behavior of young crabs may also contribute to the depensatory effect (Clark 1974), and the survey data indicate the geographic distribution of Bristol Bay RKC is slightly contracted in recent years than in the 1970s. Ancillary information also lends mixed support for a depensatory S-R relationship. The chance of delayed spawning or failure to spawn of multiparous females was higher in the 1980s than in the 1970s, but overall embryo clutch size was not different over time (Otto et al. 1990). Increased mortality due to predation and disease remains a key area of speculation on recruitment failure (Otto 1986; Blau 1986; Schmidt et al. 1992). Potential egg predators of RKC are found in Bristol Bay, Norton Sound, and Kodiak (Otto et al. 1990; Blau 1986), but they have not caused significant embryo mortality in Bristol Bay and Norton Sound populations (Otto et al. 1990).

The autocorrelated Ricker curve offers an alternative interpretation of the S-R data. Although this curve suggests that spawning stocks play a role on recruitment success, the most important factor on recruitment variation is autocorrelated events. Extremely strong year-classes occurred successively during the late 1960s and the early 1970s, which cannot be explained by spawning biomass alone; very weak recruitment occurred during recent years. Although the length-based model itself may generate a certain level of autocorrelation on recruitment, the most likely causes for recruitment autocorrelation are environmental conditions. The effects of environmental conditions on recruitment are further evident with lower than expected recruitment in the early 1980s when effective spawning biomass decreased. But causative environmental factors are unknown. A study of relationships between environmental conditions and recruitment is needed to fully understand crab recruitment dynamics, but effects of long-term environmental conditions and spawning stock can be very difficult to distinguish, particularly with autocorrelated errors (Walters and Collie 1988; Deriso et al. 1986).

In our case, strong recruitment was associated with a similar range of effective spawning biomass, and effective spawning biomass was very important at low stock sizes for both the general and autocorrelated Ricker curves. The main difference between the two curves is the level of effects of effective spawning biomass on recruitment success. The general Ricker curve emphasizes the importance of effective spawning biomass, whereas the autocorrelated curve focuses on environmental conditions. These two curves provide two alternative hypotheses for future S-R studies.

Stevens (1990) pointed out that the major problems with defining an S-R relationship for a crustacean population are lack of aging techniques and temperature-dependent growth of juveniles. Aging problems can be resolved with sophisticated statistical tools if a sufficient time series of length frequency data is available and if growth is a function of time. Temperature-dependent growth remains a challenge in establishing an S-R model. When juvenile growth is a function of degree-days, changes in the lag between spawning and recruitment complicate the S-R relationship. Definition of recruitment coming from a broad range of CL, as done in this study, can partially overcome this difficulty. If accurate temperature data are available and a reliable relationship between growth and temperature is established, the results from studies such as Stevens (1990) could be incorporated in length-based population models. Unfortunately, such information is currently unavailable. The autocorrelation of both recruitment and spawning stock may alleviate the impact of temperature-dependent growth of juvenile crabs on the S-R relationship.

The S-R relationship has an important implication for fisheries management and stock recovery of Bristol Bay RKC. First, the steepness of the ascending limb of the S-R curve suggests that recruitment will more likely fail with low spawning stocks. Ideally, the stock is managed to minimize the chance of its falling below an abundance level (threshold) where recovery is difficult. Currently, the stock is at such a low level that recovery will be difficult unless extremely favorable environmental conditions prevail to radically improve recruitment. Because these are rare events, the chance of Bristol Bay RKC recovering in the near future may be slim. Secondly, the dome-shaped S-R curve will result in low or intermediate recruitment when spawning stocks are extremely high. This compensation suggests that at high stock abundances harvest of females may lead to higher recruitment, higher long-term yield, and a more stable population (Botsford 1991).

Although our S-R relationship shares a dome-shaped feature with previous studies (Reeves and Marasco 1980; Reeves 1990; NPFMC 1990; Matulich et al. 1988, 1990; Greenberg et al. 1991), fundamental differences exist. Our results show that extremely low recruitment occurred under low spawning stocks, whereas strong year-classes were observed under low spawning stocks in all previous studies. The female spawning biomass (in thousand t) associated with maximum recruitment is 14.1 from Reeves (1990), 13.1-23.0 from Matulich et al. (1988), and 18.0-49.0 from Greenberg et al. (1991) with mature male biomass ranging from 0 to 150. In our study, effective spawning biomass ranged from 33.1-42.9 at maximum recruitment. Note that Reeves (1990) used fertilized females as spawning stock, which is converted into spawning biomass by multiplying average weight of mature females (0.785 kg) and dividing by average clutch size (77.7%) from 1970 to 1986 (Reeves 1988). Our results are closer to Greenberg et al. (1991) than to Reeves (1990) or Matulich et al. (1988). These differences result from different methods, assumptions, and data. In contrast to all previous studies that fitted stock-recruitment curves to the survey data directly, we estimated recruitment and spawning stock indices from the length-based population model and then fitted an S-R model to them. The advantages of our approach are that (1) the assumption of a one-to-one relationship between length and age of recruits is relaxed, and (2) measurement errors have been minimized by smoothing before fitting the S-R model. All previous studies also made a questionable assumption of constant catchability of survey gears before and after 1973. Crab abundances in all length-classes since 1973 are much higher than those before 1973 (Blau 1985; Stevens et al. 1992); this indicates to us a probable change in trawl catchability. Our results show that the survey data collected in 1972 are inconsistent with those collected in subsequent years (Fig. 1-4).

While our results for the S-R relationship share common grounds of density-dependent effects with several other studies (e.g., Reeves 1990; NPFMC 1990; Greenberg et al. 1991), they contradict the conclusion by Schmidt et al. (1992) of density-independent recruitment for the Kodiak RKC population. Schmidt et al. (1992) assumed a one-to-one relationship between length and age of recruits and constant catchability of the survey gears. There are some similarities in recruitment between the populations in Bristol Bay and Kodiak; e.g., extremely strong year classes occurred in both areas in the early 1970s (Blau 1985), but differences are also apparent. All year-classes after 1974 were very weak in Kodiak (Schmidt et al. 1992), whereas some average year classes occurred during the same period in Bristol Bay. Different results from these two populations may be due to fundamental differences in the population dynamics of both stocks, divergent trends in environmental conditions or disparities in methods to derive the S-R relationships.

Two alternative population models have been constructed for Bristol Bay RKC. Our length-based model is an extension of the two-stage model by Kruse and Collie (1991) in which only legal crabs are modeled. While the two-stage model lacks the capabilities of the length-based model to establish S-R relationships, predict future populations, and provide a framework to evaluate harvest strategies, it does have the flexibility to model error structures of observed abundances and catchability and requires less data. Only annual recruits to legal abundance, post-recruits, and total catch are required for the two-stage model. Both our model and recursive age-structured models developed by Matulich et al. (1988, 1990) and Greenberg et al. (1991) model the entire surveyed population. We modeled abundances by length and shell condition, and estimated a parameter set which produces a population as close to the observed population as possible, whereas the recursive age-structured models used one set of observed abundances by age to explain another set of observed age-specific abundances. The recursive age-structured models require only abundances by age and total annual catches. In cases in which shell condition data are unavailable, only the recursive age-structured models can be applied. On the other hand, only the two-stage model may be applied in cases where length and age data are unavailable or unreliable. Our model and recursive age-structured models have an advantage in that they can be used to explore the influences of sex ratio on reproductive potential of crab stocks.

