Lowell Wakefield Fisheries Symposia Series

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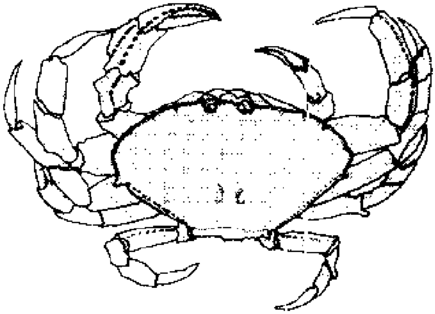
Proceedings of the
Symposium on Dungeness Crab Biology and Management



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Lowell Wakefield Fisheries Symposia Series

Proceedings of the Symposium on Dungeness Crab Biology and Management

October 9-11 1984
Anchorage, Alaska, USA

Brenda R. Melteff
Symposium Coordinator

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

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Acknowledgments

Sponsors of the Symposium on the Biology and Management of Dungeness Crab, the third in the Lowell Wakefield Fisheries Symposia Series, are the Alaska Department of Fish and Game, The Crustacean Society, and the Pacific Sea Grant College Program.

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Preface

The Dungeness crab, *Cancer magister*, has traditionally been commercially fished in California, Oregon, Washington, and British Columbia. In recent years these stocks have declined while the Dungeness fishery of Alaska has increased. This symposium, the third in the Lowell Wakefield Fisheries Symposia Series, was convened to review the biology and management of the Dungeness crab in relation to its recent decline and to discuss prudent management of the fishery in Alaska. Sponsors of the symposium are the Alaska Department of Fish and Game, The Crustacean Society, and the Pacific Sea Grant College Program comprised of the Sea Grant programs at the Universities of Alaska, California, Hawaii, Washington, and Oregon State University.

The symposium program was structured by a program planning committee whose members are:

Steven K. Davis	North Pacific Fishery Management Council
Al Kimker	Alaska Department of Fish and Game
Paul Larson	Alaska Department of Fish and Game
Robert S. Otto	National Marine Fisheries Service
Thomas C. Shirley, Chair	University of Alaska, Juneau

Welcome and Introduction

Welcome

Ole Mathisen
Dean, School of Fisheries and Science
University of Alaska, Juneau

I have been given the privilege of extending a hearty welcome to all the participants of this symposium on Dungeness Crab Biology and Management. I am afraid that my credentials are not fully impeccable since my interest has been directed toward other organisms. However, this meeting strikes an early chord in my memory. The first trip I ever made aboard a fishing vessel in the USA was with a crab boat from Aberdeen, Washington.

As I scan the program and the list of attendants and look at this audience, it appears like a "Who's Who" in contemporary invertebrate marine biology along the Pacific Coast. The symposium committee has worked hard to organize a constructive program and has assembled an array of impressive speakers dealing with life history, population dynamics and management problems. Clearly, the proceedings of this symposium will result in a volume which will remain as a storehouse of our present knowledge of the Dungeness Crab.

But since I am pulling up in years and have participated in a number of meetings and symposia, both national and international, permit me to strike a disconsonant chord by asking: Are we really making progress, or, phrased in another way, Are we really asking the kind of questions which should be raised in this decade? I have witnessed the period with the breakthrough of formal population dynamics in the 50s, and elaborate management models in the 60s, both single and multi-species models, which were partly made obsolete or inadequate in the 70s. We are finally gaining some insight into the structure of an aquatic population and the way life history strategies have evolved. As a result, we catch glimpses of the capacity of the living organisms to respond in a manner which ultimately will benefit survival of the species in question. The harvest process involves much more than removing a certain number of specimens from a population. What really is happening is an alteration of the structure of the population.

Perhaps the changes which we are observing in vital population parameters, decline in abundance and susceptibility to stress and diseases, are primarily due to changes in the underlying population genetics. This brings the conference back into a more general and penetrating framework of all the processes taking place in the environment and especially in the case of an important decapod the coupling existing between primary and benthic production.

I suppose that what I am trying to bring across is the new era which we are entering with a need for a much more basic understanding of this particular organism, its evolutionary history and its latent possibilities to respond favorably to an altering environment in the context of survival values, rather than a fragmented study of single or limited events.

This again brings us back to another central theme for species under harvest. Regardless of how much we study and how many facts we are assembling, there will always remain a large residue of unknown factors. For exploited species, this is tantamount to making management decisions in the face of uncertainties. Again the question is raised about the underlying risk function which must govern the decision making process. If observed from this angle, this symposium may produce some important side benefits.

I encourage participants in this conference, in addition to delivery of their prepared speeches, to engage freely in expression of the thoughts that we all harbor of the underlying processes which govern the external manifestations and ultimate survival of the peculiar creature we know as Cancer magister.

In this endeavor, I extend to the participants of this conference my best wishes for new and innovative solutions to old problems.

Introduction

Steve Pennoyer
Deputy Commissioner
Alaska Department of Fish and Game, Juneau

Dungeness Crab Management

The dungeness crab fishery in Alaska historically has been a very small part of our total shellfish fisheries picture. In 1980, the statewide harvest of king and tanner crab was 315 million pounds, compared to only 6.4 million pounds of dungeness (about three percent of total value). The dungeness crab harvest has provided a season to certain small boats in Alaska in limited areas, but overall, was not a significant economic factor to our crab fleet. Our total crab management and research budget was only 2.5 million dollars in 1984 and quite naturally, a very small amount of it (about five percent) was spent on dungeness crab research and management.

Reviewing our management of the past few years, I can find very little in the way of flexible management applied to the species. In-season emergency orders, when issued, have generally revolved around softshell periods and concern about high CPUE and handling mortality. I could only find one emergency order in recent years related to a decline in CPUE and a concern for associated handling of mortalities due to high effort. Statewide, size limits for males and restrictions against taking female crab are the same for all areas. Seasons are also similar, with some variation in opening dates by area, based primarily on local desires, more than any biological data. Generally, the seasons are very lengthy and there appears to be no direct relationship between regulatory seasons and sensitive periods of breeding/molting for crab. Closed seasons in some areas seem to have just been a mechanism to force removal of the pots from the water during periods of relatively low CPUE to avoid incidental harvesting and derelict pot problems. Apparently, management has been entirely the three-S system in its least restrictive form, with harvest related more to the amount of effort placed on the stocks than any direct management of the fishery.

Most of our past reports imply that the size of the Alaskan harvest has been more an economic factor related to the status of stocks and the market along the west coast. A relationship probably does exist, but the degree to which Alaskan stock status--and the status of other shellfish fisheries in Alaska--influences the relationship is not clear. A dramatic upturn in the last three years is obvious.

It is common knowledge that economics drive the fishery, and that simple protection by sex and size limits with some seasonal monitoring would be adequate to protect the stocks and insure sustainable utilization of the harvestable surplus. Recently, however, this fishery has expanded dramatically. From 1980 to 1983, the number of vessels increased by 347 percent, and the catch by 263 percent. Dungeness became eight percent of the total shellfish value statewide, and 12 percent of the total landings. The tremendous increase in effort and harvest in recent years, coupled with a lack of concrete biological data, should lead us to question this simplistic approach to management. Work to date has certainly not given us the answers to what the correct approach should be.

Our documentation on dungeness crab populations in Alaska has been, at least until recently, very poor. Exploitation rates, population size, recruitment levels, growth rates, and even age structure for most populations are largely unknown. We need to analyze whether current size limits are appropriate for stocks throughout the range in Alaska. Work is needed to determine the amount and impacts of handling that occurs on sublegal male and female crab. There has been no gear research done on mesh size or escape ring effectiveness. While there has been some tagging, for most areas, we have little knowledge of what comprises a stock of dungeness crab.

It seems to me there are a number of questions about our program direction here in Alaska that need to be answered. We need to examine the data base available on Alaska dungeness crab and ask ourselves if it is adequate, and then suggest either further monitoring or research, as might be appropriate. We need to look at our three-S system of management and decide if it is doing the job. What are the advantages and disadvantages of the current system? Are we really addressing the adequacy of seasonal restrictions versus softshell periods? Should we be attempting to achieve some level of exploitation rate? Should we be somehow restricting the amount of handling of sublegals and females that occurs, and is this a problem? Should we be considering some sort of rotational management by area, or other management schemes? Our department needs to answer all of these questions to carry out our conservation mandate.

In addition, the Alaska Board of Fisheries may wish to consider various socioeconomic allocation questions in regard to the dungeness crab, depending on the life history of the animal. If, in fact, recruitment is highly variable and successful fisheries are maintained on single age classes over a long period of time, it is possible the board may wish to spread economic harvest over a number of years. Dungeness crab are also important to local area commercial fisheries and local area sport and personal use fisheries. About 90 percent of the dungeness crab commercial permit holders are residents of Alaska, and about 85 percent of these operate out of boats under 50 feet in length. Do we have an adequate data base for the Board of Fisheries to address these questions? Dungeness crab are an important recreational fishery, and they are also important to the tourist industry, yet there are problems in stringing out the harvest to cover these types of activities in an intense commercial fishery. I do not have answers to most of these questions, but from a management sense, they need to be addressed and I am hoping they can be at this symposium.

I understand the symposium will be providing us with regional perspectives on management strategies, data collected and research under way. Hopefully, we can eliminate assumptions about what is and what is not known about the animal. We all have limitations on our time, and it is difficult to keep current. We may be able to pool resources to coordinate research activities and data analysis. Our budgets are always limited and all fisheries are demanding more attention, more precise data/management, and more accurate allocations to competing users. The symposium will allow the experts on dungeness crab population dynamics and biology to meet with the managers to discuss their different perspectives on the central questions of conservation and allocation.

We need to decide if dungeness crab are in need of a more aggressive management program in Alaska. I am sure that dungeness, like any other of our resources, do lend themselves to some estimation of optimum and maximum sustained yield. I am sure that a rational system of regulations could be developed that would ensure that biological surplus would be harvested in an orderly manner by users, according to priorities established by the Board of Fisheries. I am not sure what such a program would cost or what level of sophistication would be justified by the value of the resource. I think this symposium is an excellent chance to start trying to address this issue.

Selfishly, from the department's standpoint, I hope that suggestions for an adequate Alaskan fisheries management program is the primary output of this forum. I hope that department managers can learn about the biology of the animal, can gain knowledge about other west coast management systems, and can develop, in concert with peer scientists and managers, new potential research plans and potential management schemes. I think your agenda is excellent, and covers most of the necessary ground. In the area of research, it does contain a workshop on future research needs chaired by the department. I guess the one additional thing I would like to have seen on the agenda is a parallel workshop critique of the Alaskan management system and suggestions for improvement based on the aggregate experience from all the sessions in the symposium. If this cannot be formally or informally a part of the symposium, I am going to suggest, within my own department, that at some point after the symposium proceedings is published, a group of managers and research scientists get together and perform such a critique. I would like to see that critique presented to the Alaska Board of Fisheries at their spring shellfish meeting, and the recommendations incorporated into our FY 87 budget process next spring.

Session I

Overviews

Overview of the California Dungeness crab, *Cancer magister*, fisheries

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Ronald W. Warner
California Department of Fish and Game
Eureka, California

INTRODUCTION

There are two distinct Dungeness crab, Cancer magister, fisheries in California. The northern California fishery occurs in the area from the Oregon border to Point Arena, California and includes the ports of Crescent City, Trinidad, Eureka, and Fort Bragg (Figure 1). South of Point Arena, ports of landing for the central California fishery are Bodega Bay, San Francisco, Half Moon Bay, Moss Landing, and Morro Bay (Figure 2).

MANAGEMENT

The northern California crab season has opened on December 1 since 1967 and, since 1957, has closed on July 15 (Table 1). The season may be extended to August 31 by order of the Director of the Department of Fish and Game if it is determined that the extension will not harm the resource (Table 2). In central California crabs are in marketable condition about 1 month earlier, so the season opens on the second Tuesday in November and closes June 30. If requested, the season may be extended under the aforementioned conditions to July 31.

Only male crabs, 6¼ inches carapace width, may be taken. Not more than 1% of any load or lot of crabs may be less than 6¼ inches and none less than 5 3/4 inches may be possessed. The standard unit of gear is a circular trap, approximately 40 inches in diameter, and 75 pounds in weight. Every crab trap must have two 4¼-inch diameter escape openings. If side openings are used, one of those openings must be located so that at least one-half of the opening is in the upper half of the trap. Traps may be set 18 hours in advance of the opening of the season; however, gear dropped prior to that time must be unbaited and have unhooked lids.

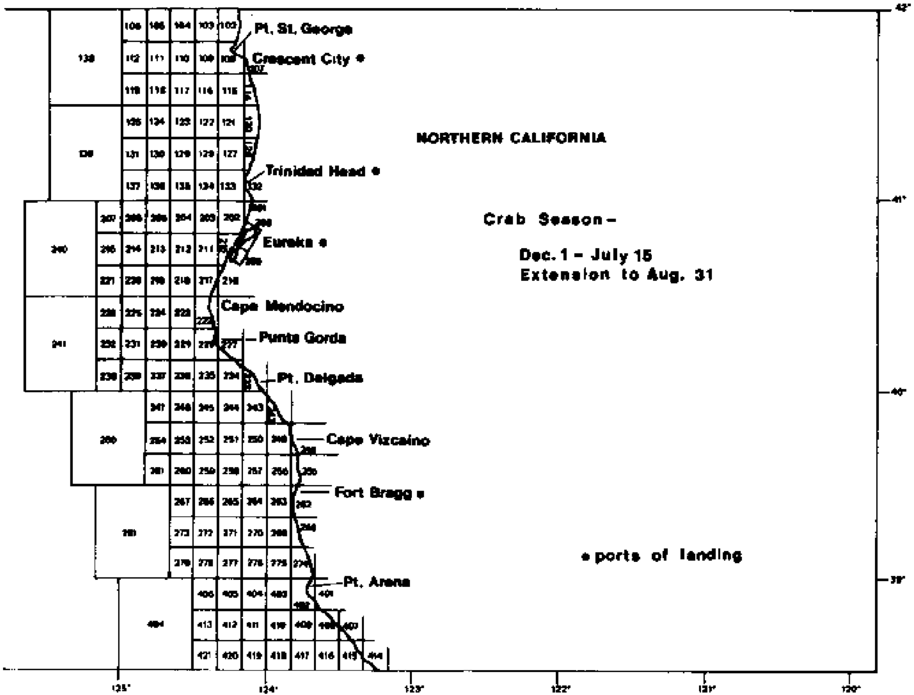

FIGURE 1. Northern California ports of landing for the Dungeness crab fishery

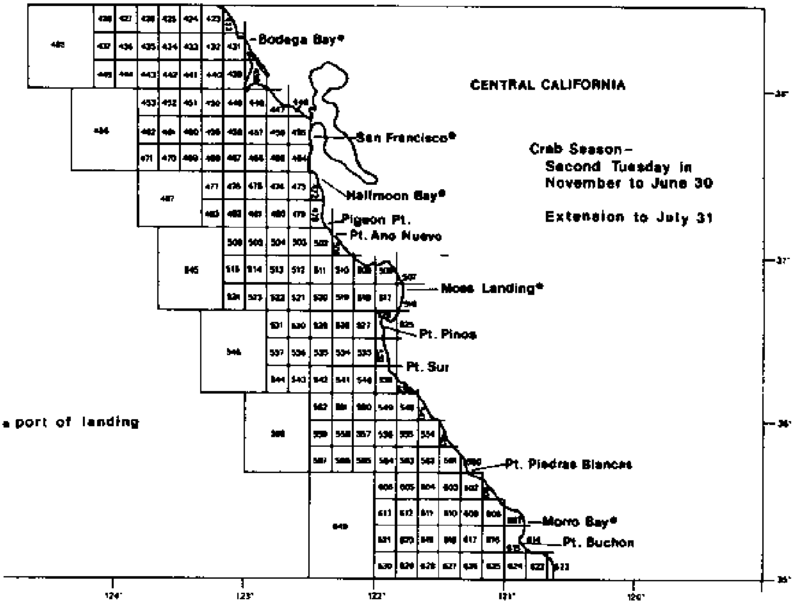

FIGURE 2. Central California ports of landing for the Dungeness crab fishery

Table 1. California Crab Seasons, 1950-1984

	Northern California (Oregon border to Pt. Arena)		Central California (Pt. Arena to Mexican border)	
	Open	Close	Open	Close
1950-51	Nov. 15	July 31	Nov. 15	July 31
1951-52	Dec. 15	July 31	"	"
1952-53	"	"	"	"
1953-54	"	"	"	"
1954-55	"	"	"	"
1955-56	Dec. 15	June 30	Nov. 15	May 31
1956-57	"	"	"	"
1957-58	Dec. 15	July 15	"	"
1958-59	"	"	"	"
1959-60	"	"	2nd Tues.Nov.	May 31
1960-61	"	"	"	"
1961-62	"	"	2nd Tues.Nov.	June 30
1962-63	"	"	"	"
1963-64	"	"	"	"
1964-65	"	"	"	"
1965-66	Dec. 8	"	"	"
1966-67	"	"	"	"
1967-68	Dec. 1	"	"	"
1968-69	"	"	"	"
1969-70	"	"	"	"
1970-71	"	Aug. 31	"	"
1971-72	"	"	"	"
1972-73	"	"	"	"
1973-74	"	July 15	"	"
1974-75	"	"	"	"
1975-76	"	Aug. 31	"	"
1976-77	"	"	"	"
1977-78	"	July 15	"	July 31
1978-79	"	Aug. 31	"	"
1979-80	"	"	"	"
1980-81	"	"	"	"
1981-82	"	"	"	June 30
1982-83	"	July 15	"	"
1983-84	"	Aug. 31	"	July 31

Table 2. Dungeness Crab Commercial Fishery Landings During Season Extension (July 16-August 31) in Northern California.

Season	Total Season Landings/lb	Total Extension Landings/lb
1983-84	4,478,548	28,000
1982-83	4,696,337	No extension
1981-82	10,104,432	--
1980-81	10,889,831	1,284
1979-80	12,233,334	1,743
1978-79	6,993,965	4,201
1977-78	12,898,761	No extension
1976-77	24,811,936	617,261
1975-76	15,381,870	49,600
1974-75	1,400,485	No extension
1973-74	323,982	No extension
1972-73	1,046,245	4,929
1971-72	2,355,063	17,138

A California law which requires trawl vessels to operate 3 miles beyond the coastline was enacted to avoid conflict between crabbers and trawlers and also serves to protect juvenile bottomfish which use that area as a nursery. No more than 500 pounds of trawl-caught Dungeness may be landed per trip. Most crab landings by trawlers are incidental and total annual landings by this gear are negligible.

Crab landings fluctuate dramatically in the northern California fishery but have remained at depressed levels for over 20 years in central California. Both fisheries have been the subject of considerable discussion and study regarding the causes of their individual patterns. Environmental and density dependent factors have been hypothesized as explanations for fluctuations in northern California, while the issues of physical oceanography, predation, and pollution have been closely examined in the central California fishery.

FISHERY

The port of Morro Bay is on the extreme southern end of the commercial range of Dungeness crab. This port also occupies the southern end of the pink shrimp, Pandalus jordani, range. The crab fishery began here in 1947 and initial landings were relatively low, peaking at 433,000 lb during the 1950-51 season (Figure 3). Subsequent landings were sporadic after that and since the mid-1970s there has been little or no effort.

To the north of Morro Bay is Moss Landing on Monterey Bay. This area is also part of the southern edge of the Dungeness crab commercial range. During the 1930s, gill nets with 8½- to 11-inch web were used in the fishery. In recent years landings have been sporadic with only minimal effort expended (Figure 4).

San Francisco has a long and colorful history of crab fishing dating back to about 1860 and from 1918 to the early 1960s, about 200 to 250 vessels engaged in the fishery which yielded as much as 8,900,000 lb in a season, 1955-56 (Figure 5). Since that time landings have been depressed and only 100 to 165 vessels fish in the area now. Landings during the 1983-84 season were only 857,000 lb, although that figure was the highest recorded in 14 years and well above the 10-year average of 511,000 lb.

Noyo Harbor at Fort Bragg is the most southerly port in the northern California area. It is home to a sizeable trawler fleet, but only 25 to 40 vessels are crabbers. Some effort is directed at a small, local population of crabs in the Usal area, but most vessels travel north to the Eel River where the bulk of the catch occurs. Fort Bragg landings fluctuate in phase with Eureka Landings (Figure 6) and the 10-year average is 517,000 lb.

Total annual landings in the northern California ports of Eureka, Trinidad, and Crescent City have experienced sharp changes. The catch dropped to a record low of 320,000 lb in 1973-74 and jumped three seasons later to a record high 25,000,000 lb (Figure 7). Eureka, a port city on Humboldt Bay, has a crab fleet composed of a mixture of vessels ranging from dories to draggers. The bar or entrance to Humboldt Bay is very rough during winter storms and on many days prevents the fleet from exiting to ocean waters. The 10-year average landings for this

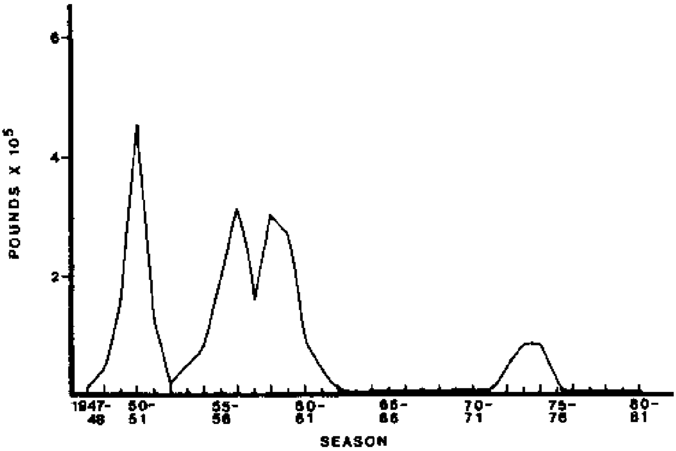

FIGURE 3. Dungeness crab commercial fishery landings in Morro Bay

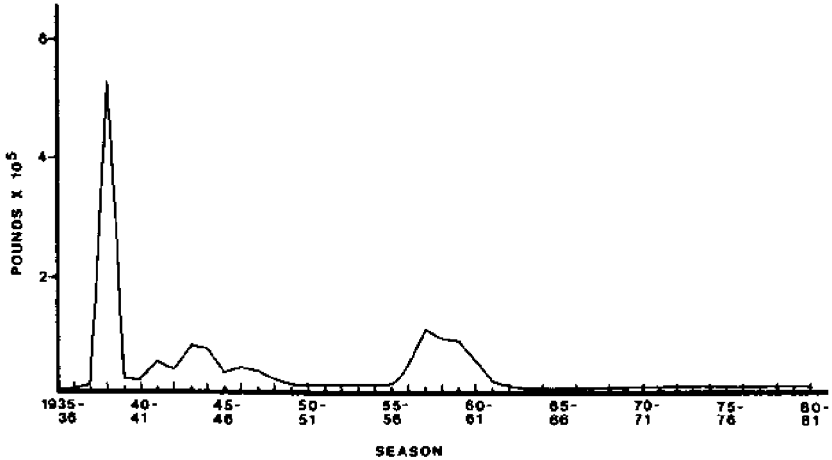

FIGURE 4. Dungeness crab commercial fishery landings in Monterey Bay

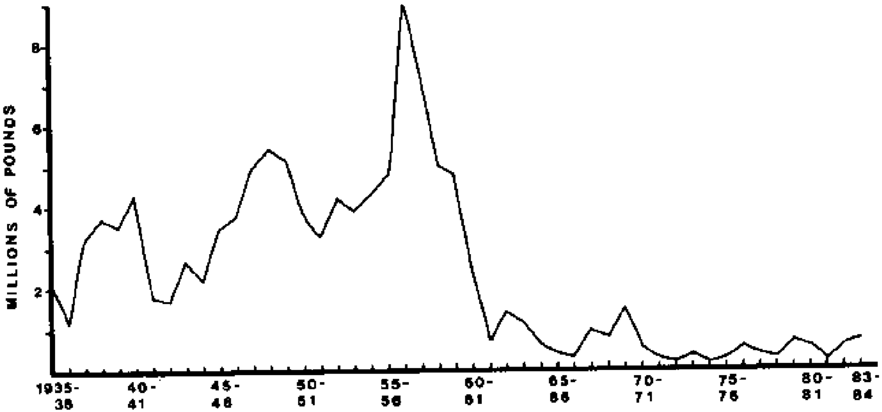

FIGURE 5. Dungeness crab commercial fishery landings in San Francisco

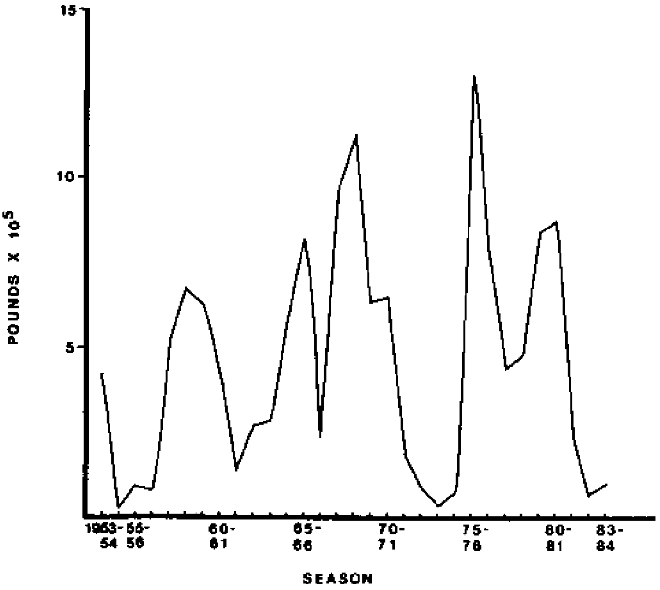

FIGURE6. Dungeness crab commercial fishery landings in Fort Bragg, California

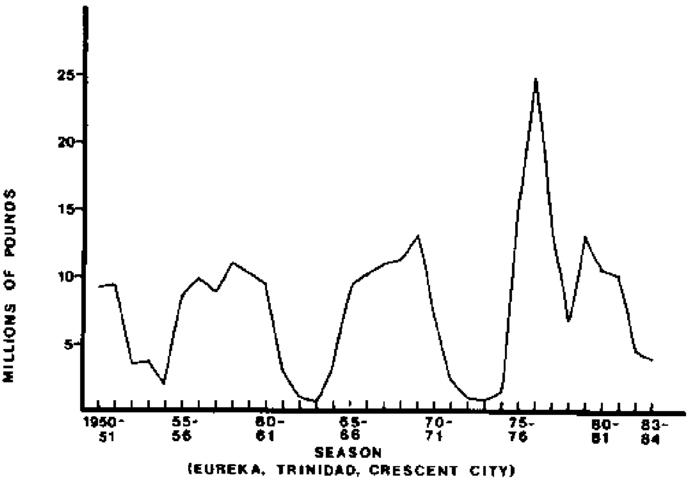

FIGURE 7. Dungeness crab commercial fishery landings in Northern California

port are 3,850,000 lb.

About 20 miles north of Eureka is the port of Trinidad, which is a small anchorage protected from northwesterly winds and very popular with summertime sport salmon fishermen. During the winter, 25 to 30 small crab boats are moored in the harbor, which is fully exposed to storms from the south. This fleet fishes primarily within a 10-mile radius of the anchorage and many fish late into the season. Average 10-year landings for Trinidad are 800,000 lb.

Crescent City, the most northerly port in California, is home to many large, multipurpose fishing vessels. Also, many boats from out of the area tie up there prior to the opening of crab season. The 200 vessels which fish crab from this port have an easy exit to the sea because there is no bar to contend with. During the last four crab seasons, over 70% of total northcoast crab landings occurred in Crescent City (Figure 8). The 10-year average is 5,740,000 lb.

LANDING TRENDS

Northern California landings display a cyclic pattern characterized by 6 or 7 years of good production followed by 4 years of poor production (Table 3). The 10- and 20-year averages are 10.4 and 8,700,000 lb, respectively.

Since landings peaked in 1976-77, there have been some significant changes in the character of the fishery. Effort in terms of vessels was greatest during the record season in 1976-77 with 439 boats (Figure 9). Thereafter, landings have dropped to low levels but effort has remained high, possibly due to hard times in other fisheries. The groundfish and shrimp fisheries have suffered from stock declines and overcapitalization; consequently, many of the large vessels involved in those fisheries now go crabbing for the first month or two of the season. An influx of dory fishermen also keeps the effort high. Dory fishing for crab became popular during the high abundance years when crabs were easy to catch. Now, these boats, with their limited capabilities, stay in business during low abundance years by fishing shallow areas not frequented by larger, slower vessels. They also fish late into the season when volume is low but price is sufficiently high to make a profit. In contrast to earlier years when the fishery consisted primarily of mid-sized, combination crab and salmon vessels, the fishing power of the modern fleet is highly mixed.

Since the late 1970s, the majority of crab landings have occurred during the first 2 months of the season (Figure 10). In the 1983-84 season, 84% of the catch was landed during the first month and 95% of total landings was across the docks after the second month of fishing. Landings have been somewhat more evenly spread out during earlier seasons because of landing limits and more limited fishing power. Improved marketing has eliminated landing limits once imposed by processors. Out-of-area and out-of-state buyers have been eager to take all the product available. Large, multipurpose fishing vessels can produce more volume than the traditional single-purpose crab boat because they handle more gear and can fish at night and during rough sea conditions. Average-sized vessels, once accustomed to 4-month seasons, now feel the pinch caused by season compaction.

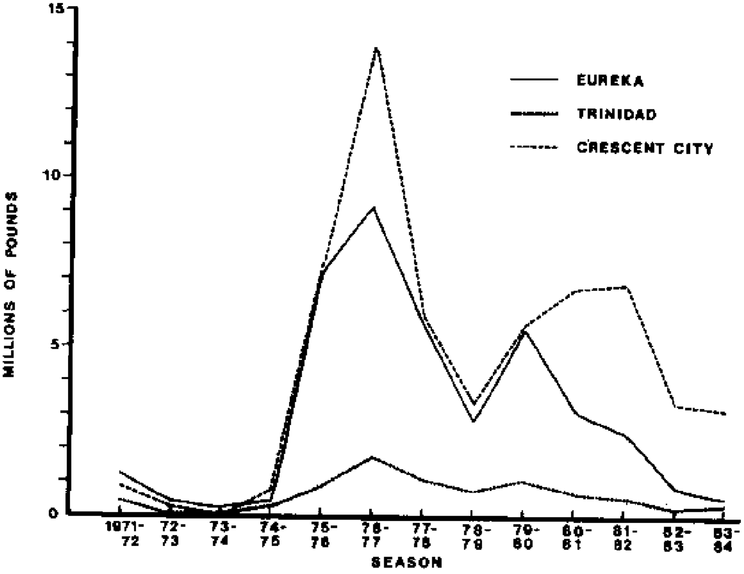

FIGURE 6. Dungeness crab commercial fishery landings in Eureka, Trinidad, and Crescent City

Table 3. Dungeness Crab Commercial Fishery Cyclic Averages (lb) in Northern California.

Season	Total Landings	Average Landings High Period	Average Landings Low Period
1955-56	7,964,877		
56-57	9,891,636		
57-58	9,103,185	9,735,310	
58-59	11,719,796		
59-60	10,105,973		
60-61	9,626,391		
1961-62	3,109,294		
62-63	640,895		1,922,148
63-64	534,536		
64-65	3,403,868		
1965-66	9,155,836		
66-67	10,076,130		
67-68	11,213,527	10,474,386	
68-69	11,728,064		
69-70	13,474,260		
70-71	7,198,499		
1971-72	2,355,063		
72-73	1,046,245		1,281,444
73-74	323,982		
74-75	1,400,485		
1975-76	15,381,870		
76-77	24,811,936		
77-78	12,898,761		
78-79	6,993,965	13,330,590	
79-80	12,233,334		
80-81	10,889,831		
81-82	10,104,432		
1982-83	4,696,337		4,587,442
83-84	4,478,548		

10-Year Average =10,388,950
20-Year Average = 8,693,249

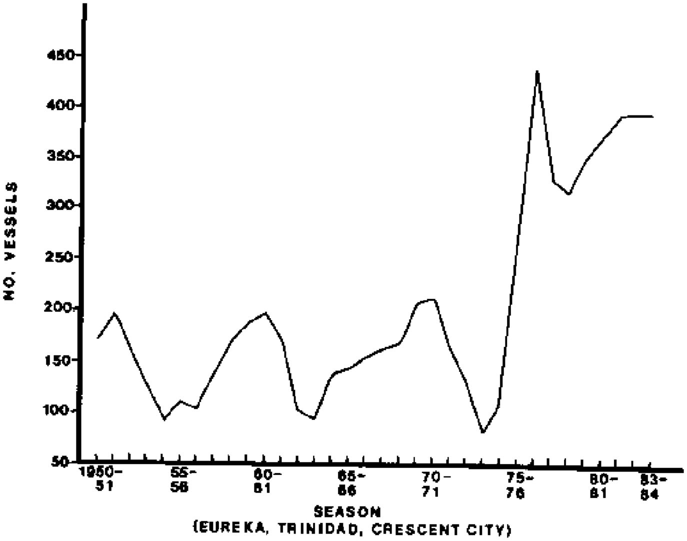

FIGURE 9. Northern California Dungeness crab commercial effort (vessels)

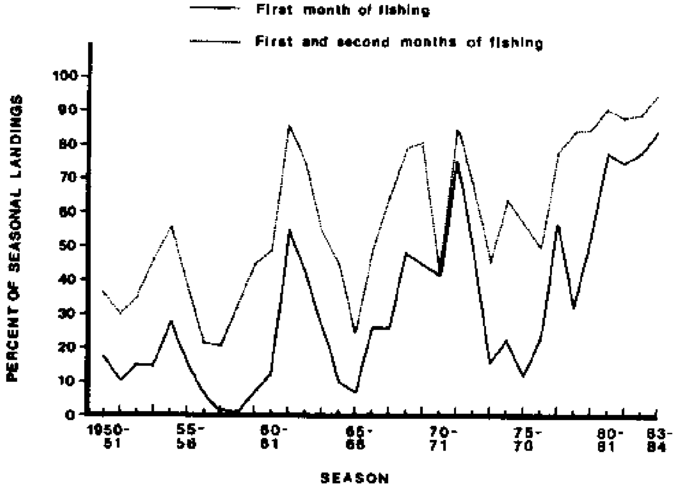

FIGURE 10. Northern California Dungeness crab commercial fishery landings during first month and first and second months of fishing.

Low crab volume and high demand have created increased prices (Figure 11). In the 1970-71 season, the initial price was $0.25 per pound; the 1983-84 season began at $1.45 per pound. Prices as high as $2.20 per pound late in the season have helped sustain small vessels with low overhead.

SUMMARY

The Dungeness crab fishery in northern California appears in good health. Historically, landings have always returned to high levels following low production years. Fishing has been poor for two consecutive seasons and the outlook for the 1984-85 season is probably for that trend to continue; however, there appears to be an extremely strong 1984 year class, which could initiate an upward swing in landings possibly as early as the 1987-88 season.

Crab abundance in the San Francisco area has remained at low levels for over 20 years. Landings during the 1983-84 season of 857,000 lb, admittedly the highest in 14 years, are still very low. The 1984 year class also looks very strong in San Francisco, but the historical record of depressed populations off that area should instill caution as far as expectations for increased production is concerned.

ABSTRACT

In California, Dungeness crabs, Cancer magister, are commercially harvested in ocean waters from Morro Bay to Crescent City. Until the early 1960s, San Francisco produced significant quantities of crabs, but since then has experienced a major decline in abundance. Landings in Morro Bay and Monterey are negligible, while the northern California ports of Fort Bragg, Eureka, Trinidad and Crescent City yield the bulk of present day landings. Crab abundance has fluctuated widely, with landings in some years shifting from 0.3 to 25 million pounds over a 4-year period. Since the mid-1950s, production in northern California has been characterized by 6 or 7 years of good fishing, averaging 10 to 14 million pounds, followed by 4 years of poor fishing with a 1 to 2 million pound average. Opening day price to the fisherman has increased from $.25 per pound in 1969 to $1.45 per pound in 1983. Intense fishing effort has accompanied increases in the value and landings of crab, and had stayed at a high level since the season of 1975-76. With increased effort, the complexion of the fishery in the north has changed to one dominated by large vessels, fishing vast quantities of gear during day and night periods, even in turbulent seas. Smaller vessels, with more limited capabilities, have experienced a financial squeeze since 80 percent, or more, of total landings now occur during the first month of fishing. In order to compete, some small vessels now concentrate in shallow areas, where less gear is set.

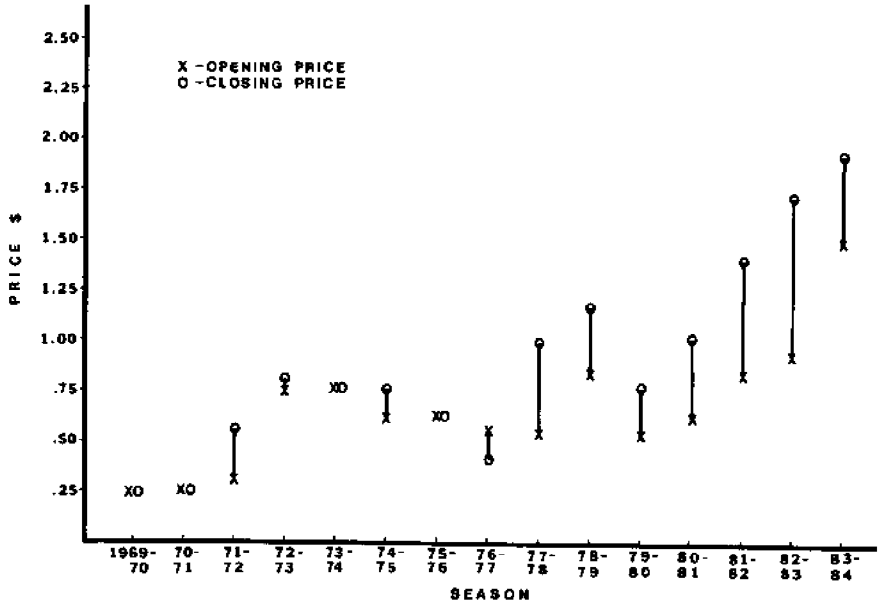

FIGURE 11. Northern California Dungeness crab prices

An overview of Oregon Dungeness crab fishery with management concepts for the future

Darrell Demory
Oregon Department of Fish and Wildlife
Newport, Oregon

Introduction

Oregon's Dungeness crab fishery is composed of commercial and sport entities with the commercial portion accounting for 98% of total harvest. The sport harvest is mostly in several estuaries while the commercial harvest is located in the ocean with a minor estuary component.

Catch and Effort

Catch records date from 1889 when 6,600 pounds of crabs were landed and remained under one million pounds until 1933. By 1937 catches had increased to five million pounds. Since 1937 catches have ranged from 3 to 18 million pounds, becoming cyclic in 1963 with highs and lows occurring at 7 to 10-year intervals.

Effort statistics date from 1948 and up to 1970 fewer than 150 boats participated in the fishery. Since 1970 there has been a steady increase in the number of boats which peaked at 570 in 1980. The number has since declined to 325 in 1984.

Prior to 1960 catch and effort peaked in March, April and May, but in more recent years most of the harvest takes place during the first 2 months of the season.

Management Strategy

Management of the Dungeness crab fishery evolved, in part, from fishing practices and dictates of dealers. In 1947 the state legislature transferred the responsibility from local counties to a state agency.

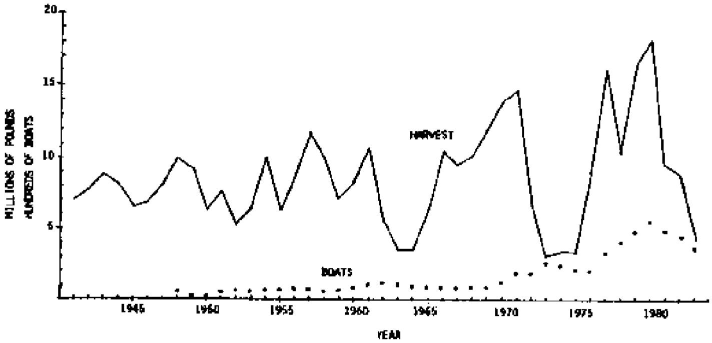

Figure 1. Oregon Dungeness crab harvest and number of boats.

Regulations

Regulations have been few and relatively simple and pertained to season, gear, and crab sex and size.

Season. Prior to 1948 the season was open all year. There were summer and fall closures in 1948 and 1949 and from 1950 through 1963 the area south of Cascade Head opened November 15 and closed August 15 while the area north of Cascade Head opened December 15 and closed September 15. In 1964 the split areas were combined into one and the season closed August 15 with 30-day extensions granted 5 times. From 1978 through 1983 the season closed September 15 with one 30-day extension. In 1984 the closing date was once again set at August 15.

A closed season generally reflected the time when most crabs were molting and in a softshelled state. The rationale for the closure was to reduce handling mortality of soft crabs and to insure maximum yield from the resource. Experience taught us that molting and soft-shelled state were highly variable with a tendency for molting to occur earlier on the south coast.

Sex and size. Only male crabs at least 6-1/4 inches in width are legal in the commercial fishery. As a consequence of this regulation little data has been collected on female crabs in Oregon.

Gear. The legal gear in Oregon for Dungeness crab are ring nets or pots with escape ports. Beginning in 1983 pots must also have a destruct device that will allow crabs to escape from lost or derelict gear. Standard pots range in size from 32 to 48 inches in diameter, but pots up to 8 feet in diameter were developed for a short-lived helicopter fishery.

A buoy branding method is now pending for all pots fished in Oregon waters.

Problems

Crowding and conflicts

There was a time when the peak of the crab harvest occurred in March, April and May, but as more people entered the fishery more of them began fishing at an earlier time. Over the past 10 years well over 50 percent of the harvest is taken in the first two months of the season. The glut of boats and gear in traditional fishing areas on opening day is a sight to behold. This, in turn, has prompted some fishermen to expand fishing into nontraditional areas both inshore and out to 80-100 fathoms and has resulted in conflicts with shipping, trawlers, trollers and other crabbers, as inshore crabbers reason that the deep water crabbers are intercepting crab on their way to inshore waters.

One rationale held by some crabbers for keeping pots in certain areas is to keep drag fishing away from crab grounds. That trawlers catch crab is well known, but how much real damage is done by trawlers is poorly documented. When the crab season closes and pots are removed a number of trawlers immediately move into the vacated areas.

Poor Utilization

During the last month of the season in the past 4 years a major fishery has developed on recently molted crab. Heavy sorting at sea was required and some fishermen did a much better job than others, but a substantial amount of marginal quality crab was landed. In a very short time matters got out of hand and more marginal crab was landed which enticed more fishermen into the fishery. The result was that considerable low yield crab meat was put on the markets which drove the price to fishermen down. Excessive handling at sea with a higher than acceptable mortality and waste of the resource resulted. In 1984 the season was shortened by two weeks although a similar request by staff in 1983 was rejected.

Sport-commercial conflict

For all practical purposes the sport fishery is confined to estuaries along with a small commercial fishery. A series of meetings with both users revealed that many sport crabbers are opposed to commercial crabbing in estuaries on philosophical grounds. Others site crowding, unfair advantage and overfishing by commercial users. The bottom line was that commercial crabbing in estuaries is now prohibited on weekends and all holidays, and gear limited to rings only and no more than 15 rings per boat.

The Common Denominator

All of the above problems have a common denominator--too many boats and too many pots. With the rapid increase in the number of boats came a similar increase in the number of pots, from 30,000 in 1970 to 130,000 in 1980. As long as entry into the fishery is unlimited the problems will continue and most likely worsen.

What To Do

Given enough time many fishery problems solve themselves. However, the current situation has been greatly influenced by some actions of the past. A big push for easy money for boat loans during a few years of abundant resources inticed many people into fisheries both to catch and to process. Markets, dollar value, inflation and product quality (or lack of it) are only a few of the factors that have put us where we are today. As resources diminished and hard economic times beset us the reality of free enterprise has hit us hard. Perhaps just waiting for something to happen will demand too high a price.

I do not have the space nor time nor expertise to thoroughly explore the complexities of modern day comrephensive fisheries management. But I do offer some thoughts.

First, we need to recognize that there are differences in and among resources, resource users and managers. In that context we need to look more to regional management scenarios and not just our own states. Crabs don't recognize our boundaries, neither do fishermen nor the market place. My pitch is to identify and quantify the problems and then resolve them through a rational management plan. Starts have been made through the state-federal project in 1974 and the PMFC draft plan of 1977-79. Let us proceed, preferably on a state level.

Effort control

I mentioned excessive effort as being the common denominator to most of our fishery problems. To affect any such measure of control several things must happen. First, there must be a major policy change at top level from one of "let industry come up with something" to one of promoting orderly development. Some small steps in some fisheries have been made, i.e., the roe herring fishery in Yaquina Bay, limitations on squid trawling permits, and the Puget Sound crab fishery. Once the policy change is made, we will then have to develop the data base for entry control. Since much of the information will be economic in nature new staff will be required and the tools to do the job. And we must work in a multifishery context because we, as crab managers, are not in this alone.

Some Requirements

My vision of regional management centers around area licensing similar to that of Alaska where differences are recognized and incorporated into a management strategy. Along with licensing would be gear identification and adequate enforcement capability.

Some Benefits

There will, of course, be many problems and questions encountered with any significant change in management policy. But we need to dwell on the benefits.

If fishing power is matched reasonably well to resource capability then the overall worth of the resource should improve. We should see both the price and market much more stable than at present. We should also see more of the catch spread out over more of the year and lessen the first of the year glut. What I'll call the Oregon experience, where large amounts of unfilled crab are caught and processed, will be greatly reduced to nonsignificance, thus, improving the utilization of the resource. With less effort economic impacts in lean times will be reduced as will conflicts with other users.

Communication

I realize that this is an oversimplification of a complex and dynamic situation. What we must do is talk to one another in our agencies, the industry, the consumer, and the final entity, the lawmakers.

To borrow someone elses title: If not now, when; If not here, where; If not us, who?

References

Catch and effort data from unpublished reports, Oregon Department of Fish and Wildlife.

Abstract

Catch records date from 1889 when 6,600 pounds of crab were landed, and remained under one million pounds until 1933. By 1937 catches had increased to five million pounds. Since 1937, catch has ranged from 3 to 18 million pounds annually, becoming cyclic in 1963 with highs and lows occurring at 7-10 year intervals.

Effort statistics date from 1948 and up to 1970 fewer than 150 boats participated in the fishery. Since 1970 there has been a steady increase in effort which peaked at 570 in 1980. The number has since declined to 370.