The RKC fishery in Bristol Bay harvests only legal crabs. Mature male and legal male harvest rates were computed by dividing total catch by the mature male abundance and legal crab abundance estimated in scenario 2, respectively. The legal male harvest rates ranged from 0.36 to 0.53 in the 1970s and the early 1980s, and fluctuated between 0.15 and 0.41 in recent years (Fig. 9). The mature male harvest rates were close to 0.2 in the early and middle 1970s and peaked at 0.38 in 1980 (Fig. 9). These high harvest rates and legal crab abundances produced the record catches in the late 1970s and early 1980s, which were followed by the quick collapse of the population. Harvest not only removes legal male crabs but also reduces abundances of sublegal male and female crabs through handling mortality (Kruse *in press*). Although we have no estimates of handling mortality, the ratio of bycatch of combined sublegal male and female RKC to the catch of legal males in the Bristol Bay RKC fishery was about 1.7 in 1990-1992 (Beers 1991, 1992). The mortality of this bycatch could be substantial after exposures to cold temperatures for a period of time (Carls and O'Clair 1990) or due to injuries caused by handling (Kennelly et al. 1990). In summary, our results indicate that high natural mortality coupled with high harvest rates may have contributed to the collapse of the Bristol Bay RKC population. Low spawning biomass in the early 1980s appears to be responsible for its continued lack of recovery.

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Figure Captions

Figure 1. Comparison of observed and estimated length frequencies of Bristol Bay male red king crabs by year for two scenarios of instantaneous natural mortality.

Figure 2. Comparison of observed and estimated legal male red king crab abundances in Bristol Bay using two scenarios of natural mortality. Boxes denote observed values we calculated from trawl survey data without post-stratification, whereas asterisks show values estimated by NMFS with the post-stratification method.

Figure 3. Comparison of estimated probabilities of molting of male red king crabs in Bristol Bay for different periods. Molting probabilities for periods 1954-1961 and 1966-1969 were estimated by Balsiger (1974) from tagging data. Molting probabilities for periods 1972-1979, 1980-1984 and 1985-1992 were estimated under the scenario of four levels of natural mortality.

Figure 4. Comparison of observed and estimated length frequencies of female red king crabs in Bristol Bay by year for two scenarios of natural mortality.

Figure 5. Comparison of observed and estimated large (CL > 90 mm) female red king crab abundances in Bristol Bay using two

scenarios of natural mortality. Boxes denote observed values we calculated from trawl survey data without post-stratification, whereas asterisks show values estimated by NMFS with the post-stratification method.

Figure 6. Ratio of male reproductive potential to the actual mature female red king crab abundance in Bristol Bay.

Figure 7. Relationships between effective spawning biomass and the logarithm of total recruits at age 6.2 (i.e., 7-year time lag) for red king crabs in Bristol Bay. Numerical label is brood year, and two lines are general and autocorrelated Ricker curves.

Figure 8. Relationships between the logarithm of total recruits at age 6.2 (i.e., 7-year time lag) and total female spawning biomass (upper) and between the logarithm of total recruits and total male and female spawning biomass (bottom) for red king crabs in Bristol Bay. Numerical label is brood year, and two lines are general and autocorrelated Ricker curves.

Figure 9. Catch, mature male crab harvest rate, and legal male crab harvest rate of red king crabs in Bristol Bay from 1972 to 1992 under the scenario of four levels of natural mortality.

Table 1. Average weight and assumed maximum number of female mates for male red king crabs in Bristol Bay by length-class.

Male Carapace Length (mm)	Average Male Weight (kg)	Number of Female Mates
0-119		0.0
120-124	1.43	1.0
125-129	1.63	1.2
130-134	1.84	1.4
135-139	2.06	1.6
140-144	2.31	1.8
145-149	2.58	2.1
150-154	2.86	2.4
155-159	3.17	2.7
160+	3.50	3.0

Table 2. Summary of parameter estimates for a length-based population model of male red king crabs in Bristol Bay with two scenarios of natural mortality. Recruits, R_t, are in millions of crabs.

Parameter	Scenario 1 Constant M	Scenario 2 4 Levels of M
N_{72}	45.050	41.787
β	0.228	0.359
β_r	2.225	1.728
α_1	66118.620	357204.800
α_2	21.404	20525.250
α_3	43461.150	290974.700
β_1	0.069	0.082
β_2	0.027	0.077
β_3	0.077	0.091
MY_{72}-MY_{79}	0.268	0.193
$MY_{80,83,84}$	0.268	0.711
$MY_{81,82}$	0.268	1.259
MY_{85}-MY_{92}	0.268	0.180
n1	125.102	108.881
n2	0.061	0.157
n3	0.000	0.000
R_{73}	62.826	37.032
R_{74}	37.973	24.877
R_{75}	52.693	37.553
R_{76}	91.893	51.516
R_{77}	84.215	56.298
R_{78}	29.072	27.686
R_{79}	10.540	14.128
R_{80}	12.443	24.620
R_{81}	9.616	22.302
R_{82}	12.474	30.032
R_{83}	8.264	14.515
R_{84}	12.825	19.554
R_{85}	12.718	10.637
R_{86}	14.016	7.620
R_{87}	12.635	7.930
R_{88}	10.974	6.677
R_{89}	9.072	5.423
R_{90}	2.617	1.700
R_{91}	4.156	3.521
R_{92}	7.837	6.555
R_{93}	3.751	3.075
RSS	68.381	31.114
df	340	337

Table 3. Summary of parameter estimates for a length-based population model of female red king crabs in Bristol Bay with two scenarios of natural mortality. Recruits, R_t, are in millions of crabs and effective spawning biomass, SP_t, in thousand t.