Crab management prior to 1947 was controlled by each coastal county, but in 1947 the State Legislature transferred the responsibility to a state agency. Our management policy, at first, was one of maximum sustained yield, but in recent years became optimum yield.

Regulations have been fairly simple: a closed season which generally reflected the softshell stage of the crabs, a size limit of 6-1/4 inches, males only, gear limited to pots or rings, 4-1/4 inch escape ports, and a pot destruct device to allow crabs to escape from lost gear.

The management policy and strategy has worked fairly well over the long term, but as effort increased in crabbing as well as in other fisheries, problems arose.

The opening day syndrome was honed to a fine edge, traditional crabbing areas were crowded with pots, crabbing expanded into other fishing grounds and shipping lanes, sport-commercial conflicts arose, and poor use of the available resource occurred as fishermen and processors felt pressured to compete even though quality of the crabs was poor and markets suffered.

Crab fishing has a future in Oregon, but serious discussion must be given to alternative management strategies: effort control and fleet reduction to get resource and effort into balance; regional management concepts that recognize resource differences and fishermen interactions; and the political system for decision making.

Overview of the Washington coastal Dungeness crab fishery

Steve Barry
Washington Department of Fisheries
Montesano, Washington

Introduction

The coastal Washington fishery occurs primarily in the ocean between Pt. Grenville and the Columbia River in depths of up to 65 fathoms. Smaller fisheries occur in the 15 M. area south from Destruction Island and in the three large southern coastal estuaries: Grays Harbor, Willapa Bay, and the Columbia River. About 10 percent of the seasonal catch is taken in the estuaries--most of this from Willapa Bay. The Destruction Island fishery is a spring-summer fishery because crabs are usually not available earlier in the season. The main fishing ports are Westport in Grays Harbor, Bay Center and Tokeland in Willapa Bay and Ilwaco and Chinook in the Columbia River.

Tagging studies indicate that the Destruction Island stock is probably separate, although abundance appears to parallel the larger southern stock. The range of the southern Washington-northern Oregon stock extends from Pt. Grenville at least as far south as Cape Lookout, Oregon--a distance of about 118 M.

The Personal Use and Commercial Fisheries

The personal use fishery occurs primarily in the coastal estuaries in the spring and summer. Although scant data exists to estimate the personal use catch, it is probably one percent or less of the annual commercial harvest. The season is open year-round with an individual daily bag limit of six male crabs per day, six inches or larger. Each person may fish two traps or ring-nets. Traps must have one 4¼-inch escape port.

Responsibility for management of the commercial fishery has been delegated by the Pacific Fisheries Management Council to the separate states, with the provision that the states cooperatively manage the resource.

Since 1950, the commercial catch has ranged from 2.5 million pounds (1981-82 season) to 18.4 million pounds (1968-69 season). Crab abundance has been cyclical with peaks in 1948, 1958, 1969, and 1977, and lows in 1951, 1964, 1974, and 1982. Effort increased dramatically following the peak seasons of 1968-69 and 1969-70. In recent years, reduced salmon harvests have caused salmon fishermen to turn to the already over-capitalized crab fishery to replace income. This, in turn, has caused traditional crab fishermen to increase their effort. A result of this has been increased fishing effort in the spring and summer. Table I contains pertinent catch, effort and fleet size information for the commercial fishery since 1950.

Over the last 35 years, the season opening date for the commercial season has ranged from December 1 to January 1, while the season closing date has ranged from September 15-30, except in 1966 when it was October 15. The reason for the variation in season opening dates has usually been to achieve uniformity with Oregon. The need for a uniform season opening has become more important as size and mobility of the fleet has increased. Since the early 1970s, the season has been set as December 1 through September 15. The season has been extended by 15 days when crab condition warrants.

The season closure in the fall has been in effect since the early 1940s because recruitment molting of male crabs usually occurs in the late summer or fall. The season closure during this time minimizes mortality on newly molted crabs (soft-shells) due to fishing operations and increases meat yield by minimizing harvest of unfilled crabs. In some years, the scheduled season opening date may occur before optimum meat condition has been reached. In this situation, meat condition must be balanced against the need for a uniform season opening date. It has been necessary to delay a scheduled December 1 opening date twice in 15 seasons.

Basic regulations for the commercial fishery include a minimum size limit of 6¼ inches, harvest of males only and the release of soft-shells. Traps are required to have two circular 4¼-inch diameter escape ports. The newest regulation (1984) requires a vessel to have a hold inspection prior to the season opening. The purpose of this regulation is to minimize the opportunity for illegal fishing activity during the pre-season "gear setting" period which begins 88-hours prior to the actual opening date. The gear-setting period was adopted in an attempt to mitigate the competitive disadvantage in setting gear that smaller boats have at the season openings.

There are no "limited entry-type" restrictions on licenses, vessels, or the amount of gear in the coastal fishery, though there is a license moratorium and gear limitation in the Puget Sound fishery. Sentiment of fishermen on the coast for "limited entry" seems to have increased in recent years.

WDF Biological Work

Biological work can be separated into two categories: routine sampling and specific studies. The primary purpose of sampling activities is to

Table I. Catch and effort data for the coastal Washington commercial Dungeness crab fishery.

Season	Lbs. Landed	Number of Boats[1]	Estimated Number of Pots[1]	Number of Deliveries
1950-51	3,255,826	69	10,650	3,974
1951-52	3,364,112	69	10,300	5,280
1952-53	5,295,677	76	11,675	4,750
1953-54	6,418,057	116	18,300	6,123
1954-55	5,801,123	88	15,600	5,296
1955-56	8,547,876	102	18,225	6,444
1956-57	10,876,236	93	13,600	3,858
1957-58	10,961,119	93	14,900	4,224
1958-59	7,685,525	97	16,800	4,636
1959-60	6,911,299	105	21,585	4,554
1960-61	5,865,415	93	18,515	3,734
1961-62	4,384,234	88	17,550	4,083
1962-63	4,112,664	103	18,115	4,406
1963-64	3,342,341	95	17,965	4,396
1964-65	6,296,500	90	17,845	4,014
1965-66	10,165,395	83	17,275	4,250
1966-67	8,422,551	81	18,400	4,111
1967-68	10,789,893	70	17,500	4,163
1968-69	18,433,896	97	21,300	5,474
1969-70	17,745,643	138	33,000	7,376
1970-71	12,552,037	--	--	5,721
1971-72	9,199,701	173[2]	40,600	6,200
1972-73	4,339,221	147	41,000	5,153
1973-74	3,663,958	129	31,100	4,378
1974-75	5,119,105	127	29,100	4,850
1975-76	8,516,055	138	37,400	5,580
1976-77	11,673,995	141	34,900	5,599
1977-78	7,368,660	135	37,100	5,616
1978-79	7,979,403	135	42,400	5,515
1979-80	6,546,544	123	40,300	4,492
1980-81	2,689,142	105	33,400	3,470
1981-82	2,564,766	95	30,300	3,522
1982-83	3,972,555	101	32,400	4,693
1983-84	4,700,000	121	--	--

[1] Figures given for 1950-51 through 1966-67 seasons from U.S. Fishery Statistics; accuracy is unknown. 1968 to 1984 data from WDF.

[2] Includes 21 boats from Oregon and California.

monitor the molting cycle of adult male crabs. Samples for size and shell condition data are routinely taken from commercial landings and aboard commercial or WDF vessels. Shell condition grading is based on the hardness of the carapace when moderate finger pressure (i.e., squeezing) is applied to the ventral carapace. Grade I is characterized as "hard-shelled". A Grade III is a crab in the "soft-shelled" stage as a result of a recent molt. Grade II is an intermediate stage. Grade I crabs may be noted as "old shells" based on the appearance of their exoskeleton. High percentages of "old shelled" sublegal-sized male crabs are sometimes noted in summer samples; this can be an indicator of impending molting activity. Sampling during the closed season is conducted during October and November to obtain shell condition data. Although we are frequently asked by some fishermen and the press for pre-season abundance predictions, we feel that the CPUE from our sampling, which is usually only one sample-set of 30 traps for two days each month, is an unreliable index of abundance. However, low CPUE in conjunction with other indicators may suggest low recruitment. Samples of female crabs, noting size, shell condition and reproductive status are also routinely taken.

The specific studies have covered a variety of areas. Tagging studies on the southern coast were conducted in 1980 and 1981 using Peterson disc tags on legal-sized males to determine distribution and movement. The results indicate that a general in-shore movement occurs during the fall with a tendency for movement to be directed toward one of the three estuaries. Experiments on handling mortality of large, soft-shelled male crabs have been conducted. Preliminary results indicate a substantial mortality rate occurs--probably in the range of 20 percent to 40 percent. Weight-width data was collected to determine if this type of data could be used as a replacement for the shell grading system as a method for assessing crab condition i.e. meat content/-quality. Results were mixed and therefore inconclusive. Sampling of juvenile populations in Grays Harbor and Willapa Bay was discontinued after several years when it was learned that adequate sample levels could not be obtained with the available manpower.

The Dungeness crab, *Cancer magister*, fisheries of British Columbia

G. S. Jamieson
Department of Fisheries and Oceans
Nanaimo, British Columbia

Abstract

The Dungeness crab fishery in British Columbia consists of geographically distinct subfisheries, the major ones of which are located in McIntyre Bay and northern Hecate Strait, Chatham Sound, the Fraser River estuary, the west coast of Vancouver Island, and the southern Gulf Islands near Saanich. During the 1960s, north coast landings dominated the total catch, but since then, landings have been relatively low. In contrast, south coast landings have remained relatively constant and now account for most of the provincial catch. Landings from each subfishery have fluctuated substantially over time.

It is estimated that at least 20% of landings are unreported, and this combined with the widespread nature of the overall fishery makes data interpretation difficult. Nevertheless, fleet characteristics and the multispecies nature of each subfishery are discussed. The overall fishery is a dynamic one, with about 40% of the fleet being replaced on an annual basis. About one-third of the 350 or so vessels involved in the fishery each year land crab exclusively, with the main alternate species exploited being salmon. Economic data by species, vessel size and area are discussed in the context of exploitation patterns.

Introduction

Dungeness crab (Cancer magister) have been fished in British Columbia since the late 1800s. Until recently, crab was the most valuable Pacific invertebrate species commercially exploited in Canada. In 1983, crab ranked eighth (Table 1) among all Pacific fisheries, second among invertebrates, in landed value ($2.6 million). Landing statistics for many high price invertebrate species are known to be underestimated, since a significant portion of the catch is often sold directly to the

Table 1. Landed weight and value of British Columbian fisheries for 1982 as reported on sales slips. Source: Annual Summary B.C. Catch Statistics 1982. Economics and Statistics Branch.

	Catch (t)	Landed value (10^{-3} $)	Rank
Salmon	62,563	165,102	1
Herring	28,598	31,799	2
Halibut*	2,382	7,094	3
Sablefish	3,912	6,847	4
Herring spawn-on-kelp	177	4,130	5
Rockfish	10,366	3,902	6
Geoduck	3,135	2,814	7
Crab**	1,002	2,627	8
Lingcod	4,040	2,439	9
Shrimp and prawns	689	2,196	10
Pacific cod	4,689	2,099	11
Soles	2,897	1,627	12
Intertidal clams	1,159	1,141	13
Abalone	54	457	14
Dogfish	2,037	413	15

*Includes landings of B.C. fishermen at U.S. ports.

**Includes 107 t not reported on sales slips because of export market.

public without any documentation. It is estimated that about 8% of crab sales slip data were missing in 1983 from vessels reporting at least some crab catch and that an additional unreported catch of 10-20% of the reported catch is landed by other fishermen (R. Harbo pers. comm.). However, in the absence of better quality fishery data for the Canadian Dungeness crab fishery, I have assumed that underreporting of catch has been generally consistent between years and areas. In this paper, I use sales slip data to characterize geographically distinct Dungeness crab fisheries in British Columbia. Existing management rationalle and regulations are presented and the impact of alternate, competing fisheries in a multi-species fishing environment is discussed. Methot (in press) has recently addressed the rationale behind American management regulations and has discussed American exploitation of Dungeness crab in the context of the excessive fishing capacity of American Dungeness crab fleets. This paper provides a complmentary Canadian perspective, expanding on the management overview of the Canadian Dungeness crab fishery by Jamieson (in press).

The Fishery

The Canadian Dungeness crab fishery has been centered at the northeastern corner of the Queen Charlotte Islands, Chatham Sound, the west coast of Vancouver Island around Tofino, the Victoria area, and the estuary of the Fraser River (Fig. 1). Some of these fisheries were briefly described a few decades ago (Tofino area: Spencer 1932; Queen Charlotte Islands: McMynn 1951) and the Georgia Strait fishery has been recently summarized by Ketchen et al. (1983). In general, however, little published fishery information is available.

Canadian Dungeness crab landings peaked in 1967 at 2405 t (Fig. 2) and at this time, the primary fishing grounds were in the shallow water banks adjacent to the Queen Charlotte Islands in Hecate Strait and Dixon Entrance. In the late 1960s, northern crab landings decreased and although effort (days fished) has subsequently increased substantially (Fig. 2), crab landings from this region have remained relatively low. Landed price was relatively stable prior to 1971, but has since increased about seven-fold (Fig. 2). In real terms, ie. accounting for inflation (Vancouver Consumer Price Index, Statistics Canada), crab price has increased 2.6 fold. New markets have also been developed, and northern crab are regularly transported alive by sea or air from the Queen Charlottes directly to American buyers.

In the south of the province, effort has also increased although landings have remained near historic levels (Fig. 2). Most Dungeness crab populations in the province are now exploited commercially (Bernard 1982) and any future major increase in landings is expected to reflect fluctuations in year-class strength or a price increase rather than expansion of the fishery into previously unfished areas.

Present crab landings as reported on sales slips include all _Cancer_, _Paralithodes_ and _Lithodes_ landings. There have been some minor king crab (_Paralithodes_ _camtschatica_ and _Lithodes_ _aequispina_) landings from the north coast in recent years. Little, if any, commercial fishing of _C_. _productus_ or _C_. _gracilis_ has occurred.

The British Columbian coast has been divided into eight geographical areas (Fig. 1, Table 2) representing what I perceive to be relatively discrete crab fisheries. These areas do not necessarily define

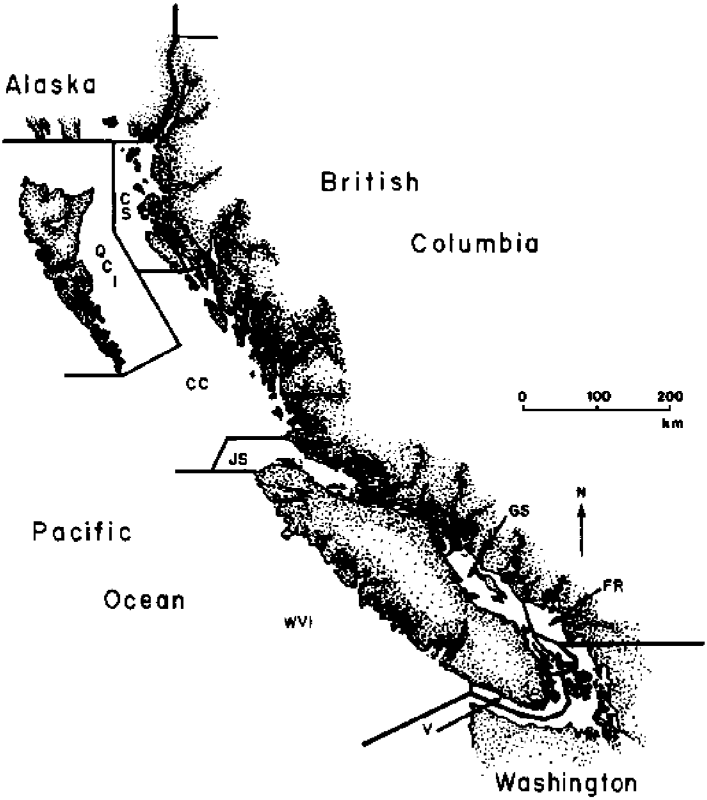

Fig. 1. The geographic boundaries of the eight, geographically distinct Dungeness crab fisheries identified in British Columbia. Reference symbols are: QCI, Queen Charlotte Islands; CS, Chatham Sound; CC, Central Coast; JS, Johnstone Strait, WVI, west coast of Vancouver Island; GS, Georgia Strait; FR, Fraser River estuary; V, Victoria.

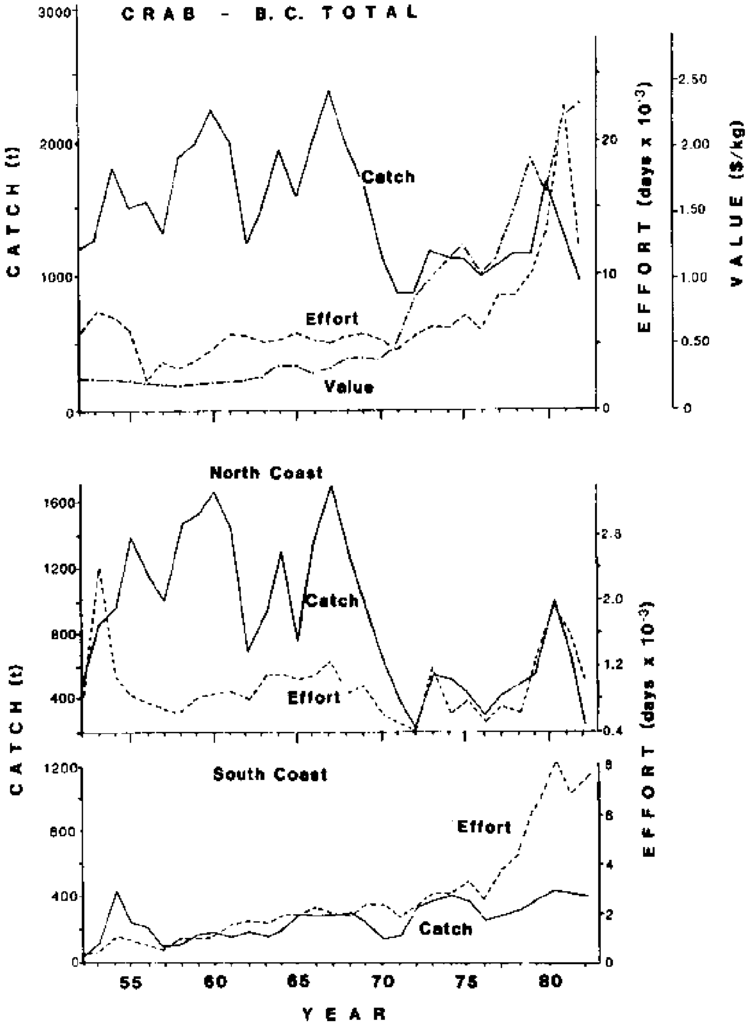

Fig. 2. Annual Dungeness crab catch, effort and unit price statistics for British Columbia in the years 1952-82. North and South coasts refer to north and south of Cape Caution respectively.

Table 2. Definitions of geographical and species groupings used in this paper.

A. Geography

Designated names	Area code	Statistical districts
Queen Charlotte Islands	(QCI)	1, 2
Chatham Sound	(CS)	3, 4, 5
Central Coast	(CC)	6-10, 30
Johnstone Strait	(JS)	11-13
Georgia Strait	(GS)	14-18
Victoria	(V)	19-20
West Vancouver Island	(WVI)	21-27
Fraser River	(FR)	28, 29

B. Species

Species code	Species
Salmon	all salmonids (*Oncorhynchus* and *Salmo*)
Halibut	*Hippoglossus stenolepis*
Herring	*Clupea harengus pallasii*, including herring spawn-on-kelp
Rockfish	all rockfish (*Sebastes*) species
Roundfish	*Hexagrammidea* including lingcod (*Ophiodon*) and greenlings (*Hexagrammus*); Gadidae; sablefish (*Anoplopoma fimbria*); and dogfish (*Squalus acanthias*)
Flatfish	Pleuronectidae, excluding *Hippoglossus*; Rajidae
Shrimp	all pandalid species (shrimp and prawn)
Crab	*Cancer magister* with possible minor landings of *Cancer productus*, *Lithodes aequispina* and *Paralithodes camtschatica*
Molluscs	all mollusc species
Other	any other species landed commercially

different crab stocks, as population mixing in the larval stages at least undoubtedly occurs among many of these areas, but it does consider geographical differences, the relative mobility of fishing vessels in each area and historical fishing patterns.

C. magister is one of the few major species fished in British Columbia for which there is unlimited entry to the fishery. Any vessel licensed in category A, B, or N (all salmon), C (general), G (geoduck: *Panope abrupta*), K (sablefish: *Anoplopoma fimbria*), L (halibut: *Hippoglossus stenolepis*), S (shrimp trawl), or T (groundfish trawl) may fish for crabs using trap gear. On average, 7300 vessels have been licensed to fish each year over the past 15 years, but because some vessels are multi-licenced, simple addition of the numbers for the various licence categories in a given year cannot be used to establish accurately the number of vessels that may potentially fish crab. Of the 8583 vessel licences issued in British Columbia in 1983, 6715 licences would permit crab fishing, suggesting that about 5000-6000 vessels of the 7217 vessels actually licenced might potentially do so. Only about 350 vessels annually actually did so in recent years (Table 3).

A defined Dungeness crab fleet, consisting of vessels dedicated to fishing crab over a number of years, appears to be very small in British Columbia, as the turn-over rate of vessels participating in the crab fishery is high (Table 3). Over the years 1979-83, 37% of the vessels participating in the previous year have on average dropped out of the fishery each year; 41% of the vessels participating each year have been new to the fishery. Of the 948 vessels which participated in the fishery from 1978-83, 52% participated for only one year and only 5% participated for all six years.

Canadian crab landings as a whole do not demonstrate clearly the cyclical fluctuations in abundance (Fig. 2) which have characterized some geographically more discrete, American crab fisheries, and in particular the northern California crab fishery (McKelvey et al., 1980). Subfishery landings fluctuate (Fig. 3) but with the present preliminary analysis, it is unclear how landings reflect crab abundance *per se*.

With respect to landings from the Queen Charlottes, the recent decrease may partially reflect a changing market and associated catch reporting problems; some crab fishermen fishing Queen Charlotte waters are inadvertently not providing sales slip data to Canadian authorities. However, there is anecdotal evidence from fishermen that a prolonged decrease in crab abundance has occurred since the late 1960s. A more comprehensive evaluation of past Canadian crab fishery statistics to determine if other such vagaries exist seems justified before more rigorous analyzes are initiated.

When a fishing fleet is not dedicated to exploiting a specific species, catch of a species does not always reflect the relative abundance of that species but may be influenced by the relative economic return from other competing fisheries. Relative to Dungeness crab landings in American states (Table 4), recent British Columbia crab landings are relatively low in magnitude. An explanation for this low Canadian harvest is not known and it is unclear as to whether fishery, habitat, oceanographic or biotic factors are most important.

The characteristics of those vessels fishing crab in 1983 (Table 5)

Table 3. Number of vessels actively participating in the Dungeness crab fishery on an annual basis, and the number of years of participation by vessels between 1978 and 1983.

A.

Year	Range* of potential number of active crab vessels	No. of active vessels			
		Old	New	Departed	Total
1978	4677 - 6444	-	-	-	252
1979	4602 - 6961	147	168	105	315
1980	4543 - 6787	191	150	124	341
1981	4547 - 6735	227	140	114	367
1982	4470 - 6617	238	114	128	353
1983	4364 - 6715	235	128	118	363

* number of licences in the largest single licence category (ie. A) to the total number of licences issued in all licence catagories permitting crab fishing (A, B, C, G, K, L, S, T and N), assuming complete and no multi-licencing of vessels respectively.

B.

No. of years of active participation 1978-83	No. of active vessels	
	n	%
1	493	52
2	193	20
3	91	10
4	65	7
5	57	6
6	49	5
Total	948	

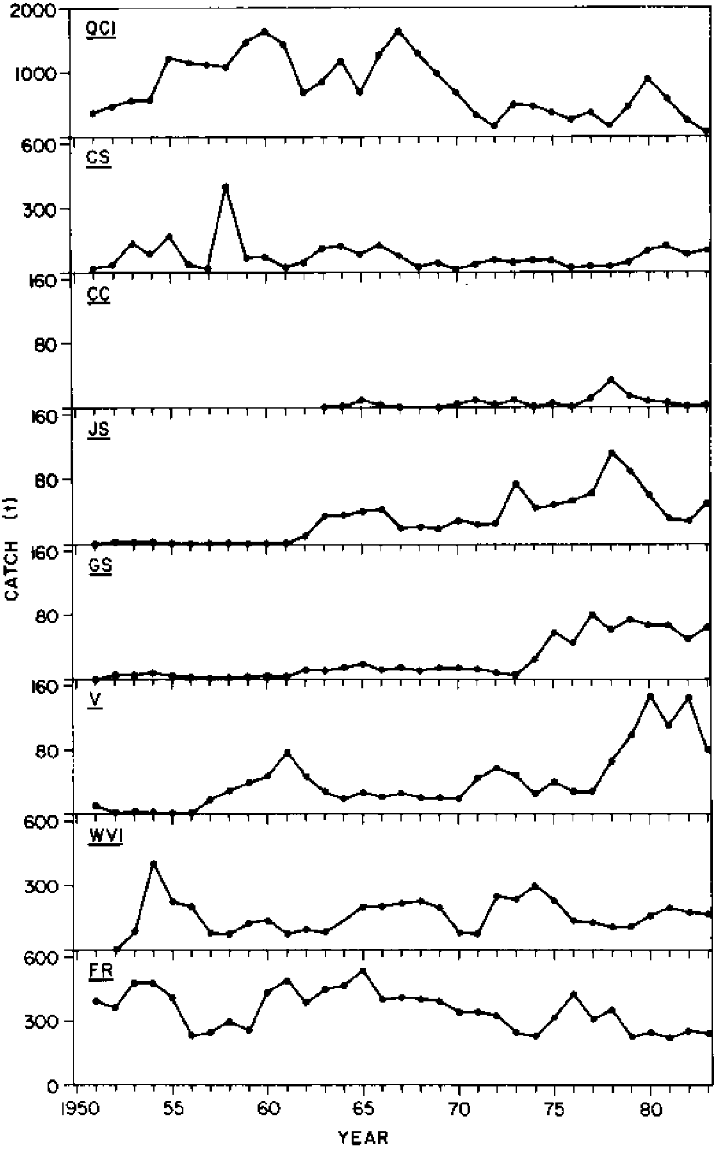

Fig. 3. Annual Dungeness crab landings in the eight fisheries identified in British Columbia. Reference symbols and geographic boundaries are described in Table 2 and Fig. 1 respectively.

Table 4. Dungeness crab landings (t) by political region for the years 1978-83 (Source: Pac. Mar. Fish. Comm. Annual Rep., 1978-83).

Fishing season	California	Oregon	Washington	Calendar year	B.C.	Alaska
1977-78	6260	4717	3266	1978	1089	3266
1978-79	3765	7439	3765	1979	1043	2903
1979-80	6214	8255	2948	1980	1542	2676
1980-81	5352	4309	1179	1981	1270	7076
1981-82	4763	3946	1163	1982	1002	7348
1982-83	2404	1859	1814	1983	843*	5216

*landings reported as of September 1, 1984

Table 5. Number of vessels fishing crab in 1983 and their average length, presented by geographical area (see Table 2 for area code explanation). Data was available for only 338 of the 363 vessels which fished crab in 1983.

Area code	Number of vessels fishing and their average length (m)					
	<10		10 << 20		>20	
	n	L	n	L	n	L
QCI	3	9.0	28	13.4	2	20.8
CS	10	7.7	40	12.8	3	21.4
CC	11	7.4	25	12.0	0	
JS	29	7.6	67	12.2	3	30.9
GS	62	7.8	51	11.8	2	35.6
V	45	7.4	34	12.3	1	22.6
WVI	41	7.4	67	12.4	4	29.6
FR	51	8.1	53	11.4	0	
Total	149	7.7	182	12.0	7	26.1

indicate that crab fishing is predominantly a small boat fishery. Of the 363 vessels fishing crab in 1983, length information was available for 338 vessels and of these, 44% were <10 m in length, 54% were 10 m << 20 m, and only 2% were >20 m. The overall average length was 10.4 m, slightly shorter than the average length of vessels reported for the California crab fishery (Dahlstrom and Wild 1983; Methot in press). Evaluation of the mobility of Canadian crab fishing vessels between identified fishing areas was determined by comparing locations of fishing activity with the vessel's designated home port, which was estimated from the registered mailing address of each vessel owner. Actual home port information was only available for 1981 and for only about 25% of all licensed vessels, but of the 101 crab fishing vessels in that year for which both data were available, 90% had identical address and home port area locations. On the basis of this high correlation, the fishing areas of the 251 vessels in 1983 for which owner addresses could be found was determined from sales slip data (Table 6). Of the total number of fishing records reported by crab-fishing vessels, an average of 47% for all species fished, including crab, and 68% from crab alone were made by fishermen in the area in which the owner resided. Fishing in other areas thus largely occurred while fishing species other than crab and this was most often in geographically adjacent areas, as might be expected from the relatively small size of the vessels involved.

Between areas, the greatest number of fishing records in 1983 was from Georgia Strait around to the west coast of Vancouver Island (68% of the landing records for all species; 83% of crab landing records). Only 2% of the total number of crab fishing records were from the Queen Charlotte Islands, although some landings are known to be missing. Nevertheless, the region with the greatest intensity of crab fishing at the present is the south coast of the province.

Current Regulations

Methot (in press) has described in detail much of the management rationale behind American crab regulations and to a large extent, these apply to the Canadian fishery as well (Miller 1976; Jamieson in press). Canadian crab fishery regulations have as general objectives conservation of the resource, maintaining stability of landings, maintaining product quality and recognizing and addressing social concerns. Restrictive measures include control of gear type, minimum crab size at landing, season and areas closures, and although operationally ineffective, a license requirement (Table 7). In contrast to American regulations (Methot 1985), Canadian fishermen may legally fish female crabs, berried or not, so long as they meet the minimum shell width, spine to spine, of 165 mm (115 mm for *Cancer productus*). This minimum size limit applies to both sexes but because female crabs seldom reach this size, relatively few female crabs are actually fished. On occasion, though, large female crabs may occur in abundance and landings from certain locations may primarily consist of only female crabs.

When a minimum size limit for crab was first introduced into Canadian fishery regulations is uncertain, but it appears to have been in the 1910's and was presumably set so that male crabs would be mature for 2-3 years before they recruited to the fishery. There is no published evidence that this specific minimum size is optimal.

Table 6. Mobility of the dungeness crab fleet for all species fished and for crab alone in 1983. (See Table 2 for area code explanation.)

Vessel owners address	No. of vessels	Species fished	No. of records by area (%)								No. of records
			QCI	CS	CC	JS	GS	V	WVI	FR	
QCI	8	All	69	27	2	1	0	1	0	0	271
		Crab	100	0	0	0	0	0	0	0	20
CS	30	All	20	68	5	3	2	0	0	1	1197
		Crab	11	84	1	0	0	0	0	4	221
CC	1	All	18	0	27	0	55	0	0	0	11
		Crab	0	0	67	0	33	0	0	0	3
JS	27	All	8	1	5	57	2	0	26	0	1140
		Crab	0	3	0	75	7	1	14	0	190
GS	41	All	0	1	4	28	24	2	38	3	1881
		Crab	0	1	2	9	62	1	1	13	289
V	45	All	0	2	0	2	34	31	29	2	2791
		Crab	0	0	0	1	32	57	5	5	707
WVI	30	All	2	1	1	8	0	8	80	0	1451
		Crab	0	0	0	4	0	23	73	0	428
FR	69	All	1	2	4	11	8	11	17	45	2218
		Crab	0	0	0	1	10	8	8	73	671
Total	251*	All	5	9	3	15	15	12	31	10	10960**
		Crab	2	8	1	8	19	22	18	23	2529**

*71% of all active vessels; **80% of the total record number, 78% of crab records.

Table 7. Presence or absence of specific fishery regulations in the recreational and commercial dungeness crab fisheries of British Columbia.

Regulation	Recreational fishery	Commercial fishery
Gear type	Yes	Yes
Closed areas	Yes	Yes
Closed seasons	No	Yes
Licence required	No	Yes
Gear limitations	Yes	No
Escape ports required	No	Yes
Trap destruct device required	No	No
Gear identification required	Yes	Yes
Unlawful to have gear in water during a closure	Yes	Yes
Minimum frequency of tending traps specified	No	Yes
Minimum carapace width	Yes	Yes
Females retainable	Yes	Yes
Soft-shell crab defined	No	No
Return sublegal crabs unharmed (unharmed undefined)	Yes	Yes
Bag limit	Yes	No

While a minimum size limit is the main management tool, area and season closures of the commercial fishery have been introduced in specific bays and areas to address local concerns, including navigation, pollution, the landing of soft-shell crabs, and the preservation of native and sports fisheries. The decision to close and/or open local crab fisheries may be made by fishery officers, management biologists and/or area managers. Existing, pre-determined closures to prevent the landing of soft-shelled crabs may be a relatively poor method of maintaining a high product quality, as depending on ocean climate, the temporal occurrence of moulting can vary on an annual basis. In-season monitoring should really be effected if optimal closure dates are to be determined; present closure dates are established at least one year in advance. Alternate methods might be: 1) to expect buyers to control product quality through a differential price structure based on shell hardness, and the absence of such a scheme suggests that poor product quality is not as important to the processor as perceived by the resource managers. This approach has the additional advantage of minimizing enforcement and management costs; 2) to routinely moult stage a subsample of the commercial crab catch, using a method similar to Aiken's (1973) for lobster, and to close the fishery when moulting of a predetermined fraction (eg. > 20%) is imminent. This is being proposed in the management of Gulf of St. Lawrence snow crab (Chionoecetes opilio) (R. Elner, pers. comm.)

Gear restriction in the commercial fishery appears ambiguous as the Pacific Shellfish Regulations (Anon. 1983) state that only traps, dip nets, and ring nets may be used, while the 1984 Commercial Fishing Guide, Pacific Region, a less authoritative publication but one more widely distributed, states that only spears, jigs, gaffs, rakes, or sharp pointed instruments are restricted. The status of trawling is thus uncertain, although relatively few crab are reported as being landed by this fishing method (1 t in 1983).

Only one escape port is required in Canada in commercial traps, in contrast to the two required by American state regulations. The escape port must be a minimum of 100 mm in diameter if circular or 50 by 100 mm if rectangular, and must be located not more than 10 cm below the frame at the top of the trap. This is smaller than the 108 mm (110 mm in Alaska) diameter escape ports required in American traps. The disadvantage of having only one escape port is that occasionally a crab will block it. Escape port size could probably be slightly larger, allowing the release of more sublegal size crabs with little increase in the escapement of legal size crabs, as indicated by Wild and Tasto (1983). The cost of requiring all new traps to meet new specifications would likely not be great, but such a requirement might be unattractive to fishermen. No programme is presently planned in British Columbia to investigate this subject.

There is some concern that lost traps will continue fishing (ie. ghost fishing), since no trap destruct devices are required in British Columbia. The extent of such fishing is difficult to assess and the number of traps lost annually is presently unknown. Methot (in press) reports that about 10% of American traps are lost annually.

In summary, Dungeness crab have been managed passively in that regulations have not generally been used to modify landings on an annual basis. Present regulations have mostly been in effect for decades. Jamieson (in press) has suggested that the widespread nature of the fishery and the absence from it of the larger fish processing companies may have hindered in the past development of an effective lobby for crab interests. The collapse of northern crab landings in the early 1970's resulted in little new research and no change in the management of the resource. Fishermen have become more organized in recent years and their participation in discussions on the study and management of crab is encouraged.

Multi-species Aspects

Vessels used for fishing crab are mostly small, inshore vessels and include herring skiffs, salmon trollers, and long-liners. A few larger vessels, such as seiners, draggers and blackcod vessels also participate, making the Dungeness crab fishery only a part of a much larger multi-species fishery complex.

To put the relative magnitude of the crab fishery into perspective, one first has to appreciate the dominating effect salmon fishing has over other British Columbian fisheries (Table 1). In 1982, salmon represented 71% of the total landed value ($202.3 million) from all fisheries in British Columbia. In contrast, the landed value of crab ($2.6 million) was 1.1% of this total. The total landed value of all species fished by vessels which landed crab was only 3% of the total landed value of all regional fisheries. This relative importance contrasts significantly with the fisheries of central and northern California, where the landed value of Dungeness crab in 1983 was $U.S. 7.9 million, or 19.1% of the total landed value of all species (Methot, 1985).

To investigate the characteristics of multi-species fishing by crab fishing vessels, the species fished by these vessels were allocated among 10 species grouping (Table 2) which include all commercial species fished in British Columbia. Crab landings from vessels which could not be identified were excluded. Table 8 indicates the total number of vessels involved during the years 1978-83, their relative involvement in each species fishery, and the average annual dollar return per vessel. Relatively little fishing occurred for flatfish and molluscs and so data for these species groups was combined with the 'other' group in this table. There were relatively large increases in the number of vessels fishing crab in 1978 and 1979, but since then, number of active vessels per year has been about 350 (Table 8). Among these vessels, there has been a general increase in their involvement in salmon and shrimp fishing, but for the other species groups, no consistent pattern appears evident. In terms of average price in recent years, only crab showed both a general annual increase and a real price increase (Table 8), after accounting for 58% inflation between 1978-83 (Vancouver Consumer Price Index, Statistics Canada). Average annual dollar return per vessel peaked in 1982 and in 1983, it dropped to a level ($19,100) last encountered in 1978-79. The relatively high price of crab suggests that over the near future, there is likely to be sustained pressure on crab in an effort by fishermen to increase their income. Any increase in crab price or abundance will likely be reflected by increased effort as indicated by the recent tendency of fishermen to remain in the fishery (Table 3).

A similar analysis was conducted for each geographical area (Table 9) for the major species groups fished there, and it was evident that the provincial pattern is largely the result of changes in fishing activity

Table 8. Economic data for the years 1978-83 by species grouping for all geographical areas combined for all vessels which landed crab in British Columbia.

Yr	Salmon	Halibut	Herring	Rockfish	Roundfish	Shrimp	Crab	Other *	Total
					Number of vessels fishing				
83	92	22	15	102	102	70	363	77	363
82	68	17	17	104	97	87	352	83	353
81	79	20	24	110	103	79	366	120	367
80	67	23	14	117	119	86	343	124	343
79	59	19	23	104	120	69	316	123	315
78	48	35	17	66	80	27	253	93	252
					Average price ($.kg^{-1})				Average annual return (10^{-3}\$) per vessel
83	1.72	3.46	1.23	0.71	0.51	4.08	3.42	-	19.1
82	2.23	3.06	1.15	1.26	1.19	4.01	2.67	-	26.2
81	1.83	2.93	1.04	1.41	0.95	4.12	2.25	-	22.1
80	2.23	2.76	0.71	1.08	0.40	5.03	1.68	-	22.6
79	2.62	5.89	1.87	1.01	0.40	4.81	1.92	-	22.0
78	1.76	4.41	0.62	0.71	0.49	4.45	1.52	-	18.6

*includes flatfish, mollusc and 'other' species (see Table 2).

Table 9. The (A) number of active fishing vessels and (B) average return for vessel ($\$10^{-3}$) by year for the major species groups fished (see Table 2 for code explanation).

A. Number of vessels

	QCI			CS			WVI			
	Salmon	Halibut	Crab	Salmon	Halibut	Crab	Salmon	Roundfish	Shrimp	Crab
1983	14	13	13	24	7	36	53	49	11	74
1982	18	11	20	21	5	26	31	34	15	69
1981	26	12	31	24	8	39	33	24	13	52
1980	18	16	21	17	8	31	31	20	7	39
1979	13	12	21	20	6	30	17	21	8	44
1978	15	17	14	19	16	22	14	16	4	25

	V				FR		
	Salmon	Roundfish	Shrimp	Crab	Salmon	Shrimp	Crab
1983	2	22	16	75	28	9	92
1982	5	22	16	87	24	22	105
1981	7	18	17	68	28	14	97
1980	6	26	16	64	26	14	106
1979	7	16	5	40	26	22	108
1978	4	12	4	31	18	7	86

B. Average return per vessel ($\$10^{-3}$)

	QCI			CS			WVI			
	Salmon	Halibut	Crab	Salmon	Halibut	Crab	Salmon	Roundfish	Shrimp	Crab
1983	16	27	19	12	20	10	15	3	2	9
1982	17	23	19	25	23	8	32	17	6	8
1981	35	23	34	14	17	7	18	6	5	10
1980	27	19	64	11	30	6	10	1	2	9
1979	42	39	44	13	48	4	25	1	11	5
1978	33	13	39	12	31	2	14	2	4	8

	V				FR		
	Salmon	Roundfish	Shrimp	Crab	Salmon	Shrimp	Crab
1983	19	6	2	4	4	8	9
1982	28	7	1	4	5	3	6
1981	10	1	3	4	6	6	5
1980	35	1	1	4	10	6	4
1979	5	1	2	4	8	1	4
1978	6	0	1	3	4	2	6

in a few specific geographic areas. In terms of number of crab vessels actively participating in each fishery, the only areas showing major increases were the west coast of Vancouver Island (WVI) and Victoria (V). Off the west coast, increased participation by crab fishing vessels in salmon, roundfish and shrimp fishing occurred. Around Victoria, shrimp and groundfish fishing showed increased crab vessel participation. In both areas, number of vessels fishing crab also increased. These trends were not generally correlated with an increase in the landed dollar return per vessel by species grouping, which suggests that increased effort may have negated any increase in income. The only instance of a consistent increase in income per vessel by species group was for crab in Chatham Sound, a location where the number of vessels fishing showed no clear trend over the six-year time period.

When fishing activity and economic return among subfisheries and species groups is compared for a specific year (1983), it is evident that most earned income by vessels which fish crab is actually from crab (Table 10). Thirty-nine percent of the total landed value for all species fished was represented by crab. However, this was only because 32% of the vessels fished crab exclusively (Table 12), and in a comparison of average dollar return per vessel between species groups, crab ranked a distant fourth ($7500) behind herring ($30,600), halibut ($26,200), and salmon ($21,600)(Table 10). The greatest total landed value by area ($1.9 million) occurred off the west coast of Vancouver Island, whereas the largest average income per vessel was in the Queen Charlottes ($28,100), followed by the west coast of Vancouver Island ($16,900) and Chatham Sound ($16,700).

The income earned from a vessel is both a function of the species fished and often, its relative size. Crab accounted for 63, 32, and 29% of the total average income from small (<10 m), medium (10<<20 m) and large (>20 m) vessels respectively (Table 11). The smaller the vessel, the less it was used for multi-species fishing. While this generalization may apply to the province on a whole, for vessels in the Fraser River estuary, relatively little multi-species fishing was evident. Almost the entire income earned by these vessel categories came from crab fishing.

The effect of vessel size on crab landings was further analyzed by comparing income earned through crab fishing alone among those vessels used to fish crab exclusively and those vessels used in fishing other species as well (Table 12). On the west coast of Vancouver Island, full-time crab fishermen earned considerably more through crab fishing than did fishermen fishing crab along with other species, and for these latter fishermen, crab fishing appeared to be a relatively minor activity. In contrast, in the Fraser River esturary, the highest crab income was earned by the numerically fewer, multi-species fishermen, while a large number of fishermen appeared to fish only crab but in relatively small quantities. This may reflect the close geographical proximity of this latter site to Vancouver, a major urban area, and the resulting participation of many part-time fishermen who have primary jobs in other industries.

Finally, the seasonal nature of crab fishing was analyzed to establish how fishermen allocated their effort among alternate fisheries open at the same time. The major species landed in the major crab fishing areas were considered (Table 13), and the most obvious feature was that alone

Table 10. Economic data on all landings by geographical area fished for all vessels which landed crab in British Columbia in 1983. Area and species codes are explained in Table 2.

Area	Species (year = 1983)										
	Salmon	Halibut	Herring	Rockfish	Roundfish	Flatfish	Shrimp	Crab	Molluscs	Other	Total
	A. Number of vessels fishing										
QCI	14	13	2	3	10	0	2	13	0	1	33
CS	24	7	0	4	6	0	6	36	6	6	54
CC	21	1	6	0	2	1	4	8	2	2	37
JS	33	2	0	37	29	3	22	70	7	3	106
GS	18	0	12	32	21	11	20	81	8	3	119
V	2	0	0	18	22	11	16	75	8	2	84
WVI	53	4	3	36	49	9	11	74	12	5	115
FR	28	0	0	3	3	0	9	92	1	6	112
Total	92	22	15	102	102	20	70	363	35	22	363
	B. Mean value ($10^{-3}) by species group landed per vessel actively fishing										
QCI	16.1	27.4	49.1	0.3	0.2	0.	1.2	18.5	0.	0.	28.1
CS	12.0	19.9	0.	0.6	0.2	0.	12.1	10.2	5.0	0.	16.7
CC	6.0	6.6	14.5	0.	0.	0.	15.9	1.5	0.4	0.	8.0
JS	11.1	13.0	0.	2.0	0.7	0.4	6.0	2.5	0.2	7.4	7.7
GS	2.4	0.	13.4	0.8	3.2	1.6	2.4	2.6	2.2	0.4	5.0
V	18.7	0.	0.	0.3	6.4	3.2	1.9	3.5	0.7	0.2	6.2
WVI	15.0	14.6	37.5	1.9	2.7	3.6	1.6	8.9	4.5	1.5	16.9
FR	3.8	0.	0.	0.	0.3	0.	8.0	8.5	0.1	0.2	8.6
Total	21.6	26.6	30.6	1.7	3.6	4.3	6.2	7.5	3.1	1.5	19.1
	C. Total value ($10^{-3}) of species group landed										
QCI	226	355	98	1	2	0	2	241	0	0	926
CS	288	139	0	2	1	0	72	368	30	0	900
CC	126	7	87	0	0	0	64	12	1	0	296
JS	365	26	0	75	20	1	132	173	1	22	815
GS	200	0	161	26	68	18	48	208	17	1	590
V	37	0	0	5	141	36	31	261	6	0	517
WVI	794	58	112	69	132	32	17	662	53	7	1938
FR	107	0	0	0	1	0	72	780	0	1	961
Total	1987	586	458	178	366	87	438	2705	109	33	6944

Table 11. The number of vessels fishing and the average value of a vessel's 1983 landing by vessel length and area (see Table 2 for area code explanation), All = all species included; Crab = only crab landings.