Parameter	Scenario 1 Constant M	Scenario 2 4 Levels of M
N_{72}	66.394	55.657
β	1.060	1.580
β_r	1.710	0.542
MY_{72}-MY_{78}	0.591	0.311
MY_{79}-MY_{81}, MY_{85}	0.591	0.561
MY_{82}-MY_{84}	0.591	2.097
MY_{86}-MY_{92}	0.591	0.260
n1	119.679	109.482
n2	0.063	0.067
n3	0.009	0.019
R_{72}/SP_{72}	na /31.693	na /29.398
R_{73}/SP_{73}	66.079/37.402	32.522/34.956
R_{74}/SP_{74}	62.190/50.705	30.112/47.573
R_{75}/SP_{75}	47.901/45.742	23.380/46.892
R_{76}/SP_{76}	56.033/48.053	34.148/51.180
R_{77}/SP_{77}	110.888/78.786	75.969/74.168
R_{78}/SP_{78}	83.283/72.080	56.438/84.078
R_{79}/SP_{79}	44.686/50.283	21.688/74.433
R_{80}/SP_{80}	46.792/45.632	47.947/61.776
R_{81}/SP_{81}	22.098/22.382	17.420/30.624
R_{82}/SP_{82}	17.347/14.232	26.146/12.033
R_{83}/SP_{83}	4.176/11.431	6.880/ 5.339
R_{84}/SP_{84}	8.559/10.123	14.814/ 7.145
R_{85}/SP_{85}	4.885/ 6.901	7.686/ 3.861
R_{86}/SP_{86}	5.955/ 6.211	5.604/ 4.602
R_{87}/SP_{87}	19.115/13.024	11.775/ 9.461
R_{88}/SP_{88}	17.417/13.856	7.622/11.813
R_{89}/SP_{89}	18.659/15.063	7.924/13.543
R_{90}/SP_{90}	7.460/ 9.357	1.265/11.886
R_{91}/SP_{91}	9.737/ 9.147	4.780/11.684
R_{92}/SP_{92}	6.128/ 6.860	3.977/11.309
R_{93}/SP_{93}	7.472/ 6.856	4.090/10.884
RSS	44.201	13.784
df	204	201

Table 4. Comparison of CPUE, legal crab abundance, mature male abundance, mature female abundance and effective spawning biomass of red king crabs in Bristol Bay from 1968 to 1973 for four levels of natural mortality. The Japanese and Russian CPUE data are from Hoopes et al. (1972) and the U.S. CPUE data are from Phinney (1975). The legal and mature male and female crab abundances, and effective spawning biomass in 1971 are an average of those in 1970 and 1972.

Year	1968	1969	1970	1971	1972	1973
No. crabs/pot lift (U.S.)	26.9	17.8	17.4	20.3	19.5	24.9
No. crabs/tan of net (Japan)	7.5	7.2	7.3	NA	NA	NA
No. crabs/tan of net/day (Russia)	0.25	0.20	0.18	NA	NA	NA
Legal crabs (×1000)	13817	13561	10078	10457	10835	11787
Mature male crabs (×1000)	23186	27949	20108	20080	20051	25818
Mature female crabs(×1000)	126774	88250	44061	44118	44174	53293
Effective spawning biomass (thousand t)	34.83	36.57	25.53	27.46	29.40	34.96

Table 5. Parameter estimates of Ricker stock-recruitment models (equations (13) and (14)) for Bristol Bay red king crab. Spawning stock is measured by effective spawning biomass in t. Recruitment is measured by male recruits, female recruits, or total male and female recruits combined at age 6.2 in thousands (i.e., 7-year time lag). Degrees of freedom are 16.

	General Model			Autocorrelation Model		
	Male	Female	Total	Male	Female	Total
r1	1.7137	2.0855	1.9132	NA	NA	NA
r2	-6.2514	-9.3511	-7.2050	0.0571	0.2011	0.8389
r3	4.79e-5	6.67e-5	5.78e-5	2.09e-5	2.59e-5	2.33e-5
a1	NA	NA	NA	0.6635	0.4862	0.6029
R^2	0.58	0.62	0.62	0.66	0.58	0.65
σ	0.67	0.69	0.65	0.55	0.71	0.59

Table 6. Comparison of published and estimated instantaneous natural mortality for male red king crabs in Bristol Bay.

Reference	Carapace Length (mm)										
	87	102	115	125	135	145	152	157	162	167	170
					0.07	0.06	0.21	0.36	0.63	0.86	0.93
2	0.51	0.37	0.57	0.30	0.09	0.24	0.46	0.57	0.93	0.63	1.22
3	0.06	0.12	0.12	0.08	0.08	0.15	0.52	0.66	0.75	0.81	
4						0.11	0.23	0.50	0.57	0.61	0.76
5	0.58	0.70	0.71	0.34	0.33						
6	1.21	0.72	0.49	0.65	1.13						
7		0.48	0.08	0.07							
8		0.75	0.23	0.50							
9					0.30	0.30	0.30	0.30	0.30	0.30	0.30
10		1.10	0.50	0.27	0.27	0.27	0.27	0.27	0.27		
11		0.57	0.19	0.19	0.19	0.19	0.19	0.19	0.19		
12		2.10	0.71	0.71	0.71	0.71	0.71	0.71	0.71		
13		3.71	1.26	1.26	1.26	1.26	1.26	1.26	1.26		
14		0.53	0.18	0.18	0.18	0.18	0.18	0.18	0.18		

1: Hirschhorn, G. 1966.

2: Balsiger, J.W. 1974. (based on 1954-1961 data set)

3: Balsiger, J.W. 1974. (based on 1966-1968 data set)

4: Reeves, J.E. and R. Marasco. 1980.

5: Reeves, J.E. 1988. (based on 1969-1980 data set)

6: Reeves, J.E. 1988. (based on 1981-1986 data set)

7: Greenberg, J.A., S.C.Matulich, and R.C.Mittelhammer. 1991. (Based on 1977-1980 data set)

8: Greenberg, J.A., S.C.Matulich, and R.C.Mittelhammer. 1991. (Based on 1981-1989 data set)

9: NPFMC. 1990.

10: Scenario 1 of this study.

11: Scenario 2 of this study, for 1972-1979.

12: Scenario 2 of this study, for 1980 and 1983-1984.

13: Scenario 2 of this study, for 1981-1982.

14: Scenario 2 of this study, for 1985-1992.