Area code	Species	Number of vessels fishing and the average value of landings (10^{-3}\$) by vessel length (m)					
		< 10		10 << 20		> 20	
		n	V	n	V	n	V
QCI	All	3	3.2	28	25.6	2	99.7
	Crab	3	0.4	8	10.4	2	78.2
CS	All	10	6.6	40	18.0	3	37.9
	Crab	9	4.9	24	13.1	2	5.2
CC	All	11	9.8	25	7.2	0	
	Crab	2	0.3	6	1.9	0	
JS	All	29	3.0	67	31.2	3	31.2
	Crab	21	1.1	41	3.0	1	0.1
GS	All	62	4.8	51	5.5	2	4.9
	Crab	43	2.7	35	2.6	0	
V	All	45	4.7	34	6.9	1	55.0
	Crab	41	4.0	29	2.9	1	0
WVI	All	41	9.2	67	21.3	4	32.2
	Crab	32	7.7	37	11.0	2	2.4
FR	All	51	8.7	53	9.2	0	
	Crab	45	8.9	40	9.0	0	
Total*	All	149	10.7	182	25.5	7	85.8
	Crab	149	6.7	182	8.1	7	24.5

*not the total of the number of vessels from each area since a single vessel may fish a number of areas.

Table 12. The number of vessels fishing and the average value of a vessel's 1983 landing by vessel length and area (see Table 2 for area code explanation). C = those vessels that fished only crab; C+ = the value of crab landings for those vessels that fished other species as well as crab.

		Number of vessels fishing and the average value of landings (10^{-3}) by vessel length (m)					
		<10		10 << 20		>20	
Area Code	Species	n	V	n	V	n	V
QCI	C	2	0.6	4	10.8	1	86.1
	C+	1	0.1	4	10.0	1	70.3
CS	C	7	5.9	12	8.0	0	
	C+	3	1.2	12	13.2	2	5.2
CC	C	2	0.3	3	1.4	0	
	C+	0		3	2.4	0	
JS	C	8	0.5	16	3.8	0	
	C+	13	1.5	25	2.5	1	0.1
GS	C	24	2.1	14	2.4	0	
	C+	19	3.5	21	2.6	0	
V	C	23	3.3	18	2.4	0	
	C+	18	5.0	11	3.8	1	0.0
WCI	C	20	10.0	12	21.1	1	3.0
	C+	12	3.9	25	6.2	1	1.8
FR	C	35	6.3	30	7.8	0	
	C+	10	18.0	10	12.8	0	
Total	C	63	8.5	53	11.4	1	3.0
	C+	86	5.4	129	6.7	6	28.1

Table 13. Seasonal pattern of landings (10^{-3}\$) by month for 1983 for the major species fished in the five major crab fishing areas of the coast.

	Queen Charlotte Islands				Chatham Sound			Victoria		
Month	Salmon	Halibut	Herring	Crab	Salmon	Halibut	Crab	Salmon	Roundfish	Crab
Jan.				5			19		26	12
Feb.				4			21		19	18
Mar.			98	5			14		13	17
Apr.	3			12			9		11	43
May.	3	186		20	3	41	25		2	54
June	14	26		22	12	0	27	2	4	33
July	85	144		22	159	98	15	30	6	16
Aug.	85			3	118		41	5	2	13
Sept.	29			10	5		65		19	14
Oct.	7			71	1		67		19	15
Nov.				41			32		9	8
Dec.				31			33		11	18
Total	226	355	98	241	288	139	368	37	141	261

	West Vancouver Island				Fraser River			Major areas combined
Month	Salmon	Roundfish	Herring	Crab	Salmon	Shrimp	Crab	Crab
Jan.				28			14	76
Feb.		1		22		9	9	74
Mar.		4	112	34		3	9	77
Apr.	25	13		82		1	22	168
May	33	20		157		2	30	286
June	64	17		93		6	5	160
July	286	34		83	8	9	196	332
Aug.	234	19		39	36	9	272	368
Sept.	135	9		24	63	9	131	244
Oct.	18	12		37		9	49	239
Nov.		2		31		5	28	140
Dec.		1		32		1	15	129
Total	794	132	112	662	107	72	780	2312

among all the species groups considered, crab fishing occurred in all months of the year in every area. Bad weather during the winter months reduced landing in most areas, and for all areas combined, landings peaked in July and August but were substantial from May to October. The occurrence of other fisheries has little obvious effect on monthly crab landings by area, which seem to be most influenced by local seasonal crab closures. Thus, in the Fraser River and Dixon Entrance, closure of major grounds in the spring (May 1 to July 15: soft shell) and the summer (July 10 to Sept 20: soft-shell) respectively reduced some month's landings. The Fraser River closure seems to result in high landings on reopening of the fishery, presumably because of both the expectation by fishermen of high landings and a resulting effort increase, and an increase in crab catchability because of warmer water temperatures and their recent moulting.

In conclusion, crab fishing in British Columbia is part of a large, multi-species fishing complex with pronounced geographical area differences. It is difficult to characterize, and is a very dynamic fishery with many participants entering and leaving on an annual basis. Although crab fishing is of significance in terms of dollar value, it has been so over-shadowed by salmon and herring fisheries that relatively little research and management effort has been devoted to it. However, studies are presently underway or are being proposed to investigate more fully crab biology and multi-species fishery implications arising from change in existing regulations in any of the associated fisheries. This should permit improved understanding of how fisheries impact on each other and of the importance of having relatively minor, unlimited entry fisheries to buffer fluctuations in income from larger, higher profile fisheries.

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A brief review of the commercial fisheries for *Cancer magister* in southeast Alaska and Yakutat waters, with emphasis on recent seasons

Timothy M. Koeneman
Alaska Department of Fish and Game
Petersburg, Alaska

Description of Fisheries

Yakutat.

Two distinct fisheries exist within Statistical Area A. Dungeness crab, Cancer magister, are harvested from the exposed open-ocean coast between Cape Fairweather and Cape Suckling which encompasses the Yakutat Fishery (Fig. 1). This fishery is most similar to major Dungeness fisheries in other areas, in that prime fishing grounds are shallow portions (4 to 30 fathoms) of the continental shelf influenced by adjacent estuaries. Vessels participating in the Yakutat fishery have primarily been non-resident vessels, utilizing standard ocean Dungeness gear, which is independently suspended from buoys in sets along depth contour lines. Common bait is a mixture of squid and herring, and natural populations of subtidal razor clams, Silqua patula, are present in the substrate. Dungeness crab harvested in the Yakutat fishery are of extremely good quality in terms of size and shell color. Waters on either side of Icy Bay have been traditionally good harvest areas, with waters of Yakutat Bay to Cape Fairweather contributing to a lesser degree. Historically, the greatest production of the harvest is taken during June and July.

Southeast Alaska.

The Southeast Alaska fishery is conducted in the convoluted bays, and estuaries south and east of Cape Fairweather, extending to Dixon Entrance (Fig. 2). This fishery is primarily a bay fishery with districts 5, 6, 8, 13, and 14 contributing significantly. The Stikine River delta of district 8 and the Duncan Canal estuary of district 6 have been historically important fishing locations. Vessels participating in this fishery are primarily smaller vessels ported in various Southeast Alaska communities. However, beginning with the 1981/82 season, an influx of larger non-resident vessels entered the fishery. Pots are individually fished

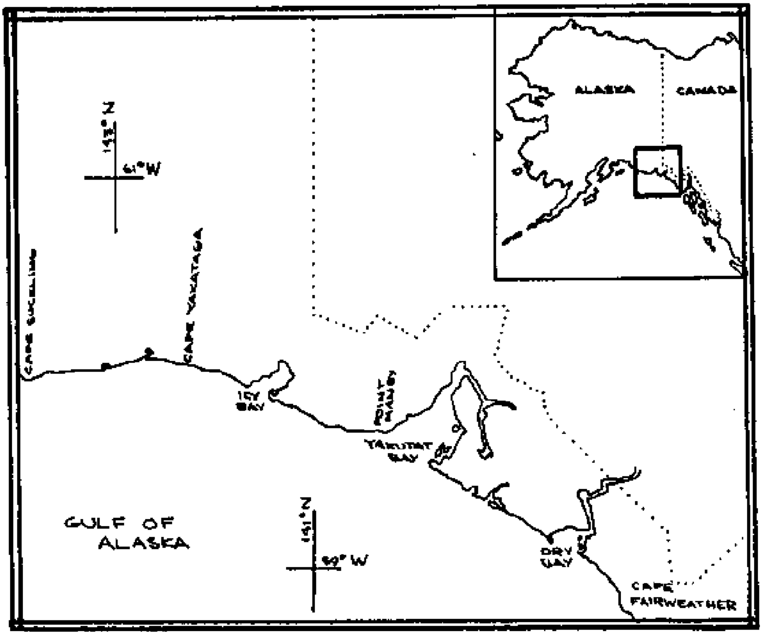

Figure 1. Location of the Gulf of Alaska Coastline Utilized in the Yakutat Commercial Dungeness Crab Fishery.

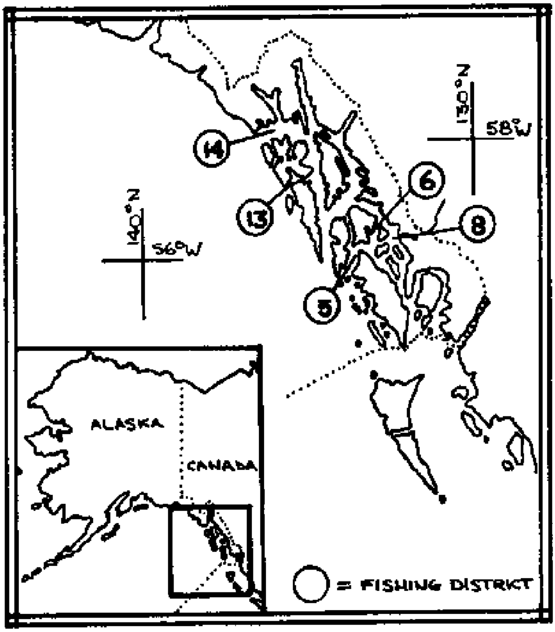

Figure 2. Location of the Gulf of Alaska coastline utilized in the Southeast Alaska commercial Dungeness crab fishery.

in small numbers in bays and along straits and sounds. Fishing along the edge of the Stikine River delta is similar to the large-stringed ocean fishery. Historically, significant harvests occur from June through September. Most crab of ocean quality are processed for a meat-pack product. In recent years, some of the harvest has been flown live to market.

Regulations

Existing regulations concur to traditional size and sex regulations implemented in other Dungeness crab fisheries, but compromise traditional regulations by allowing the fisheries to be conducted during potential molting and mating seasons. Historic notes from the commercial fisheries and past research information indicate that molting, mating and egg-bearing periods in Southeast Alaska and Yakutat are very similar to other Dungeness stocks. During low effort levels and slow-paced fisheries the effects of handling crab during sensitive life history stages may be significantly less than during high effort levels and intense fisheries. The magnitude of such handling mortalities have not been determined to date, but intuitively high effort levels during intense fisheries from May through August are a detriment to stock conditions. Handling mortalities are increased as inexperienced operators enter the fisheries.

Major regulations pertaining to the Yakutat and Southeast Alaska Dungeness fisheries are very similar at the current time.

1. Male only harvest.
2. Minimum legal size of 6.5 inches in carapace width (excluding tenth antero-lateral spines).
3. No water storage of gear during closed seasons.
4. Registration prior to fishing.
5. Alaska Department of Fish and Game number marked on each buoy.
6. Both the Yakutat and Southeast Alaska districts are super-exclusive. Valid registration in one district precludes that vessel from fishing in another district or area in that registration year.
7. Two 4-3/8 inch escape rings are required, and a maximum tunnel perimeter of 30 inches is prescribed.
8. In Southeast Alaska, the season begins on July 1 and extends through February 28, except for a small area near Sitka where the season is September 10 through February 28. In Yakutat, the season extends from May 1 through February 28.
9. In the Southeast Alaska fishery no more than 300 pots per vessel may be fished, and in Yakutat the pot limit is 600 pots per vessel. Also, a number of closures in the vicinity of population centers in Southeast Alaska have been established to provide a priority for subsistence users.

Historic Perspective, 1915-1959

Available documentation for the period 1915 through 1959 is scant and consists primarily of short paragraphs on all species of crab for all regions of Alaska. Very little mention is made of market conditions, effects on production levels from other fisheries, or other factors. Initial mention of the commercial fishery for Dungeness crab in the Petersburg district occurred in 1915 when a small quantity, 14,395 pounds of various products (Table 1),were either consumed locally or shipped to Puget Sound ports (Bower and Aller 1917). In 1921 the fishery expanded significantly in Southeast Alaska and some interesting notes were provided: Harvest was restricted to males over 6 inches in carapace width; primary molting period was from June through August; and meat yield from a 6 to 9 inch crab was slightly less than 8 ounces (Bower 1922). A marked expansion in this fishery occurred in 1933 (Fig. 3), particularly in the Cordova area (Bower 1922) and this may have been in response to improving market conditions mentioned for 1934 (Bower 1935). In 1935 a two-month summer closure was instituted, but the specific reason was not elucidated (Bower 1936). In 1936 the minimum legal size was increased to 7 inches carapace width (including tenth antero-lateral spines) but factors leading to the increase are not mentioned (Bower 1937). The discussion in the 1936 report introduces the assumption that prior discussions of minimum legal sizes reflected an inclusion of the tenth antero-lateral spines. Beginning in 1936, harvest data was presented in tabular form and identifies three basic products: canned, cold packed meat, and whole-in-shell. Within the canned product four different sizes were utilized (6-1/2 ounce, 1/2 pound, 1 pound, and 20 ounces), and cold packed meat was available in either 1, 5, or 10 pound cans (Bower 1937). Documentation identifying reasons for harvest fluctuations during the period 1940 through 1959 were not available, with the exception of poor market conditions effecting the 1956 fishery (Thompson and Erickson 1960). It has generally been acepted that significant effort in the Southeast and Yakutat fisheries have been a result of improved markets for Alaskan crab due to declining harvests in other Pacific Coast areas.

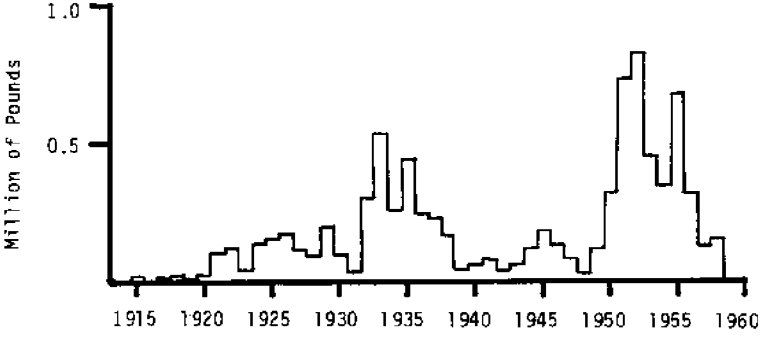

Figure 3. Historic commercial harvests of Dungeness crab, *Cancer magister*, from Statistical Area A (Dixon Entrance to Cape Suckling). Portions of 1925-1927, 1930, 1932, and 1933 harvests include Prince William Sound. Data are in pounds of processed product.

Table 1. Historic commercial harvests of Dungeness crab, *Cancer magister*, from Statistical Area A (Dixon Entrance to Cape Suckling). Data from 1925-1927, 1930, 1932 and 1933 includes Prince William Sound harvest. Data from 1915 through 1959 in pounds of processed meat.

Year	Pounds	Year	Pounds	Year	Pounds
1915	14,935	1940	55,988	1965	3,302,670
1916		1941	65,915	1966	2,496,177
1917	2,160	1942	29,475	1967	4,064,616
1918	4,320	1943	46,966	1968	3,996,809
1919	480	1944	109,707	1969	2,324,400
1920	8,030	1945	172,206	1970	2,289,300
1921	99,000	1946	122,397	1971	1,668,700
1922	113,274	1947	77,184	1972	2,592,900
1923	33,360	1948	22,633	1973	3,085,900
1924	121,374	1949	114,537	1974	1,726,800
1925	140,093	1950	306,706	1975	1,208,600
1926	167,253	1951	738,983	1976	1,054,500
1927	101,372	1952	813,078	1977	237,700
1928	93,940	1953	444,118	1978	2,569,100
1929	193,291	1954	336,872	1979	2,158,719
1930	92,105	1955	670,783	1980	1,381,241
1931	19,401	1956	302,832	1981	6,751,159
1932	296,625	1957	122,462	1982	8,838,900
1933	523,074	1958	149,813	1983	4,555,200
1934	249,247	1959	1,422,292	1984	1,728,100
1935	435,530	1960	1,993,167		
1936	234,255	1961	1,695,000		
1937	215,045	1962	3,922,990		
1938	146,142	1963	4,679,660		
1939	41,514	1964	4,633,240		

Recent History, 1960-1984

Documentations of occurences in the Dungeness fishery for this period can be found in numerous Alaska Department of Fish and Game documents including: Annual Management Area Reports, Regional Shellfish Analyses, and reports to the Alaska Board of Fisheries. Beginning at this time, harvest data for Southeast Alaska and Yakutat were separated (Tables 2 and 3). However, similar trends have been exhibited in both fisheries. Declining harvests in other Pacific Coast Dungeness fisheries produced good market conditions for Southeast Alaska and Yakutat products during the early 1960's. The Southeast Alaska fishery peaked in 1964 and declined through the 1970's (Fig. 4).

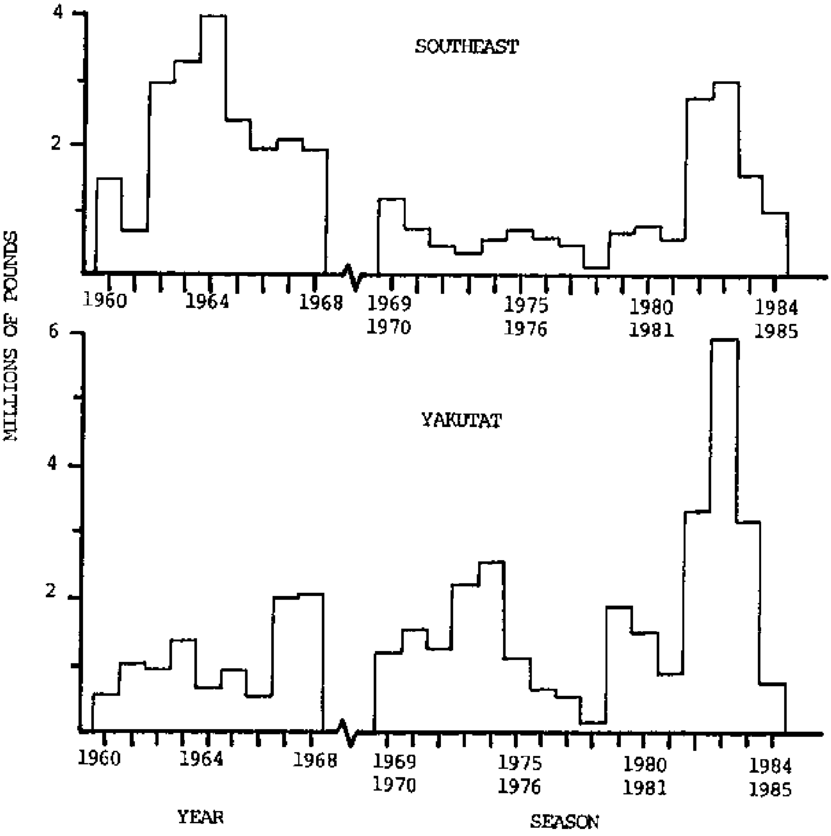

Figure 4. Recent Commercial Harvests of Dungeness Crab, Cancer magister, from the Southeast and Yakutat Fisheries.

Table 2. Recent harvest statistics from the commercial Dungeness crab, *Cancer magister*, fishery of Southeast Alaska (Dixon Entrance to Cape Fairweather).

Year/Season	Catch in Pounds	Number of Vessels	Number of Landings
1960	1,449,405		
1961	671,455		
1962	2,985,939		
1963	3,296,362		
1964	3,996,100		
1965	2,392,395		
1966	1,968,117		
1967	2,033,156		
1968	1,900,690		
1969/70	1,149,111	20	392
1970/71	700,168	21	375
1971/72	413,361	23	309
1972/73	383,100	30	301
1973/74	563,148	41	442
1974/75	647,733	43	435
1975/76	562,768	32	331
1976/77	476,650	15	165
1977/78	124,276	11	85
1978/79	679,175	22	192
1979/80	719,277	32	280
1980/81	516,245	17	224
1981/82	2,685,627	55	649
1982/83	2,929,916	103	1,087
1983/84	1,492,815	139	1,164
1984/85	964,056	136	

[1] Recent year's data should be considered preliminary; season closes February 28, 1985.

Table 3. Recent harvest statistics from the commercial Dungeness crab, *Cancer magister*, fishery of Yakutat, Alaska (Cape Fairweather to Cape Suckling).

Year/Season	Catch in Pounds	Number of Vessels	Number of Landings
1960	543,762		
1961	1,023,545		
1962	937,051		
1963	1,383,298		
1964	637,140		
1965	910,278		
1966	528,060		
1967	2,031,460		
1968	2,096,119		
1969/70	1,207,397	11	107
1970/71	1,589,945	10	88
1971/72	1,250,118	8	91
1972/73	2,207,061	12	99
1973/74	2,532,778	22	274
1974/75	1,097,508	19	173
1975/76	628,879	16	129
1976/77	542,726	8	28
1977/78	131,052	2	11
1978/79	1,875,088	13	134
1979/80	1,474,149	19	99
1980/81	881,681	7	56
1981/82	3,300,158	16	175
1982/83	5,880,409	33	356
1983/84	3,133,531	54	493
1984/85[1/]	763,994	39	

[1/] Season closed July 15, 1984.

Results of research projects indicated that survival of the 1964 year class was poor, and resulted in reduced legal stock abundance in the Petersburg area during 1967. The reasons for low harvests in the 1971 through 1974 period are not explained. Intuitively, Southeast Alaskan markets should have been good. With the most recent decline in the Washington, Oregon, and California fisheries, which began with the 1979/80 season, effort and subsequent harvests in Southeast Alaska increased dramatically to a peak of over 2.9 million pounds during the 1982/83 season. Since that season, effort has remained high, exvessel prices have increased, and harvests have decreased significantly. It is apparent that effort during the past four seasons have been sufficient to capture a high proportion of the available legal stock, and these recent harvests are a fair estimate of stock abundance. Average size, expressed as carapace shoulder width, peaked during the 1982/83 and 1983/84 seasons. Perhaps this is an indication that the strongest year-class contributing to the fishery during recent seasons was the 1978 year-class. Economic conditions, and the unavailability of viable alternative fisheries for many Southeast Alaska fishermen has resulted in a petition for limited entry in this fishery.

As previously mentioned, occurrences in the Yakutat fishery are similar with the exception that reasonably high harvests did occur from 1971 through 1974. These high harvests may be attributable to the greater proportion of Washington ported vessels that participate in the Yakutat fishery. As such, these vessels are more sensitive to market and stock abundance conditions in Washington, Oregon, and California.

Harvests during the 1981/82 through 1983/84 seasons have been the highest on record and correspond to record effort levels. Effort was high once again during the 1984/85 season and the resulting harvest was low. It is apparent that the available stock has been harvested and future harvests will depend upon recruitment entering the fishery. Extensive dockside sampling was conducted in the Yakutat fishery, and results suggest that the most recent fisheries were a result of a strong 1978 year class. This aspect will be discussed to a greater degree in another presentation.

Available Research Information

From approximately 1965 through 1969 various Dungeness crab research projects were conducted by Alaska Department of Fish and Game employees in the Petersburg-Wrangell area. Data was collected primarily by Mr. Carl Lehman and summarized through the Bureau of Commercial Fisheries Quarterly Progress Reports. Mr. Oliver Osborn first attempted to formally summarize the data at a later date (1970) but did not complete this project. Additional analysis of methods, data, and summarization should be accomplished. But, due to the current interest in the Alaskan Dungeness fisheries, some of the summarized data is presented as previously written.

Growth.

Between 1965 and 1969 plastic, spaghetti ephemeral line tags were placed on 5,250 male and female Dungeness crab in the Duncan Canal and St. John Harbor areas. A total of 230 males and 67 females were recaptured after molting. Linear regression analysis of premolt carapace width (measured just anterior to the tenth antero-lateral spines) versus postmolt carapace width was accomplished from data for males (Table 4) and females (Table 5).

Table 4. Average carapace width, absolute increments and percentage increments for male Dungeness crab, *Cancer magister*, in Southeastern Alaska (Lehman and Osborn, Unpublished).

Carapace Width Range (mm)	Number Crab Sampled	Carapace Width		Growth Increments	
		Premolt	Postmolt	Absolute	Percent
70-74	1	74.0	90.0	16.0	22
120-124	2	122.5	147.5	25.0	20
125-129	6	126.7	155.5	28.8	23
130-134	9	132.6	161.6	29.0	22
135-139	13	136.9	163.3	26.4	19
140-144	11	142.8	169.8	27.0	19
145-149	23	147.2	175.2	28.0	19
150-154	33	152.2	180.2	28.0	18
155-159	64	157.2	185.4	28.2	18
160-164	51	162.0	189.9	27.9	17
165-169	11	165.8	193.8	28.0	17
170-174	4	172.8	199.5	26.7	16
175-179	2	177.5	207.5	30.0	17
Total	230				

Table 5. Average carapace widths, absolute increments, and percentage increments for female Dungeness crab in Southeastern Alaska (Lehman and Osborn, Unpublished).

Carapace Width Range (mm)	Number Crab Sampled	Carapace Width		Growth Increments	
		Premolt	Postmolt	Absolute	Percent
50-54	1	51.0	65.0	14.0	27
85-89	1	89.0	106.0	17.0	19
100-104	1	100.0	113.0	13.0	13
110-114	2	113.0	130.0	17.0	15
115-119	8	116.9	132.4	15.5	13
120-124	1	120.0	138.0	18.0	15
125-129	6	126.5	146.3	19.8	16
130-134	12	132.5	149.7	17.2	13
135-139	14	137.1	153.7	16.8	12
140-144	12	141.7	158.5	16.8	12
145-149	6	146.2	160.5	14.3	10
150-154	3	151.7	167.7	16.0	11
Total	67				

Resulting least squares regression equations are:

For males - $Y = .943x + 36.6$ and
for females - $Y = .924x + 27.8$ where

Y = postmolt carapace width in mm and
x = premolt carapace width in mm.

These data were compared to similar data from British Columbia (Butler 1961). which had been adjusted to exclude the tenth antero-lateral spines and found to be comparable (Figure 5).

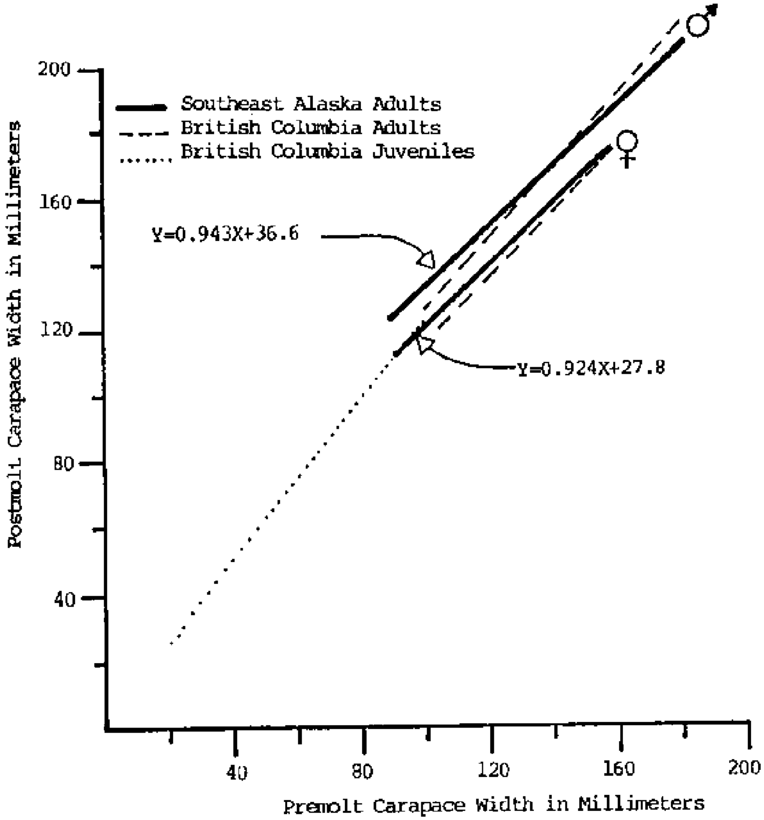

Figure 5. Increase in Carapace Width Per Molt of Adult Dungeness Crab, in Southeast Alaska (Lehman and Osborn, unpublished), and a Comparison with Similiar Canadian Data (Butler 1961). Canadian data adjusted from carapace width including tenth antero-lateral spines to carapace width excluding tenth antero-lateral spines according to Poole (1965).

Molt frequency.

Data was gathered from 335 recaptured males and 179 recaptured females. Results indicate that males molted annually up to the 155 to 159 mm size range, and began to molt with decreasing frequency after attaining that size (Table 6).

Females began to show a similar tendency to molt with decreasing frequency after reaching the 135 to 139 mm size range (Table 7).

Molt timing.

Data indicating population molt times was collected from Duncan Canal and St. John's Harbor from 1965 through 1969. These data suggest that most males molted between late winter and mid-summer months (Table 8). Based upon observations of females with eggs, it appears that most females molt and mate during the summer months, as eggs are carried from September through March (Table 9).

It appears that the life history of Dungeness crab in portions of Southeast Alaska is similar to that described in other geographic locations. However, the above research information should be viewed with caution due to the limited geographic area and time frames within which the data was collected. Additional research is needed to confirm previous findings.

Table 6. Molt frequency of 335 recaptured male Dungeness crab, *Cancer magister*, in millimeters of carapace width, excluding tenth antero-lateral spines (Lehman and Osborn, Unpublished).

Size Class (carapace width in mm.)	Molted Prior to Recapture		Recaptured After 1 Year Without Molting		Recaptured After 2 Years Without Molting	
	Number	%	Number	%	Number	%
130-134	3	100	-	-	-	-
135-139	3	100	-	-	-	-
140-144	1	100	-	-	-	-
145-149	3	75	1	25	-	-
150-154	2	100	-	-	-	-
155-159	10	59	7	41	-	-
160-164	4	17	19	79	1	4
165-169	3	6	43	90	2	4
170-174	1	2	38	88	4	9
175-179	1	2	52	85	8	13
180-184	-	-	42	86	7	14
185-189	-	-	35	81	8	19
190-194	-	-	23	92	2	8
195-199	-	-	11	100	-	-
200-204	-	-	1	100	-	-

Table 7. Molt frequency of 179 recaptured female Dungeness crab, Cancer magister, in millimeters of carapace width, excluding tenth antero-lateral spines (Lehman and Osborn, Unpublished).

Size Class (carapace width in mm.)	Molted Prior to Recapture		Recaptured After 1 Year Without Molting		Recaptured After 2 Years Without Molting	
	Number	%	Number	%	Number	%
130-134	11	92	1	8	-	-
135-139	12	71	5	29	-	-
140-144	11	26	31	74	-	-
145-149	6	17	29	83	-	-
150-154	1	3	31	94	1	3
155-159	-	-	28	87	4	13
160-164	-	-	4	80	1	20
165-169	-	-	2	100	-	-
170-174	-	-	1	100	-	-

Table 8. Summary of data on the occurrence of softshell male Dungeness crab, Cancer magister, from Duncan Canal and St. John's Harbor, 1965 through 1969 (Lehman and Osborn, Unpublished).

Month	Number of Crabs Examined	Number of Soft Crabs	Percent of Soft Crabs
January	no data	no data	no data
February	128	7	5.5
March	73	3	4.1
April	74	9	12.2
May	900	39	4.3
June	677	6	0.9
July	1034	82	7.9
August	1345	9	0.7
September	849	4	0.5
October	390	2	0.5
November	319	2	0.6
December	129	2	1.6

Table 9. Summary of egg occurrence data on untagged female Dungeness crab, *Cancer magister*, from Duncan Canal and St. John's Harbor, 1965 through 1969 (Lehman and Osborn, Unpublished).

Month	Crab Sampled	Number of Crab with Eggs	Percent of Crab with Eggs
January	-	-	-
February	51	6	11.8
March	32	4	12.5
April	7	0	0.0
May	782	6	0.8
June	1296	4	0.3
July	1764	4	0.2
August	1457	1	0.1
September	693	35	5.5
October	357	66	18.5
November	232	87	37.5
December	41	15	36.6

Table 10. Comparison of Dungeness crab size and age data between British Columbia (Butler 1961) and Southeast Alaska populations (Lehman and Osborn, Unpublished).

		Males		Females	
Instar	Age	British Columbia	Southeast Alaska	British Columbia	Southeast Alaska
1		6.5		6.5	
2		9.3		9.3	
3		12.9	12.0	12.9	12.0
4		17.3	16.0	17.3	16.0
5	I	22.6		22.6	
6		29.0		29.0	
7		36.0	35.0	36.0	
8		46.6	47.0	46.6	
9		58.3	65.0	58.3	
10		72.7	76.0	72.7	
11		90.1		90.1	
12	II	111.5		109.9	
13	III	137.1		127.5	
14	IV	164.4		142.3	
15	V	193.6		156.4	
16	VI	224.9		169.0	

Note: British Columbia data adjusted to exclude tenth antero-lateral spines to allow comparison.

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Overview of the Prince William Sound management area Dungeness crab fishery

Al Kimker
Alaska Department of Fish and Game
Cordova, Alaska

Abstract

The Prince William Sound Management Area is adjacent to northcentral Gulf of Alaska and extends from Cape Suckling to Cape Fairfield.

Historically there are two major areas in the Prince William Sound Management Area where Dungeness crabs (*Cancer magister*) are commercially harvested: (1) Orca Inlet District and (2) Copper River District.

The Orca Inlet District, which is immediately adjacent to the community of Cordova, has provided a fishery that allows participation by small vessels in an area protected from adverse sea conditions. Historically the fishery has occurred in the fall months with annual catches ranging to 1.5 million pounds. Recent arrival of a large group of sea otters (*Enhydra lutris*), a major predator of the Dungeness crab, has led to a dramatic decline in abundance of crabs.

The Copper River District is usually a summer-fall fishery. This exposed area is subject to heavier sea conditions and longer running distances to market, thus requiring larger vessels. Harvests have ranged from 78,000 to 1.5 million pounds. Salmon drift gillnet mortalities have effected stock conditions.

General

The Prince William Sound Management Area is adjacent to northcentral Gulf of Alaska and extends from Cape Suckling to Cape Fairfield (Figure 1).

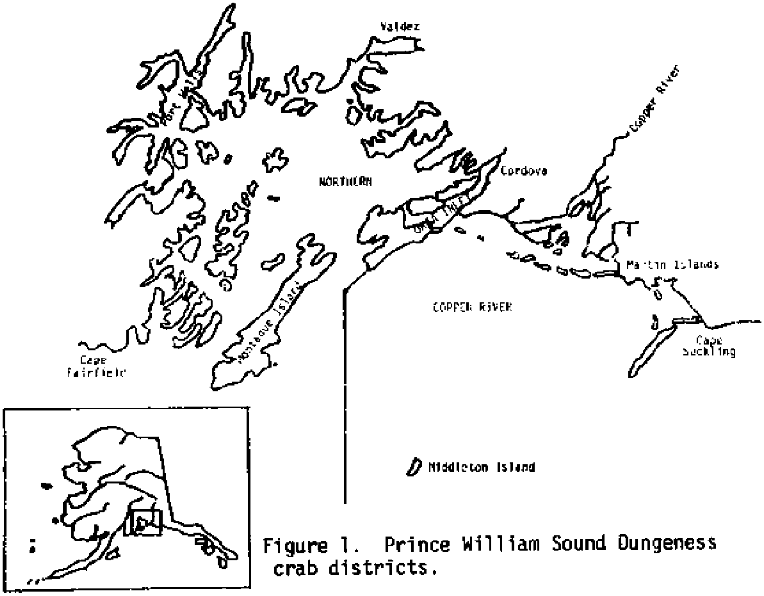


Figure 1. Prince William Sound Dungeness crab districts.

There are two major areas in Prince William Sound where Dungeness crabs (Cancer magister) are commercially harvested: (1) Orca Inlet District and (2) Copper River District. Dungeness are also taken from the Orca Bay portion of the Northern District as well as western Prince William Sound; however, this harvest is proportionally very small and is either taken incidental to the Tanner crab fishery or by one or two small vessels targeting on Dungeness crab.

Historical catch from the entire management area has fluctuated from a low of 300 thousand pounds taken in 1976 to two million pounds taken in 1978 (Figure 2). Prices, which are inversely effected by the success or failure of the traditional Dungeness crab fisheries in Washington, Oregon and California, have until recently dictated the effort level and resultant catch; i.e. in years of low price, such as 1976, the effort level was low and the resultant catch was not a true reflection of stock abundance. However, since 1980, when general crab abundance in the state began to decline, fishermen have been forced to fish for lower profit margins thus maximizing effort in shellfish fisheries regardless of price.

Management strategy for both the Copper River and Orca Inlet Districts is as follows:

1.) Generally avoid fishing during significant softshell periods.
2.) A minimum legal size of 6.5 inches.
3.) Males only, and
4.) Recruit fishery.

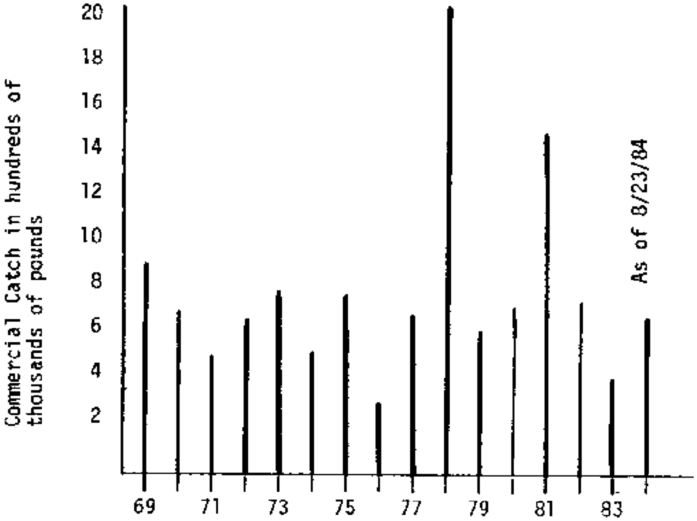
Copper River District

The Copper River District is a late spring through early fall fishery due to prevailing adverse weather conditions which prohibit fishing in the winter. Vessel sizes range from small seine type vessels of 32 feet up to medium sized crab vessels of 70 feet. A 250 pot limit, which is successfully enforced due to fishermen cooperation, generally inhibits larger crab vessels from fishing the district. Fishing normally occurs between the mean low water line and 10 fathoms. This is a reflection of the location of legal males.

Commercial harvest in the Copper River District has fluctuated significantly. Since 1978, when effort level has been consistently high, the catch has varied from a low of 379 thousand pounds in 1983 and 1.5 million pounds in 1981 (Table 1).

The season for the Copper River District opens April 1 and continues through December 31, except for the Controller Bay area which closes on October 15. The season dates are set to coincide with the time of year when the weather permits fishing. The crabs are consistently in their firmest shell condition in late fall through spring; however, sea and icing conditions during winter are such that the majority of the time the district is unfishable. Also, stuck and lost gear caused by this seasonally bad weather creates an unnecessary source of mortality on the large crabs which are in the gear and cannot get out via the escape rings.

Another extraneous source of mortality which cannot be avoided is loss to gillnets. The Copper River Drift Gillnet Fishery for three species



Year

Figure 2. Commercial Dungeness crab catch, Prince William Sound Management Area, 1969 - 1984.

Table 1. Prince William Sound Area Dungeness crab catch, 1960-1984.

Year	Copper River Pounds	Vessels	Orca Inlet Pounds	Vessels	Total Catch Pounds
1960	data not available		1,524,326		
1961			990,242		
1962			1,353,190		
1963			1,216,846		
1964			1,290,929		
1965			1,240,372		
1966			999,341		
1967			No data available		
1968			579,279		
1969	336,696		541,822		878,696
1970	78,223		660,411		738,634
1971	78,848		430,976		509,824
1972	437,865		286,808		724,673
1973	458,613		347,764		806,377
1974	290,149		269,015		559,164
1975	654,410		163,631		818,041
1976	254,933	4	35,399	3	290,332
1977	506,751	4	228,858	23	735,609

Year	Copper River Pounds	Vessels	Orca Inlet Pounds	Vessels	Northern District Pounds	Vessels	Total Catch
1978	1,319,451	12	684,439	34	49,571	17	2,053,461
1979	504,770	19	123,245	32	20,924	16	652,924
1980	659,667	10	No fishing		31,152	5	690,819
1981	1,503,574	18	No fishing		5,683	5	1,509,257
1982	757,911	16	No fishing		4,221	2	762,132
1983	379,094	9	No fishing		511	2	379,605
1984[1]	678,639	9	No fishing		34	1	678,673

[1] As of August 30, 1984.

of salmon, red, king and silver, occurs in the near shore area where crab concentrations are heaviest. Crabs become entangled in the nets as they drag across the bottom causing nearly 100 percent mortalities of entangled crabs during the softshell period.

There is also a gear conflict between the drift gillnets and crab pots. Unfortunately this is sometimes resolved with cut crab lines as opposed to cooperation. Nevertheless, this gear loss is a source of Dungeness mortality that could be avoided.

Fishing in the spring and early summer, when the molt and softshell periods normally occur, causes a unique management problem. The Department's Prince William Sound Management Area policy on closures due to softshells is dependent upon two factors: 1) the relative abundance of softshells, and 2) the level of vessel participation. During the 1979 season, when the softshell abundance was average and the effort was high, the district was closed until the crab reached a condition where handling mortality and limb loss were diminished. However, in 1984, the abundance of softshells was high, but only three vessels were fishing, thus the season remained open as fishermen avoided areas of softshell abundance.

Orca Inlet District

The Orca Inlet District, which is immediately adjacent to the community of Cordova, has provided a fishery that allows participation by small vessels in an area protected from adverse sea conditions. The largest vessels were in the 40 foot seiner class; however, the majority of the vessels were smaller than 40 feet with some as small as the 24 foot stern-picker gillnetter. Crab fishermen could leave the harbor in the morning, lift their 100 pots (the pot limit in this district), and deliver to the processors by early afternoon. Concentrations of legal crabs were found from mean low water to 10 to 15 fathoms.

This protected body of water was not effected by seasonally adverse weather conditions thus the fishery was not opened until the crabs were in a hardshell condition.

Prior to the decline in abundance in 1979 due to otter predation, the Dungeness population was beginning to recover from another decline which was caused by habitat loss and degredation as a direct result of the 1964 earthquake and siltation from the Copper River. Catch varied from 35 thousand to 684 thousand pounds (Table 1).

In the early to mid 1960's the annual catch exceeded one million pounds (catch records prior to this are not reliable as to specific location of harvest). The 1964 earthquake caused an average uplift of six feet in Orca Inlet thereby resulting in a significant habitat loss.

The resultant habitat loss, due to uplift, and the continuing substrate change caused by the Copper River outflow had dramatic effect on both the Dungeness crabs and its primary prey species, razor clams (*Siliqua patula*) (Nickerson 1975).

The Orca Inlet season was not opened in 1984, as it hasn't been since 1980, because of extremely low abundance as identified by the pre-season index value, which was less than one legal male per pot.

The reason for the continued suppression of the Dungeness crab population in Orca Inlet is predation by the sea otter (Enhydra lutris). The otter arrived in large numbers during 1979 and immediately impacted the Dungeness crab stock. The most recent count of sea otters in Orca Inlet in 1983 tallied well in excess of 500 animals (Schmidt 1983). According to a recently completed study, when Dungeness crab are available, adult otters are capable of eating 14 crabs per day (Garshelis 1983). Needless to say this equates to significant predation and a continued suppression of the stock.

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The Lower Cook Inlet Dungeness crab fishery from 1964-1983

Margaret F. Merritt
Alaska Department of Fish and Game
Homer, Alaska

Abstract

Dungeness crabs have been harvested in the inner bays of Lower Cook Inlet, Alaska, since the early 1900's. In 1973 a relatively large stock of Dungeness crab was located in outer Kachemak Bay off Bluff Point and the majority of the fishing effort has shifted to this area in recent years. The Lower Cook Inlet Dungeness crab fishery is primarily dependent on market demand and natural fluctuations in the population. When catches of crab on the west coast are low, Lower Cook Inlet Dungeness crab landings tend to increase. From 1968 to 1983, the ex-vessel value of the fishery has ranged from an estimated $7,200 to $1,598,200, with a mean value of $440,100 per year. The mean catch from 1961 to 1983 is 615,200 pounds, with the highest reported at 2.1 million pounds in 1979. The number of vessels participating in the fishery between 1961 and 1983 has ranged from 2 to 117, with a mean of 36. Management is based on area closures, gear restrictions, and sex and size limitations. There are no established guideline harvest levels for Lower Cook Inlet Dungeness crab. No biological assessment program has been developed for Lower Cook Inlet Dungeness crab, although some tagging studies have been conducted. A bivariate covariance matrix was used to estimate area covered by tagged Dungeness crab. The model indicated that size of area covered differs between geographical areas and the sexes. Non-overlapping adult movements and morphological variation may suggest the existence of various stocks of Dungeness crab in Lower Cook Inlet.

History of the Fishery

The Lower Cook Inlet area is described as those waters west of a line extending south from Cape Fairfield and north of a line extending east from Cape Douglas (Figure 1). The Lower Cook Inlet Dungeness crab fishery primarily occurs within bays: Kachemak Bay, Seldovia Bay, Sadie Cove, etc. Local residents from Homer, Seldovia and Port Graham

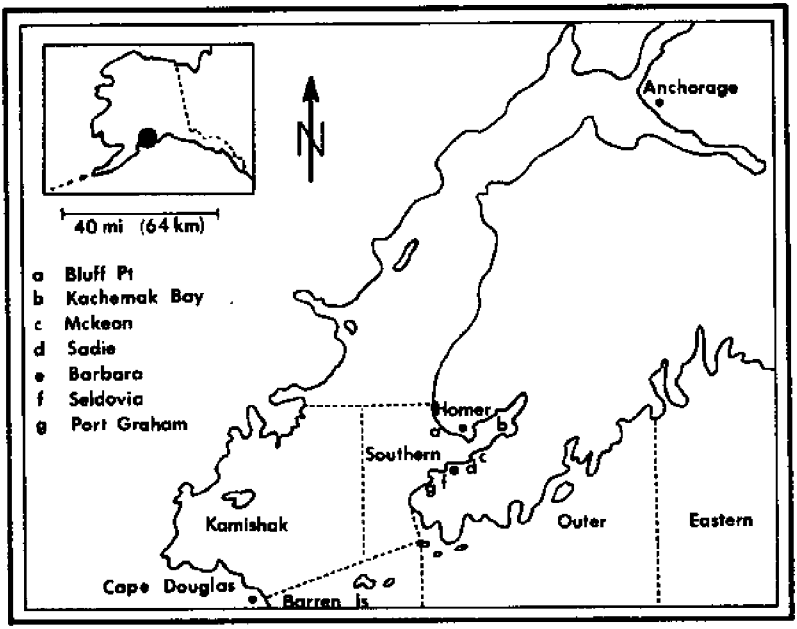

Figure 1. Lower Cook Inlet, Alaska.

are the primary participants in the fishery. The majority of Dungeness crab are harvested from the Southern District. While some landings have historically occurred in the Outer and Eastern Districts, fishing Gulf of Alaska and Cook Inlet waters is not as productive as bay fishing and offers greater hazards.