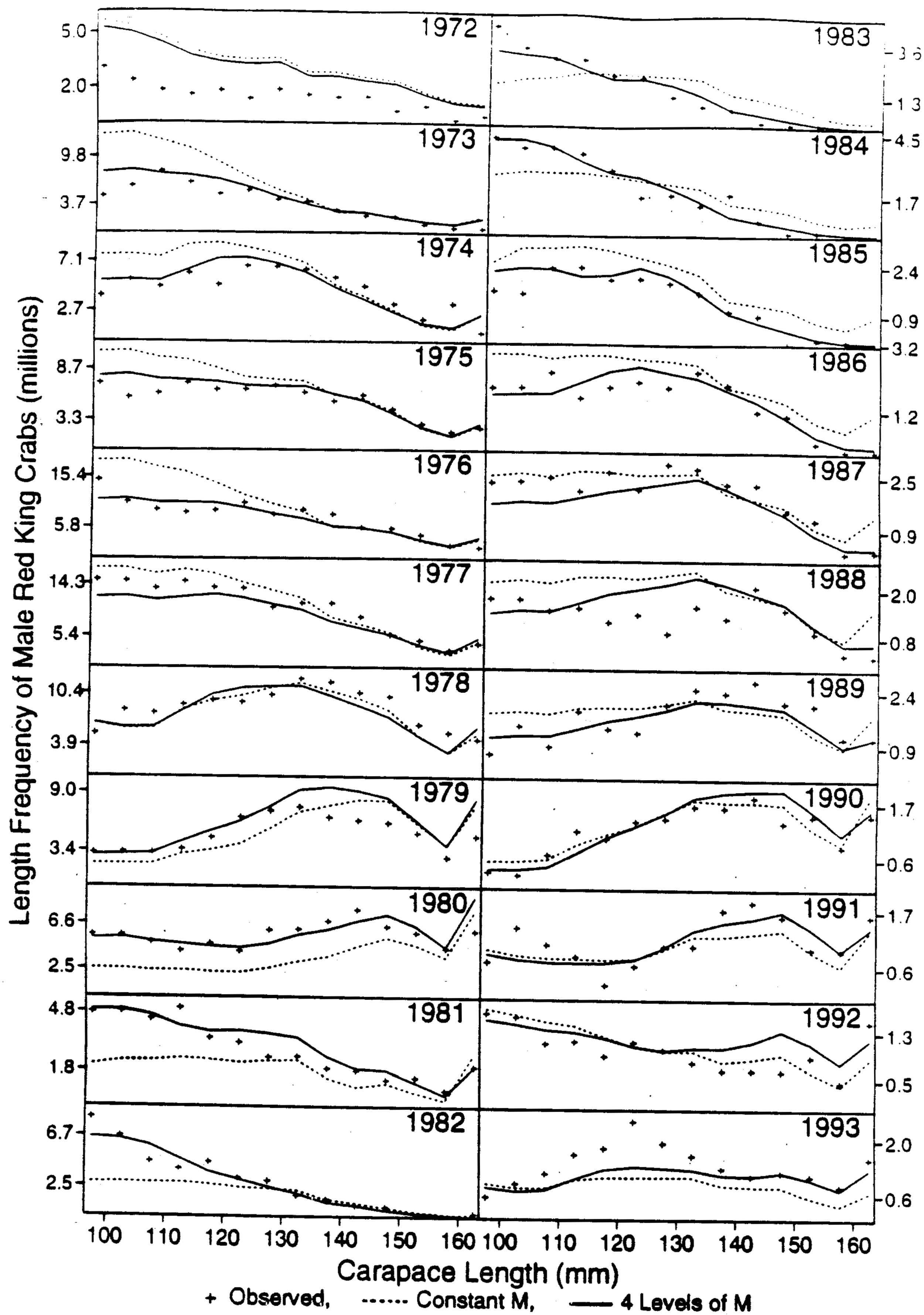

Length Frequency of Male Red King Crabs (millions)
Carapace Length (mm)
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
1982
1983
1984
1985
1986
1987
1988
1989
1990
1991
1992
1993
5.0
2.0
9.8
3.7
7.1
2.7
8.7
3.3
15.4
5.8
14.3
5.4
10.4
3.9
9.0
3.4
6.6
2.5
4.8
1.8
6.7
2.5
1.3
4.5
1.7
2.4
0.9
3.2
1.2
2.5
0.9
2.0
0.8
2.4
0.9
1.7
0.6
1.7
0.6
1.3
0.5
2.0
0.6
100
110
120
130
140
150
160
100
110
120
130
140
150
160
+ Observed,
------ Constant M,
—— 4 Levels of M

Figure 1

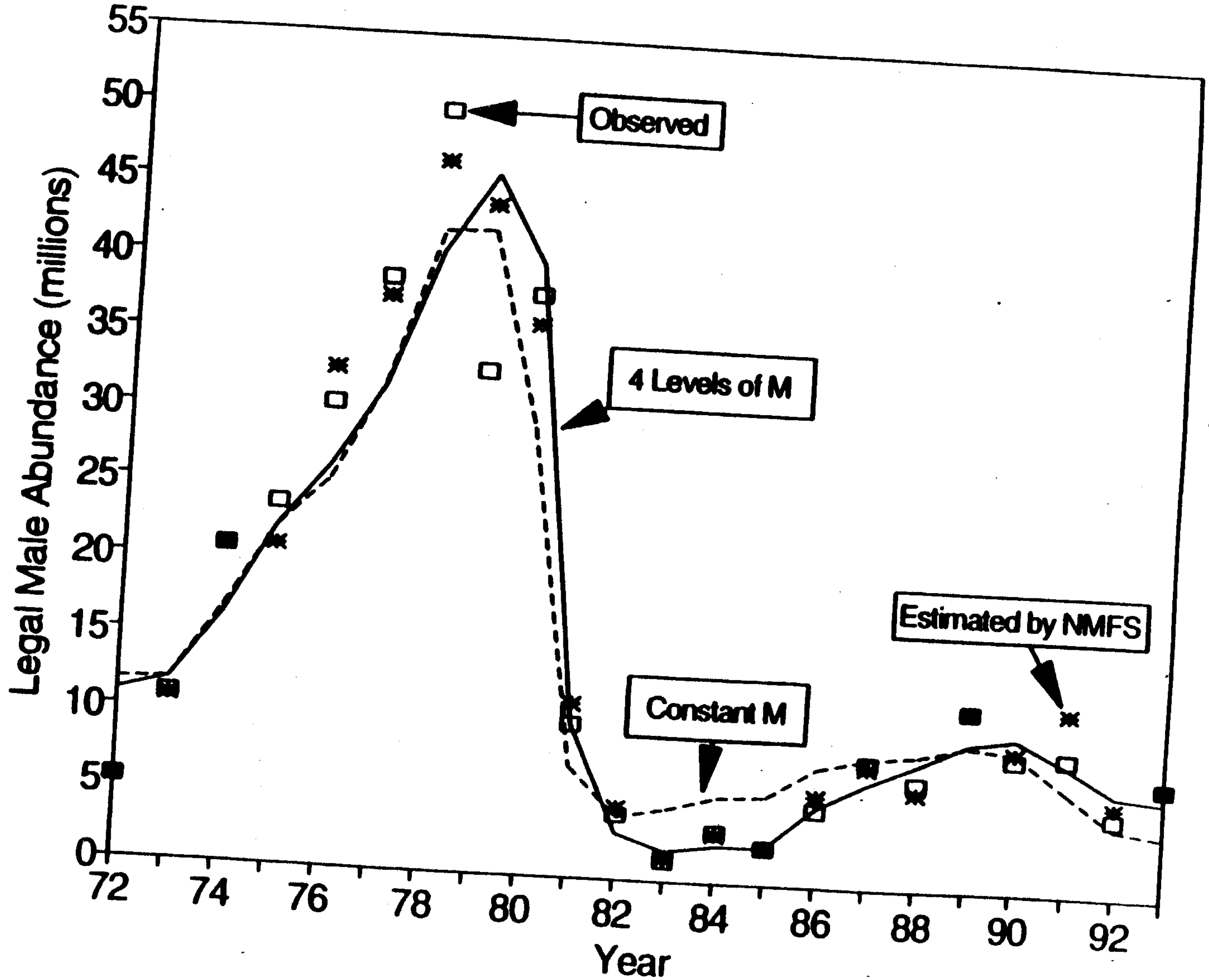
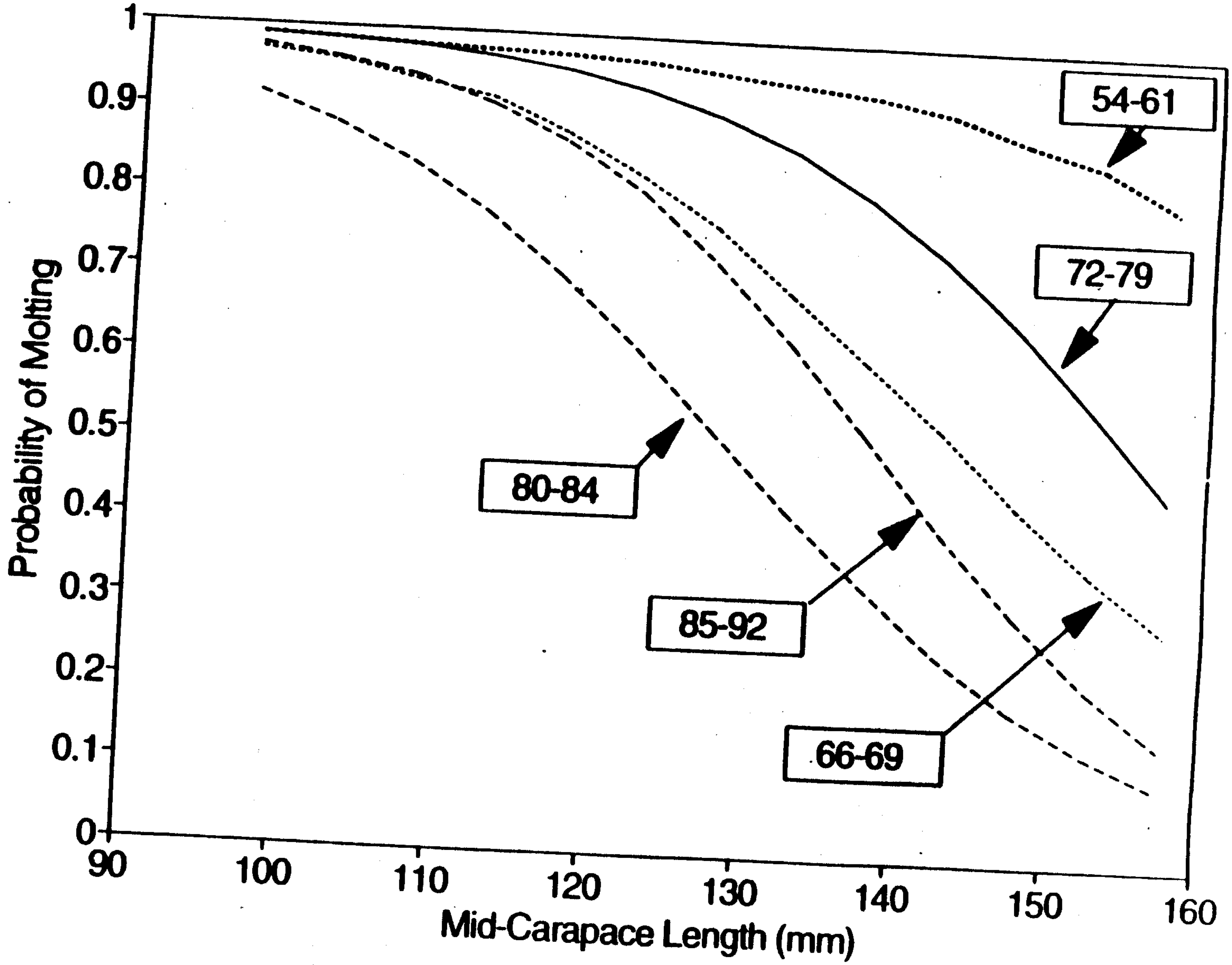