Dungeness crabs have been harvested intermittently in the Lower Cook Inlet area since the early 1900's. Canning of Dungeness meat was conducted in Seldovia from 1920 to 1925. The next major effort was in the early 1950's when a yearly peak catch of 1.5 million pounds (680.4 metric tons) was recorded. Prior to 1973, fishing was conducted entirely in the inshore waters of Kachemak Bay and the smaller bays of the Lower Kenai Peninsula. During 1973 a relatively large stock of Dungeness crab was located in the Bluff Point area of outer Kachemak Bay. The majority of the fishing effort has shifted to this area in recent years and is conducted in the depth range from 15-40 fathoms (27-73m).

The Lower Cook Inlet Dungeness crab commercial fishery is primarily dependent on market demand. Historically, when catches of crab in Washington were depressed, Lower Cook Inlet Dungeness crab landings increased (Figure 2). A change in relationship became apparent in 1977, when Lower Cook Inlet catches became parallel to those of Washington.

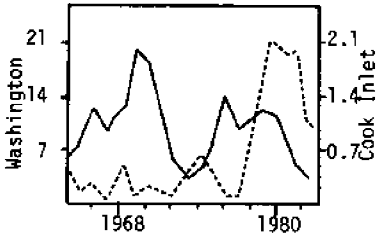

Figure 2. Dungeness crab commercial catch from Washington (solid line) and Cook Inlet in millions of pounds by year.

This may indicate that Lower Cook Inlet catches are now tied more directly to overall market demand for crab product rather than to the harvest of Dungeness crab from Washington. Sustained high prices may be responsible in part for the recent changes in market action of Lower Cook Inlet Dungeness crab.

Additional limiting factors to the Dungeness crab fishery in Lower Cook Inlet are tidal action and inclement weather, particularly in the Bluff Point area. During extreme tidal fluctuations, which occur normally twice per month in summer through fall, pot buoys sink below the surface except at slack tide periods, limiting the amount of time boats can pick their gear. Regulations allow a twelve-month season on Dungeness crab, but fishermen generally confine harvest to July through October - storms and ice passage severely restrict winter harvest. Due to inconsistent fleet effort, it cannot be determined to what degree crab abundance affects the harvest. Certainly market demand, environmental conditions and crab abundance all play a significant role in determining fleet effort and harvest of Dungeness crab in Lower Cook Inlet.

Table 1. Lower Cook Inlet Dungeness crab catches, number of participating vessels, number of landings, (M.T. = 2,204.62 pounds), and ex-vessel values.

Year	Number Vessels	Number Landings	Catch Pounds	Catch Metric Tons	Ex-vessel Value Price per Pound	Ex-vessel Value Total
1961	12	189	193,683	87.8		
1962	15	269	530,770	240.8		
1963	50	1,360	1,677,204	760.8		
1964	22	341	423,041	191.9		
1965	14	105	74,211	33.7		
1966	5	28	129,560	58.8		
1967	2	13	7,168	3.3		
1968	7	224	487,859	221.3	$0.14	$ 68,300
1969	9	41	49,894	22.6	.145	7,234
1970	10	50	209,819	95.2	.13	27,726
1971	22	136	97,161	44.1	.15	14,574
1972	24	206	38,930	17.7	.39	15,182
1973	54	625	310,048	140.6	.52	161,224
1974	34	619	706,910	320.7	.55	388,800
1975	36	402	362,815	164.6	.536	194,468
1976	12	123	119,298	54.1	.515	61,438
1977	18	94	75,834	34.3	.40	30,286
1978	51	680	1,214,716	551.0	.65[1]	789,565
1979	82	1,326	2,130,963	966.6	.75	1,598,222
1980	65	1,183	1,866,696	846.7	.50	933,348
1981	96	2,072	1,859,759	843.6	0.70	1,301,831
1982	117	1,870	832,603	377.6	0.83	691,060
1983	77	1,283	750,838	340.6	1.01	758,346

Data Source: ADF&G Statistical Catch Reports

[1] Price per pound ranged from $0.45 to $0.75, majority purchased at $0.65 plus.

From 1968 to 1983, the ex-vessel value of the fishery has ranged from an estimated $7,200 to $1,598,200, with a mean value of $440,100 per year (Table 1). The mean catch from 1961 to 1983 is 615,200 pounds, with the highest reported at 2.1 million pounds in 1979. The commercial catch and ex-vessel value show similar trends in fluctuations through time, except in 1980, when the catch remained high while the price per pound dropped. In 1983, the price per pound increased while the catch decreased (Figure 3).

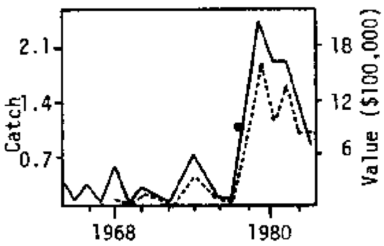

Figure 3. Ex-vessel value of Dungeness crab in Cook Inlet compared to commercial catch in millions of pounds (solid line) by year.

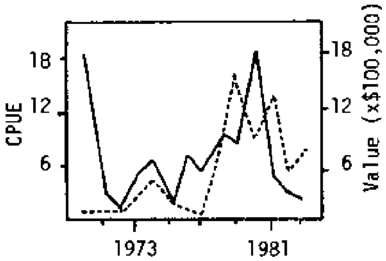

Figure 4. Ex-vessel value of Dungeness crab in Cook Inlet compared to CPUE (solid line) by year.

The catch per unit effort or CPUE (number of crabs per pot) shows little correlation to ex-vessel value. While the CPUE and value appeared to be directly correlated from 1972 to 1975, CPUE has recently declined (1981 to 1983) while the value of the harvest has increased (Figure 4).

Monitoring of the Southern District sport/subsistence fishery for Dungeness crab was initiated in 1978 with an interview creel census, and it was estimated a total of 3,570 crab (or 7,140 pounds) were taken, comprising 0.6 percent of the total 1978 harvest for Lower Cook Inlet. No census was conducted in 1979 or 1980. In 1981, monitoring of the harvest was initiated through a mail-out questionnaire, and it was estimated that 22,928 crab (45,856 pounds) were taken, or 2.4 percent of the total harvest. In 1982 and 1983, the estimated sport harvests were 9,956 crab (2.3 percent of the total catch) and 14,130 crab (3.6 percent of the total catch), respectively (Mills, 1982,1983). By regulation, males of any size may be taken in this fishery.

Management of the Fishery

Management strategy is based on the 3-S concept: sex, season, size. There are no established guideline harvest levels for Dungeness crab in the Lower Cook Inlet area. Only males greater than 6.5 inches (165 mm) may be harvested, with seasons varying according to regulation (Table 2). Upper Kachemak Bay was historically closed May-August (1975-1978) to prevent harvest of crab in the soft-shell condition, but in 1979 this regulation was repealed. The Bluff Point area was historically closed (1977-1983) January-April to force fishermen to pick up their gear when fishing success declined in the fall. This closure

Table 1. Historical development of Cook Inlet Dungeness crab commercial fishery regulations, 1964-84.

Pot limit	
1964-78:	150 in Southern District 250 in remaining Cook Inlet districts
1979-80:	No limit
1981-84:	150 in Southern District No limit in remaining Cook Inlet districts
Seasons	
1964-74:	No closed season
1975-76:	Upper Kachemak Bay closed May - August
1977-78:	Upper Kachemak Bay closed May - August Bluff Point area closed January - April
1979-83:	Bluff Point area closed January - April
1984 :	No closed season
Size and Sex	
1964-75:	No limit
1976-84:	Females and males less than 6.5 inches (163mm) may not be taken
Gear Specifications	
1964-84:	Buoy identification
1978-84:	Tunnel eye opening not greater than 30 inches (76mm)
1979-84:	Two circular escape rings of 4 3/8 inches (11mm)

was repealed in 1984.

Pot limits have varied by regulatory year, with the majority of the regulations limiting pots to 150 in the Southern District; other Lower Cook Inlet districts have either had a requirement for a 250 pot limit or no limit. Pot specifications include a tunnel eye opening not greater than 30 inches (76 cm). This regulation was established in 1978 to prevent king crab pots from being used prior to the king crab season under the guise of Dungeness gear. Effective in 1979, pots must have two circular escape rings of 4 3/8 inches (11 cm).

Lower Cook Inlet is a non-exclusive registration area for Dungeness crab, which requires fishermen to register prior to fishing, but does not limit the number of non-exclusive areas they may fish during a season. This is in contrast to exclusive registration areas, which limits the fisherman to fishing in that area only.

Economics of the Fishery

Consumer demand is the driving force behind harvest of a resource. Since the decline in king crab abundance and harvest, demand for Dungeness crab has increased, and some Lower Cook Inlet crab fishermen have become dependent in recent years on Dungeness crab for economic survival (Figure 5). From 1969 to 1976, the Dungeness crab harvest in Lower Cook Inlet comprised 0.3 to 3.0 percent of the total shellfish catch (Queirolo et al 1977). In 1983, Dungeness crab comprised 11 percent of the total catch. There are five processors based in Lower Cook Inlet and similar to local fishermen, the smaller processors

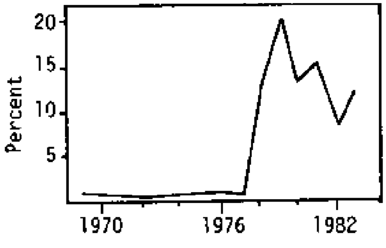

Figure 5. Percent value of Dungeness crab catch relative to total Cook Inlet shellfish value by year.

currently rely on Dungeness crab for their business success, which consists of local marketing. The larger processors interviewed have increased the proportion of Dungeness crab handled over previous years to 10 to 15 percent of their total purchases, but since the decline in king crab some must expand into new bottomfish markets to operate successfully.

The largest plant processes about 75 percent of the Lower Cook Inlet Dungeness crab catch and ships a minimum of 99 percent of its purchase of Dungeness crab to the west coast for marketing; less than one percent is marketed in Alaska. Another large plant markets about 90 percent of its Dungeness crab outside Alaska. Lower Cook Inlet crab is shipped frozen and competes with the west coast fresh market. Processing capabilities enable a single plant to process the current Dungeness crab catch in Lower Cook Inlet. This signals over-capacity and indicates the necessity for market diversification.

Examination of the fleet composition provides indicators of the local bioeconomics. The Lower Cook Inlet Dungeness crab fleet average vessel length is about 36 feet (11m) and average engine size is 240 hp, which, according to Butcher et al (1981) categorizes the fleet size as "small", relative to all vessels operating in Alaska. Small vessels are typically local Alaskan fishing operations (versus large vessels originating outside Alaska) and tend to be involved in the harvest of other fisheries (salmon, halibut, shrimp). Dungeness crab fishermen interviewed realize a net profit of approximately 30-35 percent. This contrasts with the estimate by Butcher et al (1981) of a 20 percent net profit for small vessels.

The mean gross ex-vessel value per vessel participating in the Lower Cook Inlet Dungeness crab fishery from 1974-78 was $7,768, ($1,554 to $2,719 net). From 1979-83 the mean gross value per vessel was $12,633, (2,526 to $4,421 net). (These are minimum values, because the total number of vessels registered as fishing Dungeness crab are not considered the "core" fleet. Several boat owners register for the fishery but are not active participants). Thus, the mean gross profit to Dungeness crab fishermen has increased by 38.5 percent during the past five years, and is reflective of increased demand. However, the low net profits realized necessitate participation in additional fisheries.

Unfortunately, the Alaska Departments of Revenue, Commerce and Economic Development and Fish and Game do not have available data bases on the bioeconomics of a given fishery by locality. Thus, the relationships between Lower Cook Inlet Dungeness crab harvest, local market development and dependency on west coast Dungeness crab demand can only be speculated. Based on interviews with local processors, it appears that harvest of Lower Cook Inlet Dungeness crab is still dependent on the west coast catch which sets the price and market demand for frozen Alaskan Dungeness crab.

Biology of the Fishery

Tagging of Dungeness crab has provided information on adult movement and rates of dispersion. Tagging of females and sublegal males occurred in upper Kachemak Bay and on the coast between Port Graham and China Poot in 1963. Tagging of legal males off Bluff Point occurred in 1975, 1976, 1978 and 1979, although returns from 1975 and 1976 did not provide accurate information on location (Davis 1976, 1977, 1979, 1981).

In a review and re-analysis of the Dungeness crab tagging data in Lower Cook Inlet, Merritt (1984) examined movements for size of area covered by recaptured individuals from a given tagged population. Studies on small mammal demographics has produced many statistical techniques to define home ranges of tagged individuals, and a bivariate covariance matrix (Jennrich and Turner 1969) was chosen to estimate area covered by tagged Dungeness crab. This model assumes that activity is distributed according to the bivariate normal distribution. Van Winkle (1975) contends that the matrix model is free of sample size bias and can be used for quantitative comparisons. Quantitative estimates allowed relative comparisons between areas and sexes, and also indicated degree of overlap of adult movements from different areas.

The model indicated that size of area covered by tagged crab differs between geographic areas and sexes (Table 3).

Table 3. Estimated home range sizes (A_4) and rates of dispersion (a^2) for tagged Dungeness crab in Cook Inlet by area and year.

Year	Tag release area	No. Tagged	No. Recovered	A_4 (mi^2)	a^2 (mi^2/day)
1963	Port Graham	125	23	0	0
	Barabara/ Nubble	147	22	21.5	0.07
	Seldovia	373	67	44.6	0.08
	Sadie Cove	60	10	81.3	0.24
	Homer	145	19	207.2	0.32
	McKeon	271	18	257.7	0.82
1978	Bluff Pt.	210	79	121.1	0.68
1979	Bluff Pt.	323	121	132.5	0.62

The mean square coefficient of dispersion (Skellam 1951) shows some correlation with size of area covered. Tag returns from the fleet in 1963 indicated that crab in Port Graham and Seldovia Bays during the tag recovery period tended to remain in the general area of those bays, but crab tagged along McKeon Flats tended to migrate extensively along the coast. Interviews with fishermen support the thesis that certain bays contain Dungeness crab which tend to remain within the general area of those bays.

Tag returns from the fleet in 1978 and 1979 indicated that Bluff Point crab migrate within an approximately 121 to 133 mi^2 (313 to 344 km^2) area off Bluff Point during the tag recovery period, and area covered does not tend to overlap with those crab tagged along the coast between Port Graham and China Poot or in upper Kachemak Bay. Non-overlapping movements of adults tagged in different areas suggests that these adults may be to some extent reproductively isolated. Larval drift movements must be considered prior to suggesting the existence of separate stocks. Oceanic currents in Kachemak Bay consist of several stable and predictable gyres (Krull and Williamson 1969, Patchen et al 1981) which may increase localization of larval settlement. Catch sampling observations note morphological variations between inner bay crab, which tend to be more bluish in color and larger. Processors recognize Bluff Point crab and offer a higher price to fishermen. These observed variations may be more environmentally induced than genetic, but still point to differences in growth conditions. The concept of Dungeness crab stocks along the same coast line is not novel. California Fish and Game has identified Dungeness crab stocks and manages each with different fishing seasons based on environmentally induced differences in crab condition (Soule and Tasto 1983). Study of Lower Cook Inlet Dungeness crab biology by area may reveal that the great degree of variability in shell condition observed in the overall Southern District population may in fact be correlated to microhabit, and may occur on a predictable basis. Shell condition can be a significant limiting factor in marketable catch per unit effort because of variability in shell condition between areas and years. Processors in general do not purchase soft-shell crab. Fishermen interviewed stated their catches of soft-shell legal males can vary between 5 to 90 percent, with the percentage of hard-shell tending to increase (but not consistently) over the season.

The only shell condition data gathered during the tagging operations was in 1963, when 71.8 percent of the sublegal males examined were found in a soft-shell condition, as compared to 1.1 percent of females, in the same tagging areas during the same time interval. The greater incidence of soft-shell males captured may indicate behavioral differences between the sexes. Fishermen contend that females bury in the sand during soft-shell condition and are thus not as susceptible to pot capture. The difference in shell condition may also indicate that males and females vary in their reproductive cycles and in their responses to extrinsic factors affecting the molt. Changes in growth rate after sexual maturity may also occur between the sexes.

Tagging also provides estimates on fishing mortality, which in the Bluff Point area ranged from 19.5 percent in 1978 to 38.3 percent in 1975. These estimates are considerably less than the estimated fishing mortality of legal males (63 to 87%) in California (Gotshall 1978).

Length frequencies for Dungeness crab were obtained from sampling commercial landings in Homer and Seldovia in 1973 to 1975, 1978 to 1980, and 1982, and from tagging studies off Bluff Point in 1975, 1978 and 1979. Commercial catch sampling of Bluff Point crab occurred during the initial years of this fishery and reflects the size distribution of a previously unexploited population. The mean carapace width of Bluff Point legal males sampled in the commercial fishery from 1973 to 1975 ranged from 190 to 200 mm. No changes in size distribution were noted during this time period, except that the very large crab (230+mm) caught in 1973 were not available in subsequent years. In 1978, mean carapace widths of tagged legal male crab were eight percent smaller (182.7 ± 10.0 mm) than in 1975. In 1979 and 1980 a larger cohort appeared to enter the Bluff Point fishery. Mean width in September 1979 was 193.3 mm and in 1980 was 195.7 mm.

Catch sampling indicates that Bluff Point legal male crab tend to be slightly larger than upper Kachemak Bay crab. In 1980, mean carapace widths of Bluff Point crab were 195.7 mm, 14.8 percent larger than upper Kachemak Bay crab. In August 1982, mean width of Bluff Point crab was 187.7 mm, 6.5 percent larger than Bay crab (Figure 6).

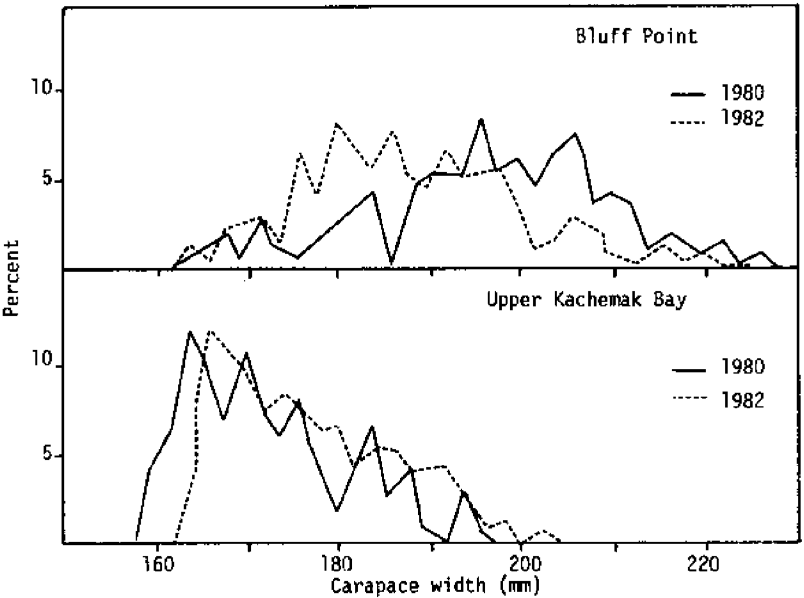

Figure 6. Percent carapace width in 2 mm increments of legal male Dungeness crab from the Bluff Pt. and Upper Bay commercial fisheries.

The average weight of legal male Dungeness crab in the Bluff Point commercial fishery from 1978 to 1983 was 2.35 pounds (1066 g). This is 15 percent greater than the average weight of legal male crab in the inner bay fishery east of the Homer Spit (2.04 pounds or 925 g) during the same time period. Differences in size between the Bluff Point and upper Kachemak Bay Dungeness crab may result from 1) different rates of growth per molt or 2) different exploitation rates as they affect the size distribution of a given population.

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Kodiak Island commercial Dungeness, *Cancer magister,* fishery

Martin F. Eaton
Alaska Department of Fish and Game
Kodiak, Alaska

Introduction

The Kodiak Archipelago located between 56° N. latitude and 58°50' N. latitude and 151° W. longitude and 156° W. longitude is some of the most productive waters for shellfish in the north Pacific Ocean (Figure 1). Since the beginning of statehood in 1959, these waters have produced 620 million pounds of king crab (Paralithodes camtschatica), 280 million pounds of tanner crab (Chionoecetes bairdi), 743 million pounds of shrimp (Pandalus borealis) and 64 million pounds of dungeness crab (Cancer magister). It is quite apparent from these catch figures that dungeness crab has been a minor fishery, when compared with the other shellfish fisheries. The primary reason that dungeness production has been lower than the other fisheries is that dungeness habitat is limited in area and competition from the other crab species is very fierce on the prime dungeness grounds. A secondary reason the production was suppressed is that the Alaska product has had to compete in the market place with crab caught on the west coast of the United States and Canada. When production was large on the west coast, Alaska catches were held artifically low, as can be seen from Table 1 and Figure 2. For example in 1962 when the Kodiak fishery began, the harvest for the West Coast and Canada was only 14.7 million pounds compared to 10.1 million pounds for Alaska and 1.9 million pounds for Kodiak. The low harvest led fishermen and processors to tap the Kodiak resource for the first time in 1962 (Table 2). Not only did the Kodiak dungeness fishery depend on catches of West Coast crab, but the catches from the Cook Inlet, Prince William Sound and Southeast areas in Alaska also influenced Kodiak production. In 1963, the catch in Kodiak was 2.4 million pounds; in 1964, 4.1 million pounds; in 1965, 3.3 million pounds; but in 1966, it decreased to 1.1 million pounds primarily because the rest of Alaska's dungeness catch increased from 1.7 million pounds in 1965 to 10.4 million pounds in 1966.

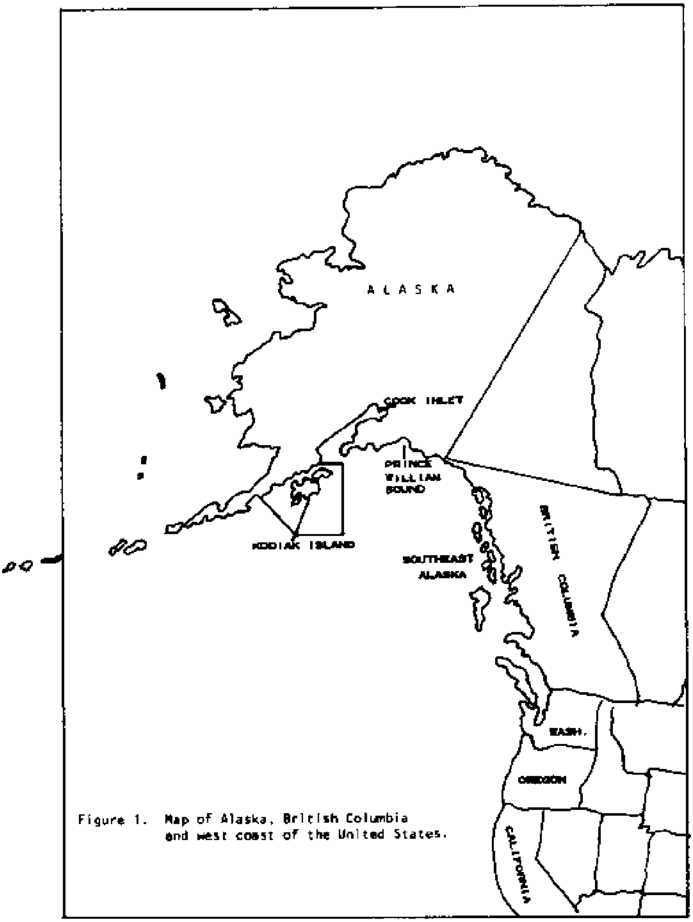

Figure 1. Map of Alaska, British Columbia and west coast of the United States.

Table 1. Historic dungeness catch from Kodiak, Alaska, west coast states and Canada in thousands of pounds, 1962-1981.

Year	Kodiak	Alaska	Canada & U.S. West Coast	Total
1962	1,904	10,180	14,731	26,815
1963	2,487	10,221	14,883	27,591
1964	4,162	4,733	22,186	31,081
1965	3,311	1,742	36,793	41,846
1966	1,148	10,449	34,719	46,316
1967	6,663	6,579	39,482	52,724
1968	6,829	4,475	48,605	59,909
1969	5,834	3,863	50,636	60,333
1970	5,741	3,388	38,410	48,113
1971	1,445	2,304	21,725	25,474
1972	2,059	3,238	12,806	18,103
1973	2,000	4,386	11,446	17,832
1974	750	4,583	13,560	18,893
1975	639	2,323	38,515	41,477
1976	87	1,451	58,896	60,434
1977	113	1,063	36,004	37,180
1978	1,362	5,854	37,613*	44,829
1979	1,313	4,260	30,347*	35,920
1980	2,011	8,991	16,649*	31,545
1981	2,614	12,287	14,597*	29,498

*California catch not included.

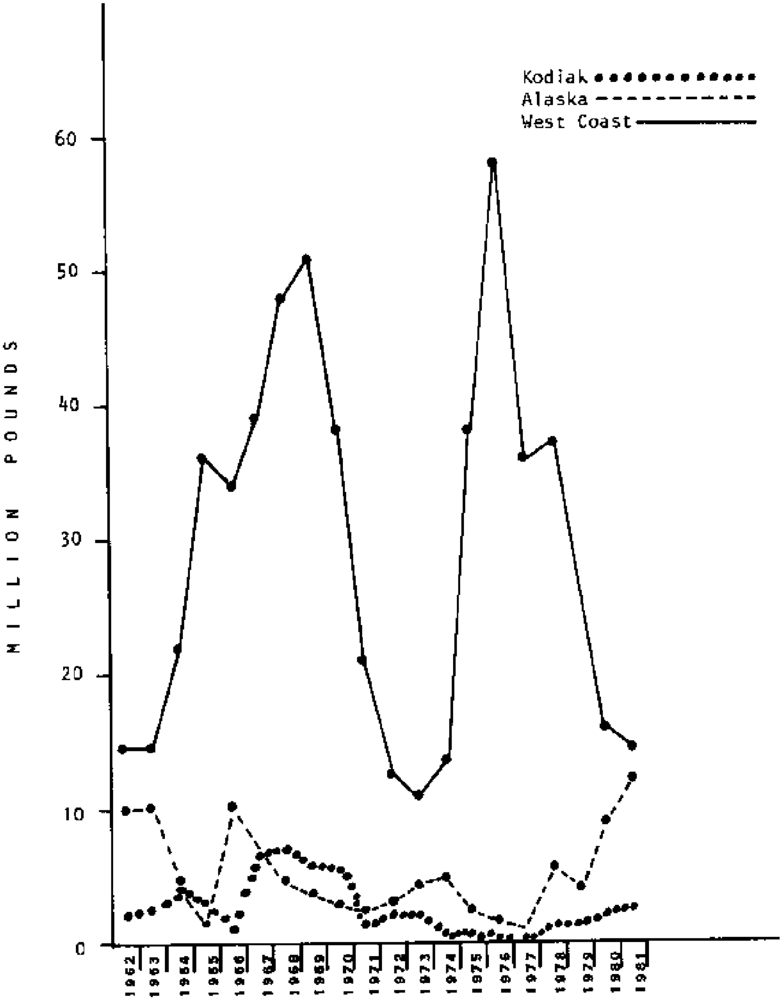

Figure 2. Alaska's dungeness catch production compared to West Coast catch production 1962 - 1981.

Table 2. Dungeness catch by geographic area, by year, in thousands of pounds.

Year	Northeast	Eastside	Southeast/ Southwest[1]	North Mainland	South Mainland	Westside
1962	-	-	493.1	1,085.9	-	314.6
1963	165.3	63.9	201.7	1,774.2	-	312.4
1964	180.7	830.1	1,088.4	1,621.8	-	533.6
1965	159.8	832.4	944.6	881.6	97.3	395.9
1966	64.9	605.6	289.0	241.0	139.7	76.0
1967	89.4	1,331.9	4,658.7	313.5	-	270.1
1968	265.9	930.1	4,273.8	801.1	13.0	545.2
1969	219.2	907.8	3,930.0	617.3	66.8	72.6
1970	131.1	1,211.8	3,242.8	934.7	10.0	204.0
1971	37.6	400.4	545.0	248.6	11.7	202.5
1972	180.2	617.0	730.9	284.9	-	246.4
1973[2]	NA	NA	NA	NA	NA	NA
1974	30.1	331.2	42.7	29.4	116.3	200.3
1975	.9	259.0	7.5	43.5	120.4	208.3
1976	-	.3	-	-	19.9	66.9
1977	-	103.3	-	1.6	1.2	6.9
1978	35.4	420.7	244.9	17.8	366.4	277.1
1979	61.5	459.1	380.6	68.7	192.5	148.6
1980	89.1	224.2	513.5	154.5	229.5	800.8
1981	131.2	510.8	1,475.0	1,087.9	811.2	1,550.2
1982	363.4	484.1	1,409.3	855.0	577.4	856.9
1983	206.4	437.5	2,571.3	516.3	454.6	564.6
TOTAL	2,412.1	10,961.2	27,042.8	11,579.3	3,227.9	7,853.9
PERCENT	4%	17%	43%	18%	5%	12%

[1] Combine from 1962 to 1976 and called Southend.

[2] Data not available.

The most dramatic illustration of the U.S. West Coast and Canadian ability to influence dungeness catches in Alaska is seen in Figure 2. Beginning in 1977, West Coast and Canadian production has been steadily declining while Alaskan and Kodiak production has been increasing. The graph lines on Figure 2 for 1981 almost touch each other indicating the strong interaction and dependence the catches have on the two areas.

Description of the Area

The Kodiak dungeness fishery occurs in the geographical area defined in the 1983 Shellfish Regulation book as the Kodiak District. The Kodiak District includes all waters south of the latitude of Cape Douglas (58°52' N. latitude), west of the longitude of Cape Fairfield (148°50' W. longitude) and east of the longitude of Cape Kumlik (157°27' W. longitude) (Figure 3).

The district is further divided into seven management sections for dungeness crab (Figure 3). Dungeness crab are found in all these section; however, some are more productive than others. Beginning with the Northeast section; which comprises the area from Cape Chiniak north to the northernmost tip of Shuyak Island including Chiniak Bay, Marmot Bay and Southeast and Northeast Afognak Island. Most of the land area is heavily timbered with Sitka spruce. The bays of Kodiak Island, where dungeness are caught, are large broad sheltered shallow bays (averaging 60 meters in depth). The potential habitat for dungeness crab could be quite large; however, these bays are also inhabited by king and tanner crab which are fierce competitors with dungeness. During high populations of king and tanner crab, dungeness catches in these bays are very small. Fishermen report that their dungeness pots catch king crab. It is not known whether the dungeness populations are low during high king crab populations, or whether the king crab are more active feeders keeping the dungeness crab out of pots.

The Afognak Island bays, where dungeness are found, are characterized by being long, narrow and deep bays (600 meters) with shallow areas (60 meters) formed by stream mouths. These areas are quite small and appear to be marginal habitat for dungeness, as the Afognak Island catches have been historically very small. In fact, the Northeast section has produced only four percent of the historic harvest of dungeness crab.

The Eastside section includes primarily two large bays, Ugak and Kiliuda, which are relatively long, broad and deep (600 meters). These bays are characterized by having large shallow water areas inhabited by dungeness crab. These areas are located in the numerous small bays inside the two larger bays. In addition to these large productive bays, shallow water habitat exists on the exposed beaches from Cape Chiniak south to Dangerous Cape. This area is one which would compare to the open ocean habitat found on the west coast of Oregon and California. The shallow water (60 meters) extends three miles off shore in some areas.

It is in these waters that dungeness are found co-habitating with razor clams. The Eastside section production has accounted for 17 percent of the Kodiak dungeness historic harvest (Table 2).

The Southeast section includes the waters south of Cape Barnabas to Cape Trinity, including Sitkinak Island. The Southeast section has

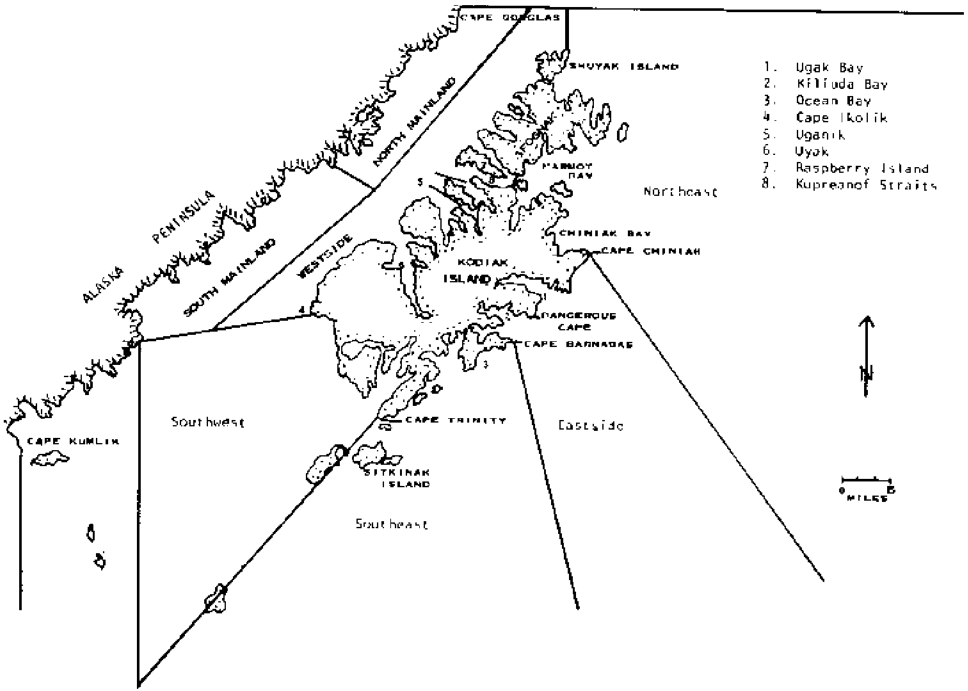

Figure 3. Kodiak management area, districts/sections for Dungeness crabs.

some minor production areas located in typically deep water bays with narrow bands of shallow water near shore where dungeness are found. The major production areas, however, are located at Ocean Bay and in the water surrounding Sitkinak Island. In 1983 this section accounted for 1.9 million pounds.

The section which most resembles the West Coast fishery of open ocean beaches is the Southwest section, which extends north of Cape Trinity to Cape Ikolik then to the southernmost tip of Cape Kilokak. In 1977 the Southwest and Southeast sections were created from a section called the Southend. These two sections have historically accounted for 43 percent of the Kodiak dungeness harvest (Table 2).

The Alaska Peninsula also supports a dungeness crab fishery. The Peninsula is divided into two sections; the North Mainland and South Mainland sections (Figure 3). The North Mainland and South Mainland sections are comprised of primarily open ocean beaches with a few deep and narrow bays. The North Mainland has historically been more productive than the South Mainland accounting for 18 percent of the Kodiak dungeness harvest.

The final geographic area that comprises the management units of the Kodiak dungeness fishery is called the Westside. This area covers the waters west and south of the northern tip of Shuyak Island to Cape Ikolik. This area has an extremely rugged, high cliffed, rocky coastline. Dungeness crab are found in long narrow deep bays such as Uganik and Uyak bays (Figure 3). They also occur in Kupreanof straits along the southern shore of Raspberry Island. The Westside section has traditionally produced 12 percent of the Kodiak harvest.

In summary, the Kodiak Island, Afognak Island and Pacific side of the Alaska Peninsula comprised the Kodiak dungeness fishery. The habitat is highly variable, as are the dungeness populations found in each of the areas.

Distribution of Species

No population estimates of dungeness crab have been calculated using standard survey techniques in the Kodiak Management area. Dungeness crab distribution is obtained from the fishing fleet. All dungeness crab fishermen are required to report their catch of legal males by statistical catch area (Figure 4 Table 3). The commercial catch data certainly is a good indicator of legal male distribution; however, no sublegal male or female distribution estimates can be calculated since females and sublegal males are returned to the sea. As can be seen on Figure 4, the majority of crab are concentrated around the Trinity Islands.

Dungeness crab have traditionally been fished in waters less than 30 meters; however, some catches have been reported in water depths greater than 160 meters. The species seem to inhabit primarily shallow water areas (less than 30 meters) in both bays and beach areas exposed to wave action. The crab seem to prefer sandy or mud bottom substrate.

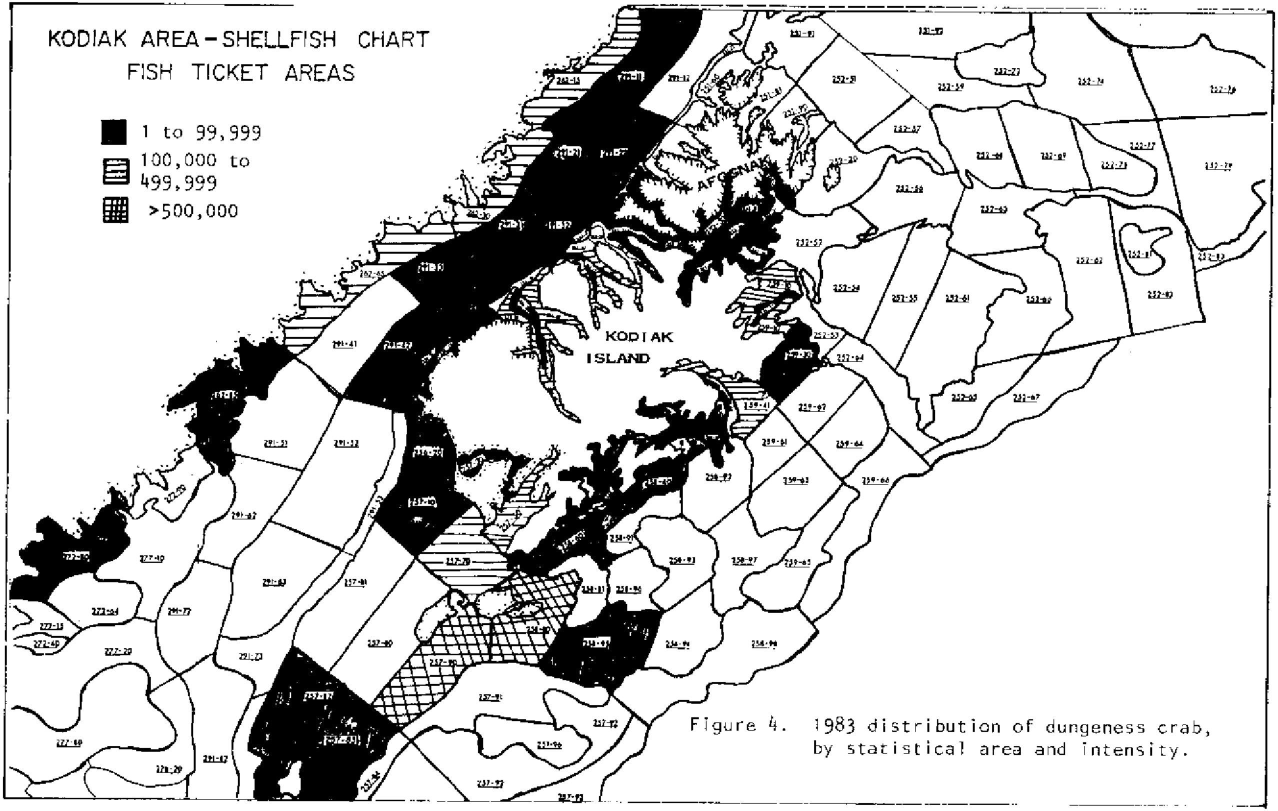

Figure 4. 1983 distribution of dungeness crab, by statistical area and intensity.

Table 3. Dungeness crab catch, landings, vessel effort, catch per pot (CPUE), and catch per month by statistical subarea, Kodiak District, 1983-84. Average catch per pot unstandardized for soak period and gear type.

Stat. Area	Vessels	Lndgs.	Pounds Harvested	Avg. Wt.	CPUE	Catch In Pounds By Month May	June	July	August	September	October	November	December	January
251-20	1	1	45	2.5	1.5	-	-	-	-	-	-	45	-	-
252-30	2	3	2,429	2.1	2.7	2,046	-	-	-	-	-	-	383	-
252-33	5	8	9,191	2.3	3.0	405	2,256	-	4,509	1,112	-	-	909	-
252-35	10	27	29,513	2.2	2.9	3,246	2,247	2,655	9,220	1,411	7,337	3,256	-	141
252-38	17	63	54,692	2.1	2.2	14,030	12,505	7,474	8,752	7,650	3,241	940	-	100
253-11	1	1	708	2.2	3.3	-	708	-	-	-	-	-	-	-
253-12	7	11	13,418	2.1	2.2	2,230	991	4,612	500	4,005	1,080	-	-	-
253-31	7	11	8,595	2.3	2.4	-	1,063	-	2,304	1,901	575	2,147	470	136
253-33	18	106	247,464	2.4	2.7	36,748	24,504	60,933	52,317	40,698	21,756	6,577	3,013	916
254-30	2	6	43,921	2.1	2.5	-	-	4,699	-	13,907	19,160	6,155	-	-
254-40	17	50	195,464	2.1	2.3	34,506	18,191	34,336	47,273	15,810	17,201	14,851	10,229	3,068
256-20	3	6	37,898	2.2	3.1	-	11,280	26,618	-	-	-	-	-	-
257-10	1	2	889	2.5	0.1	-	-	-	-	-	-	-	889	-
257-30	1	2	8,066	2.4	5.2	-	-	-	8,066	-	-	-	-	-
257-50	20	63	392,927	2.3	4.6	-	83,695	68,218	59,967	79,183	76,625	11,803	10,567	2,869
257-70	10	19	107,716	2.3	5.2	-	-	62,438	14,764	20,135	6,194	4,185	-	-
257-80	4	4	40,161	2.4	7.6	-	15,751	-	-	15,125	9,285	-	-	-
257-82	1	1	3	3.0	0.1	-	-	-	3	-	-	-	-	-
257-83	1	1	3	3.0	0.0	-	-	-	3	-	-	-	-	-
257-90	29	117	1,225,778	2.5	5.2	-	15,751	412,366	372,135	209,095	178,922	34,056	3,453	-
258-10	10	17	62,269	2.1	4.1	-	5,990	7,876	9,560	17,863	2,504	16,248	2,228	-
258-20	1	1	445	2.1	1.0	-	-	-	-	-	-	-	445	-
258-40	5	10	67,482	2.1	6.3	-	-	724	50,062	14,156	948	1,592	-	-
258-54	3	3	14,557	2.2	6.2	-	-	6,010	-	-	8,547	-	-	-
258-55	1	2	2,179	2.4	6.0	-	-	-	-	-	2,069	-	110	-
258-60	3	3	36,371	2.3	6.7	-	-	36,371	-	-	-	-	-	-
258-80	21	61	604,395	2.4	5.5	-	4,200	178,780	188,588	140,558	63,655	22,578	4,813	1,223
258-95	1	1	44,598	2.4	9.3	-	-	-	-	44,598	-	-	-	-
259-10	27	327	139,445	2.2	2.1	17,300	9,945	31,778	40,623	24,512	9,248	4,108	1,306	625
259-21	1	1	629	1.8	3.5	-	-	-	-	-	-	-	629	-
259-30	4	10	42,190	2.3	4.0	14,585	1,843	-	9,281	13,026	3,456	-	-	-
259-41	21	109	332,573	2.2	3.7	33,345	54,551	86,386	65,515	47,091	35,571	8,691	936	407
262-15	7	21	193,120	2.3	5.4	-	9,133	73,494	32,792	27,691	43,909	6,101	-	-
262-30	8	28	273,700	2.2	4.3	31,421	72,818	69,838	58,588	28,047	7,403	4,285	1,300	-
262-65	8	40	367,336	2.3	4.2	98,115	25,013	110,808	35,922	66,556	30,992	930	-	-
262-85	2	2	51,955	2.2	5.2	-	-	25,264	26,691	-	-	-	-	-
272-80	1	1	1,440	1.8	0.6	1,440	-	-	-	-	-	-	-	-
291-11	3	4	46,551	2.7	7.0	-	-	-	14,503	15,708	16,340	-	-	-
291-21	1	1	2,090	1.9	5.5	-	-	-	2,090	-	-	-	-	-
291-22	2	2	513	1.9	1.8	218	-	-	-	-	295	-	-	-
291-31	1	1	828	2.0	4.1	-	-	-	828	-	-	-	-	-
291-32	4	8	7,975	2.0	4.2	-	964	1,990	1,850	-	-	-	3,171	-
291-33	2	6	35,355	2.2	2.4	5,465	25,448	4,442	-	-	-	-	-	-
291-42	1	1	5,271	2.1	2.5	5,271	-	-	-	-	-	-	-	-
TOTAL	103	1,079	4,752,148	2.3	4.1	300,370	398,847	1,318,110	1,116,708	848,838	566,314	148,548	44,853	9,564

The Commercial Fishery

The dungeness fishery has historically held minor economic importance, when compared to the salmon, shrimp, king crab and tanner crab fisheries. As was mentioned in the introduction of this report, the fishery started only in 1962. The amount of harvest seems to be dictated by the West Coast dungeness harvest, and to some extent, stock status of salmon and other shellfish in the Kodiak area.

The fishery began in 1962 when 1.9 million pounds were harvested. The fishermen were paid nine cents a pound. It was not until 1964 that the number of vessels were recorded, and in 1969, the number of pot lifts were recorded. In 1971, the number of crab were also reported (Table 4).

In 1967, vessel size was recorded by ten foot increments. As can be seen from Table 5, 66 percent of the fleet has traditionally been composed of vessels less than 49 feet keel length. The shallow water and protected bays of Kodiak can be efficiently fished by smaller vessels. The larger vessels have been primarily fished in offshore waters. The Department has conducted gear surveys since 1979 gathering the number of pots fished by each vessel. In 1979, skippers reported averaging 441 pots per vessel; and in 1983, this figure jumped to 501 pots per vessel.

The largest production months in the Kodiak fishery have traditionally been in July and August. When the fisheries were open for 12 months a year, for example, the catch in 1968 for July and August was 3.2 million pounds compared to 3.6 for the other ten months (Table 6).

Regulations

In most fisheries the amount of regulations governing the fishery is directly proportional to the effort level and population size of the target species. In the 1962 Kodiak dungeness crab fishery, the season was open for 12 months a year, only seven inch male crab could be retained and the crab had to be captured using pots or ring gear. In 1963, the fishermen had to identify their gear by marking their buoys with the Department registration number; and in 1964, the State forbid transporting live dungeness crab using fishing vessels from state waters.

In 1969 king crab stocks were at very low levels in Kodiak. In order to protect these king crab stocks, dungeness crab fishing was curtailed from these grounds during the molting period from May 1 to June 15. In 1971, the Department defined a dungeness pot as a pot with a tunnel eye opening which does not exceed 30 inches in perimeter. By 1975, all dungeness vessels were required to be registered and tank inspected prior to fishing in each statistical area. In addition, vessel skippers had to notify the Department before leaving these statistical areas.

Table 4. Dungeness crab commercial catch and effort by fishing year for the Kodiak Management District, Statistical Area (J), 1962 and 1983-84.

			Commercial Catch						
Year	Lndgs.	Vssls.	No. Crab	No. Pounds	Pots Lifted	Avg. Catch Per Lndg. (Pounds)	CPUE	Avg.Price Per Pound	Ex-Vessel Value
1962[1]	149	-		1,904,567		12,782		.09	171,000
1963	354	-		2,487,512		7,026		.09	224,000
1964	395	29		4,162,182		10,537		.09	375,000
1965	351	25		3,311,571		9,434		.12	397,000
1966	144	12		1,148,600		7,976		.13	149,000
1967	439	18		6,663,668		15,179		.13	866,000
1968	536	43		6,829,061		12,741		.14	956,000
1969	455	29		5,834,628	190,967	12,823	12	.16	934,000
1970	318	33		5,741,438	249,800	18,055	9	.14	804,000
1971	173	24	515,653	1,445,864	90,913	8,358	6	.18	260,000
1972	316	34	766,960	2,059,536	140,921	6,517	6	.40	824,000
1973	487	42	879,484	2,000,526	251,467	4,108	3	.50	1,000,000
1974	172	23	337,839	750,057	104,062	4,361	3	.47	353,000
1975	154	15	307,272	639,813	76,411	4,154	4	.61	390,000
1976	6	4	38,072	87,110	4,410	14,518	9	.15	13,000
1977	16	2	46,333	113,026	3,805	7,064	12	.30	34,000
1978[2]	173	20	618,357	1,362,306	93,633	7,875	6	.75	1,022,000
1979	237	28	595,850	1,313,650	137,951	5,543	4	.75	943,000
1980	197	21	968,829	2,011,736	107,261	10,212	9	.45	905,000
1981-82[3]	466	50	2,614,545	5,566,463	295,138	11,945	9	.70	3,897,000
1982-83[4]	991	111	2,004,075	4,546,311	481,542	4,588	4	.75	3,410,000
1983-84[4]	1,079	103	2,044,505	4,752,148	503,464	4,408	4	1.05	4,989,000
TOTAL				64,731,773					22,916,000
AVERAGE	346	33	902,898	2,942,341	182,106	8,504	5	.37	1,042,000

[1] Season open year around 1962-1977.

[2] Open May 1 through December 31, 1978 - 1980.

[3] Open February 27, 1981 through February 1, 1982.

[4] Open May 1, 1982 through February 1, 1983.

Table 5. Kodiak dungeness crab vessel numbers and lengths, 1967-1983.

	VESSEL LENGTH (IN FEET)										
Year	10/ 19	20/ 29	30/ 39	40/ 49	50/ 59	60/ 69	70/ 79	80/ 89	90/ 99	100/ 109	TOTAL
1967	-	-	5	5	3	3	-	2	-	-	18
1968	1	3	7	11	8	4	3	3	3	-	43
1969	2	5	11	5	1	2	1	1	-	-	29
1970	1	3	5	8	5	2	4	5	-	-	33
1971	1	4	3	6	2	4	1	2	-	1	24
1972	1	1	9	7	6	4	2	4	-	-	34
1973	10	3	11	12	4	5	4	2	-	-	51
1974	-	-	7	7	2	1	5	-	-	-	22
1975	-	-	3	4	-	5	3	-	-	-	15
1976	-	-	1	1	-	1	1	-	-	-	4
1977	-	-	-	2	-	-	-	-	-	-	2
1978	-	1	7	8	1	-	2	1	-	-	20
1979	-	1	8	12	3	1	3	-	-	-	28
1980	-	2	4	7	2	1	1	3	-	-	21
1981	1	4	7	14	5	5	3	3	-	-	42
1982	2	22	20	29	10	10	7	5	1	-	106
1983	3	15	27	30	7	14	4	2	-	-	103
TOTAL	22	64	135	170	59	62	44	34	4	1	595
AVERAGE	1.2	3.8	7.9	10.0	3.4	3.6	2.6	2.0	.2	-	35
PERCENT	3%	11%	23%	29%	10%	10%	7%	6%	-	-	

Table 6. Kodiak area dungeness catch, in pounds, by year and month.

YEAR	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.	TOTAL
1962	-	-	-	-	47,550	573,175	415,787	456,061	397,605	14,389	-	-	1,904,567
1963	-	-	-	-	48,490	361,505	921,853	679,186	357,305	60,359	47,059	11,755	2,487,512
1964	-	-	-	-	51,146	468,461	812,083	1,335,928	997,450	373,113	111,953	12,048	4,162,182
1965	105	974	3,411	56,626	462,30	526,728	861,424	977,179	655,072	128,453	54,677	692	3,311,571
1966	-	15,841	-	-	29,150	218,248	170,242	350,981	264,142	49,743	42,748	7,505	1,148,600
1967	13,352	5,335	9,811	1,450	414,967	1,200,028	2,021,921	1,332,017	903,094	527,542	195,233	18,918	6,663,668
1968	-	92	3,323	41,536	342,335	1,321,935	1,974,251	1,384,323	822,707	676,828	214,831	46,900	6,829,061
1969	14,955	813	460	6,895	104,708	422,329	1,983,621	1,765,757	999,113	352,060	146,870	37,047	5,834,628
1970	3,789	-	-	-	156,352	732,837	1,906,177	1,512,963	779,188	550,753	126,798	22,581	5,741,438
1971	9,110	-	52,109	-	5,278	44,289	188,333	304,714	368,498	424,158	44,595	4,780	1,445,864
1972	7,380	2,814	-	-	9,834	155,165	536,355	558,635	445,349	190,250	85,702	68,072	2,059,536
1973	427	15,265	1,960	35,464	148,867	277,312	552,192	377,665	328,189	112,974	111,335	38,876	2,000,526
1974	12,718	2,530	4,750	2,110	23,929	157,075	202,143	88,647	82,695	113,757	43,324	16,379	750,057
1975	-	2,940	520	-	4,534	67,752	153,969	165,269	94,945	106,508	42,582	794	639,813
1976	2,480	250	-	-	-	15,000	-	39,235	-	-	30,145	-	87,110
1977	- - - - - C L O S E D - - - -				-	-	20,905	44,920	23,802	11,661	5,736	6,002	113,026
1978	- - - - - C L O S E D - - - -				58,163	185,802	313,805	478,351	170,223	105,114	35,615	14,071	1,362,306
1979	- - - - - C L O S E D - - - -				62,584	196,034	455,313	391,790	109,855	49,767	43,364	2,568	1,311,275
1980					13,834	183,526	548,134	641,565	258,020	271,116	56,864	24,087	1,997,146
1981	-	-	13,726	47,896	274,258	602,258	1,429,914	1,508,068	924,139	449,573	228,225	32,580	5,510,637
1982	23,038	9,123	- C L O S E D -		141,977	464,116	1,117,180	1,122,639	603,745	575,028	402,914	84,139	4,543,899
1983	22,600	5,940	- C L O S E D -		300,246	398,527	1,305,742	1,116,546	848,838	566,314	148,398	44,851	4,758,002

In 1976, the season was set at May 1 through December 31, and during the closed period all crab pots had to be stored on dry land. By 1977, fishermen were concerned with non-commercial crab escaping from their gear and instituted the requirement of two circular 4 3/8 inch escape rings in each pot located on the upper half of the vertical plane. Also, the size limit was decreased to six and one-half inches inside measurement from seven inches outside measurement in 1977. In 1978, all pots had to contain a termination device which would render the pots inoperable, if the pot was lost. Finally in 1981, the season was changed from May 1 to February 1.

In summary, these are the regulations in effect that are currently used to manage the dungeness fishery in Kodiak.

Fishery Management

The Kodiak area dungeness fishery management strategy is based on three main criteria: size, sex and season. The fishermen are allowed to harvest as many male crab over six and one-half inches (carapace width) from May 1 until February 1. This management strategy has been in effect since 1962; and as can be seen on Table 6, the harvest has fluctuated from a high of 6.8 million pounds in 1968 to a low of 87,000 pounds in 1976.

No quotas have been set on dungeness crab in the Kodiak area for primarily two reasons. First, no Alaska Department of Fish and Game population estimates are available on which to base a quota. Second, the harvest of six and one-half inch crab assures that the reproductive potential of the stock is protected.

As was mentioned in the Regulatory section, fishermen must abide by many administrative regulations in addition to size, sex and season. The Department of Fish and Game monitors and requires fishermen to provide information about their commercial catch of crab. The fishermen must report every landing made to the Department with the following information: a. date of landing; b. area caught; c. number of crab; d. number of pounds, e. number of pots pulled; and f. of course, the vessel name and skipper. This information is reported by the Department on a monthly basis. In addition to data provided by fishermen, Department personnel interview fishermen while they are unloading their catch; sampling crab for width, condition and average weight. These dockside samples were instituted in 1968, when 746 crab were measured to obtain a mean carapace width of 189 mm (Table 7).

Research

In April of 1968, the first research data on dungeness crab was collected by Morris in Saltery Cove. Morris used the dungeness crab vessel, JAN M, to catch dungeness in pots and recorded width frequencies, shell age and egg condition. In May of 1968, McMullen collected the same information from trawl surveys conducted in Santa Flavia, Ugak, Kalsin and Middle bays.

Table 7. Catch per pot and mean carapace width dungeness crab, Kodiak area.

Year	Average Catch/Pot	Sample Size	Mean Carapace Width (mm)[1]	Average Wt./Crab
1968	-	746	189	-
1969	12	-	-	2.6
1970	9	2,041	193	2.7
1971	6	542	189	2.6
1972	6	50	189	2.5
1973	3	996	179	2.2
1974	3	209	186	2.2
1975	4	1,101	178	2.0
1976	9	NA	NA	2.3
1977	12	163	186	2.4
1978	6	928	181	2.2
1979	4	474	180	2.0
1980	9	1,097	177	2.0
1981	9	622	180	2.1
1982	4	561	181	2.3
1983	4	1,978	180	2.3

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[1] Measured immediately. Anterior to the 10th lateral spine.

In 1970, the first formal research program was started by Brown and Jackson. Jackson began a tagging program with the objectives to define growth per molt, age class composition and migration. He tagged 1,915 crab in 1970 releasing them around Kodiak Island from four different vessels (Table 8). Jackson recorded depth the crab were caught, measurement inside and outside spines and carapace damage. The tagging program continued until 1972. Unfortunately, these studies have not been published, and the information was retrieved from Department files. No intensive analysis of the data has been attempted. Table 8 presented in this report summarizes tag release and returns, and Table 9 lists the incidence of molting. It appears from Table 9 that, of those crab measured, on the average one millimeter a month is gained by molting crab.

No current dungeness crab research program exists in the Kodiak area. After reviewing the unpublished data on dungeness in the area; the author would recommend continuation of the tagging program, and the documentation of the molting period in each major producing area.

Stock Status

The Kodiak dungeness crab stocks are at the edge of their known range (MacKay 1942). The only indicator of population size in the area is based on commercial harvest. The commercial harvest figures may have appropriately mirrored the population size in years of intensive harvest; however, for those years (1974-1977) the harvest was held artifically low because of market resistance. The abundance of crab will fluctuate as a result of natural cycles in the populations; and the current management strategy objective to harvest all males over six and one-half inches will, undoubtedly, perpetuate the cyclic fluctuation. The harvest is strictly dependent on the strength of the incoming recruit class, as most known habitat is presently commercially fished.

The dungeness crab populations has sustained harvests of over four million pounds each year since 1981 (Table 4). Compared to the historic average harvest of three million pounds, the stocks appear to be at moderately high levels.

Conclusions

The Kodiak area dungeness crab fishery began in 1962 on stocks that inhabit the periphery of their range. The harvest has been primarily dictated by market conditions, which have been based on dungeness harvests on the west coasts of Canada and the United States. The dungeness fishery has held relative minor importance in the Kodiak area, until recently with decline in the shrimp stocks and closure of the king crab fishery. With the fisheries greater economic impact on the community, the Department of Fish and Game should establish a permanent dungeness research program to provide growth information which would be used to set a biological size limit that would insure the reproductive potential of the stock be protected.

Table 8. Dungeness crab tag release and subsequent recovery[1] for Kodiak, Alaska, 1970-72.

Release Area			Recovery By Year										Total	
		No. Tags	1970		1971		1972		1973		1974		To Date	
Bay	Stat.Area	Released	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
1970														
Uganik	253-33	204	0	0	10	4.9	0	0	1	.5	0	0	11	5.4
Uyak	254-40	155	0	0	11	7.0	4	2.6	0	0	1	.6	16	10.3
Alitak	257-50	978	0	0	15	1.5	11	1.1	4	.4	0	0	30	3.0
Trinity Is.	257-90	21	0	0	0	0	0	0	0	0	0	0	0	0
Sacramento R.	259-30	173	1	.57	8	4.6	0	0	0	0	0	0	9	5.2
Ugak	259-41	234	2	.85	4	1.7	6	2.6	1	.4	0	0	13	5.5
Mainland	262-15	150	0	0	5	3.3	0	0	1	.7	0	0	6	4.0
Subtotal	7	1,915	3	.15	53	2.8	21	1.1	7	.36	1	.05	85	4.4
1971														
Sharatin	252-38	98	-	-	0	0	7	7.1	6	6.1	0	0	13	13.2
Anton Larsen	252-38	86	-	-	0	0	2	2.3	3	3.5	0	0	5	5.8
Alitak	257-50	183	-	-	0	0	0	0	0	0	0	0	0	0
Kiliuda	258-10	800	-	-	5	.6	26	3.2	4	.5	1	.12	36	4.5
Ocean Beach	258-40	57	-	-	1	1.7	4	7.0	0	0	0	0	5	8.7
Subtotal	5	1,224	-	-	6	.49	39	3.2	13	1.1	1	.08	59	4.8
1972														
Sharatin	252-38	1,223	-	-	-	-	0		82	6.7	8	.65	90	7.4
Subtotal	1	1,223	-	-	-	-	0		82	6.7	8	.65	90	7.4
TOTAL 1970-1972		4,362	3	.06	59	1.4	60	1.4	102	2.3	10	.2	234	5.4

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[1] Complete 1974 recovery through December 15, 1974.

Table 9. Dungeness crab molting incidence for tags recovered 1971-1974[1], Kodiak Island, Alaska.

Size at Release (mm)	Number Recovered	Number Molted	Percent Recoveries Molted	Average Growth/ Month (mm)
130-134	2	1	50	1.12
135-139	0	0	0	-
140-144	0	0	0	-
145-149	1	1	100	.80
150-154	7	5	71	.88
155-159	18	6	33	1.20
160-164	47	11	23	.99
165-169	36	6	17	.84
170-174	16	1	6	.90
175-179	19	1	5	.86
180-184	12	0	0	-
185-189	8	0	0	-
190-194	2	0	0	-
195-199	0	0	0	-
200-204	2	0	0	-
TOTAL/AVERAGE	170	32	18.8	.97

[1] Those crab which were recovered and measured.

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Session II

Life History

Ecology, growth, and population dynamics of juvenile Dungeness crab, *Cancer magister* Dana, in Grays Harbor, Washington, 1980-1981

Bradley G. Stevens
National Marine Fisheries Service
Kodiak, Alaska
and
David A. Armstrong
University of Washington
Seattle, Washington

Abstract

Dungeness crabs, Cancer magister were collected regularly from May 1980 to July 1981 in Grays Harbor, Washington. Distribution, growth, and feeding habits were studied for several age groups. Many crabs entered the estuary as megalops in April of both years; intertidal mudflats were important habitats for the earliest instars. Highest densities of crabs occurred in summer, and in the outer estuary. Crabs emmigrated from the estuary at various ages. Mature females must leave to spawn. Prey preferences changed with age/size; the most important were shrimp (Crangon spp) and juvenile fish. Crabs followed shrimp movements into littoral areas, especially at night. The differential use of habitats by age groups of crabs was probably more closely related to food preferences than salinity; no differences in osmoregulatory ability were demonstrable between large and small crabs. Population size ranged from 3.3 to 39.0 million crabs (winter to summer); 75% of the summer population estimate were early instars. Grays Harbor is an important resource which contributes substantially to recruitment of coastal Dungeness crab populations, and may serve as a model for crab-estuary interactions.

Introduction

The Dungeness crab, Cancer magister Dana, supports a large commercial fishery in Washington coastal waters and is a top benthic predator in the marine ecosystem. Numerous authors have published studies on C. magister ecology (MacKay, 1942; Cleaver, 1949; Butler, 1960; Gotshall, 1978b,c), but only a few have conducted studies on estuarine populations (Butler,

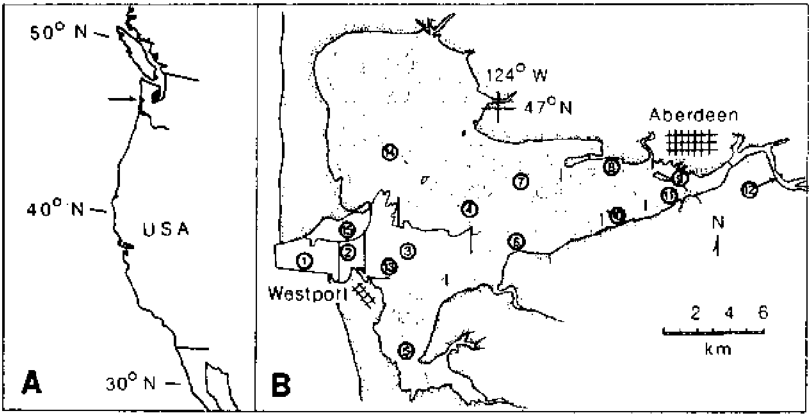

Fig. 1. A. West coast of North America; arrow indicates site of Grays Harbor, Washington, USA; B. Map of Grays Harbor, showing sites of <u>Cancer magister</u> collection (1-13). Stations 14 and 15 were not sampled regularly. Solid lines indicate boundaries of strata used for population estimation.

1956; Gotshall, 1978a), and those that did indicated that estuaries may be important nursery areas.

Grays Harbor is a large, shallow estuary on the coast of Washington State (Fig. 1). It has a total surface area of about 200 square km, of which about half is exposed mudflats at low tide. Annual rainfall exceeds 100 inches. Located at the mouth of the estuary is Westport, site of one of the largest Dungeness crab fisheries on the coast. Aberdeen, at the eastern (upstream) end of the estuary, is a major log exporting center, serving the Olympic Peninsula and southwest Washington. For this reason, artificially deepened navigation channels have been maintained to Aberdeen since about 1910 by the U.S. Army Corps of Engineers (USACE).

In 1978, the USACE funded a study of the effects of dredging on Dungeness crabs in the estuary which showed that large numbers of crabs were killed and injured during channel maintenance dredging (Stevens, 1981). During that study, I observed large numbers of juvenile crabs in most portions of the estuary, and concluded that it was probably an important nursery area, but that it's role as such had been largely overlooked. As a result of these observations, I requested and obtained funding from the USACE to study the ecology and distribution of juvenile Dungeness crabs in the estuary.

The objectives of the research program were:

1. to determine the distribution of crabs in the estuary,

2. to determine their diel activity patterns,
3. to estimate growth of crabs in the estuary,
4. to determine how crab distribution was related to
   a) food habits, and
   b) salinity tolerance,
5. to estimate the estuarine population size of juvenile crabs, and
6. ultimately, to understand why crabs lived in the estuary and how important this resource was to them.

Because of the multiple goals of this study, I will treat the methods and results of each objective separately.

Distribution and Abundance

Habitats sampled ranged from deep to shallow, sandy to muddy, and oceanic to freshwater regions (Fig. 1). Crabs were collected at stations 1-9 with a 4.9 m otter trawl with a 6 mm stretch mesh cod end liner, and ring nets with 12 mm mesh were used at stations 10-12. Trawls were made within 2 h of spring low tides, and were measured by placing anchored buoys at each endpoint, then fixing their positions by compass triangulation. Distance towed was converted to area swept, and crab density standardized to crabs per hectare. ANOVA and regression analyses were conducted on log-transformed data.

Crab density was greatest in summer at all stations, and decreased to very low values in winter (Fig. 2). Additionally, crab density was greatest near the estuary mouth, and decreased with distance upstream. These differences were both statistically significant at $p<0.01$ (F test; Stevens and Armstrong, 1984).

In April of 1980 and 1981, large numbers of megalops stage larvae entered the estuary as free swimmers or attached to _Velella velella_, and first through third instars were abundant by late May. Three major carapace width (cw) frequency modes were distinguishable in the spring of both years (Fig. 3), which were concluded to represent distinct year classes. Abundance and growth data were analysed separately for each age-class (size-group). In 1980, young-of-the-year (YOY), or 0+ age crabs, were present at all trawl sampled stations. These were most abundant at station 5, in the south branch of the estuary, near mud flats and extensive eelgrass (_Zostera_ spp.) beds. The 1+ crabs were the most widespread throughout the estuary, comprising almost 80% of crabs collected at the farthest upriver sites, 9-12 (Fig. 4). The 2+ crabs were most abundant in the outer estuary, with small numbers elsewhere. Age 3+ crabs were collected infrequently by the trawl (but were numerous in the harbor, as shown by trap collections; Stevens, 1981) and were restricted to the outer estuary, especially stations 1 and 3. Closer examination of mudflats adjacent to station 5 and similar areas in the northern portion of the estuary revealed fairly high densities (>1 per square m) of early

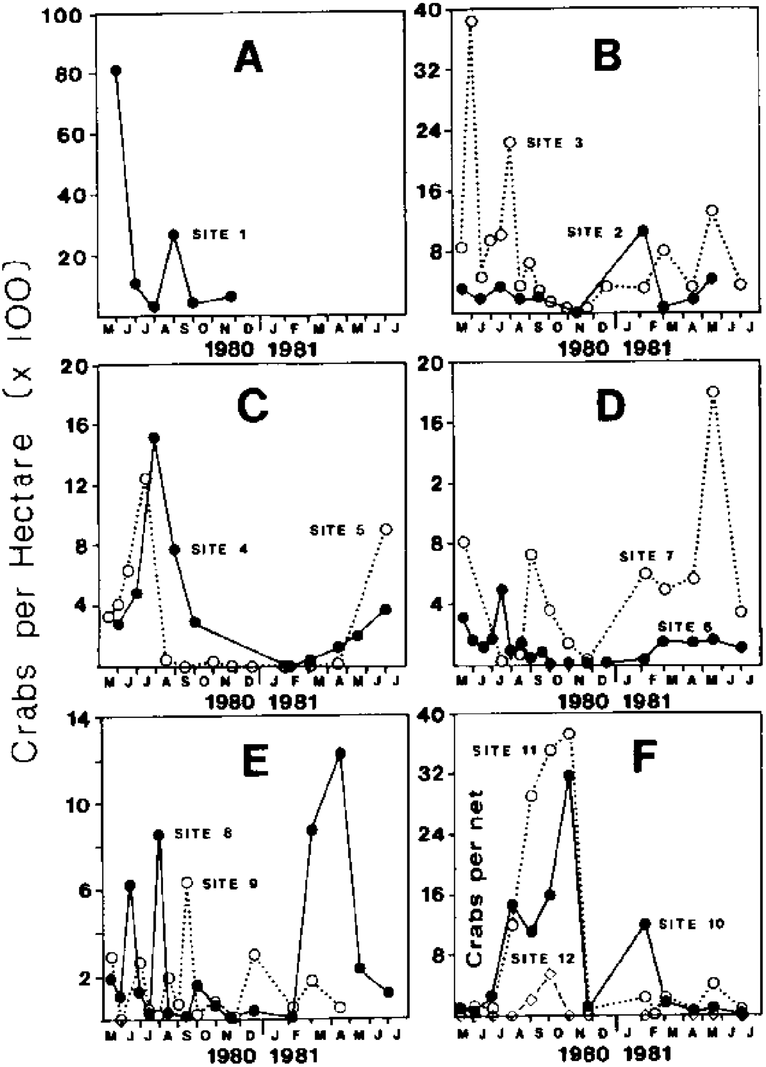

Fig. 2. Crab density for all stations in Grays Harbor sampled in 1980-81. (A) Station 1; (B) Stations 2 (filled) and 3 (open); (C) stations 4 (filled) and 5 (open); (D) Stations 6 (filled) and 7 (open); (E) Stations 8 (filled) and 9 (open); (F) Stations 10 (filled), 11 (open), and 12 (diamonds). Trawl sampling stations 1-9 shown as crabs/ha; ring net sampling stations (10-12) shown as crabs/net. Each point represents a single sample.

instars buried in the mud which was exposed at low tide. I calculated that trawl-estimated densities of this size-group reflected only 0.033 of the probable actual densities.

Growth

Growth analysis was based on the assumption that three major modes present each spring represented separate year classes. By September, YOY crabs averaged about 40 mm cw. This size group virtually disappeared during winter, but reappeared in spring of 1981, with an average cw of about 45 mm, thus they did not appear to grow appreciably during winter (Fig. 5). This pattern of slow winter growth occurred among all age groups. Dry weight vs. width regressions were not significantly different for males (<132 mm) and females (<112 mm), so a combined regression equation was calculated:

$$\log_{10} \text{weight (g)} = -4.064 + 2.832 \log_{10} \text{cw (mm)}$$

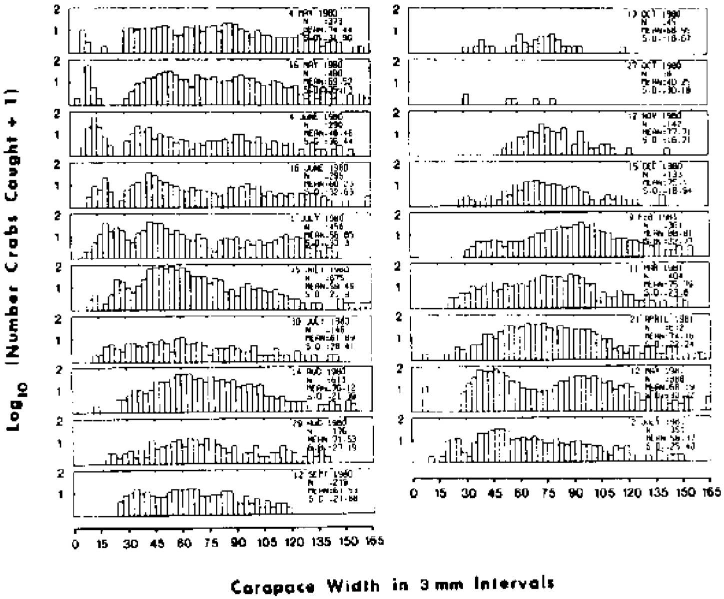

Fig. 3. Carapace width frequencies of all crabs caught by trawl at stations 1-9 in Grays Harbor, 1980-81. Numbers expressed as log (base 10) (catch + 1). Box for each sampling period shows date, number of crabs measured, mean carapace width overall (in mm), and standard deviation.

This equation was used to calculate mean weight from mean widths. There appeared to be an inflection point in the growth curve about late August, so k values were calculated separately for spring-summer and fall-winter growth stanzas (Table 1). The dry weight of YOY crabs approximately doubled each month until September. One year after metamorphosis, they weighed, on average, 282 times the dry weight of a first instar.

From studies of San Francisco Bay, Tasto (1983) and Collier (1983) concluded that only one year-class occupied that estuary, and that crabs grew to about 100 mm cw in one year, compared to ocean-reared crabs which grew only half as fast.

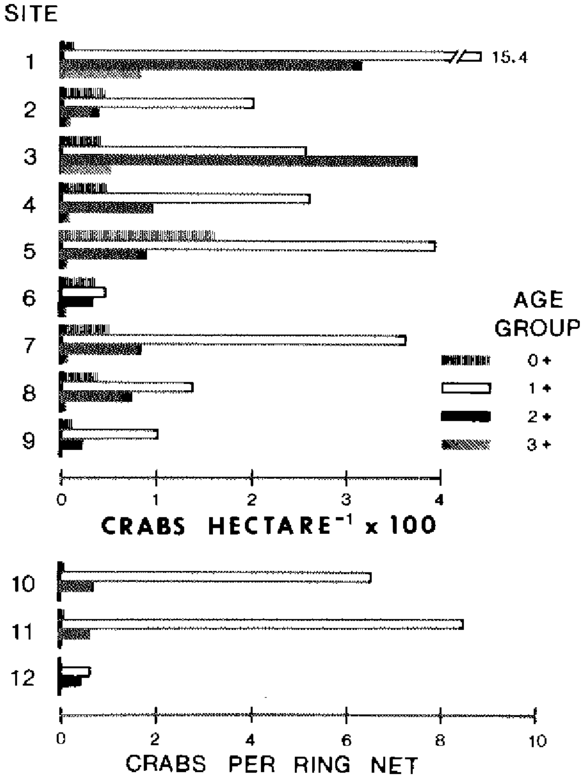

Fig. 4. Mean number of crabs/ha (stations 1-9) or crabs/net (stations 10-12) over the entire study period, by age-class. Age 0+ (vertical dashed lines), 1+ (open bar), 2+ (filled bar), and 3+ (slanted dashed lines) shown.

Table 1. Weight-specific growth rates and percent dry weight increase of three year-classes of <u>Cancer magister</u> in Grays Harbor, WA. Weights calculated from mean carapace width of each year-class by regression equation. Growth per month calculated for Spring-Summer (May-August) and Fall-Winter (September-April) growth stanzas.

Year class	Dry Weight 4 May 1980	Dry Weight 29 Aug 1980	Dry Weight 22 Apr 1981	May-August k	May-August % wt gain	Sept-April k	Sept-April % wt gain
1980	0.02	1.75	5.56	1.118	206	0.147	15.8
1979	4.02	11.75	21.46	0.268	31	0.075	7.8
1978	24.30	59.70	98.71	0.225	25	0.063	6.5

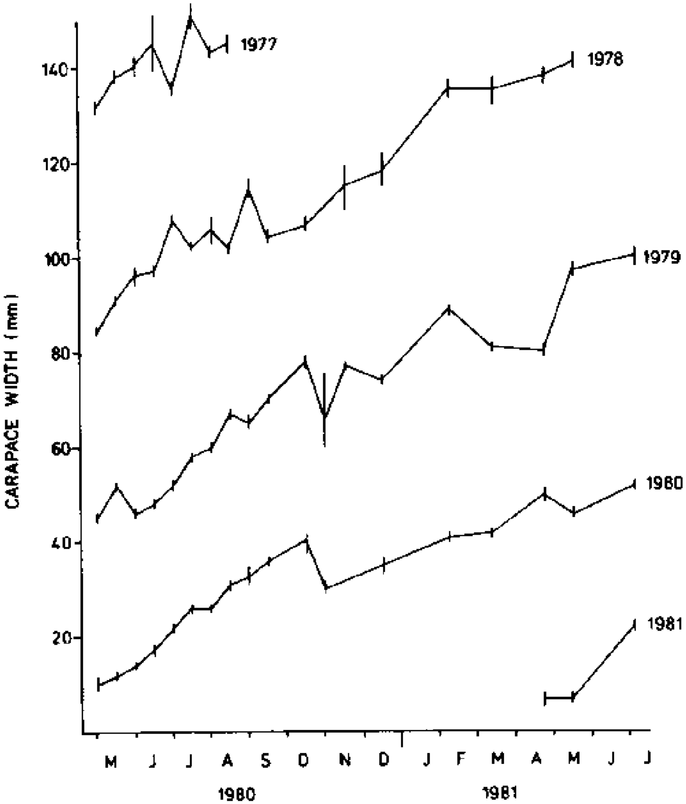

Fig. 5 Mean width of four age-classes of crabs (0+, 1+, 2+, 3+) in Grays Harbor, 1980-81. Mean width (+ 1 SE) shown for each age-class within each sampling period.

This contradicts my interpretation of growth in Grays Harbor, and would indicate that growth is much faster in San Francisco Bay, or that Tasto's sampling techniques did not efficiently catch the smallest crabs. Although it is conceivable that growth rates could differ between estuarine and ocean reared crabs, it is unlikely that growth rates would differ so drastically between these two estuaries. A large proportion of the California study was conducted by sampling crabs with ring nets with 25 or 45 mm mesh. This width was probably too great to capture the first 5 to 7 instars, and may explain why the smallest crabs were so infrequent in their bay area collections. Furthermore, my interpretation is supported by periodic diel collections in Grays Harbor (see below) in which thousands of crabs were measured over a 3 day time period. These samples were an order of magnitude larger than those collected in San Francisco-San Pablo Bays by Tasto or Collier.

Diel Activity

Diel trawl sampling was conducted at two stations, one in a deep channel (station 3) and one on an adjacent tidally inundated sand-mud flat (station 13). During four quarterly 3-day sampling periods (June and September, 1980, and January and April, 1981), tows were made during every slack tide at the channel site, and during high tides only at the flats site (Stevens et al., 1984).

In the channel, crab densities tended to be greater at low tide, but not significantly. This pattern occurred in all seasons except spring, when it was reversed, probably as a result of heavy rainfall and consequent high river flows. Generally, crab densities tended to be greater in the channel than on the flats, due to frequent exposure of the latter. Catches in the channel decreased at night, whereas densities on the flats increased at this time, producing a significant interaction effect in January and over all data combined (Fig. 6). Since regression analyses showed very little dependence of catches on salinity, I concluded that these differences were a response to the movements of prey organisms, primarily the shrimp *Crangon franciscorum*, and two congeners, *C. nigricauda*, and *C. stylirostris*, whose total abundance on the flats increased by 1-2 orders of magnitude at night (Stevens et al., 1984).

Food Habits

The previous conclusion relating to food availability was well supported by studies on the food habits of the crabs in Grays Harbor. Stomach contents were analysed from 410 crabs collected at both diel-sampling sites in all seasons, and at two additional sites farther upstream (stations 7 and 8). Data were analysed by the use of the Index of Relative Importance (Stevens et al., 1982).

Prey preferences showed few differences between day and night, or sites sampled. Some seasonal changes in diet were

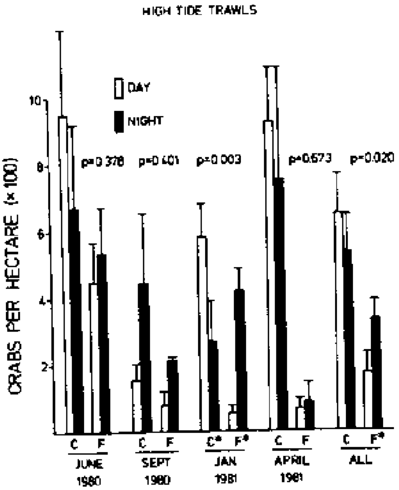

Fig. 6 Mean densities (+ 1 SE) of *C. magister* during high tides showing differences between day and night trawls at channel and flats sites. Day/night differences were significant (p<0.05) where marked wityh an asterisk. Significance levels of the light/site interaction are noted above each season. C: channel; F: flats. N=3 for all means except April, flats (n=2).

apparent, related to prey availability. Diel patterns of stomach fullness showed no consistent pattern, being different in every season. The greatest differences were apparent when diets were compared between size-classes of crabs (Fig. 7). Small crabs (<60 mm cw) preyed most heavily on small bivalves. Medium crabs (61-100 mm cw) preyed less on bivalves and more on crustaceans and juvenile fish. Larger crabs (>100 mm cw) preyed mostly on small fish, and proportionately less on bivalves and crustaceans. The most important prey items overall were the Crangonid shrimp, consumed by all size groups to some degree. A small amount of cannibalism also occurred, especially among the smallest and largest size groups (Stevens et al., 1982).

Osmoregulatory Ability

Although regression analyses of catch data showed little influence of salinity, this variable still appeared to be a good general indicator of crab distribution, if not abundance. In particular, 0+ and 1+ crabs were more abundant in lower salinity areas than were larger crabs, thus indicating that smaller crabs might have better

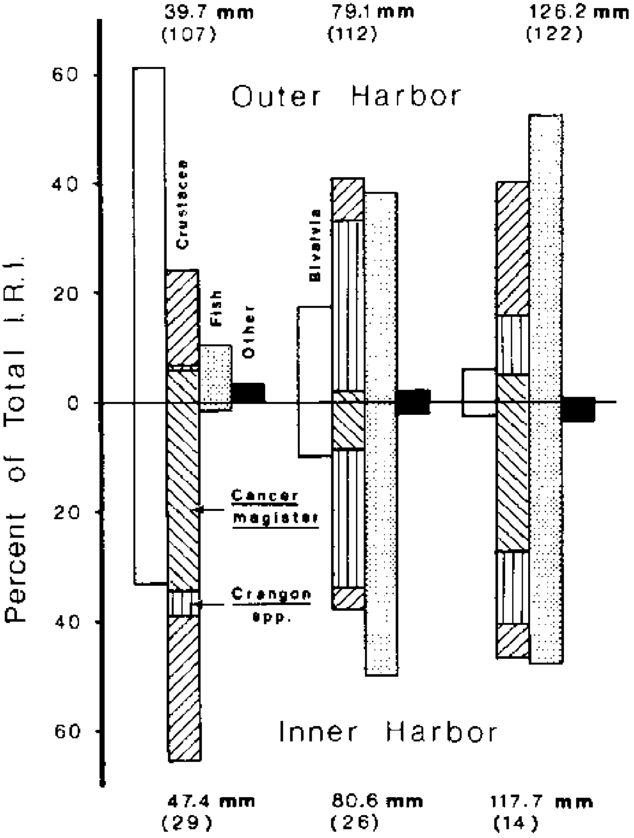

Fig. 7 Relative composition of diet of 3 size-classes of C. magister collected from outer estuary (stations 3 and 13) or inner estuary stations (7 and 8). Mean carapace width and number of crabs are shown for each group. Bar lengths are equivalent to percent of total IRI for each prey category.

physiological adaptation or tolerance to such habitats. Many other studies of crustacean osmoregulation show differences in osmoregulatory ability related to age, size, sex, or developmental stage (Gilbert, 1959; Hunter and Rudy, 1975; Bishop et al., 1980)

To test for differential osmoregulatory ability, crabs were captured from the outer estuary in March, 1981, and classified as small (56-97 mm, mean 80.3 mm, n=58) or large (103-157 mm, mean 126.1 mm, n=26). Crabs of both size-groups were placed in traps in a tidal creek where salinities varied from 0 to 10 ppt, at two sites ("dock", and farther upstream, "creek") about 3 km apart. Blood and ambient water samples were collected periodically over a 55 h period and frozen. Samples were later thawed and their osmolality was determined with a Wescor vapor-pressure osmometer.

Blood osmolality dropped rapidly in both size groups of crabs at both sites, from an initial mean of 850 mOsm to about 620 mOsm after 32 h (Fig. 8). From then on it remained fairly stable, and did not appear to fluctuate with ambient levels, which were much lower and fluctuated greatly. Contrary to my initial expectations, there were no significant differences in blood osmolality between large and small crabs (t-test, p>0.05).

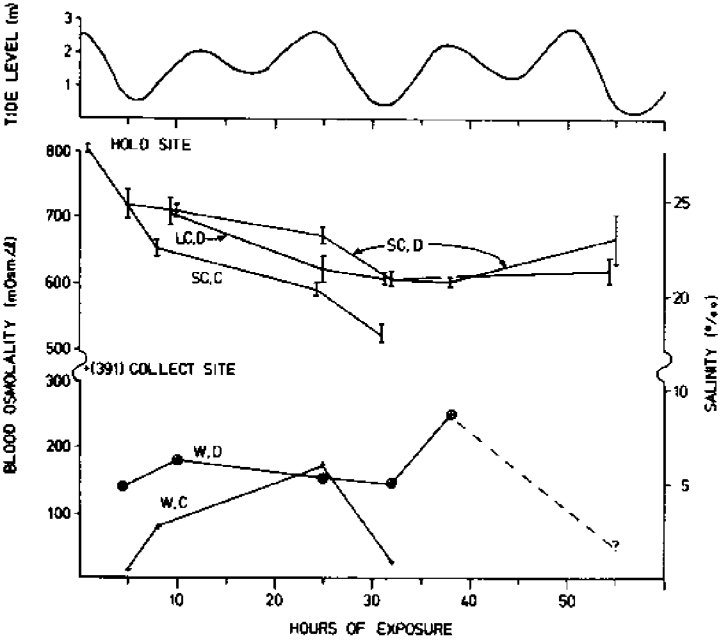

Fig. 8 Mean osmolality (+ 1 SE) of <u>Cancer magister</u> hemolymph and ambient water. Two size-classes tested at two sites. First point measured after overnight holding at collection site in outer estuary. Tide levels shown at top. SC,C= small crabs in creek. SC,D= small crabs at dock. LC,D= large crabs at dock.

General Ecological Hypothesis

From the above data it is now possible to construct a general hypothesis concerning early life history of Dungeness crabs in Grays Harbor (Fig. 9). Although mating may occur in the harbor, all spawning takes place offshore (no gravid females were ever found inside the estuary; Reilly (1983) reached the same conclusion for San Francisco Bay). Larvae develop offshore (Lough, 1976) but eventually return to the nearshore zone and enter the estuary as megalops in April or May. Some crabs may enter as first or second instars also. These first stages settle on or near mudflat areas, where they consume abundant small bivalves and crustaceans. As they grow and develop they show an ontogenetic change in habitat preference that is more closely keyed to dietary preferences than to salinity patterns. All size classes become less abundant in winter, possibly leaving the estuary, and many return in the spring. During their second year they spread out through the estuary seeking larger food sources (shrimp). As they mature, they concentrate near the estuary mouth where large numbers of juvenile fish are available as prey. Eventually the females leave the estuary for spawning, and perhaps for better food sources as well (e.g. razor clams). Some mature males remain in the estuary and support a small commercial fishery there.

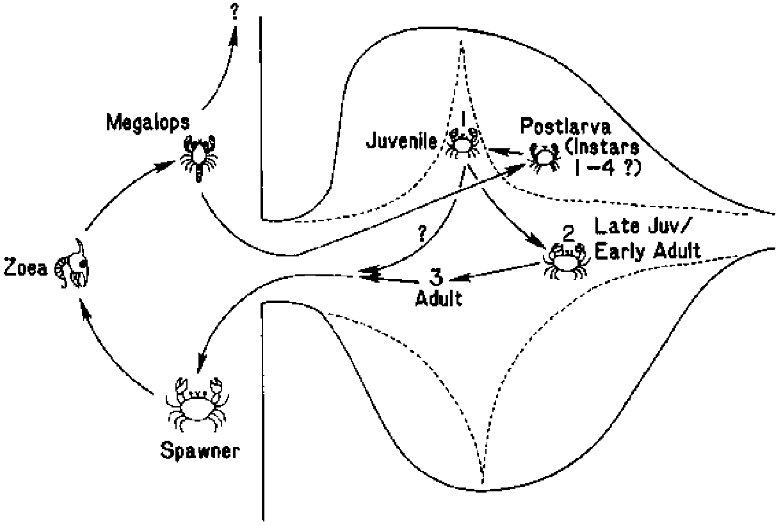

Fig. 9. General hypothesis for early life history of <u>Cancer magister</u> in estuaries. Relative magnitude of postlarval settlement along coast is unknown. Numbers indicate predominant location of age groups. Many probably leave the estuary after age I. All spawning is oceanic.

Population Estimation

In order to guage the relative importance of the estuary to crabs, and the relative magnitude of impacts from dredging, crab density data were used to calculate the population size of juvenile crabs in the estuary. A stratified random technique was used for which strata were defined encompassing each sampling station, and replicates were the tows taken there within a given seasonal period (Fig. 1)(See Stevens and Armstrong, 1984, for confidence limits and other details). Crab abundance was calculated for each age-class in each of 3 seasonal periods: summer, fall-winter, and spring. Separate trawl efficiency factors were derived for YOY crabs in summer (0.033, as described above), adult crabs (0.5, based on Gotshall, 1978a), and YOY crabs from fall through spring (0.25, an interpolated value). "Corrected abundance" was calculated by applying these factors to initial abundance estimates. No confidence intervals could be calculated for the final estimates (Table 2).

The "corrected" density estimate of 39.0 million crabs in summer of 1980 is the most dense estimate of a population of _C. magister_ ever reported (calculated for an area of 100 square km, or approximately 0.4 crabs per square m). The winter population dropped by an order of magnitude. Whether this decline was due to burial, emmigration, mortality or other factors is currently unknown. The population increased again the following spring, prior to arrival of the 1981 year-class.

Table 2. Results of the population size estimation for juvenile _Cancer magister_ in Grays Harbor.

Seasons Age-Group	Initial Estimate (millions)	Efficiency Factor	Total Crabs (millions)
Summer			
0+	0.96	0.033	28.9
1+	3.96	0.5	7.9
2+	1.08	0.5	2.2
Total			39.0
Fall-Winter			
0+	0.19	0.25	0.8
1+	1.16	0.5	2.3
2+	0.10	0.5	0.2
Total			3.3
Spring			
0+	0.23	0.25	0.9
1+	1.48	0.5	3.0
2+	1.95	0.5	3.9
Total			7.8

Mortality rates for adult crabs are approximately 0.2 (Jow, 1965). Rates for juveniles are unknown but are probably much higher in their first year. Using rates of 0.8, 0.5, and 0.2 for 0.5, 0.5, and 2.5 years respectively, I calculated that the 1980 cohort of 29 million YOY crabs would be reduced to 4.6 million adult males by age 3.5, at which time they should be recruited to the commercial fishery (Stevens and Armstrong, 1984). If the assumption is made that equivalent recruitment of early instars occurred to Willapa Bay, a nearby estuary of similar size to Grays Harbor, then about 9.2 million adult male crabs could have been made available to the coastal fishery by January 1985. This amount represents about 240% of the annual mean landings in Washington coast ports for the period 1971-1980 (about 3.85 million crabs). Since landings have fluctuated greatly in that time period, these estimates, if taken literally, may indicate a good year class in 1980. However, due to the speculative nature of these estimates and the many assumptions involved, they should be interpreted simply to imply that the recruitment of juvenile crabs to these two Washington estuaries probably represents a relatively significant contribution to Washington coastal crab stocks.