Legal Male Abundance (millions)
55
50
45
40
35
30
25
20
15
10
5
0
72
74
76
78
80
82
84
86
88
90
92
Year
Observed
4 Levels of M
Constant M
Estimated by NMFS

Figure 2



Probability of Molting
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
90
100
110
120
130
140
150
160
Mid-Carapace Length (mm)
54-61
72-79
80-84
85-92
66-69

Figure 3

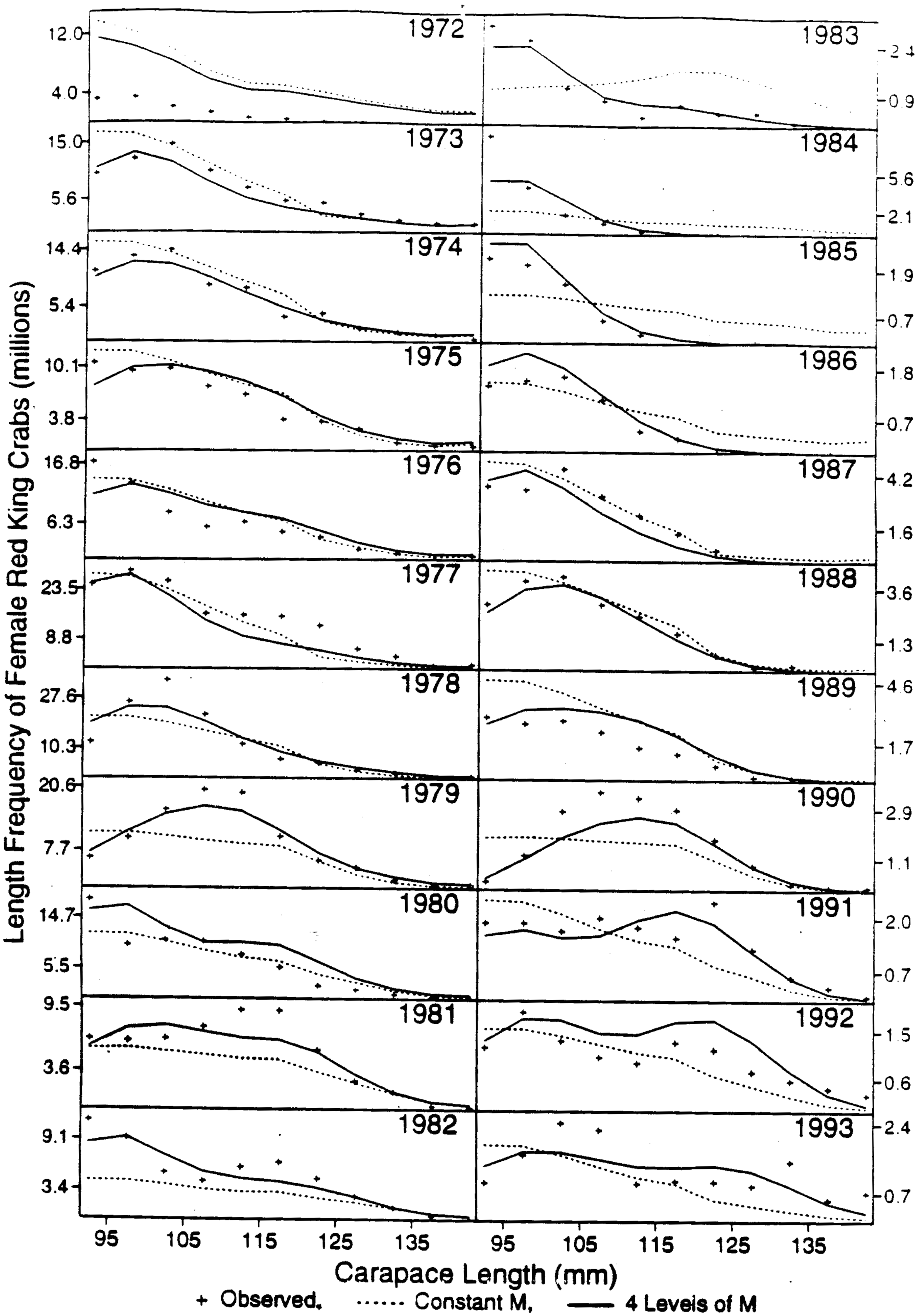

Length Frequency of Female Red King Crabs (millions)
Carapace Length (mm)
+ Observed, ... Constant M, —— 4 Levels of M
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
1982
1983
1984
1985
1986
1987
1988
1989
1990
1991
1992
1993
95 105 115 125 135

Figure 4

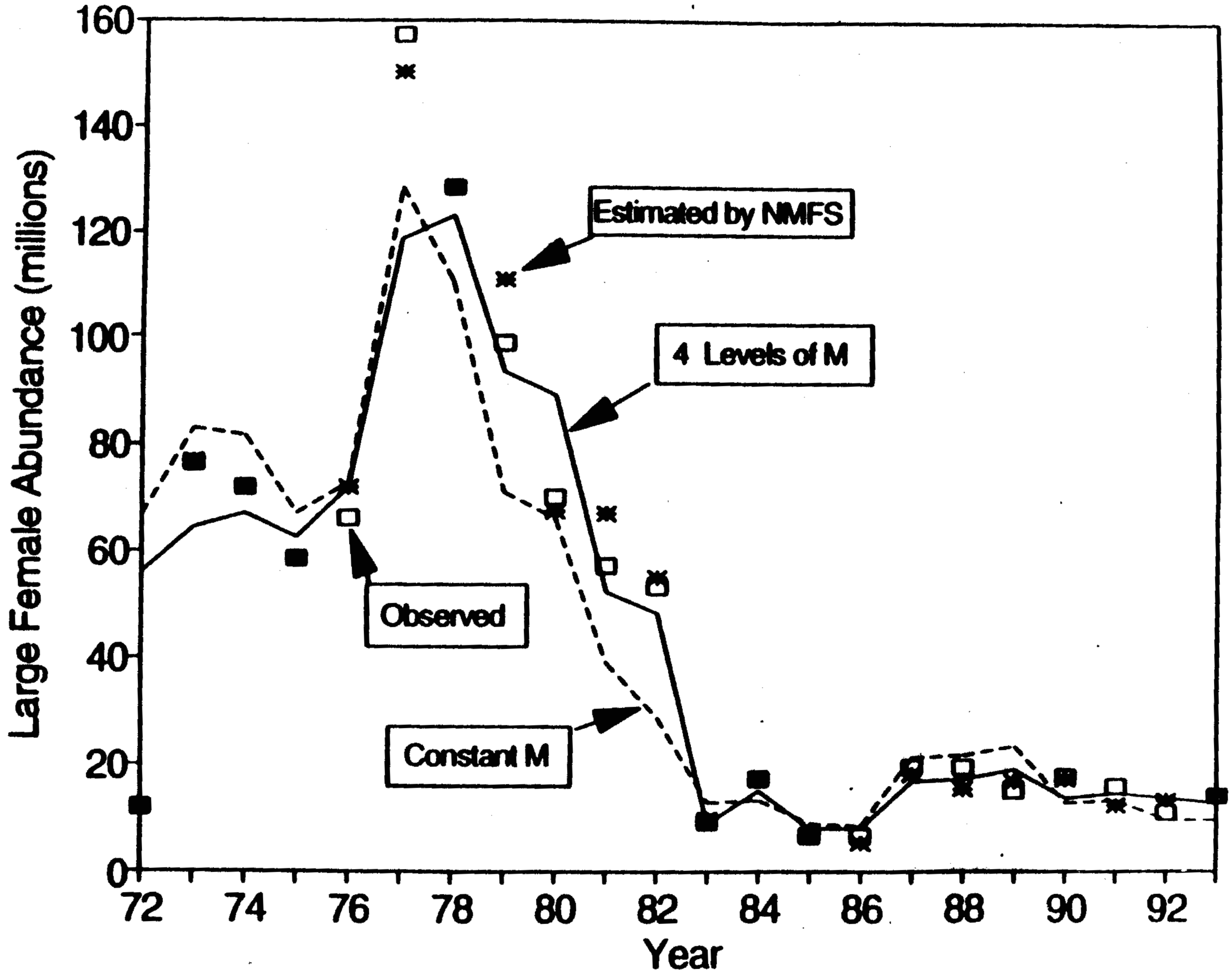

Large Female Abundance (millions)
160
140
120
100
80
60
40
20
0
72
74
76
78
80
82
84
86
88
90
92
Year
Estimated by NMFS
4 Levels of M
Observed
Constant M