Future Directions

The results of this research serve to emphasize a number of important questions concerning *C. magister* biology which remain to be answered.

1. What is the exact nature and extent of intertidal habitat usage by early instar crabs?
2. What is the relative importance of nearshore coastal habitat for YOY crabs, compared to estuaries like Grays Harbor?
3. What is the burial behavior of Dungeness crabs, and how does this behavior affect trawl density estimates and dredging impacts?
4. Is growth in the estuary more rapid than offshore, and how does differential growth affect the interpretation of year classes and growth rates?
5. If estuaries are as important for nursery areas as they now seem to be in Washington, what is the relative importance of numerous small estuaries along the Oregon coast to commercial fisheries there?

The potential contribution of estuaries as nurseries for marine life is very great. Therefore it is imperative that extensive ateration or development of these habitats should be permitted only after careful consideration of possible impacts to indigenous fauna, particularly those of obvious economic importance.

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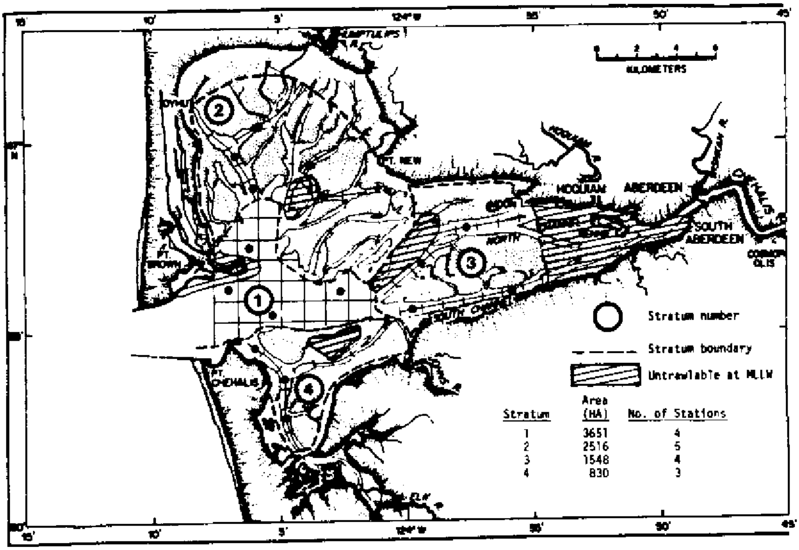
Sampling design and methodology for juvenile Dungeness crab surveys

Donald R. Gunderson, David A. Armstrong and Christopher Rogers
University of Washington
Seattle, Washington

Direct population estimates of juvenile Dungeness crabs, where the goal is to use area swept and quadrat sampling methods to determine population sizes, presents a number of challenges. First instar juvenile crab are known to settle out in a variety of habitats, ranging from open coast to estuaries, and from continental shelf to littoral zone. In addition, they are quite small (down to 6mm carapace width) and closely associated with the substrate, burrowing into it at times. In the course of a Sea Grant investigation on population sizes and dynamics of Dungeness crab in Grays Harbor and the adjacent Washington coast (Armstrong and Gunderson; Carrasco et al., this symposium), an approach has been developed to deal with these characteristics in a manner that is as operationally and statistically efficient as possible. This involves a combination of three different surveys: a transect line-quadrat survey of the intertidal zone within Grays Harbor, a stratified random trawl survey of the subtidal zone within Grays Harbor (Figure 1), and a systematic (by depth) trackline survey of the adjacent continental shelf (Figure 2).

Gear Employed

Otter trawls are quite effective for sampling demersal fauna, and they are of proven effectiveness in resource assessment surveys (Hayes, 1983). The horizontal net mouth opening is maintained through hydrodynamic forces generated by trawl doors, however, and is highly variable. The mouth opening has been shown to vary with water depth, scope ratio, bottom conditions, towing speed, and rigging features (Wathne, 1977; Main and Sangster, 1979; West, 1982).



Stratum	Area (HA)	No. of Stations
1	3651	4
2	2516	5
3	1548	4
4	830	3

Figure 1. Survey design used to sample Dungeness crab density within Grays Harbor 1983. Four strata are shown, each divided into one kilometer grids (subtidal areas only). Randomly selected stations are shown as dark circles.

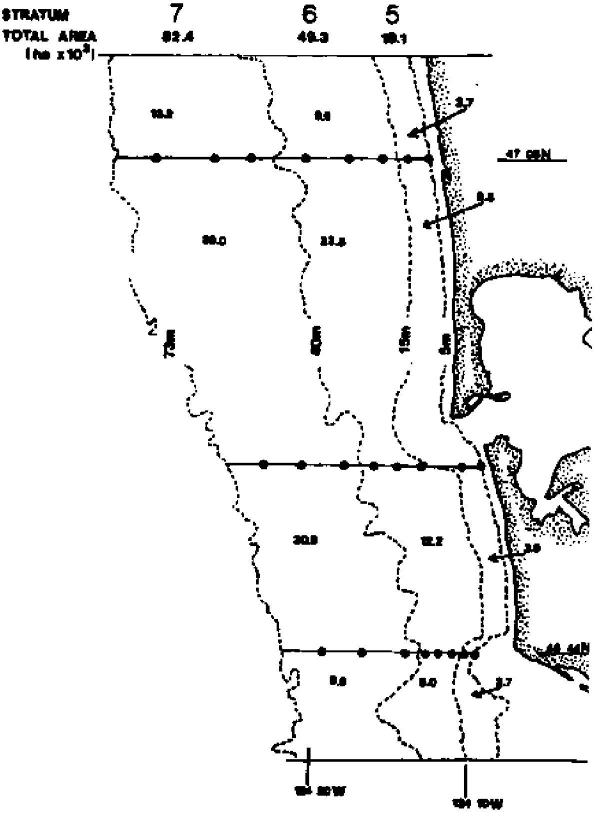


Figure 2. Continental shelf survey area and station array (dark circles) used to estimate populations of juvenile Dungeness crab. Shown are three strata (5, 6, 7) that include stations in common depth intervals from 5 m to 73 m (3 fm to 40 fm).

This is probably a minor problem with full-scale commercial trawls, but is of greater significance in the case of scaled-down otter trawls that have been developed for use off small boats (Mearns and Allen, 1978; Gibbs and Matthews, 1982) in shallow coastal waters. This is particularly true when the doors are rigged so that only a short distance separates them from the net itself.

Traditional beam trawls (Carney and Carey, 1980), where the mouth of the trawl is completely surrounded by a rigid metal frame, provide an alternative to the otter trawl in small-boat sampling, but are more awkward to store and deploy. The plumb staff beam trawl has a long history of commercial use (Amos, 1984), and offers an additional alternative. A nearly constant mouth opening is maintained by a rigid "beam" (aluminum conduit in our application), which can be removed after each set. Little storage space is required, and the net can be deployed and retrieved from a small vessel by hand.

The Ellis Highliner demersal sampling system, a modified plumb staff beam trawl developed for our work on Dungeness crab (Gunderson and Ellis, 1984) is shown in Figure 3. This system was scaled for use aboard a 6.4 m Boston Whaler within coastal estuaries, and for larger commercial fishing vessels (11-21m) in nearshore areas of the open coast.

Small juvenile Dungeness crab (down to 6 mm carapace width) and flatfish (down to 20 mm total length) were the principle targets in our surveys, and the sampling system was designed to sample them as effectively as possible. The net was designed and rigged to follow the contours of the seabed closely while the "tickler" chain array scrubs the bottom in advance of the net. The net is of relatively light construction and is fished with 30-60 m of 3/8-in. (.95 cm) nylon towline. Nylon stretches when under strain, acting as a shock absorber when the net "hangs up" on the bottom, reducing gear damage or loss.

Three series of SCUBA dives were undertaken in order to evaluate the effectiveness of the net when pulled from the Boston Whaler, and to measure its mouth opening. In addition, the net was compared with a shrimp try net (Headrope length = 4.9 m) used previously in Dungeness crab survey work (Gotshall, 1978; Stevens, 1982).

These observations showed that the final trawl design (Figure 3) maintained the desired shape and configuration under operational conditions, with good bottom contact along the entire length of the footrope. The footrope tended to dig into the substrate where it was sandy, and the main crossing chains in the tickler chain array also maintained good bottom contact. The tickler chain array, together with the turbulent zone created behind it, dislodged small organisms from the substrate and lifted them into the water column where they could be trapped by the net.

The horizontal spread (net width) could be readily determined either by measuring the net opening itself while the gear was in operation, or by measuring the distance between tracks left in the sand by the two lower wingtip weights. The effective width was determined to be 2.3 m, while the vertical opening was estimated at .6 m.

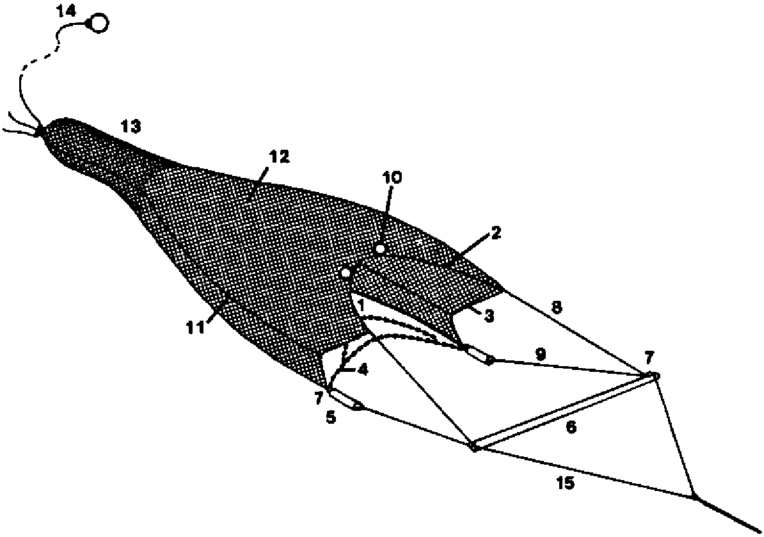


Figure 3. System developed for sampling juvenile Dungeness crabs and flatfish. 1 - 5.1 m footrope; 2 - 4.1 m headrope; 3 - 1.0 m breastlines; 4 - tickler chain arrays, 4.3 and 4.9 m sections of 1.9 cm chain; 5 - wingtip weight, 6.0 x 40.6 cm, 9.5 kg; 6 - beam, 3.8 cm x 3.1 m aluminum conduit; 7 - quick release snap; 8 - upper net bridle, 1.0 cm x 1.8 m; 9 - lower net bridle, 1.3 cm x 1.4 m; 10 - 7.6 cm cork float; 11 - ribline; 12 - main body of net, 14 mm (lumen) square knotless nylon; 13 - cod-end, with 5.5 mm liner; 14 - emergency retrieval line, with 20 cm float; 15 - beam bridle, 1.3 cm x 3.1 m. Total length, wings to cod-end is 7.9 m. Further information available from Ellis Highliner Fishing Gear, P.O. Box 55028, Seattle, WA 98153.

The shrimp try net used in previous Dungeness crab surveys failed to contact the bottom adequately, a feature which greatly reduces its utility for species such as Dungeness crab and flatfish. The footrope never got closer to the bottom than about 5 cm, and only the loops of chain attached to it actively contacted the substrate. This was true even with scope ratios in excess of 10:1 and towing speeds as slow as 1 kn.

Day-night comparisons of trawl efficiency were conducted during September 12-14, 1983, in order to examine the sampling efficiency of the trawl. These comparisons were all conducted from the 15 m offshore fishing vessel "SPIRIT", and a total of 15 pairs (30 total) of usable tows were made. The tows were made outside the entrace to Grays Harbor, Washington (Lat 46°50' to 46°56'N, depth = 23 to 38 m), within an 8 x 2 nautical mile survey area. Mean towing speed was 2.0 kn during the daytime hauls and 1.8 kn at night. A 5:1 scope ratio was used during these tows although this was increased at shallow depths (50 m of warp for depths less than 5 m, 100 m for depths of 5-20 m).

Mean day-night catch rates were compared statistically using a t-test after log (x+1) transformation (Sissenwine, 1978). Size composition data were also collected during the day-night studies, in order to evaluate size-specific differences in capture efficiency. Size data were compared statistically by using X^2 tests for homogeneity.

The day-night comparisons failed to detect any statistically significant differences (0.05 level) in mean catch per nautical mile or size composition for Dungeness crab. Although mean catch rate was greater during the night (37.2 versus 23.1 crabs/km), the difference was nonsignificant both for the t-test (P=.242) and the Mann-Whitney test (P=.141). This suggests that the net was equally effective during both periods.

Dungeness crab are known to burrow into the substrate during the day (Barr, 1980), and the system was designed to dislodge them. A single nighttime SCUBA dive by Barr (op cit) indicated that burrowing did not occur at night, so that the failure to detect any significant day-night difference in either catch rate or size composition for Dungeness crab suggests that the system design tended to successfully overcome any burrowing behavior that may have occurred.

In contrast, Gotshall (1978) found highly significant (.05 level) differences in catch rate between 6 pairs of day-night tows for Dungeness crabs when using a try net similar in size and design (4.9 m headrope, 3 m mouth width) to the one observed during our SCUBA work. Catch per tow was 75 percent greater during the night than it was during the day.

Sampling Methods

Four different strata were delineated within Grays Harbor (Figure 1), and each was divided into 1x1 km grids. Several of these were then selected randomly from each stratum, with the constraint that no two stations could be adjacent. The number of stations selected from each was proportional to the estimated abundance (Armstrong et.al., 1982) of crabs there, the largest number of stations being allocated to those strata where abundance was greatest. Few crabs exist in the upstream portion of the estuary, east of stratum 3 (Armstrong et.al., op. cit.). The allocation procedure was reviewed once the data from the 1983 survey became available, and an additional station was added in both stratum 1 and stratum 2.

We attempted to sample each station bimonthly, from April to September, sampling during low tide series, when the network of channels that characterize the Grays Harbor estuary (Figure 1) are easiest to locate and navigate. Trawling had to be confined to slack tide periods, in order to insure proper operation of the gear. In order to allow for a full working day the stations situated in smaller, unmarked channels were occupied during low slack, while stations in the more easily navigable main channels were occupied at high slack. Mean towing speed was 1.4 kn.

The small mesh (5.5mm) used in the cod-end liner frequently resulted in the net filling with detritus, gravel, mud etc. so that all tows had to be relatively short. In 1983, the mean distance fished in the estuary was 289 m. This made it imperative that the distance fished be measured as accurately as possible in order to keep the percent error within acceptable bounds.

Within Grays Harbor, a method was developed whereby an anchored buoy was deployed at the point where the net first contacted bottom after setting, and where it was estimated to leave the bottom during the retrieval process. The distance between these buoys was measured with an optical range finder, and by taking the measurements from a position between the two buoys, the precision was usually within about ±10%.

The sampling design for the continental shelf survey consisted of a systematic series of stations placed along three tracklines (Figure 2). The tracklines were oriented perpendicular to the bathymetry, and located off Copalis Head, Grays Harbor and Cape Shoalwater (Willapa Bay). Stations were originally placed at 3, 5, 10, 15, 20, 25, 30 and 35 fm (5.5, 9.2, 18.3, 27.5, 36.6, 45.8, 54.9, and 64.1 m). Where rocky or untrawlable bottom was encountered, the station was moved off transect until a trawl could be successfully completed at that depth. The transects were sampled in May, July, August and September of 1983. In 1984, replicate trawls were added at 15 and 20 fm, and the 35 fm stations were dropped at each transect, based on a review of the previous year's findings on bathymetric distribution.

Distance fished in the continental shelf area was determined by using Loran C, and estimating the time the gear arrived on bottom and left bottom from the wire angle. Most of the error in determining distance fished probably came from the latter process, since Loran C has a precision of ±15-90 m.

Twenty minutes was the usual target for tows made in the continental shelf area. However, large catches of sand dollars were frequently encountered inside of 5 m, and rocky bottom characterized several other sites, so that tows at some stations were eventually reduced to only 5 to 10 minutes. In 1983, the average distance fished in the continental shelf area was 1.2 km. Mean towing speed was 1.8 kn.

Catch processing and sampling procedures were similar in both the Grays Harbor and continental shelf survey areas. The catch was sorted, weighed, and length observations taken for selected species. The usual practice was to measure carapace width for each crab in the catch. In a few instances, where large catches of 0-age crab were encountered, random subsamples (never less than 20%) of the catch were taken for width measurments.

Surveys of the intertidal zone within Grays Harbor have been restricted to detailed quadrat sampling for seasonal trends in abundance within eelgrass and "shellhash" areas that provide refuge for small Dungeness crabs. In September 1984 transects of the entire Grays Harbor study area were made from an HH-3 Albatross helicopter, quantifying the percent ground cover and areal extent of both eelgrass and shellhash. The helicopter was made available by the U.S. Coast Guard, and all transects were flown during low tide. More thorough temporal coverage of eelgrass habitat is anticipated in 1985.

Future Studies

Research to date has indicated that substrate type is an important determinant of the distribution and abundance of juvenile Dungeness crab. In 1984, we began systematically noting any evidence of gravel, mud, detritus and epiphytic vegetation in trawl catches, and plan to undertake detailed mapping of substrate types using side-scan sonar and underwater video in 1985/86. In 1984, the Army Corps of Engineers surveyed a 70 square mile area off Grays Harbor using these techniques, and analysis of the results is currently underway. Ideally, the delineation of sampling strata and allocation of sampling effort would take the distribution and importance of habitat type (sand, mud, gravel, shellhash, rocks, etc.) into consideration.

In 1985, the overall scope of the surveys will be expanded considerably and surveys within Willapa Bay will be added. Offshore, two more transects will be added, bringing the total number to 5. These transects will be spaced more closely and the southernmost transect will extend south to Leadbetter Pt. We also anticipate further examination of the efficiency of the plumb staff beam trawl system, using direct SCUBA observations of crab densities, and comparing the results with the densities determined from trawl hauls made in the same area.

ACKNOWLEDGEMENT

This project was supported by Washington Sea Grant and we are indebted to the director and staff for their help and encouragement.

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Abstract

In order to obtain quantitative estimates of the size of subtidal juvenile crab populations in Grays Harbor, Washington, a stratified systematic (grid) sampling design was developed. Strata were selected on the basis of homogeneity of habitat, and sampling effort was allocated among these strata on the basis of previous estimates of crab abundance. A series of tracklines was set up in the open coastal region around Grays Harbor and Willapa Bay, in order to compare the density and population dynamics of continental shelf populations with estuarine populations.

A new type of demersal trawl was designed specifically for quantitative sampling of subtidal juvenile crabs, and some preliminary evaluations of its performance and efficiency were undertaken. Because of the small mesh used in the cod-end, the net was frequently filled with debris, making short tows and precise estimation of distance fished a necessity.

Juvenile crabs also make extensive use of "shellhash" and eelgrass habitat within the intertidal zone at Grays Harbor. This necessitates estimating both the geographical extent of these habitat types, and the density of crabs within each.

Future plans for alterations in the scope, sampling design and sampling methodology of these surveys, are also discussed.

The role of estuaries in Dungeness crab early life history: A case study in Grays Harbor, Washington

David A. Armstrong and Donald R. Gunderson
University of Washington
Seattle, Washington

Introduction

Although most of the Dungeness crab fishery and all reproductive events occur along the coast, there are several studies that point to the importance of estuaries in the life cycle of Cancer magister. During the life history of this species, ovigerous females are found only along the open coast where eggs hatch and five zoeal stages develop (Lough 1976). However, upon molt to megalopae there is a well documented movement of this last larval stage toward shore (Lough 1976; Cal. Fish and Game 1981; Reilly 1983) and entry directly into estuaries (Stevens and Armstrong 1984 for Grays Harbor; Reilly 1983 for San Francisco Bay). Newly metamorphosed first instars are abundant in estuaries (Butler 1956, 1961; Gotshall 1978; Stevens and Armstrong 1984; Tasto 1983) which has led to the notion that they serve as nursery grounds for young-of-the-year (YOY=0+) and 1+ age class crab.

Present management plans for Dungeness crab can put no specific value on the importance of estuaries to the fishery other than to say in general terms that they may be significant. It is therefore difficult to argue to what extent estuaries like Grays Harbor and Willapa Bay should be protected, what sort of development should be allowed and where its location within an estuary might be compatible with habitat requirements of crab.

Plans to alter and develop estuaries will be proposed for decades to come. A warning as to the possible impact on Dungeness crab resulting from extensive and poorly planned development of Washington estuaries can be taken from San Francisco Bay. In 1957 landings of crab at San Francisco exceeded 9 million lb. but by 1960 and for the last two decades landings have usually been about 0.5 million lb. (Farley 1983). Hypotheses to account for the demise of this fishery include impacts to the bay caused by extensive dredging, landfill, municipal and industrial development and concommitant pollution, and the enormous agricultural drainage that enters the bay complex (see review by Armstrong 1983; Wild and Tasto 1983). The San Francisco estuary has been estimated to shelter up to 80% of incoming YOY in some years (Tasto 1983), which suggests that loss of vital habitat could significantly reduce recruitment to the offshore fishery.

Due to the commercial importance of Dungeness crab in Washington state and the potential impact on the species caused by an expanded dredging program in Grays Harbor, the Army Corps of Engineers (COE) sponsored research work in 1980-81 on both crab populations and dredge entrainment that provided substantive data on the magnitude, abundance and distribution, timing of movement and habitats of the species (Armstrong et al. 1982; Stevens and Armstrong 1984). Based on calculations of crabs entrained per cubic yard removed by different gear in several seasons, these authors predicted that up to 2.6 million crab would be killed during operations through summer while 1.5 million might be killed if dredging was restricted to an extended winter season of September through February. As a fraction of the annual population (estimated to be 28 million in 1980, Armstrong et al. 1982, but revised upward to 39 million by Stevens and Armstrong 1984), a year-round operation might kill 4.6% of the population each year, but a winter operation could kill 26% of a much smaller resident population in that season (see Stevens this symposium proceedings).

The contribution of YOY juveniles in Grays Harbor to the offshore fishery 3.5 years later was calculated by Stevens and Armstrong (1984) based on an initial 0+ population of 29 million (revised upward from 18 million calculated by Armstrong et al. 1982). By using a variety of mortality rates from $Z = 0.8$ to 0.5 in the first year and 0.2 (Jow 1965) thereafter, they calculated that 4.6 million males might survive to the fishery, a number that could be doubled to account for recruitment from Willapa Bay. The ten year average landings from the Washington coast are about 3.85 million crab (based on an average weight of 0.9kg/crab), which leads to the conclusion that Washington's fishery could be supplied entirely from recruits that settled initially in coastal estuaries; this conclusion, however, is tentative because of sweeping extrapolations required from the data.

While this study provided the best estimate of crab density and population abundance in Grays Harbor or any west coast estuary to that time, it still embodied two important problems: 1) sample stations were restricted to an area in and near the main navigation channel and, thus, the extrapolations from station density to total population abundance was based on no information for large segments of the estuary including several habitats thought to be important for juvenile crab (e.g. shallow eelgrass flats); and 2) the gear (a small otter trawl) was considered inefficient for very small crab although no study of this issue was made.

As an outgrowth of this first program, we acquired funding from Washington Sea Grant to begin a program in 1983 that has as its objectives the following:

1. Contrast juvenile crab abundance in Grays Harbor estuary to that offshore.

2. Improve the survey design for the estuary by increasing spatial coverage, and using improved gear.

3. Include, for the first time along the Washington coast, an offshore trawl survey coincident with that in the estuary (see Carrasco et al. this symposium).

4. Contrast crab population structure, mortality and growth rates between the two systems.

5. Study the occurrence of juvenile crab on different substrates in order to identify sediment type and/or materials of greatest importance to early instars.

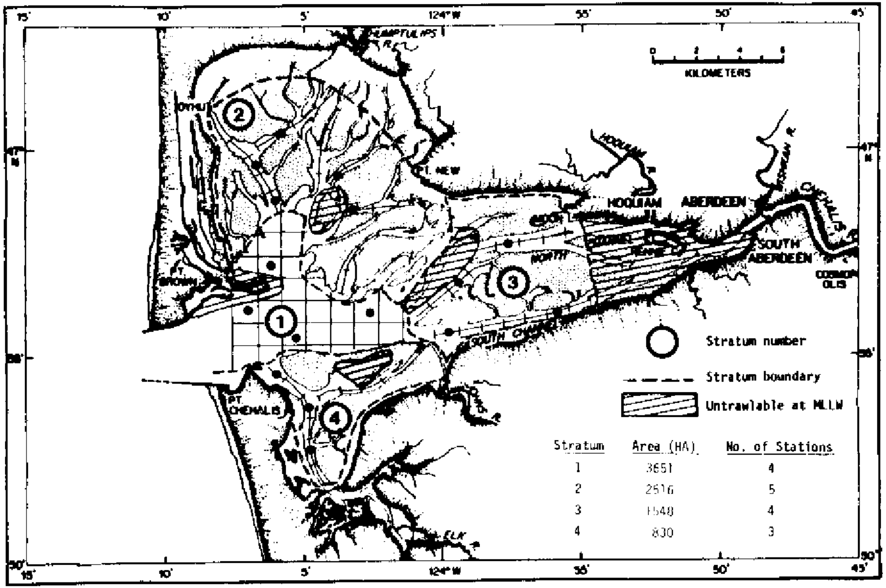
Methods and results to date for certain components of this project are reported elsewhere in this symposium proceedings by Gunderson et al. on sampling design, methodology and gear, and by Carrasco et al. on crab populations offshore. In this particular report we describe research and results in Grays Harbor estuary during 1983, and consider data in light of other studies of Dungeness crab population dynamics and general ecology of the species.

Methods and Materials

Sampling Design and Gear.

Details of these aspects of the project are given by Gunderson et al. (this symposium) and only paramount features will be noted here. The stratified random survey design of Figure 1 was based, in part, on work of Stevens and Armstrong (1984) in Grays Harbor but was expanded to include sample stations throughout navigable areas of the estuary; notably the North Bay (stratum 2) and South Bay (stratum 4) where virtually no work was done previously although the areas were thought to be important to juvenile crab based on habitat such as eelgrass. The subtidal area up to mean lower low water (MLLW) was digitized and stored on the National Marine Fisheries Service computer (Seattle) to use in calculations of population abundance from station density. The largest subtidal area occurs in stratum 1 (3651 ha) and the smallest in stratum 4 (830 ha). The total area of 8,545 ha is about 17.6 times smaller than that (150,800 ha) digitized for calculation of offshore populations (see Carrasco et al. this symposium). (It is important to remember that all estimates of population size given in this paper are for subtidal areas only; the intertidal is treated separately on a small scale).

Twelve sampling trips were conducted in 1983 from April to early October and 17,102 crabs were caught, sexed and measured. The survey gear described by Gunderson et al. (this symposium) worked well and, in all respects, seemed to be superior to the semiballon otter trawl used by Stevens and Armstrong (1984). It is our impression that the net actually excavates slightly on certain substrates since catches containing large amounts of sand, mud and fine detritus were rather common. Although more efficient than the otter trawl, no specific measure of efficiency of the plumb staff beam trawl has been made to



Stratum	Area (HA)	No. of Stations
1	3651	4
2	2516	5
3	1548	4
4	830	3

Figure 1. Survey design used to sample Dungeness crab density within Grays Harbor, 1983. Four strata are shown, each divided into 1 km grids (subtidal areas only). Randomly selected stations are shown as dark circles.

date and thus no correction factors are applied to population estimates in this report (as done by Stevens and Armstrong 1984).

Population Estimates

Population estimates are based on the area swept method, using the estimator,

$$\hat{P} = \sum_{i=1}^{h} \frac{A_i}{a} \bar{C}_i$$

where P = population estimate

A_i = area of stratum i

a = area swept per km by the trawl, assuming an effective width of 2.3m

$\bar{C}_i$ = mean catch rate (number caught per km fished) for stratum i, based on n_i hauls

$$\bar{C}_i = \frac{1}{n_i} \sum_{j=1}^{n_i} C_{ij}$$

h = number of strata.

This corresponds to the three depth strata 5-15m, 16-40m, and 41-73m (see Carrasco et al., this proceedings) for the offshore survey area, and to the four geographic strata defined in Figure 1 for the Grays Harbor survey area.

On assumption that the survey stations within each stratum are randomly distributed with respect to the crab population, and that total population estimates are normally distributed around the actual population for that area, 95% conficence limits for P were approximated by:

$$\hat{P} \pm t_{(0.95,\, n_e)} \; (\mathrm{Var}\ \hat{P})^{\frac{1}{2}}$$

$$\text{where } \mathrm{Var}\ \hat{P} = \sum_{i=1}^{h} \left(\frac{A_i}{a}\right)^2 \mathrm{Var}\ \bar{C}_i$$

$$\mathrm{Var}\ \bar{C}_i = \frac{1}{n_i(n_{i-1})} \sum_{j=1}^{n_i} (C_{ij} - \bar{C}_i)^2$$

n_e = number of effective degrees of freedom (Cochran 1962).

Size frequency observations were obtained for each catch, usually by measuring each individual in the catch. Subsampling was occasionally necessary, particularly when large numbers of YOY were encountered in the catch. These length frequency observations, weighted to the catch per unit effort (numbers/ha), were then expanded from the total estimated population to obtain estimates of population size for each millimeter increment, by stratum. These estimates were then summed across all strata and plotted on a percentage basis to obtain size composition data which, in turn, provided the basis for modal analysis and analysis of the catch by age group. In addition, size-at-age data from Cleaver (1949) and Stevens and Armstrong (1984) were also used to set width ranges for several year classes (0+, 1+, and others) over time.

Intertidal Survey

A limited intertidal survey of two areas was conducted, one in the South Bay (Stratum 4; Fig. 1) in an eelgrass habitat and one along the South Channel on an expansive mudflat with patchy covering of shellhash and eelgrass (see inset of Fig. 8). Small quadrat areas of $0.2\text{-}1.0 m^2$ were excavated to a depth of about 2 to 5 cm and sorted for crab on nine sampling trips at the South Channel site and on four trips in the South Bay. A population estimate was calculated for a large portion of the intertidal flat at the South Channel site by estimating the percentage cover of shell and eelgrass from a series of randomly arrayed transect lines. A mean value of 16.5% optimal cover in this area (n=10, ± 1 S.D. = 7.8%) was used as a multiplier to correct the total area of the estimate ($15.8 \times 10^6 m^2$) to $2.6 \times 10^6 m^2$ considered to be well suited for crab (see Fig. 8). Helicopter flights over this region in summer, 1984, were used to verify that the entire area depicted in Figure 8 is qualitatively like that used for ground cover transects in a restricted area near the South Channel proper.

Results

Size and growth.

First samples collected in April, 1983, indicated that YOY crab had not arrived in the estuary in peak numbers, and that the population was composed primarily of 1+ and 2+ animals from approximately 30 to 120 mm carapace width (CW; Fig. 2). In early May, arrival of the 1983 year class produced a strong mode between 7 to 10 mm, the size of first and second instar juveniles. Thereafter, the size mode for 0+ remained distinct from the rest of the population as the YOY grew from a mean CW of about 7 mm in early May to 38 mm by October, 1983 (Figs. 2 and 3).

Modal analyses and size-at-age discrimination were not so straightforward with older juveniles. The size boundary between smallest 2+ and largest 1+ crab was never easy to distinguish but was set at about 70 to 90 mm over time between May and September (Fig. 2; Table 1) in order to calculate population abundance by age class. In several months (e.g. April, June, August), 1+ juveniles appeared to be

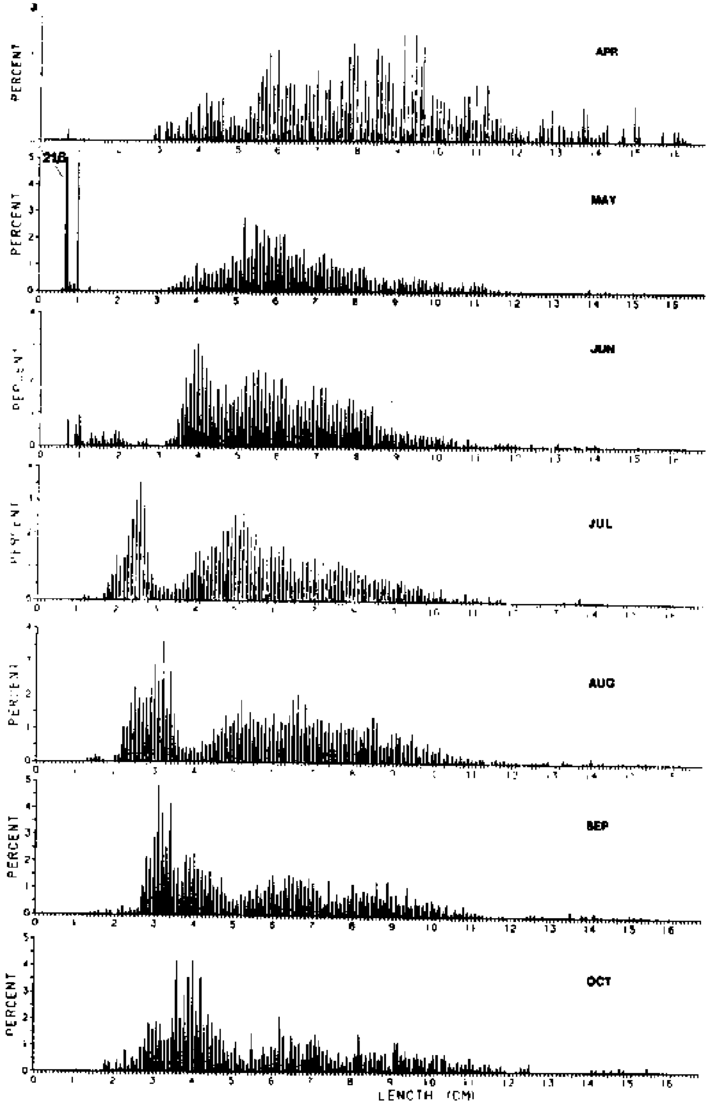


Figure 2. Size composition of the Dungeness crab population in Grays Harbor (strata combined) by month in 1983. Data are combined for two trips per month in April-August, one each in September and October.

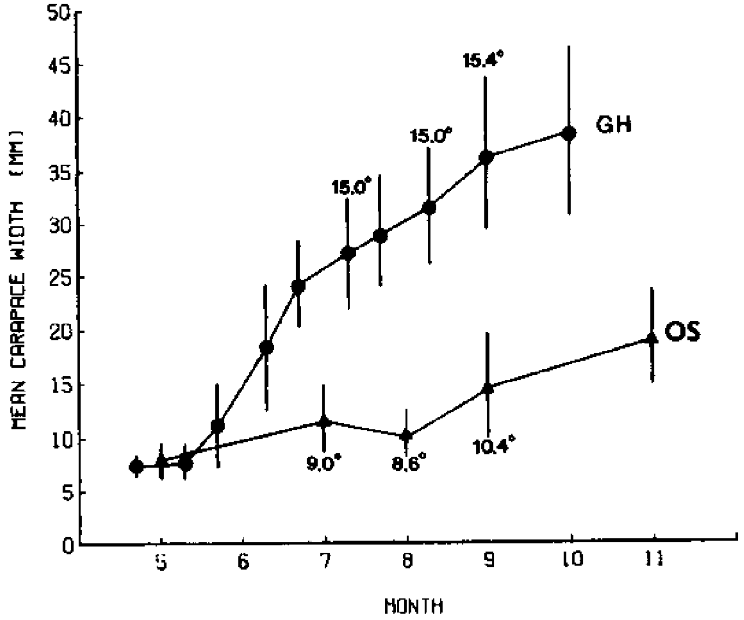


Figure 3. Mean carapace width of 0+ Dungeness crab from settlement in late April through early fall. Size of Grays Harbor population shown as solid circles; offshore populations shown as triangles. Also shown are mean bottom water temperatures during several months in both study areas. Bar = ±1 SE.

Table 1. Approximate size range (mm) of crabs collected in Grays Harbor, based on modal analysis. Data from the 1983 Sea Grant survey were used for age 0+, while information presented in Cleaver (1949), Stevens (1982) and Stevens and Armstrong (1984) and obtained during the 1983 Sea Grant survey was used for 1+ crab.

	0+	1+
January		
February		
March		
April	7	
May	6-10	29-69
June	7-27	33-74
July	6-34	35-84
August	7-39	40-90
September	7-49	50-95
October	11-54	55-100

bimodal in size distribution (for example in June, modes for 1+ crab occurred at about 40 and 55 mm (Fig. 2) suggesting the presence of two or more populations originating possibly as different cohorts of 0+ in the year of metamorphosis, or 0+ that settle in different habitat and subsequently grow at different rates.

Size-frequency data were used to set size ranges for the 0+ and 1+ age classes (Table 1). Population estimates for 2+ and older crab were not made (as of this report) because of our belief that the data are equivocal and require further analyses. For all age classes, there was a broad range of sizes that appeared to develop soon after settlement of an incoming year class. YOY juveniles in June, 1983, ranged in size from 7 to 28 mm or first to fifth or sixth instar, and this size differential continued through time so that 0+ in October ranged from 18 mm to more than 50 mm CW (Fig. 2).

Subtidal populations by area and age class.

Total population. The total subtidal crab population in Grays Harbor increased dramatically over a three week period from 2.5 million in late April to 18.1 million in mid-May, 1983 (Table 2; Fig. 4A). The population remained rather stable between 18.1 to 21.6 million through August and declined to 14.4 million and 11.9 million in September and October, respectively; by January 1984 only 917,000 crab were estimated for the estuary (Table 2). The precision of these data is good since ± 2 SE of the means are 42-69%.

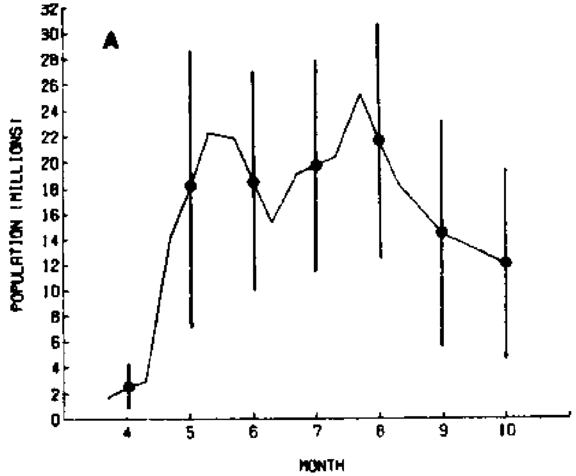
Distribution and numbers of crab within the estuary changed month to month in strata 1 and 2 but remained relatively constant in strata 3 and 4 (Fig. 4B). Populations increased quickly in stratum 1 (largest subtidal are of 3651 ha; Fig. 1) to over 13 million crab during the second trip in May, then declined to 3 million in early July (Fig. 4B). The crab population of stratum 2, however, continued to increase throughout late spring to mid summer when it reached a level of about 12.6 million due to a consistently higher density of crab, although in an area only 69% as large as stratum 1 (Table 2; Fig. 1). The sequential change in estimated populations between strata 1 and 2 might indicate passage of crab from offshore through the mouth of the estuary into stratum 1 and then redistribution elsewhere in the estuary.

Total population estimates in strata 3 and 4 were comparable throughout most of the sampling season and ranged from a few hundred thousand to about 1.5 million crab in each area (Fig. 4B; Table 2). Although stratum 4 is about half the subtidal area of stratum 3, crab density was typically twice as high in the former area.

Population by age class. The contribution of 0+ and 1+ crab to the total estuarine population was significant, and ranged from 67% in May to 92% by September (difference between total crab of Table 2 and 0+ and 1+ population values of Figures 5 and 6). The 0+ crab that entered the estuary in early May reached a subtidal population of 4.8 million in that month and were located primarily in stratum 1 (Fig. 5). This population had declined, however, to 1.2 million in June but recovered to 4.6-7.0 million in July to October, and was located primarily in the North Bay (stratum 2) after June (Fig. 5). The percentage of the total estuarine population comprised of 0+ crab

Table 2. Dungeness crab mean density and estimated population by stratum (see Figure 1) for the total estuary, April through October, 1983. RE is the relative error; the percent of the mean covered by 2 standard errors.

STRATUM AREA (HA)	DENSITY NO/HA (2SE)	POPULATION MILLIONS (2SE)	STRAT PROP	MONTH /YEAR	ESTUARY TOTAL MILLIONS (2SE)
1 3651	470(467)	1.717 (1.706)	.68	4/83	2.537(1.758)
2 2516	95(77)	0.238 (0.194)	.09		RE = 69%
3 1548	231(168)	0.358 (0.261)	.14		
4 830	271(324)	0.225 (0.269)	.09		
1 3651	2267(2642)	8.278 (9.645)	.46	5/83	18.077(11.186)
2 2516	3157(2220)	7.944 (5.586)	.44		RE = 62%
3 1548	643(561)	0.996 (0.868)	.06		
4 830	1034(440)	0.859 (0.365)	.05		
1 3651	1995(1918)	7.284 (7.001)	.38	6/83	18.976(8.428)
2 2516	3669(1839)	9.232 (4.626)	.49		RE = 44%
3 1548	778(419)	1.204 (0.648)	.06		
4 830	1512(518)	1.255 (0.430)	.07		
1 3651	1210(705)	4.416 (2.573)	.22	7/83	19.705(8.425)
2 2516	5014(3137)	12.616 (7.892)	.64		RE = 43%
3 1548	991(779)	1.534 (1.207)	.08		
4 830	1372(953)	1.139 (0.791)	.06		
1 3651	2192(1651)	8.003 (6.029)	.37	8/83	21.605(9.147)
2 2516	4446(2727)	11.186 (6.861)	.52		RE = 42%
3 1548	641(271)	0.992 (0.420)	.05		
4 830	1715(332)	1.423 (0.276)	.07		
1 3651	1546(1529)	5.644 (5.582)	.39	9/83	14.403(9.030)
2 2516	2567(2740)	6.458 (6.895)	.45		RE = 63%
3 1548	472(245)	0.731 (0.379)	.05		
4 830	1891(1980)	1.570 (1.643)	.11		
1 3651	815(404)	2.976 (1.476)	.25	10/83	11.896(7.492)
2 2516	2483(2698)	6.247 (6.789)	.53		RE = 63%
3 1548	1419(1781)	2.196 (2.756)	.18		
4 830	575(623)	0.477 (0.517)	.04		
1 3651	128(111)	0.466 (0.403)	.51	1/84	0.917(0.451)
2 2516	94(78)	0.236 (0.196)	.26		RE = 49%
3 1548	121(19)	0.187 (0.029)	.20		
4 830	33(40)	0.027 (0.033)	.03		



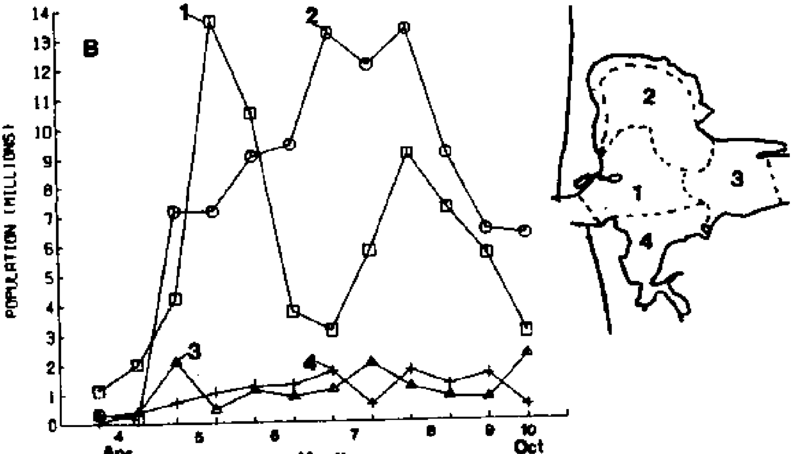


Figure 4A. Population estimates of total crab weighted by strata and combined from April-October, 1983. Shown are means and a vertical bar of ±2 SE for both cruises of each month combined (one cruise each in September and October).

Figure 4B. Same data as in Figure 4A but presented separately for each cruise and stratum (see Figure 1).

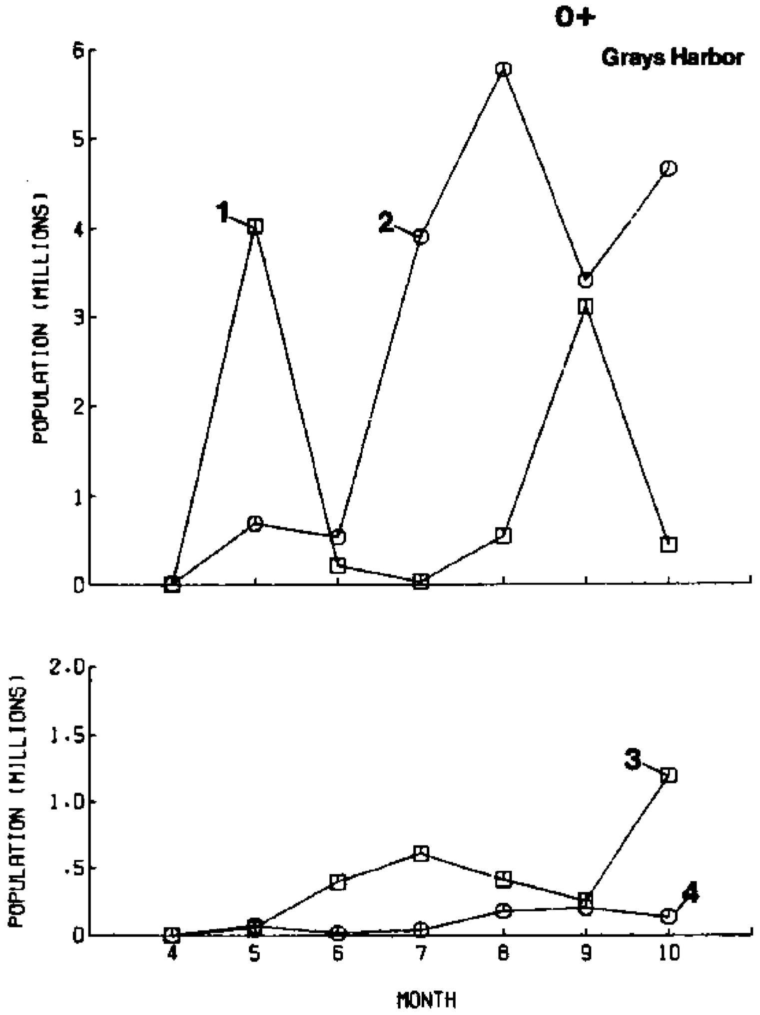


Figure 5. Population estimates for 0+ juvenile Dungeness crab in Grays Harbor from April to October, 1983. Data are shown for strata 1 through 4 (see Figure 1).

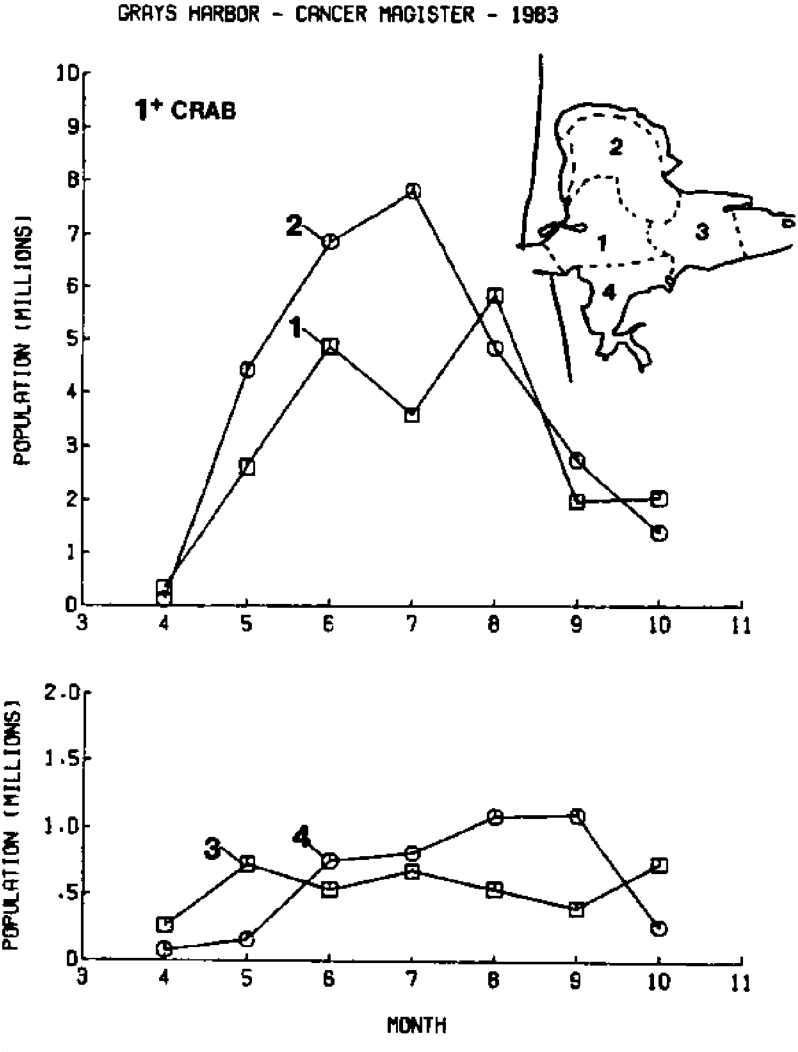


Figure 6. Population estimates for 1+ Dungeness crab in Grays Harbor, April to October, 1983. Data are population means of two trips combined per stratum from April-August, one trip each September and October.

increased from 26% in May to 54% in October, indicating either that some portion of the older 1+ and 2+ crab populations left the estuary, or that 0+ moved in from offshore or down from littoral flats into channels.

Populations of 1+ crab increased substantially between April to May in all strata particularly stratum 2 in North Bay, an area of extensive channels where bottom water temperatures are relatively high in the summer (16-17°C). The estimated number of 1+ crab in stratum 2 by July was 7.8 million but had declined to 1.4 million by October (Fig. 6). Combined across all strata, 1+ crab were the numerically dominant age group in the subtidal portion of the estuary for most of the summer and reached population levels of 12 to 13 million animals between June to August; about 70% and 57%, respectively, of total crab during that period (Table 2; Fig. 6).

Older crab were substantially less abundant than 0+ and 1+ crab in the estuary during the 1983 field season except in April and May when they were about 68% and 33% of the total population, respectively. Again, the uncertainty of size-age demarcations for 2+ crab and older caused us to forgo separate population estimates for age classes older than 1+. However, based on the length-frequency data of Figure 2, it is evident that 2+ crab in April (about 80-100 mm CW; Butler 1961; Stevens and Armstrong 1984) were a large percentage of what was otherwise a fairly low estuarine crab population at that time (Fig. 4). While the percentage of older crab declined by May to 33% of the total population, these animals were still about 6.2 million of the 18.1 million estimated for that month (Table 2; Fig. 4). However, both as a percentage of the total population and absolute number, older crab declined steadily from June to October until they were 1.1 million (9%), in the latter month.

Intertidal populations.

Three intertidal habitat types were surveyed during the summer of 1983: one in dense eelgrass (*Zostera marina*) located in the South Bay, stratum 4; one in shellhash located along the South Channel in stratum 3 (Fig. 1); and finally open mud/sand in both locations.

The only age class found in samples taken from mid May to October was 0+ juveniles. Only on the first trip in May were juveniles found in samples taken on exposed sand and mud; thereafter, no juveniles were captured on or buried in substrate that did not have some type of protective over-cover. Densities of 0+ crab in eelgrass ranged from 7/m^2 in May to 2/m^2 in July (Fig. 7), substantially higher than values of 0.1 to 0.5/m^2 for total crab found subtidally by trawl (Table 2). Shell debris contained the highest densities of 0+ crab found in 1983, with initial mean values of about 90 to 115/m^2 just after settlement in May that then declined quickly to 8-16/m^2 in June and July, and thereafter were about 2-3 crab/m^2 until October (Fig. 8).

Shell debris was composed almost entirely of *Mya arenaria* (soft

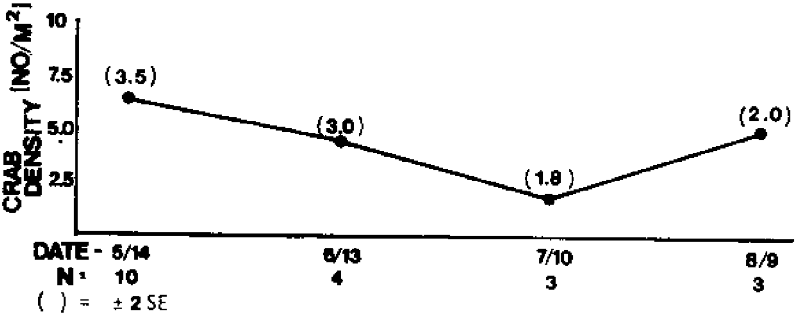
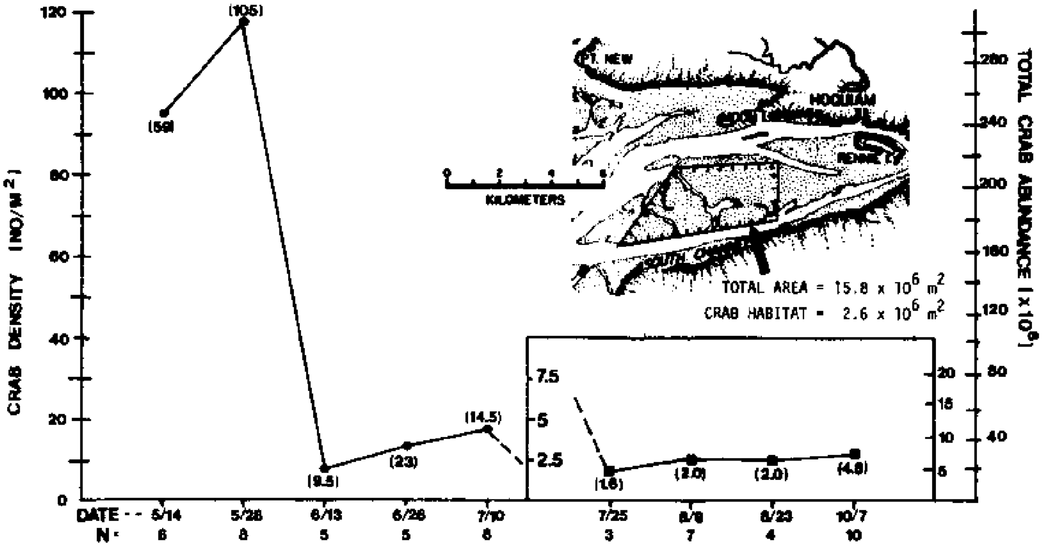


Figure 7. 0+ Dungeness crab densities in thick eelgrass beds in South Bay, Grays Harbor in the summer of 1983 (stratum 4; see Figure 1). A calculation of population abundance was not made because there is no recent measure of the extent of such beds in the estuary.



( ) = ±2 SE

Figure 8. Density of 0+ crab on a portion of intertidal flat in Grays Harbor with about a 16.7% cover of shellhash and sparse to medium density eelgrass. Population estimates were based on mean density per square meter x 2.6 million square meters as indicated (±2 SE).

shelled clam) but also contained *Macoma nasuta* (bent nose clam). Shell was distributed in patches about 0.5 to 2.0 m^2 in area, often in shallow depressions covered by 2-5 cm of water and sometimes mixed with sparse eelgrass. As noted previously, such material was estimated to cover 16.5% of the large intertidal flat between the North and South channels of stratum 3, an area equivalent to about 2.6 million m^2 of optimal juvenile crab cover (Fig. 8). Crab densities per m^2 extrapolated to the full area of shell coverage resulted in population estimates in excess of 300 million in May, 8 to 18 million in June and July, and about 5 to 7 million in August to October (Fig. 8).

Discussion

Grays Harbor estuary as a nursery.

The first definition required in a discussion of estuaries as nurseries is that for "nursery" itself and what constitutes such habitat for, in this case, a species of crab whose adult populations are primarily located in the nearshore coastal zone. Easiest is to say that a "nursery" is where young of a species occur and grow; implicitly, the very young such as YOY Dungeness crab and not so much older, subadult juveniles. To be of use in the context of the life history cycle of *C. magister*, however, the definition must be made more precise, albeit somewhat a posteriori with 1983 data inhand. From this perspective nursery habitat is where:

1. A numerically important portion of the juvenile population resides during periods or stanzas of significant growth.
    a) The extent or scope of such habitat will depend on the scale of comparison; e.g. the estuary may be truer "nursery" habitat than the open coast, but within the estuary juveniles of the species of interest may reside primarily in eelgrass, tidal channels, on mud substrates, etc.
    b) More than one juvenile (subadult) age class may utilize the nursery system; there is no attempt to apply the definition only to the youngest age class of a species. In this sense, juveniles may preferentially use the nursery for more than one year following birth (or metamorphosis) as a reflection of continued advantages in that over other habitats.
2. An advantage is imparted to siblings reared in the "nursery" compared to those within other habitats.
    a) The advantage may be conferred through a combination of biotic and abiotic factors (food, temperature, refuge, fewer predators) that enhance survival and/or growth while in the system.

b) The provision for enhanced growth relates to point No. 1 in that habitat may be "nursery" in one season but not in another if conditions deteriorate - e.g. decreased temperature in winter.

Based on this definition of nursery habitat, juvenile stages of several commercial Crustacea have been shown to depend substantially on estuaries. Blue crab, *Callinectes sapidus*, 0+ juveniles mature in Chesapeake Bay and other estuaries of the Atlantic coast where they are significantly more abundant in eelgrass compared to unvegetated areas (Heck and Thoman 1984; Summerson and Peterson 1984). The recent historic reduction in extent of eelgrass in that estuary as well as deterioration of water quality documented as increased spatial extent and temporal duration of anoxia are viewed as direct threats to survival of juveniles and vitality of the fishery (Officer 1984; Orth and Moore 1983). Juveniles of penaeid shrimp from North Carolina to Texas require warm, low salinity water for rapid growth following metamorphosis offshore and they move into estuaries to maximize these conditions (Costello and Allen 1966; Weinstein 1979). Turner (1977) found a positive correlation between commercial yields of *Penaeus* spp. and the area of estuarine vegetation at several latitudes but not area, depth or volume of estuarine water. Over the last 15-20 years, loss of estuarine habitat considered vital to juvenile penaeid shrimp poses a threat to that fishery along the Gulf Coast states (Christmas and Etzold 1977).

That YOY and older juvenile stages of *C. magister* are present in estuaries has been known for a number of years and stated in qualitative terms by several authors (Butler 1956; Gotshall 1978; Tegelberg and Arthur 1977). The supposition, however, that west coast estuaries are important in the life cycle of *C. magister* is not intuitively attractive to some biologists for two reasons primarily: 1) *C. magister* is not an exceedingly strong osmoregulator (Engelhardt and Dehnel 1973; Caldwell 1977) and thus not considered as likely an estuarine resident as blue crab, penaeid shrimp or west coast crangonid shrimp and; 2) west coast U.S. estuarine habitat is not nearly so extensive as on the east coast. The latter point is particularly important since San Francisco Bay of central California and Grays Harbor and Willapa Bay of southern Washington are the only estuaries of appreciable size along this section of coast. Northern California and Oregon have no large estuaries although small systems are numerous.

The issue of osmoregulatory capability and physiological capacity to tolerate low salinity conditions is probably not critical to the arguments concerning estuarine nurseries since the timing of settlement and use of estuaries are seasonal and miss major periods of very low salinity. From data of the present study and that of Stevens and Armstrong (1984), YOY *C. magister* enter the estuary in early May and apparently leave by fall, thereby avoiding the period of peak rainfall, November to March (Armstrong et al. 1982). Throughout most of the estuary where juvenile abundance is highest, it is uncommon for bottom water salinities to be less than 20^{o}/oo and they are typically greater than 25^{o}/oo, high enough to ensure that blood osmolarity remains stable (Hunter and Rudy 1975). In fact, lower salinity beginning in late fall may be one of several stimuli that cause crab to leave the estuary.

Estuarine versus Offshore Population Abundance

The issue of size of west coast estuaries and whether they could provide adequate habitat for YOY and older juveniles is best considered in light of our findings on relative estuarine/offshore densities, population sizes and growth rates.

Juvenile crab density was consistently higher in Grays Harbor estuary than offshore in 1983. From May through September mean crab densities were usually well in excess of 1000/ha and values from 2,000 to 4,000/ha were not uncommon in most strata of the estuary (Table 2), whereas mean densities offshore were usually less than 100 to 300/ha (only stratum 6 in May had a mean density > 1,000/ha; see Carrasco et al. this symposium). Comparing estimates of total populations, Grays Harbor supported 38%, 44% and 19% more crab than calculated for offshore in the months of July, August and September, respectively. The exception was in May when 283% more crab were calculated for the offshore than in the estuary (69 million versus 18 million); a difference that was, however, quickly attenuated in favor of a higher estuarine population (although in an area 17.6 times smaller than the area offshore). It is important to note that the potential contribution of Willapa Bay south of Grays Harbor to estuarine juvenile crab populations could equal or exceed values estimated for the latter system as noted by Stevens and Armstrong (1984). In accord with these indications that Washington estuaries are important to 0+ and 1+ crab, Tasto (1983) estimated that up to 80% of an incoming year class might reach the San Francisco estuarine complex and reside there up to a year.

In addition to a large subtidal population of juvenile crab that was dominated by 1+ animals in June through August, a substantial intertidal population of 0+ crab was calculated from less rigorous sampling in shellhash and eelgrass, which further underscores the value of an estuary to Dungeness crab. A single region of intertidal flats in the estuary (Fig. 8) was estimated to contain over 300 million 0+ crab just after settlement in May. The population declined to a more sustained number of 5 to 10 million through summer, 1983 a range comparable to subtidal estimates of 0+ crab throughout the entire estuary. The rapid decline in numbers from May to June indicates that mortality and/or emigration is high when initial densities are excessive and it seems likely that a portion of this intertidal, shellhash population continuously moves from there to stocks in the adjacent subtidal areas. Such movement may be provoked by intraspecific agonistic interactions exacerbated within limited cover, or result when crabs physically outgrow such habitat. Although the dynamics of intertidal juvenile *C. magister* populations are poorly understood at this time, the magnitude of abundance appears to be high.

While this Dungeness crab program began primarily as a study of 0+ estuarine population dynamics, evidence from ours and other studies (Stevens and Armstrong 1984; Tasto 1983) points to the importance of estuaries for 1+ juveniles. Between June through August, 1983, 1+ crab were estimated to be 12 to 13 million in the subtidal of Grays Harbor, but declined in abundance offshore from 8 to 2 million during this same period. Although much more extensive an area, the offshore regions supported only 15% as many 1+ as found in the estuary late in the summer. This ratio has caused us to examine more closely the hypothesis that the age class deriving most benefit from the estuary is 1+ rather than 0+ Dungeness crab.

Growth Rate

Several studies of juvenile growth rates indicate the process is accelerated in estuaries or within nearshore coastal embayments where water temperatures are relatively warm. Stevens and Armstrong (1984) studied growth of 0+ and 1+ juveniles in Grays Harbor and found that six months after metamorphosis (May to October) 0+ crab averaged 40 mm in carapace width (CW) and by one year were 50 mm. This indicates that 0+ crab in Washington estuaries may molt 6 to 8 times during the first summer growing season after which the frequency apparently declines with the onset of winter and larger size. A more dramatic indication of seasonal growth is based on change in dry weight over time. First instar crabs at 7 mm CW weigh 0.2 g dry weight while crabs of 50 mm CW weigh 5.7 g, a 280-fold increase. The monthly weight- specific growth rate (k) for 0+ crab in summer of 1980 was 206% dry weight per month which declined to 15.8% through winter.

Even greater growth rates were reported by Tasto (1983) for 0+ crab in San Francisco Bay that reached 90 to 100 mm CW one year after metamorphosis. However, this conclusion can be disputed on the basis that the author inadvertently combined year-classes in his length-frequency analysis and biased collections toward larger crab by using ring nets.

Despite this potential error, information from this and our 1983 crab program shows that populations of 0+ crab that settle directly offshore grow significantly slower than those in the estuary (Fig. 3). YOY in Grays Harbor grew from a first instar size of 7 mm in May to a mean carapace width of 38.3 mm (sixth instar) by October, 1983. Mean bottom water temperatures were 15°-16°C during this time while those offshore were 8.5°-10°C. Perhaps as a consequence of this, 0+ crab offshore had reached a mean width of only 15 mm in September, a mixture of third and fourth instars. This difference in size is a substantial difference in weight that equates to a mean value of 2.57 g dry weight for estuarine YOY (38 mm) and 0.18 g for offshore YOY (15 mm) based on width-weight regressions of Stevens and Armstrong (1984). YOY juveniles offshore of San Francisco Bay in the Gulf of the Farallones also grow substantially slower than estuarine crab (Tasto 1983; Fig. 3.7) although, as previously noted, the upper size range assigned to 0+ may be wrong. In the fall of 1977, the data show a 0+ mode offshore at about 28-30 mm CW while in the estuary a good proportion are up to 60 mm.

Advantages to more rapid growth include decreased time to reproduction and greater avoidance of predators. The second point may be critical to population survival since mortality of young, small instars is apparently very high. For example, Reilly (1983) showed that virtually all predation of juvenile C. magister taken from stomachs of demersal fish captured in San Francisco Bay and in the Gulf of the

Farallones was on crab 7 to 30 mm CW.

Thus, from the perspectives of both absolute population size and relative growth rate, the hypothesis that Grays Harbor provides nursery habitat for a significant portion of the Washington coast Dungeness crab population is still tenable. Quantitative estimates of juvenile density in Grays Harbor and similar levels of production in Willapa Bay would support the supposition of Stevens and Armstrong (1984) that a major portion of the offshore fishery is initially dependent on estuarine habitat. Particularly important in this regards is the role of intertidal shellhash and eelgrass to 0+ juveniles which likely face intense predator pressures both in the estuary and offshore, coming in part as cannibalism. In 1980 (Stevens and Armstrong 1984) and 1983 (present study) 1+ crab were numerically dominant in the subtidal regions of Grays Harbor, and even crab this small have been shown to be significant predators of conspecifics (Stevens et al. 1982). Thus 0+ may only survive subtidally in areas of the estuary where stick, shell, macroalgae and dislodged eelgrass afford epibenthic refuge. Otherwise, intertidal regions of such cover likely play an important role in 0+ survival since larger crab and other predators (e.g. staghorn sculpin, Leptocottus armatus) only forage there at flood tides (Stevens et al. 1984). Juvenile blue crab are always more dense in vegetated areas than in adjacent, unvegetated areas (Heck and Orth 1980; Heck and Thoman 1984) and, in part, this probably accounts for protection from their older and larger conspecifics that exert tremendous predatory pressure on fauna when they forage on more open sandflats (Summerson and Peterson 1984). Analysis of Grays Harbor intertidal data collected in 1984 and forthcoming in 1985-86 should help to clarify the extent of juvenile metamorphosis and survival in intertidal habitat.

While large estuaries may enhance juvenile survival and growth in southern Washington and central California, no large estuaries of comparable size occur for over 400 km of coastline from northern California to the Columbia River. To what extent then are crab populations of that area dependent on juvenile recruitment to estuaries as opposed to directly offshore? The area of numerous small estuaries may constitute appreciable habitat for juvenile crab given densities recorded for Grays Harbor. For example, the subtidal and intertidal areas (ha) of Coos Bay (2502, 2510), Siletz (167, 314), Nestucca (171, 234) and Netarts (121, 889) estuaries total 2960 ha and 3947 ha, respectively (Oreg. Dept. Fish Wildl. 1979); in addition to which there are the Siuslaw, Alsea, Yaquina, Sand Lake, Tillamook, and Nehalem estuaries as well. Together they could potentially provide habitat for a substantial portion of 0+ and 1+ juveniles.

Conclusion

As an expansion to this program stated in 1983, we will study Willapa Bay in 1985-86 as well as continue population surveys of Grays Harbor to establish a four year data base for the latter estuary. Futher, the offshore study (Carrasco et al., this symposium) will be increased in spatial coverage to more accurately estimate populations along the coast. We hope to better map various estuarine and coastal substrates and compare relative crab densities on each. Throughout this program we have collected additional abundance and biomass data on crangonid shrimp and several species of fish. When combined with biological and physical information from other programs we anticipate that a more comprehensive picture of Dungeness crab ecology and population dynamics will emerge in the future.

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Abstract

Population dynamics and distribution of 0+ and 1+ juvenile Dungeness crab were studied in Grays Harbor, Washington from April to October 1983 in order to compare the relative importance of that system to areas offshore. A stratified, random survey design and improved net were the bases of biweekly sampling in the estuary. Total population estimates were 2.5 million in April but increased to 18.1 million in May with the arrival of 0+ (as megalopae larvae) and 1+ juvenile age classes primarily. The estuarine population increased to 21.6 million in August but declined to 11.9 million by October; in January, 1984, less than 1 million crab were estimated to be in the estuary.

While 1+ crab were numerically dominant in subtidal regions of the estuary, 0+ crab were also abundant there but more so on intertidal flats covered by shellhash and eelgrass. Survival of 0+ crab immediately following settlement and metamorphosis seems to be dependent on refuge habitat in the form of shell, allochthonous stick, litter, dislodged eelgrass and macroalgae.

Compared to the offshore region, Grays Harbor supported consistently higher densities of juvenile crab as well as greater populations (up to 44% more) than found offshore in most of 1983 (although the estuarine area used to estimate population abundance is 17.6 x less than the offshore area). Growth of 0+ crab was significantly greater in the estuary where they were about 2.5 x wider (carapace width) and 14.3 x heavier (dry weight) by September than siblings that settled offshore. These data indicate that a major estuary like Grays Harbor can serve as important nursery habitat for 0+ and 1+ Dungeness crab.

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Abundance and growth of *Cancer magister* young-of-the-year in the nearshore environment

Kenneth R. Carrasco, David A. Armstrong,
Donald R. Gunderson and Christopher Rogers
University of Washington
Seattle, Washington

Dungeness crab megalops larvae are known to enter both estuaries and nearshore areas, either passively or actively, where they metamorphose to the first juvenile instar stage (Butler 1956, Lough 1976, Reilly 1983, Stevens and Armstrong 1984). It is not known, however, if the eventual recruitment of young-of-the-year (YOY=0+) to the adult stocks relies exclusively on either the estuaries or on the nearshore areas, or perhaps if features of both areas are exploited to favor appropriate steps in the species' ontogeny. Likewise, it is not known if the megalopae somehow target towards the mouth of an estuary, or rather if they are uniformly spread along the coast and only a fortuitous few are swept into the mouth. Although megalopae were sometimes seen more than 50 km off the coast, Reilly (1983) reported the highest densities offshore from Eureka to San Francisco in the Gulf of Farallons within 10-15 km of Pt. Reyes, and also inside San Francisco Bay itself. Evidence from Stevens and Armstrong (1984) and this present Sea Grant study indicates that an incoming year class will enter nearshore areas and estuaries as megalopae near the surface or, perhaps, deeper in the water column, and then settle on various substrates to metamorphose. However they arrive, Dungeness megalopae and first instars are found both inside estuaries as well as in the nearshore coastal zone which necessitates sampling each area with identical gear to gain a realistic assessment of the respective contribution of each system to the ultimate recruitment of YOY into the adult population.

As a part of the same two-year Sea Grant project described by Gunderson et al. and Armstrong and Gunderson (both papers, this Symposium), this paper describes results of nearshore crab sampling done concurrently with the estuarine project. The principle components of the nearshore program were to: 1) survey Dungeness crab population densities in the nearshore area, particularly as a function of depth; 2) determine size at age; 3) determine if a year class settles as a single cohort or several through the season; 4) extrapolate crab density to an estimate of population abundance for direct comparison with the estuary; 5) determine the relative growth and mortality rates of YOY, again as compared with the estuary and; 6) characterize benthic habitats to qualitatively correlate with settlement and/or survival patterns.

As the 1984 field season ended just weeks before this Symposium, the entire two year data set was not yet available for consideration. As a result, only the 1983 data is presented in this paper (the senior author will analyze both the 1983 and 1984 nearshore data as part of his Master's thesis).

A note on terminology: the terms "nearshore" and "offshore" are at times used interchangably in the literature. For the purposes of this report, which deals exclusively with the more shallow areas of the continental shelf, the term "nearshore" will be used essentially as a noun and "offshore" will be used to indicate a relative direction from a specified point.

MATERIALS AND METHODS

This section will amplify relevent points beyond those addressed by Gunderson et al (this Symposium) in their description of the equipment and sampling methods utilized in both the nearshore and estuarine segments of this project.

The area offshore of Westport, Washington, is characterized by a fairly uniform continental shelf with a shelf break at 200 meters depth about 50 or 60 km offshore. The typical spring/summer northwest winds of the Pacific Northwest of the United States are associated with upwelling events and are the norm after the spring transition, while in winter winds are variable, generally southerly, and not associated with upwelling (Huyer and Smith 1983).

Since the very limited data on offshore distribution of Dungeness YOY on the continental shelf indicates a preponderance in the relatively shallow areas (Wickham et al. 1976; and Gotshall 1978), three transect lines were established nearshore in the vicinity of Grays Harbor (Figure 1). One line was located just south of the mouth of Grays Harbor, another 28 km to the north off Copalis Head, and the third transect was located off Cape Shoalwater at the mouth of Willapa Bay, 17 km to the south of the Grays Harbor transect. In 1983, eight stations were located on each transect line at depths of 6, 9, 18, 27, 37, 46, 55, and 64 meters (or, respectively, at 3, 5, 10, 15, 20, 25, 30, and 35 fathoms). Unfortunately, even moderately poor weather often precluded sampling at the 6 meter station near the surf zone.

Three strata were defined that grouped the two shallowest stations (6 and 9 m in Stratum Number 5; Strata 1 to 4 were areas in Grays Harbor estuary) on all three transect lines, the three intermediate stations (18, 27, and 37 m in Stratum Number 6), and the three deepest (46, 55 and 64 m in Stratum Number 7). The east-west boundaries of the strata

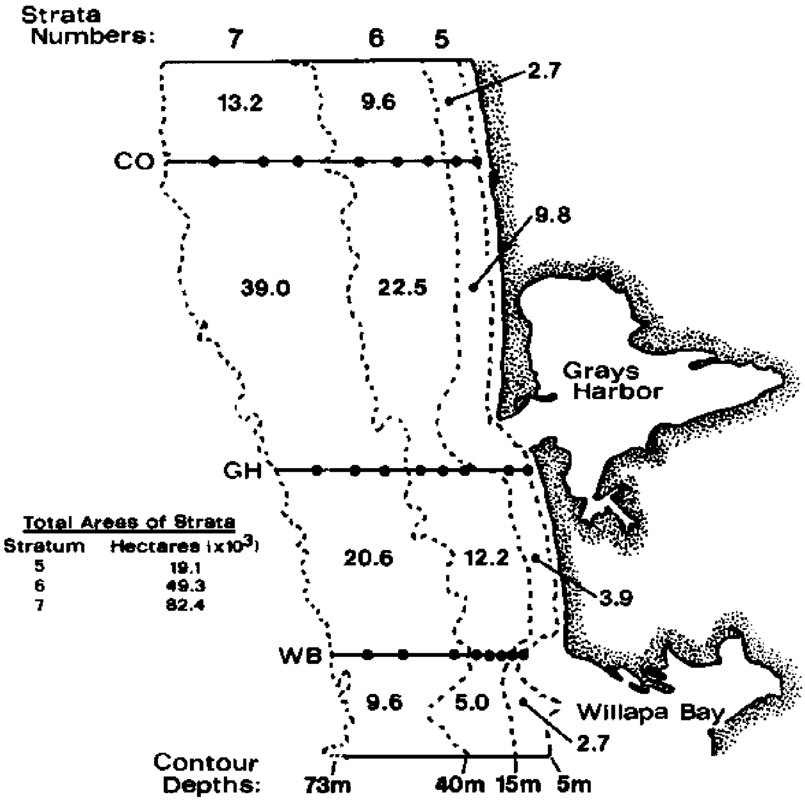

Figure 1. Nearshore survey area and station array (dark circles) used to estimate populations of juvenile Dungeness crab. Shown are three strata (5,6,7) that include stations in common depth intervals from 5 m to 73 m (3 fm to 40 fm).

were the depth isobaths midway between the most adjacent stations of any two strata, while the north-south boundaries are assumed in this report to be lines nine km north or south of the outermost transect lines. Digitizing these strata on the Burroughs computer at the NMFS Northwest and Alaska Fisheries Center in Seattle yielded areas of all three strata in hectares. The total area of all three strata is approximately 150,000 hectares (151 km^2), which is an area about 18 times greater than the subtidal area of Grays Harbor estuary. Stratum 5 constituted 13% of the total nearshore area while Strata 6 and 7 comprised 33% and 55%, respectively.

Sampling trips in 1983 were made during daylight hours on May 28 and 29 (with a third day on June 10, postponed because of weather), July 17 through 20, August 14 though 16, and September 12 through 16. A 55 ft salmon-charter boat (*Spirit* of Westport, Captain Don Samuelson, skipper) was equipped with the appropriate hydraulics and a boom arrangement to deploy and retrieve the plumb staff beam trawl described by Gunderson *et al*. (this Symposium).

Determination of distance towed was calculated from LORAN C readings obtained on board ship. The program LORAN AND DISTANCE was used on the NMFS Burroughs computer to generate latitude/longitude coordinates and calculate distance over ground. Using the area-swept technique (net width = 2.29 m), density of crab in numbers per hectare was calculated.

Commencing with the second trip in July, 1983, a Niskin bottle was lowered to the bottom by hand on alternate stations to collect water samples, and a bucket was used to collect surface water at the same location. A pocket thermometer was used to measure the temperature of the water samples and a refractometer was used to determine salinities.

Crabs were sexed and measured to the nearest millimeter on board the boat unless very large numbers of YOY were caught in which case samples were processed later in port. Data analyses were accomplished on the Burroughs 7800 computer at the Alaska and Northwest Fisheries Center in Seattle and on the CDC 170-750 Cyber computer at the University of Washington.

RESULTS AND DISCUSSION

Crab Densities

Densities of crab per hectare for each station trawled in 1983 are displayed in Figure 2 with stratum boundaries indicated by dotted lines between depth intervals. It should be kept in mind that the lack of any symbol indicates an absence or a negligible amount of crab, while a null sign indicates that no tow was made at a station (usually due to bad weather). Densities for each strata were determined by combining the appropriate stations on all three transect lines within each stratum. The mean number of crabs per hectare by stratum, two standard errors, and number of tows are displayed in Table 1. Briefly, the highest densities of Dungeness crab were found in May and decreased through the sampling season. Viewing the season as a whole, the densities were generally highest at the more shallow

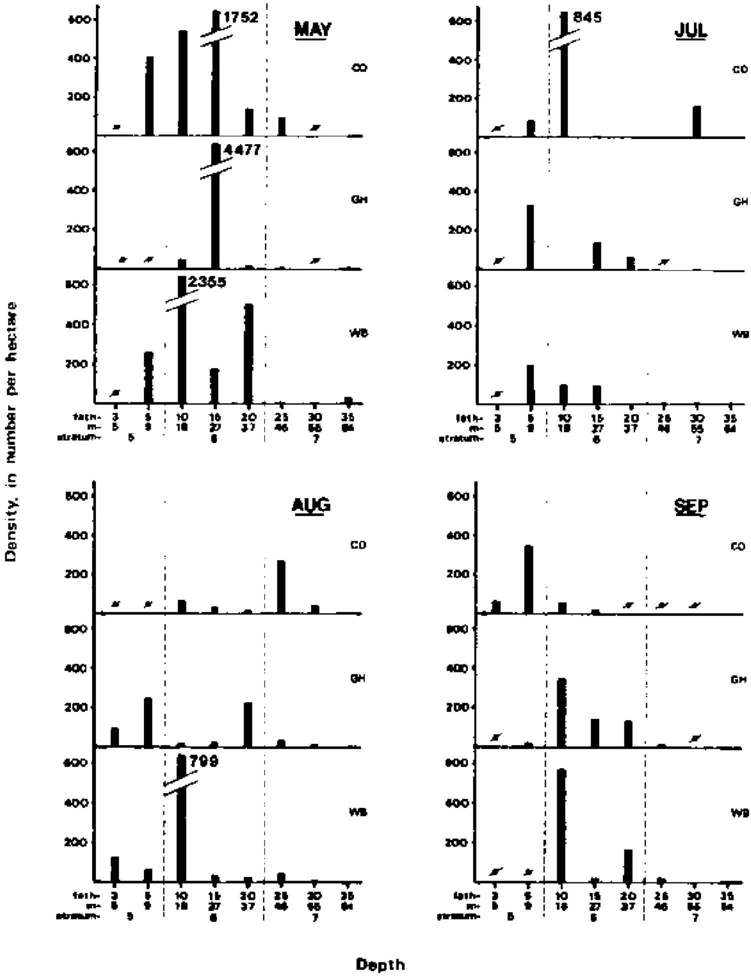

Figure 2. Absolute densities of crab per hectare for each station trawled in 1983. Each quadrat presents findings from one trip with densities at the Copalis Head (CH), Grays Harbor (GH), and Willapa Bay (WB) transects. "▰" indicates no sample was taken. Blanks indicate a sample was taken but no crabs were caught.

Table 1. Mean density of Dungeness crab by stratum, by trip, in nearshore study area in 1983, as crabs per hectare ("Mean No/HA"); two standard errors ("2SE"); and number of tows ("N").

	Stratum Number			
	5 (5-15 m)	6 (16-40 m)	7 (16-40 m)	All Strata Combined
May				
Mean No/HA	328	1114	20	601
2SE	158	1003	24	548
N	2	9	7	18
July				
Mean No/HA	203	124	25	98
2SE	145	163	42	84
N	3	10	8	21
August				
Mean No/HA	135	115	62	91
2SE	80	142	57	67
N	4	11	11	25
September				
Mean No/HA	206	152	7	131
2SE	215	48	8	42
N	5	39	6	49

Table 2. 1983 width ranges by age, by trip, using data from Figure 4; the resulting proportion of each age class relative to the whole population; and the estimated population abundance in millions for each age class in all three nearshore strata combined.

Month Age Group	Range, mm	Proportion Relative to Whole Population	Estimated Pop. Abundance, millions
May			
0+	6-16	0.84	58.0
1+	22-65	0.12	8.3
"Others"	>65	0.04	2.8
July			
0+	6-16	0.61	7.5
1+	35-66	0.23	2.8
"Others"	>66	0.15	2.1
August			
0+	6-16	0.61	7.3
1+	33-68	0.15	1.8
"Others"	>68	0.24	2.9
September			
0+	6-27	0.14	1.6
1+	33-73	0.18	2.1
"Others"	>73	0.68	7.9

stations, particularly the 18 to 37 m stations of Stratum 6, and decreased as depth increased along each transect (Table 1). At the 64-meter (35 fm) station the densities were consistently small.

Population Estimates

For the purposes of comparing the nearshore area with results from the concurrent Grays Harbor estuarine program (Armstrong and Gunderson, this Symposium) and, additionally, for comparison between years and between areas within a year, an estimate of population was derived by multiplying mean station densities by the digitized area of individual strata, and then summing the results for the entire nearshore area. Total population estimates, all strata combined, are displayed in Figure 3. From 69.0 million crab in May, the estimate dropped to 12.3, 12.0, and finally 11.6 million in July, August, and September, respectively. Overall mortality for all crab during the 1983 sampling season was estimated at 83%. In terms of depth intervals, Stratum 6 (intermediate depths) had the highest population abundance through most of the season despite a substantial decrease between late May and mid July (Figs. 3, 6, 7, 8). Significantly, however, Stratum 5 (nearest shore) had consistently high crab densities and a large total population through the summer although it constitutes only 13% of the entire nearshore area used for population estimates. Stratum 7, the deepest, supported the fewest crab, particularly in September (Figs. 6, 7, 8), despite being the largest in area.

Size and Growth

Width frequencies as one-millimeter increments are displayed in Figure 4 as the percentage of the total estimated population of all strata. YOY (0+) and 1+ juvenile crab width ranges were relatively distinct through time, but significant overlap in sizes of older crab caused us to combine them into an "Other" category (although in September 2+ crab are probably the group from about 85 mm to 120 mm). Through the summer, growth of the 0+ and the 1+ nearshore crab was slower than the estuarine crab of the same age (Armstrong and Gunderson, this Symposium). The 0+ nearshore crab grew only slightly from the 7 to 10 mm range (first and second instars) in May to the 10 to 20 mm range (third and fourth instar) in September. Similarly, the 1+ nearshore crab had a mode of about 35 to 37 mm in May and increased to about 55 mm in September. The width ranges of each age and the resulting proportions of each age category relative to the whole population are summarized in Table 2.

Age Class and Strata Populations

The width ranges were applied to the previously derived areal population estimates to find the population size of each age category and to detect trends through the season (Figure 5). Of the three age groups, abundance of YOY (0+) crab decreased most over time. From a high of 58.0 million animals estimated for May (84% of the entire population), the population declined markedly through the season to

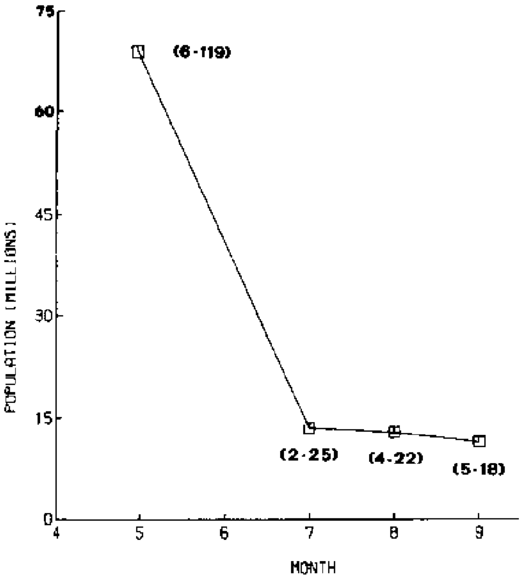

Figure 3. Population estimates through the 1983 sampling season for the nearshore area depicted in Figure 1, all ages combined. 95% confidence intervals are shown in parentheses.

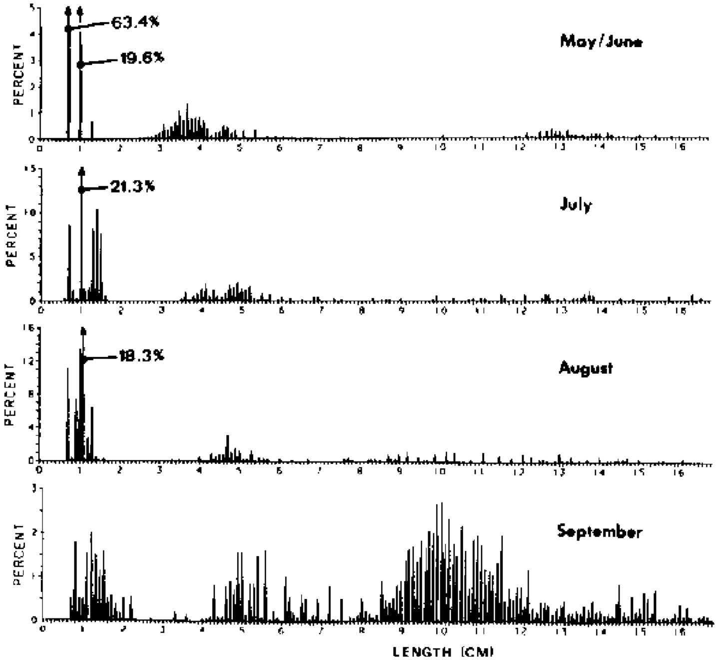

Figure 4. Size composition of the Dungeness population in the nearshore survey area, all depth strata combined, by trip in 1983. Note slow growth of 0+ crab from May to September, and the increase in percentage of 1+ and 2+ crab in September due to decrease in the percentage of 0+ crab.

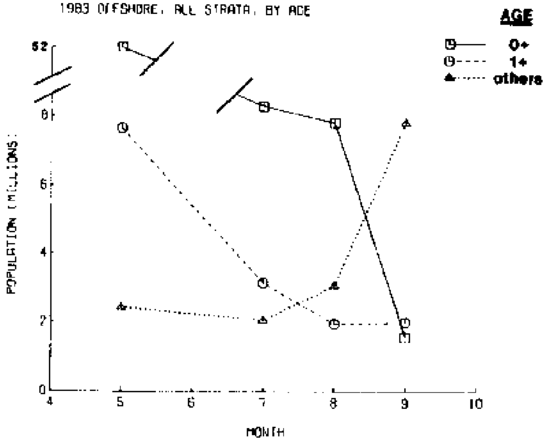

Figure 5. Population estimates of each age category through the 1983 sampling season, all three strata combined.

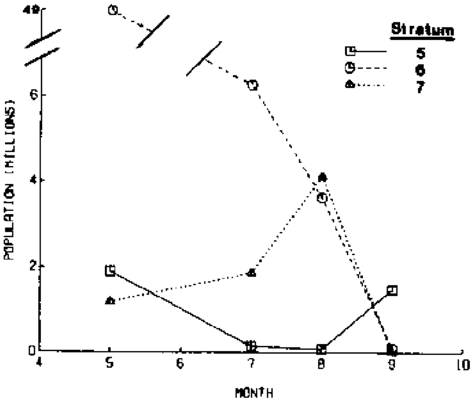

Figure 6. Population estimates of 0+ (YOY) crab in 1983, by stratum.

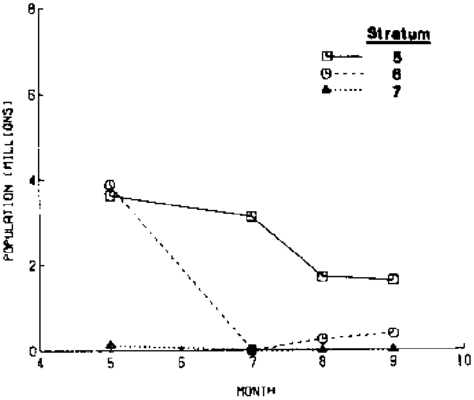

Figure 7. Population estimates of 1+ crab in 1983, by stratum.

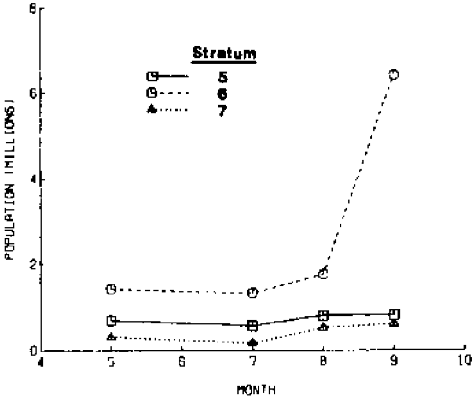

Figure 8. Population estimates of 2+ and older crab, described in the text as "others", by stratum.

about 1.6 million (14% of the population) in September. There is a similar, but less dramatic, decrease in 1+ crab through the summer. Indeed, the 1+ population essentially leveled out in August and September at about two million crabs, slightly higher than the final population of 0+ crab. The older crab, the "Others" category, increased from about 2 million in July to 8 million in September, due possibly to immigration of larger crab from the estuary in the fall when the bottom water temperature starts to decrease there (Stevens and Armstrong 1984; Armstrong and Gunderson, this Symposium). Population abundances of different age classes in the three strata are shown in Figures 6 through 8. The population trend of 0+ crab (Fig. 6) through the season underscores the initial importance of Stratum 6 where there was a very dramatic decline from about 49.2 million 0+ crab in May to a population nearly equal to that in Stratum 7 by August although both declined to virtually zero by September. In Stratum 5, however, 0+ crab were actually most abundant in September. This late summer increase of 0+ crab in Stratum 5 might also be due to some immigration from the adjacent Grays Harbor estuary, or from Stratum 6.

Compared to 0+ individuals, 1+ crab were generally less common (Figure 5). This age group was most densely distributed in Stratum 5 but was relatively rare in both the offshore and the intermediate strata. By July of the 1983 sampling season, Stratum 5 contained the highest population of 1+ Dungeness crab despite the small area of this nearshore zone.

The "Others" category (Figure 8), representing the 2+ and older crab, presented an enigma in population trends. These older crab maintained a constant population level through the sampling season until September when they increased to 7.9 million from 2.9 million in August. This increase was exclusively limited to the intermediate depths of Stratum 6, and may again represent possible movement of 2+ and older crab out of the Grays Harbor estuary beyond the well-mixed shallow stratum.

Benthic Habitat

The habitat (bottom type) sampled by the trawl generally tended to be consistent at individual sampling stations. There did appear to be some variation in epibenthic vegetation perhaps related to temporal changes in the quantity and quality of organic debris flushed from the bordering estuaries. The only real similarity between all of the transects was the presence of sand dollars (*Dendraster excentricus*) at the more shallow stations. The Grays Harbor and Willapa Bay transects consistently had many of these animals in the 6- and 9-meter (3- and 5-fathom) stations, never deeper, but they were commonly encountered through the 18-meter (10-fathom) station on the Copalis Head transect.