Figure 5

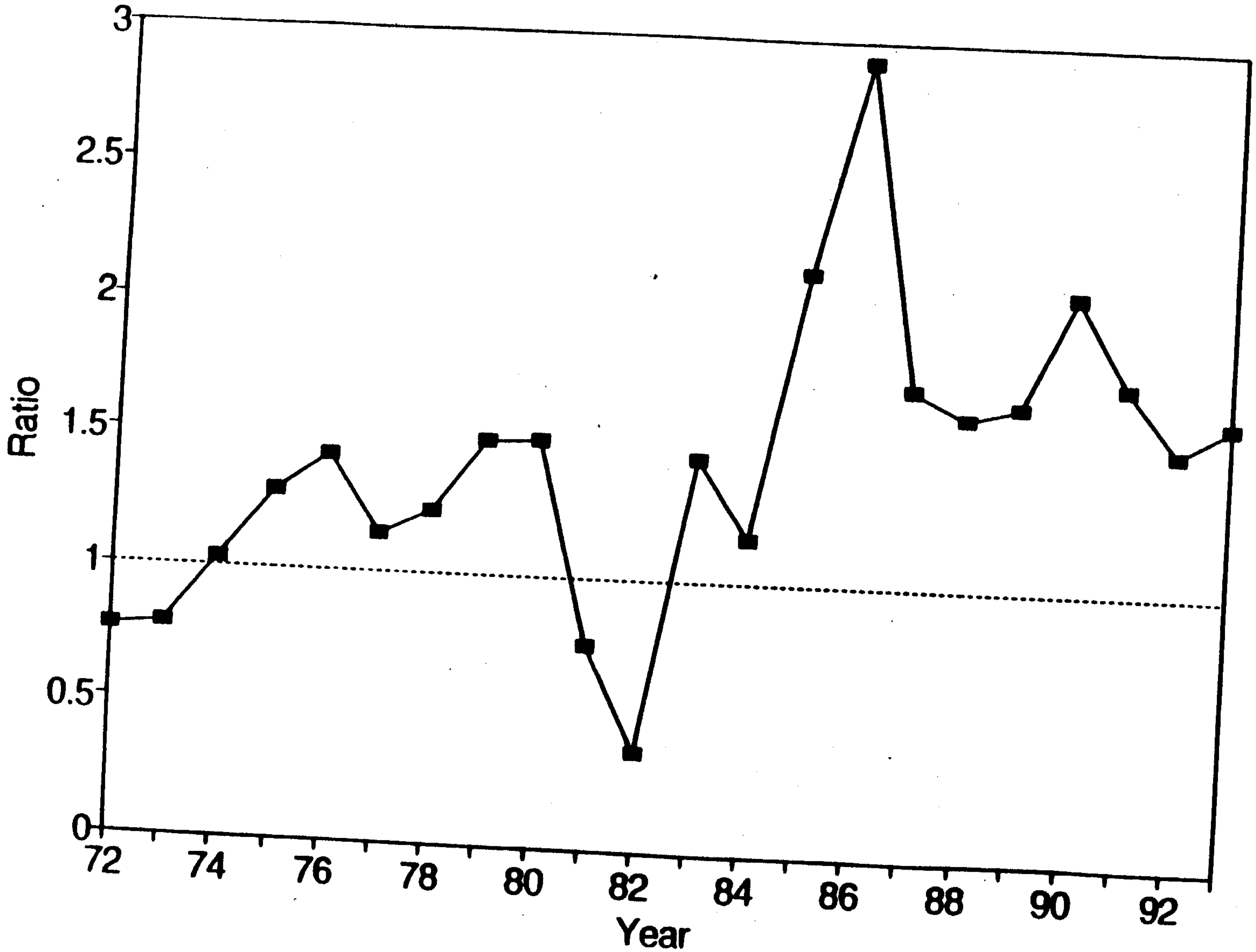


Figure 6

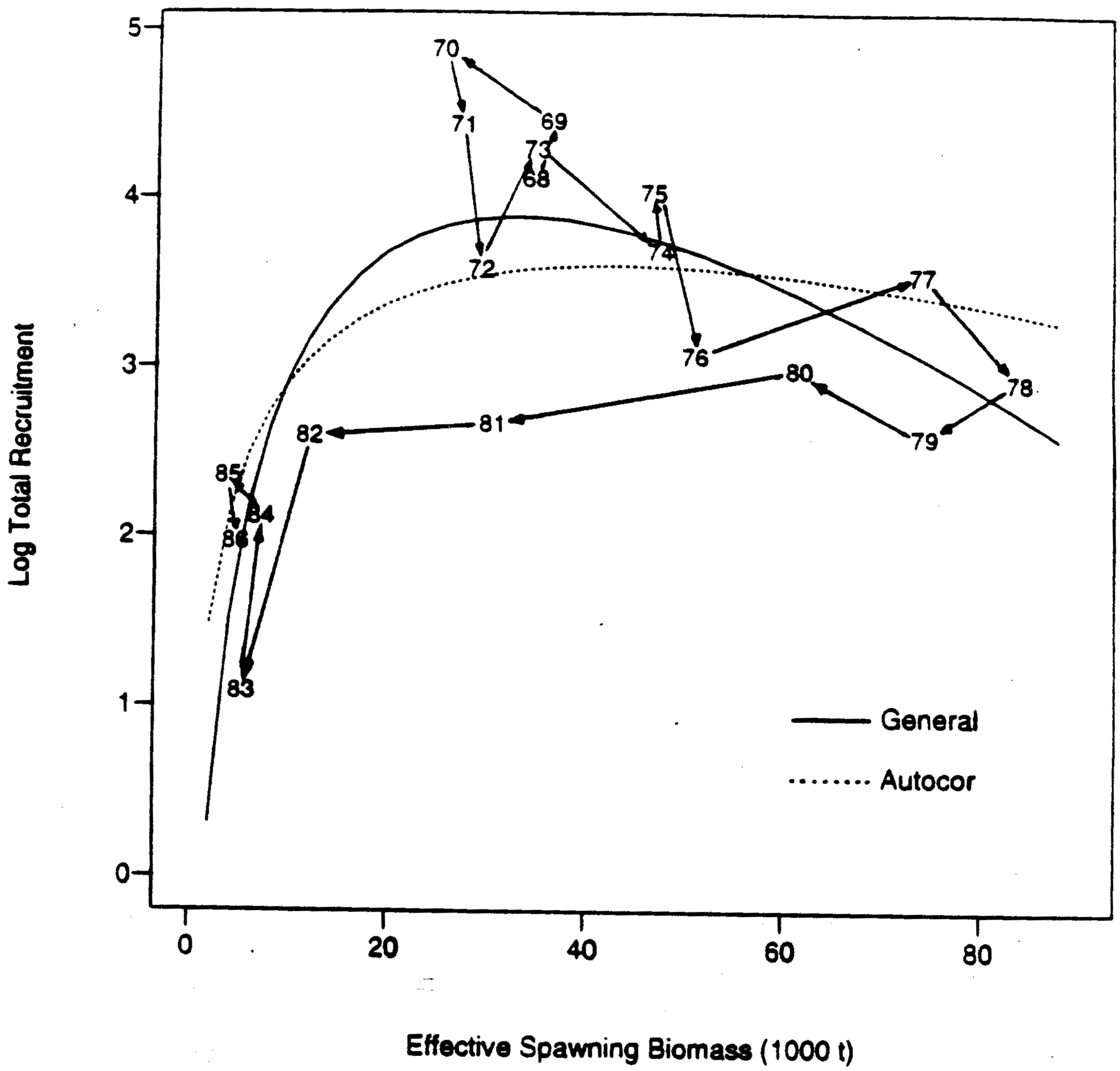

Log Total Recruitment
Effective Spawning Biomass (1000 t)
General
Autocor
0
1
2
3
4
5
0
20
40
60
80
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86

Figure 7

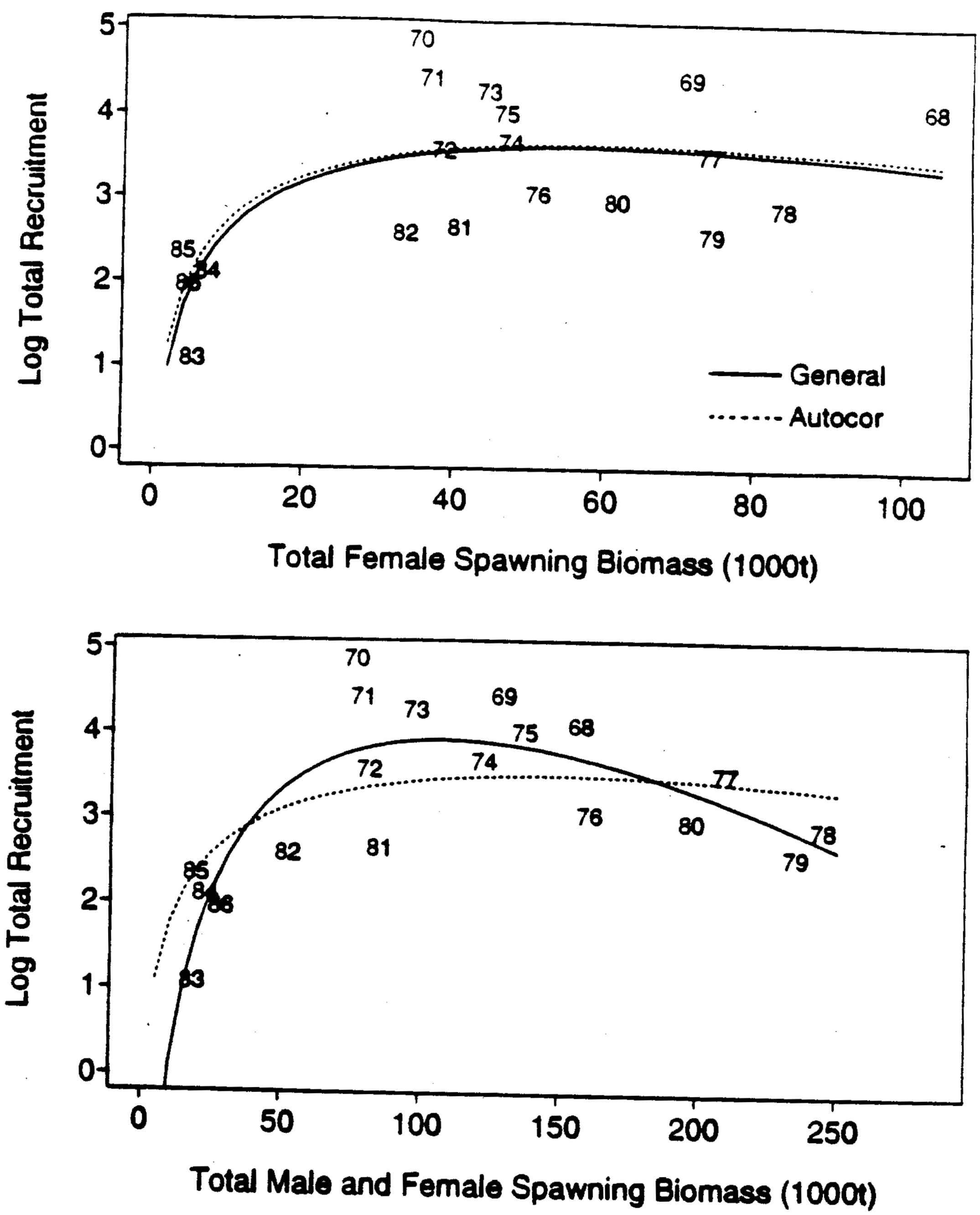
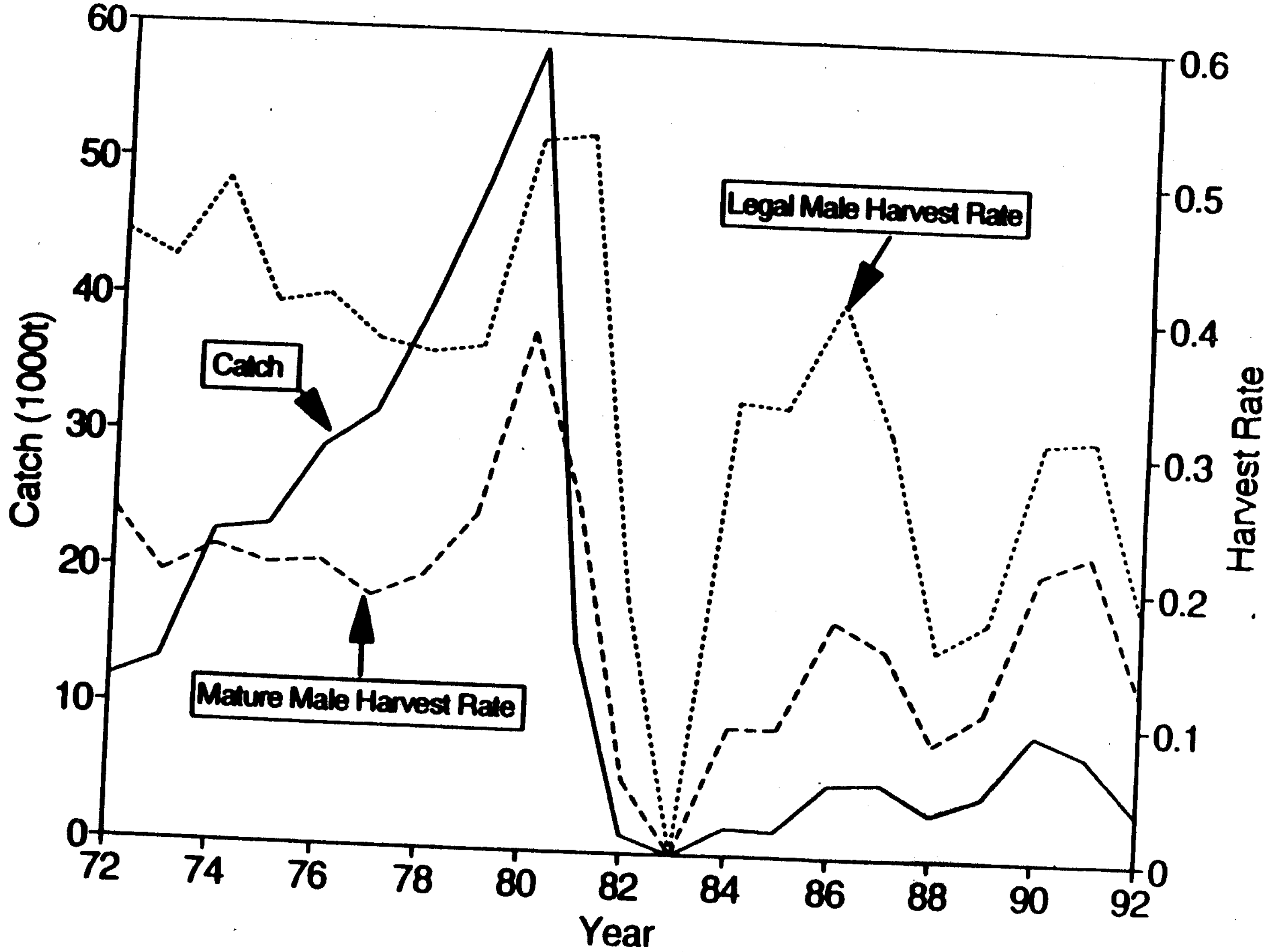

Log Total Recruitment
Total Female Spawning Biomass (1000t)
General
Autocor
Log Total Recruitment
Total Male and Female Spawning Biomass (1000t)

Figure 8



60
50
40
30
20
10
0
Catch (1000t)
0.6
0.5
0.4
0.3
0.2
0.1
0
Harvest Rate
72
74
76
78
80
82
84
86
88
90
92
Year
Catch
Mature Male Harvest Rate
Legal Male Harvest Rate

Figure 9