The Copalis Head transect often had cobble or gravel at the intermediate depths (which caused difficulty in retrieving the gear) while the two deeper stations at 55 and 64 m (30 and 35 fm) had a rock substrate that often tore the nets. Gear damage and the low abundance of crab at the deep stations on all three transects prompted us to drop those at 64 m (35 fm) in 1984. While virtually no terrestrial or marine vegetation matter was found on the Copalis transect, *Zostera* spp., *Ulva*, *Enteromorpha*, and terrestrial matter (deciduous leaves, sticks, pine cones) were found at the intermediate depths of the Grays Harbor transect. Even more of this terrestrial and marine vegetation was found on the Willapa Bay transect. Such epibenthic debris, which did not originate in the locale of the sampling station, was found on that transect from 18- through 46-meters (10 through 25 fm) peaking at 37-meters (20 fm). A substantial portion of the 1983 YOY were associated with such estuarine material suggesting an association between newly settled juveniles and "refuge" habitat.

Larval Recruitment and the El Nino

The 1983 Dungeness crab year class may have been exposed to warm surface water anomalies resulting from the well-publicized El Nino of 1982-83. As the zoeae were in the water column at the peak of the phenomenon in February and March of 1983 (Fluharty 1983), the survival, growth and food supplies of the larvae were possibly affected. The highest surface temperatures observed during our two-year project occurred in July of 1983, the first trip that temperature observations were made, of up to 17.8°C. These temperatures were significantly higher than temperatures observed in the following, more typical year of 1984 at analogous stations and dates.

In his study of the effects of temperature and salinity on the growth of Dungeness crab larvae collected off Oregon, Reed (1969) found that of five temperatures tested at various salinities, zoeae showed best survival (88%) and development at 10° to 13.9°C and 25 to 30 ppt, factors typical of those nearshore waters. Survival of zoeae was less at 17.8° (60-70%) but any further extremes of temperature resulted in much higher mortality. A decrease in salinity exacerbated the mortality, especially at temperature extremes. Similarly, Wild (1983) found that temperature effected Dungeness crab eggs as well as zoeae. As experimental temperatures increased from 10 to 17°C in normal salinities, both the egg mass volume and hatching success progressively decreased.

Indirect effects by the anomolous warm temperatures are more speculative, but there are indications that productivity in the spring of 1983, and hence food supply for the zoeae, was probably reduced because of the El Nino (Fluharty 1984). Among other influences on Dungeness larval mortality, Lough (1976) discussed the importance of food adequate both in abundance and in size for efficient ingestion. Especially crucial during the first few weeks of zoeal life, temperature anomalies could alter the optimum timing of these factors with deleterious effects on Dungeness larval survival.

The trends in year class and population abundance discussed in this paper should be viewed cautiously for several reasons. First is the inherent problem of attempting to derive reasonable conclusions from the data of a single year in a field of study of a species so subject to interannual variability. Our imminent consideration of the entire two-year data set and the continued funding of the offshore component of this project, will provide an opportunity to evaluate this variability and establish a norm. A second, unexpected reason to be cautious, which was at once a complication and an opportunity, was the El Nino of 1983. A complication insofar as our observations during that year possibly do not reflect the norm of abundance and distribution, and yet an opportunity as we fortuitously began a rigorous sampling program in a year of extremely anomalous oceanographic conditions. Again, this data will be particularly valuable once a more complete data base is collected and 1983 can be viewed in retrospect.

ACKNOWLEDGEMENT

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Abstract

The megalopae of a Dungeness crab year class are known to metamorphose and settle in both estuaries and the nearshore environment along the coast. However, the relative contribution of each habitat to the ultimate recruitment into the adult population is unknown. The newly metamorphosed crab in the nearshore area may be in an inferior environment with less refuge from predators, lower temperatures, and less available food but these factors may be compensated for by the much larger area available for settlement than could be provided by an estuary.

A two year Sea Grant project, begun in the spring of 1983, studied the population dynamics of Dungeness within the Grays Harbor estuary and along the nearshore coastal zone outside the mouth. Objectives of the nearshore component of the project were to: 1) assess Dungness crab population densities; 2) determine size at age; 3) characterize settlement; 4) estimate population abundance in the study area; 5) determine relative growth and mortality rates; and 6) characterize benthic habitats. Possible implications of the 1982-83 El Nino are briefly discussed.

The 1983 data are treated exclusively as the 1984 sampling season ended shortly before the commencement of this Symposium. Only one period of settlement of young-of-the-year (YOY=0+) was detected; these first and second instars of 7-10 mm carapace width grew to only 10-20 mm (3rd and 4th instar) by September. The highest densities of these YOY crab were found in the nearshore areas. After an initial large first and second instar population, the YOY abundance dropped dramatically through time until the only sizable population was found in the nearshore stratum of 5 to 15 meters depth. Overall mortality of all age classes through the sampling season was 82%.

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Age and growth of male Dungeness crabs, *Cancer magister,* in northern California

Ronald W. Warner
California Department of Fish and Game
Eureka, California

Age and growth studies on Dungeness crabs (Cancer magister) have been conducted in British Columbia (MacKay and Weymouth 1935); Washington (Cleaver 1949); British Columbia's Queen Charlotte Islands (Butler 1961); Bodega Bay, California (Poole 1967); and San Francisco, California (Collier 1983). Length frequency analysis, tagged crab returns, and observations of molting crabs were used in these earlier studies for growth determination. My study documents the age and growth of male Dungeness crabs in northern California with emphasis on the 1972 year class by applying these methods to an isolated year class, in time series, over several years.

Dungeness crabs were captured in ocean waters by trawl and trap on annual surveys conducted during fall months from 1972 to 1977. Periodic trawling for juvenile crabs took place in Humboldt Bay in 1972 and 1973. Crabs in bays and offshore waters were tagged with Floy anchor tags and a $2.00 reward was paid for recovered tagged crabs.

There were 103 recoveries from a total of 7,930 tagged individuals. Size at age was determined for 33 crabs. Average size of 1972-yc crabs at 3 and 4 years was 151.7 and 167.7 mm, respectively. Crabs of the 1973 yc averaged 160.5 and 181.2 mm for the same ages. One 197-mm crab was recovered at 5 years of age.

A total of 35,264 crabs was caught during the 6-year survey period. Age (size) group parameters were calculated by using the separation procedure of Macdonald and Pitcher (1980). Means for 1-, 2-, 3-, and 4-year-old 1972-yc trawl-caught crabs were 24.7, 93.8, 140.8, and 172.7 mm, respectively. Trapped crabs of the 1972 yc averaged 133.5, 151.8, 176.1, and 188.6 mm for ages 2, 3, 4, and 5, respectively. The means for 3- and 4-year-old trapped crabs were more meaningful than those for trawled crabs because of much larger trap sample sizes.

Instar sizes were computed from regression formulas by Collier (1983). A starting point of 150.7 mm for the 14th instar was used. Calculated instar sizes were plotted in conjunction with means of crabs of known age to produce a growth curve.

After comparison of instar widths for Pacific coast crabs, differences in growth rates were demonstrated which ultimately determine the percentage of legal sized crabs entering the fishery in the 14th instar. At age 3, 28% of the 1972 yc recruited to the fishery, while approximately 60% of the faster growing 1973 yc recruited in the 14th instar at 3 years of age.

Age and growth of Dungeness crabs in northern California is similar to that reported by Cleaver (1948) in Washington. Growth in British Columbia (Butler 1961) is slightly slower, with negligible recruitment at 3 years, but the majority recruited at 4 years. Botsford (1983), in a cursory examination of a portion of unpublished data used for this report, concluded that northern California crabs are slow growing, with a large portion of the crabs recruiting at 5 and 6 years of age. His conclusions are inconsistent with results presented here and by Cleaver (1949), Butler (1961), and Poole (1967).

This study has shown that male Dungeness crabs in northern California are, with minor exception, recruited at age 4. The percentage of crabs which enter the fishery at 3 years varies.

ABSTRACT

The age and growth of male Dungeness crabs, Cancer magister, was determined from studies conducted during the period 1972 to 1977. Annual ocean surveys, with concurrent trapping and trawling at selected stations, yielded length frequency data, in time series, for specific year classes. Recoveries of crabs tagged at known ages elucidated upon size at age. Observations of molting crabs and single molt tag returns provided molt increment information used to calculate instar sizes. Interpretation of length frequency data for an unusually abundant 1972 year class was facilitated by the precedence of very weak year classes which helped mitigate cohort overlap. Age(size) group parameters from length-frequency data were generated by a computer programmed separation procedure. Sizes of the 1972 year class for ages 1 to 5 years were 24.7, 93.8, 150.7, 176.1, and 188.6 mm, respectively. Corresponding calculated widths were 26.6, 100.2, 150.7, 177.9, and 206.5 mm for ages 1 to 5. Tagged 1972 yc crabs were 108.0, 151.7, and 167.7 mm for ages 2 to 4. The percentage of northern California Dungeness crabs which attain the legal size of 159 mm at 3 years is variable; however, with minor exception, they are fully recruited at 4 years of age.

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Molt increments, annual molting probabilities, fecundity and survival rates of adult female Dungeness crabs in northern California

David G. Hankin, Nancy Diamond, Michael Mohr and James Ianelli
Humboldt State University
Arcata, California

Introduction

Although the Ricker stock-recruitment, Leslie matrix and other models of population dynamics are often formulated exclusively in terms of females, studies of the Dungeness crab (Cancer magister) have concentrated almost exclusively on male crabs. Failure to devote research attention to female crabs is undoubtably explained by the facts that commercial female harvest is prohibited in most West Coast fisheries (only British Columbia allows commercial harvest of females that exceed legal size for males), and that females are smaller and have less commercial value or potential value than do males. However, as the models suggest, females are normally regarded as the more important sex from a population dynamics perspective and, in the usual fishery context, should receive more research attention than males rather than less. This is particularly true for a polygamous species such as the Dungeness crab, where very few adult males may ensure insemination of virtually all adult females (PMFC 1978; Poole and Gotshall 1965).

McKelvey et al. (1980), assuming an underlying endogenous explanation, showed that fluctuations in landings of male Dungeness crabs in the northern California fishery could be most plausibly explained by density-dependent egg/larval survival mediated through fluctuations in total egg production of the unexploited female stock (see Hankin, this Symposium, for a critique of this and other hypotheses). Because their conclusions rested on extremely tentative data concerning age and growth, fecundity and survival rates of adult female Dungeness crabs, they recommended that study of the demographic statistics of female Dungeness crabs receive immediate and priority attention.

This paper presents the principal results of a three year California Sea Grant-sponsored project specifically designed to allow determination of the vital demographic statistics of adult female Dungeness crabs in northern California. Research consisted primarily of a tag-recovery project in which more than 12,000 adult female crabs were tagged and released, laboratory generation of molt increments from 185 females removed from pre-mating embraces, and estimation of total fecundity of 122 adult female crabs. From results of these studies, we have been able to paint a remarkable picture of the life history of adult female Dungeness crabs. In particular, we found strong size-dependence of molt increments, molting probabilities, fecundity and survival rates; such dependence was often unexpected. Among females exceeding 155 mm carapace width, fecundities were often low (200-400,000 eggs), annual molting probabilities were effectively zero, and annual survival rates were about 10%; these figures were far less than those for smaller younger adult female crabs (125-135 mm carapace width). Based on these findings, and other bits of evidence, we present an argument for senescence among adult female Dungeness crabs.

The intention of this paper is to present a concise descriptive review of the more significant of our findings. As a consequence, details of certain methodologies are only briefly sketched or occasionally omitted so as to present an overall perspective of the life history of adult female Dungeness crabs within the confines of a single brief paper. Where appropriate, reference is made to existing and/or contemplated documents in which relevant details may be found. We hope that this obvious sacrifice of completeness of detail is more than compensated for by the reader's ability to quickly and easily grasp our principal findings.

Materials and Methods

The northern California commercial fishery for male Dungeness crabs opens 1 December and runs through 30 July (unless extended through August by California Fish and Game). Thus, a single commercial season spans two calander years. Project activities were necessarily closely linked with the commercial fishing season, in part because all field research took place on board a contracted commercial crab fishing vessel out of Trindad, California, and because most tag recoveries were received from cooperating commercial fishermen, but also because of Dungeness crab life history. In particular, ovigerous female Dungeness crabs are most frequently captured in traps during the months of December and January. To simplify presentation of methods and results, where it would otherwise be awkward to mention two calander years, project "years" have been defined as twelve month periods beginning 1 December of 1980, 1981 and 1982. Thus, for example, the first project year spanned the period 1 December 1980 through 30 November 1981. An additional convention involves the use of the term "large" in reference to the size of female crabs; "large" will consistently refer to female crabs of carapace width ≥ 155 mm.

More than 12,000 adult female crabs ranging in carapace width from about 85 to 172 mm were tagged and released between the mouth of the Mad River (40° 55' N) and Freshwater Lagoon (41° 15' N) during the months of January through March of 1981-1983 at depths of 10-24 fathoms (18-44 m). (See Diamond and Hankin, this Sympsoium, for site maps and detailed descriptions of release locations). Crabs were measured to 0.1 mm across the widest part of the carapace (excluding the tenth anterolateral spines), and were tagged at the posterior epimeral suture with numbered FLOY anchor tags (Model FD-68B).

During 1983 tagging activities a qualitative assessment of molting history of each tagged crab was made based on visual examination of carapace condition (degree of fouling, blackening around joints, etc.). Crabs were classified as (a) molted during most recent molting season, (b) uncertain molt history, or (c) failed to molt during most recent (and possibly previous) molting season(s). Recoveries were received primarily from commercial fishermen, although small numbers were recovered during tagging activities. Recovery data provided by fishermen included date, depth and location (LORAN-C reading or coastal landmark) of recovery. Because commercial crab traps in northern California have large mesh size (70-100 mm on diagonal) and two ≈ 10.3 cm diameter escape ports, recoveries of tagged crabs by commercial fishermen were biased toward larger crabs by trap size selection. To allow statistical adjustment for such bias, and to allow capture and tagging of small adult females (100-135 mm), specially designed crab traps, which were non-selective above about 85 mm carapace width, were fished parallel with commercial trap gear. (See Diamond 1983; Diamond and Hankin, this Symposium, for details regarding trap size selection and modified experimental traps.)

During late April through early June of 1981 and 1982 (when female molting and mating takes place in northern California), the contracted commercial fisherman and his crew collected females from pre-mating embraces for us. (Females are found paired with males in such embraces just prior to female molting; when the female molts, the hard-shelled male mates with the soft-shelled female in the true mating embrace.) These females were brought to the Telonicher Marine Laboratory in Trindad where they were held until molting took place, usually within four days. Premolt and postmolt carapace widths were recorded for 185 such females which molted in the Laboratory.

Most ovigerous females were collected during late December through early January of the second and third project years from traps fished from the contracted vessel; additional recoveries of tagged ovigerous crabs were received at the Telonicher Marine Laboratory. Collected females carried eggs which were usually bright orange in color and at an early stage of development, well before the eyed stage and larval release. Females were immediately placed in Bouin's fluid, on board the vessel or at the Laboratory, so as to minimize physical damage to egg masses; live ovigerous females tend to physically "tear" at their own egg masses when handled. Female widths were measured, molting condition was assessed as described above or known from tag-recovery records, and egg masses were removed from females and transferred to fresh Bouin's fluid in which they remained for about one month prior to processing. Processing consisted of a drying and cleaning protocol which resulted in production of a small volume of dried, cleaned, hardened and separated eggs. For the second year's collections, at least six random 0.020 g subsamples were counted from each dried egg mass. Total fecundities and variances of estimated fecundities were estimated using a mean-per-unit estimator (Cochran 1977). For third year collections, only a portion of collected specimens were actually subsampled (8 subsamples of 0.020 g each), but all specimens were processed to produce dried egg masses. For those egg masses for which estimates were not based on subsampling, total fecundities and variances of estimated fecundities were estimated from dried egg mass weight based on a regression of estimated total fecundities against dried egg mass weight among subsampled specimens. This statistical procedure allowed us to minimize subsampling effort and expand the number of specimens for the third project year. Details of sample preparation and statistical analyses will be presented in Hankin and Ianelli (in prep.).

A total of 362 female crabs were collected in non-selective traps during late May of 1983 and were classified as (a) recently molted, or (b) failed to molt during most recent molting season, according to visual examination of carapace condition. Because the molting season had only just concluded by late May of 1983 (Mohr, unpublished), visual assessment of molting history was most accurate at this time of year. Recently molted females could be readily distinguished from those that had failed to molt.

Linear regressions were used to describe the relations between molt increments and premolt carapace widths for tag-recovery data and for data generated from pre-mating embrace females that molted in the Laboratory. Techniques for comparison of regression lines (Snedecor and Cochran 1967) were used to compare tag-recovery and Laboratory/pre-mating embrace regression lines so as to examine the effects of tagging on molt increments. Annual molting probabilities for adult females were estimated using two independent methods. Estimators which accounted for biases due to tag loss and commercial trap size selection were developed and applied to tag-recovery data. For these analyses, only those crabs which (a) were released prior to 1 April and (b) were recovered after 1 June of the year of tagging but before 1 April of the following year were included in analyses. This restricted analyses to those crabs which should have had just a single opportunity to molt. Details of tag-recovery-based molting probability estimators are presented in Diamond (1983) and Diamond and Hankin, this Symposium. An independent estimator developed by Mohr (unpublished) was applied to shell condition data collected during late May of 1983 and to analagous data collected during tagging activities in January of 1983. Multiple regressions, with molting history as a dummy variable (Draper and Smith 1981), were used to statistically account for the variation in total fecundity as a function of carapace width and molting history. All tests of statistical significance were made at 5%. Finally, survival rates for large adult female crabs (those ≥ 155 mm carapace width) were estimated from the sequence of recoveries of crabs tagged in each of the three project years following techniques presented in Brownie et al. (1978, Model 1) and Youngs and Robson (1975). Survival rates for smaller crabs could not be directly estimated, but qualitative comparison of recovery sequences for smaller crabs allowed inference of relative survival rates as compared with larger crabs.

Results

Of more than 12,000 adult female crabs which were tagged and released, just over 600 crabs were recovered as of 31 August 1984. Overall recovery rate was about 5%, but recovery rates were strongly size-dependent and reflected commercial crab trap size selection. For adult females ≥ 155 mm carapace width, recovery rates were about 11%; for females falling between 124 and 136 mm recovery rates were only about 2.5%. Of the total recoveries, 289 had been at large through a single molting season and could be used for tag-recovery-based estimators of annual molting probabilities; 111 of these had molted and could be reliably used for molt increment regressions (Table 1).

Table 1. Total number of female Dungeness crabs tagged and recovered by size (as of 31 August 1984).

Mid-Point (mm)	Numbers Tagged	Numbers Recovered
86.5	3	0
89.5	0	0
92.5	2	0
95.5	4	0
98.5	1	0
101.5	6	0
104.5	12	0
107.5	23	0
110.5	43	0
113.5	75	2
116.5	131	1
119.5	215	4
122.5	301	4
125.5	491	5
128.5	611	9
131.5	782	28
134.5	918	32
137.5	1139	43
140.5	1242	52
143.5	1383	56
146.5	1148	49
149.5	922	43
152.5	915	87
155.5	768	76
158.5	497	57
161.5	253	32
164.5	119	23
167.5	27	3
170.5	8	1
Totals:	12037	607

Molt increments.

Molt increments declined linearly with increasing female carapace width for both tag-recovery and laboratory/mating embrace data. Molt increments for adult females of 100 mm averaged about 19 mm, whereas molt increments for females of 150 mm averaged about 12 mm. Regression lines of molt increments against premolt size were not significantly different between tag-recovery and laboratory-generated data, thus suggesting that tagging had no statistically significant effect on molt increments of released crabs (Figures 1 and 2). Variation about the molt increment regression (Figure 2) was approximately constant over the full range of premolt carapace widths.

Molting probabilities

A total of 289 crabs was recovered after a single molting season at large, of which only 111 had molted. Failure to molt was most evident among larger female crabs (Table 2). A total of 53 crabs was recovered

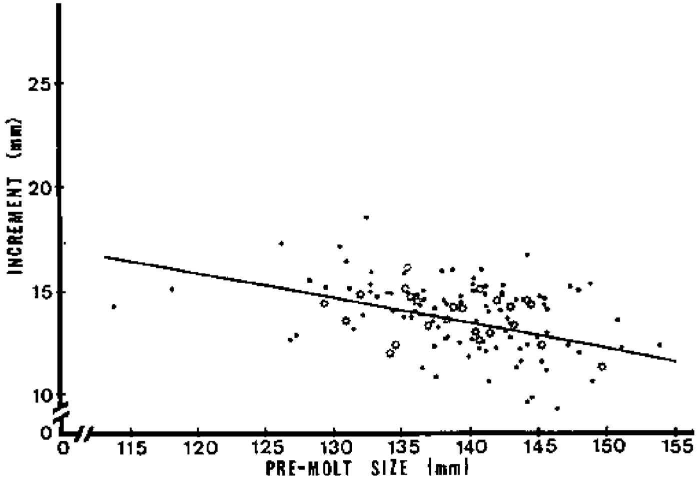

Figure 1. Molt increments plotted against pre-molt carapace widths. Solid symbols - recoveries of molted crabs at large through a single molting season. Open symbols - recoveries of crabs at large through two molting seasons, but which molted only once. Solid line indicates regression of increment against pre-molt size for solid symbols.

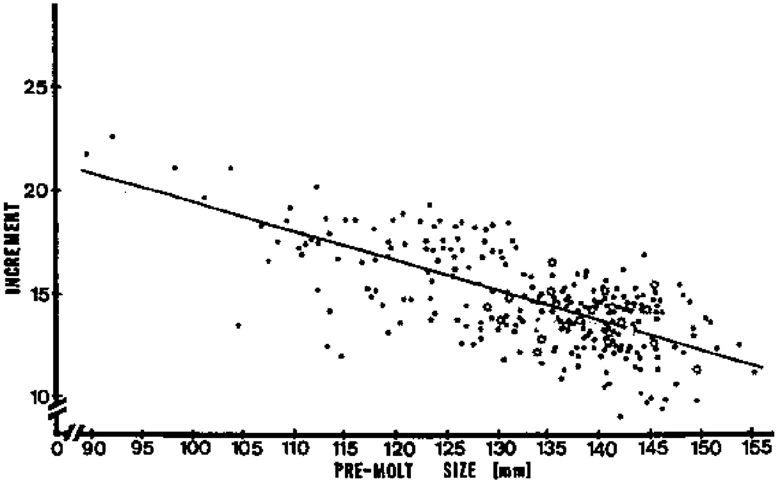

Figure 2. Molt increments plotted against pre-molt carapace widths for tag-recovery and laboratory/mating embrace data combined. Solid circles and open symbols as for Figure 1; asterisks are for laboratory-generated data. Solid line shows regression line for combined data, solid symbols only.

Table 2. Recoveries of tagged crabs at large for a single molting season. Size indicates carapace width at tagging.

Mid-Point (mm)	Not Molted	Molted	Total Recovered
113.5	0	1	1
116.5	0	1	1
119.5	1	1	2
122.5	0	1	1
125.5	1	3	4
128.5	2	3	5
131.5	5	11	16
134.5	4	9	13
137.5	7	21	28
140.5	8	18	26
143.5	11	21	32
146.5	16	14	30
149.5	17	4	21
152.5	28	3	31
155.5	25	0	25
158.5	26	0	26
161.5	11	0	11
164.5	12	0	12
167.5	3	0	3
170.5	1	0	1
Totals:	178	111	289

after having been at large through two molting seasons. Again, frequency of molting was greater for smaller crabs than for larger crabs and double molts were evident for a few small crabs (Table 3). Recoveries of crabs that had been at large through three molting seasons have been few, but displayed the same trends as seen in Tables 1 and 2; molting was more frequent among smaller crabs (Table 4). For large crabs (those ≥ 155 mm carapace width), total recoveries have been 80: of these, 79 were recovered after one molting season at large and one was recovered after two molting seasons at large. None had molted.

Data presented in Tables 2-4 are, as previously mentioned, biased by size selection in the commercial fishery recovery gear. A naive calculation, which would calculate annual molting probability simply as the fraction of recoveries which returned molted for a particular size interval at tagging, would show a steep decline in molting probabilities from about 135 mm through 155 mm; beyond 155 mm molting probabilities were effectively zero. However, these calculations would be (a) positively biased by trap size selection (a crab that molted to a larger size would be more likely to be recovered than would a crab of the same initial size that had failed to molt), and (b) negatively biased by tag loss through the molt (a crab which loses its tag while molting obviously cannot be recovered). The combined effect of these two biases is unclear, although we suspect that the principal effect is a positive bias in molting probabilities estimated via the naive calculation. Figure 3 shows results of applying the developed molting probability estimators to (a) tag-recovery data and (b) shell condition data, as well as the naive calculations. Estimates derived by the three methods

Table 3. Recoveries of tagged female crabs at large through two molting seasons. "-?-" indicates uncertainty regarding one or two molts based on increment from tagging to recovery.

Mid-Point (mm)	No Molt	One Molt		Two Molts	Total Recovered
113.5	0	0		1	1
116.5	0	0		0	0
119.5	0	0		0	0
122.5	0	0		1	1
125.5	0	0		1	1
128.5	0	2		0	2
131.5	0	6	-?-	0	7
134.5	0	5	-?-	0	6
137.5	0	6		0	6
140.5	0	7		0	7
143.5	2	8		0	10
146.5	1	5		0	6
149.5	0	2		0	2
152.5	3	0		0	3
155.5	0	0		0	0
158.5	0	0		0	0
161.5	1	0		0	1

Table 4. Recoveries of tagged female crabs at large through three molting seasons.

Mid-Point (mm)	No Molt	One Molt	Two Molts	Total Recovered
119.5	0	0	1	1
122.5	0	0	2	2
125.5	0	0	0	0
128.5	0	1	1	2
131.5	0	0	0	0
134.5	0	3	0	3
137.5	0	1	0	1
140.5	0	4	0	4
143.5	0	1	0	1

are not in agreement, but all suggest a pattern of rapid decline in annual molting probabilities (beginning somewhere between 130 and 135 mm carapace width) to effectively zero for crabs with carapace widths in excess of 155 mm.

Fecundity.

Estimated total fecundities of 35 female Dungeness crabs collected during the second project year are presented in Figure 4. Total fecundity was not significantly linearly related to carapace width for these data. Failure to discover a significant increasing trend of total fecundity with increasing carapace width prompted a more extensive fecundity sampling program during the third year. Expanded sample size was made possible by the discovery that total fecundity estimates derived by subsampling were highly correlated with dried egg mass

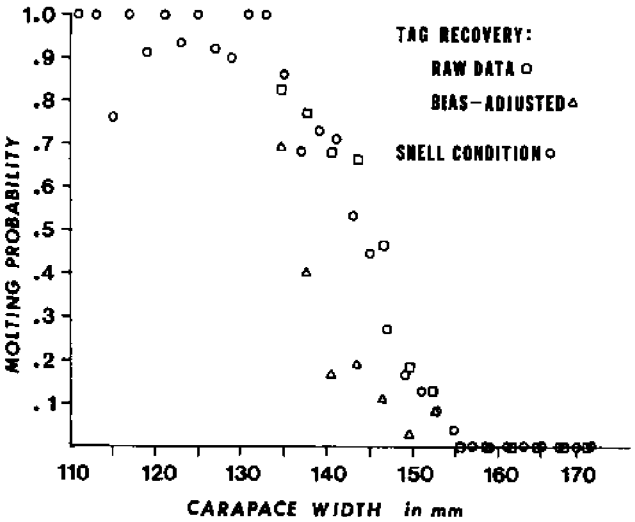

Figure 3. Estimated annual molting probabilities for female Dungeness crabs plotted against female carapace width. "RAW DATA" = naive calculations described in text; "BIA-ADJUSTED" = estimates based on tag-recovery data, adjusted for gear selection and tag loss.

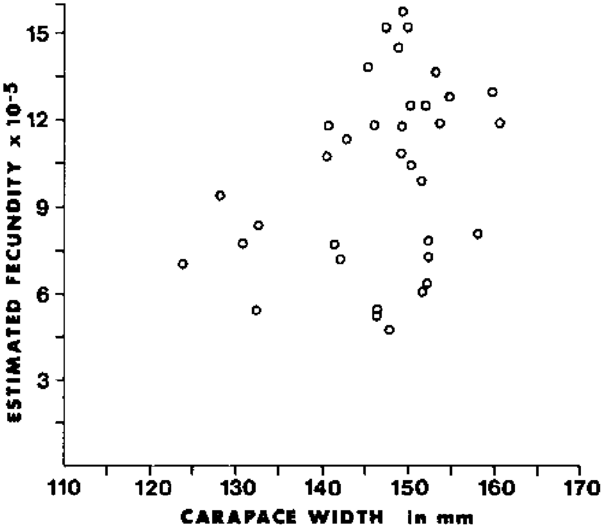

Figure 4. Estimated total fecundity plotted against carapace width for specimens collected during the second project year. All estimates are based on subsampling of dried egg masses.

weights (Figure 5). Confidence intervals based on subsampling were always within ± 10% of the estimated total; those derived from the regression of estimated total fecundity against dried egg mass weight were roughly ± 100,000 eggs and, for most specimens, were between ± 10-20% of the estimated total. Apparent variation in size-specific fecundity was therefore real and not a result of estimation methods; errors of estimation were small compared to size-specific variation among estimated fecundities. Combined fecundity estimates for the second and third project years are plotted on Figure 6 as are estimates for ten California crabs collected from the Farallone Islands which appear to belong to the same set of data (Hines, pers. comm.). Clearly, fecundity was only weakly related to female carapace width in both years' collections. A regression of total fecundity against carapace width was significant for the third year's data, but could explain only about 6% of the total variation in estimated fecundity. It is worth noting that variation among these data is far greater than among those data presented in Mayer (1973) for Washington crabs; however, Mayer had no crabs exceeding 145 mm carapace width.

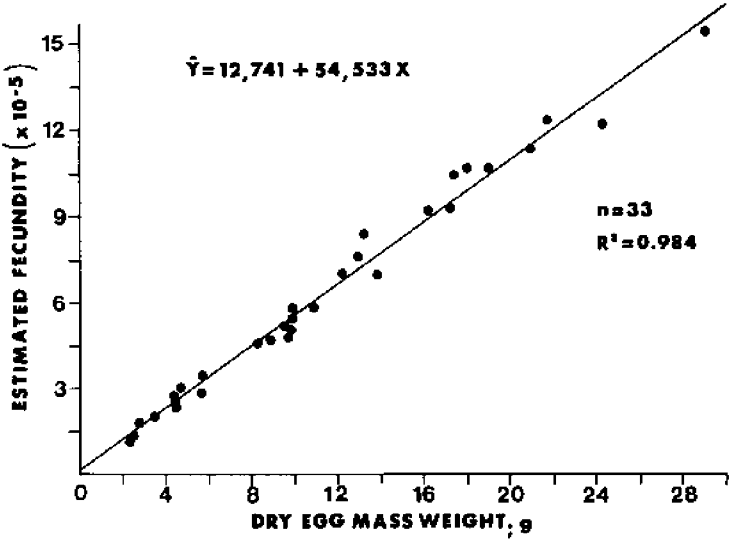

Figure 5. Estimated total fecundity, determined by subsampling, plotted against dry egg mass weight for specimens collected during the third project year. Solid line indicates regression line.

Recoveries of tagged ovigerous females revealed that female Dungeness crabs could extrude viable egg masses without having molted during the most recent molting/mating season(s). Of a total of 96 tagged ovigerous crab which were recovered after a single molting season at large, only 25 had molted. Seventeen ovigerous females were recovered after two molting seasons at large and, of these,

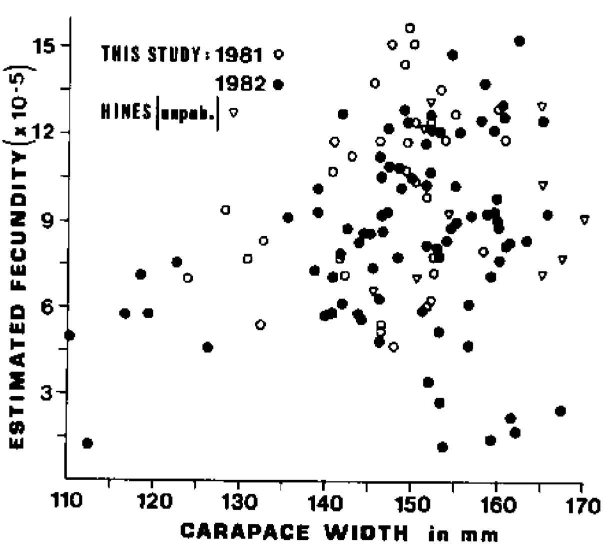

Figure 6. Estimated total fecundity plotted against carapace width for specimens collected during the second (1981) and third (1982) project years and for ten specimens collected off the Farallone Islands, California (courtesy of A. Hines, pers. comm.)

none had molted twice and three had failed to molt for two consecutive seasons. Tag recovery data thus conclusively showed that annual molting and mating were not required to allow female Dungeness crabs to extrude viable egg masses.

That female crabs could extrude viable egg masses in the absence of molting suggested to us that at least part of the apparent variation in size-specific fecundity might be attributed to molting history. When used as a categorical or dummy variable in a multiple regression context, the addition of molting history increased the amount of explained variation in fecundity from about 6% (carapace width alone) to about 30% (carapace width and molting history). For crabs which had molted during the most recent molting season, total fecundity significantly increased with carapace width. For crabs which had failed to molt in the most recent (and perhaps previous) molting season(s), total fecundity significantly decreased with carapace width. Using the "extra" sums of squares principle" (Draper and Smith 1981), we found that the regression line for the molted group was significantly different from the regression line for the group that had failed to molt, but not from the regression line for the uncertain group. The regression line for the group that had failed to molt was significantly different from both the molted and uncertain groups' regression lines (Figure 7). Details of these analyses will be presented in Hankin and Ianelli (in prep.).

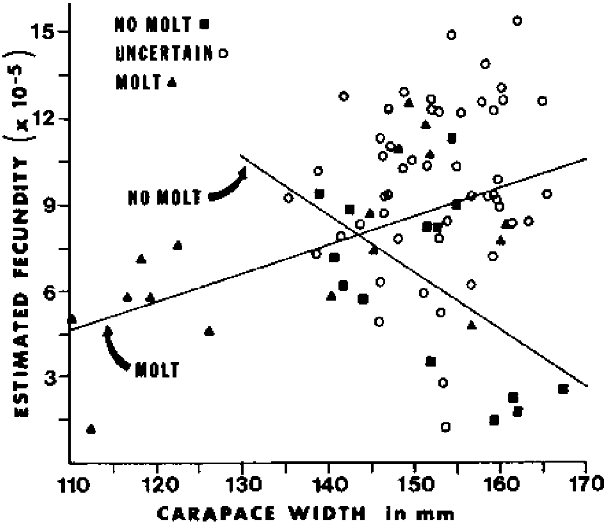

Figure 7. Estimated total fecundities for crabs which had failed to molt during most recent molting season(s) (NO MOLT), had molted during most recent molting season (MOLT), or had uncertain molting history (UNCERTAIN) plotted against carapace width. Solid lines indicate regression lines for MOLT and NO MOLT groups respectively.

Survival rates.

Because annual molting probabilities for large adult female crabs were effectively zero, and because crabs of this size were fully vulnerable to the commercial recovery gear, it was possible to use methods presented in Brownie et al. (1978) and Younge and Robson (1975) to estimate annual survival rates for these crabs based on the sequence of recoveries for each of the three year's releases. Table 5 displays the recovery matrix used for these estimates; the matrix consists of recoveries of crabs which were recovered within 365 day "years" of the original dates of release (as suggested by W.D. Younge, pers. comm.). Estimated annual natural mortality rates (M) were, on an instantaneous basis, 1.984 and 2.533 for the first and second years' releases, giving annual natural survival rates of 0.1375 and 0.0794 respectively. Confidence intervals for these two survival rate estimates overlapped, thus indicating that estimated survival rates did not differ significantly between years.

The contrast in recovery pattern between large and small females was striking. Table 6 shows an analogous recovery matrix for crabs released at sizes between 125 and 140 mm. In contrast to Table 5, there are significant numbers of these smaller crabs that were recovered in the third year after tagging. If one assumes that all crabs of this smaller size range (a) molted into fully vulnerable sizes (≥ 155 mm) by the third year at large, (b) had the same annual survival

Table 5. Number of crabs ≥ 155 mm carapace width released in each project year and number of these crabs recovered during 365 day "year" periods following date of release.

Year Released	Number Released	Year Recovered 1	2	3	4
1981	518	47	9	0	0
1982	384		58	2	0
1983	465			34	8

Table 6. Number of crabs with carapace widths ≥ 125 mm but ≤ 140 mm which were released in each project year, and number of these crabs recovered during 365 day "year" periods following date of release.

Year Released	Number Released	Year Recovered 1	2	3	4
1981	1725	30	19	13	0
1982	1922		26	13	5
1983	464			8	4

rates as did the large crabs, and (c) no tags were lost during molts, then there were nearly ten times as many small crabs recovered in their third year at large (from those released during 1981) than would have been expected based on these assumptions (13 vs. 1.39). A conclusion that smaller adult female crabs have much higher annual survaival rates than large adult females is inescapable. An annual natural survival rate of about 50% appears compatible with recovery data for these smaller females. It is worth noting that Reilly and Saila (1978) found that survival rates for C. irroratus females were 5-10% during the last two years of life, but were 40-45% for younger females; Lawton (this Symposium) suggests that C. magister and C. irroratus may be closely related in an ecological sense.

Discussion

The results presented in this paper have allowed us to develop a fascinating and unexpected description of the life history of adult female Dungeness crabs. Of the generated project results, only the finding that molt increments declined linearly with increasing carapace width was expected. Other project results caused us to radically revise our original preconceptions concerning the basic life history of female crabs. Below we give what we feel is a description of the female's life history which is consistent with our project results.

The relationship between the age of a female Dungeness crab and carapace width is clearly a complex one. The rapid decline in annual molting probabilities from about 135 mm through 155 mm, to zero beyond 155 mm, means that the correlation between age and carapace width becomes progressively weaker as females reach sizes exceeding 135 mm. Using the molt increment regression presented in this paper (Figure 2) and an average carapace width two years after settling of 110 mm, it appears that almost all females reach a carapace width of about 128 mm at three years of age (molt increments for crabs of 110 mm average about 18 mm and annual molting probabilities for a 110 mm premolt size appear close to one). At a carapace width of 128 mm, molt increments are about 15 mm and molting probabilities are still nearly one, so that the majority of females probably reach a carapace width of about 143 mm at age four. Beyond age four, females belonging to a single year class may have many possible (modal) sizes depending on succeeding molt history. A size of 155 mm could be reached as early as age five if a female molted from age four to age five. In contrast, a six year old female could conceivably still be the size of an "average" four year old female; assuming that successive molts are independent of one another and that annual molting probabilities for a premolt size of 143 mm are about 0.5, the probability that a six year old female would have the same size as a four year old female is about (1-0.5)x(1-0.5)= 0.25 . An "average" female crab probably molts annually from age three to age four but then takes two years to reach a size of about 156 mm at age six. Having reached this size, annual survival rates are very low (about 10%) implying that maximum longevity is probably not much more than 7 or 8 years of age. Mohr (unpublished) has been developing a crustacean growth model which incorporates both size-specific molting probabilities and size-specific variation in molt increments; this model should provide a far better description of the age and growth relation for female Dungeness crabs than the above crude computations. Nevertheless, the absence of a strong correlation between age and size of females means that length frequency data for female Dungeness crabs are extremely difficult to interpret. Diamond (1983) used sophisticated distribution separation methods to extract size structure from carapace width frequency data collected over the three project years, but we have not presented results of those analyses here; their interpretation is by no means straightforward.

The strong size-dependence of annual molting probabilities was unexpected because C. magister and other Cancer crabs mate only while the female is in a soft-shelled condition, immediately after molting (Hartnoll 1969). Butler (1961) first speculated that large female Dungeness crabs may not molt annually (based on observations of carapace condition) and he called our attention to a report by Lehman and Osborn (1970) which gave tag recoveries for female Alaskan Dungeness crabs; their data are entirely consistent with our much larger tag recovery data set. Clearly, many adult female Dungeness crabs do not molt and mate annually. However, recovery of tagged ovigerous crabs that had been at large through two molting seasons without having molted conclusively demonstrated that female crabs must be capable of retaining viable sperm for periods of at least 2.5 years. (The delay from mating in April-May to extrusion and fertlization of eggs in November is about six months in northern California. Hence, failure to molt for two years while still extruding a viable egg mass implies an ability to retain viable sperm for at least 2.5 years beyond an original molting/mating event.) Extrusion of egg masses by females that failed to molt has also been observed in laboratory settings by Wild (pers. comm.), Jamieson (pers. comm.) and in this study. More remarkable still is the laboratory observation by Wild (pers. comm.) that females can molt without mating and still produce viable egg masses, although these egg masses appear to be smaller than "normal".

It is possible that size-dependent declines in annual molting probabilities and sperm retention abilities are a fairly general feature of the reproductive biology of *Cancer* crabs; they are certainly not unique to *C. magister*. Declines in annual molting probabilities with increasing size have been documented for the European edible crab, *C. pagurus*, (Bennett 1974; Hancock and Edwards 1967; Hancock 1965) and for the East Coast rock crab, *C. irroratus* (Haefner and Van Engel 1975; Reilly and Saila 1978). Hancock (1965) noted the ability of *C. pagurus* females to retain sperm for long periods and to extrude viable egg masses in the absence of molting and mating. It seems likely, in fact, that the ability to retain viable sperm for long periods of time and to extrude viable egg masses in the absence of molting and mating is an evolutionary adaptation to the observed declines in annual molting probabilities as adult female crab size increases. Declines in molting probabilities are themselves probably a reflection of energetic constraints. As female crabs become larger, the energetic expense of reproduction apparently becomes large enough to eventually prevent the additional energetic expense of growth via molting; the advantages of large size and increased fecundity apparently conflict with the advantages of repeated reproduction at a smaller size. Although repeated reproduction appears to dominate this "conflict", there are obvious tradeoffs which result. Female Dungeness crabs that extruded egg masses without having molted carried significantly fewer eggs (at a given size) than did females that had molted and mated in the most recent molting season (see Figure 7). In fact, total fecundity actually declined with increasing carapace width among those crabs which were visually characterized as having failed to molt for one or more molting seasons or that were known to have failed to molt based on tag recovery data. This apparent statistical decline in fecundity with increasing size may, however, reflect declines in molting probabilities rather than a real size-dependence of fecundity among crabs which have failed to molt. It is likely that many of those females that we characterized as having failed to have molted had in fact failed to molt for two molting seasons rather than just one; this would be especially likely for females with carapace widths in excess of 150 mm. The "uncertain" group probably contained a mixture of crabs which had failed to molt for just a single season and crabs which had molted during the most recent molting season. Because the uncertain group was not statistically different from the group which had molted, but was significantly different from the group which had not molted, it seems most probable that numbers of eggs extruded (at a given size) progressively decrease with number of molts missed. At this point we can only speculate as to the biological basis for such a decline. Progressively fewer sperm or perhaps less viable sperm may remain as a female fertilizes successive broods at extrusion. Alternatively, continuing physical damage to pleopods, which are not regenerated if crabs fail to molt, may phsyically prevent a large female from carrying a "normal" sized egg mass. This issue and the issue of the tradeoff between reproduction and growth both appear to warrant basic study, from physiological and life history-theoretic perspectives.

Finally, results from this study have led us to the conclusion that adult female crabs become senescent. The decline in molting probabilities with increasing size, the decline in egg numbers among those crabs that failed to molt, and the very low annual survival rates (10%) for large female crabs are all entirely consistent with an hypothesis of senescence and all likely have a physiological basis. One cannot help but be awed by the volume of a Dungeness crab's egg mass as compared to total body volume. How long can an animal continue to make this kind of reproductive investment? Apparently, female Dungeness crabs can make such a continued reproductive investment only with diminishing success and with dramatic reduction in survival rates. And, there are other bits of evidence, some rather anecdotal, which suggest senescence. The largest female Dungeness crabs in northern California are not handsome animals; they are heavily fouled and present a dramatic visual contrast with relatively clean large males and smaller females (see also Butler 1961). The egg masses produced by these large females are often not only small, but they also look "poor", hard as it is to judge such a vague notion. Meat yields from large females are highly variable and are often lower in percentage than for smaller females (Hankin, unpublished). Furthermore, large females are lethargic animals when compared to their smaller counterparts.

Ironically, we would not have been able to develop this scenario of senescence were it not for fishery management policies that prohibit commercial harvest of female Dungeness crabs. If female crabs were harvested, then larger individuals would have been removed from the population by fishing, leaving only smaller females that showed little evidence of senescence. Although prohibition of female harvest has little biological basis, results presented in this paper suggest that the resource of large females is probably small anyway. Survival rates for large females are very low and transition to these sizes (≥ 155 mm) is probably slow due to low annual molting probabilities for crabs of about 140-145 mm. Hence, a fishery targeted on large female Dungeness crab would probably rapidly deplete available females and, over the long term, be very small compared to the existing male fishery. However, it seems unlikely that harvest of such large females would have any significant impacts on recruitment. Most large females will produce small numbers of perhaps "poor" quality eggs, and these females have only one or at most two years to live (survival rates are about 10%). McKelvey et al. (1980) pointed out that harvest of females exceeding some specified carapace width could have the beneficial effect of damping fluctuations in year class strength of Dungeness crabs, if they are caused by density-dependent egg/larval survival. It may indeed be possible to have too many females on spawning grounds. British Columbia allows commercial harvest of females that exceed the size of legal males and fluctuations in the aggregate British Columbia landings are noticeably smaller than those for other areas (see Hankin, this Symposium). It may be worth considering the possibility that limited commercial harvest of female Dungeness crabs has contributed to the relative stability of Dungeness crab landings in British Columbia.

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studies of female Dungeness crabs will meet that same test of time. This work is the result of research sponsored in part by NOAA, National Sea Grant College Program, Department of Commerce, under grant number NA80AA-D-00120, through the California Sea Grant College Program, and in part by the California State Resources Agency, project number R/F-72. The U.S. Government is authorized to reproduce and distribute for governmental purposes. We thank California Sea Grant for their support.

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Session III

Mortality

A review of Dungeness crab diseases in the Pacific Northwest and Alaska

Theodore R. Meyers, Thomas C. Shirley and Susan M. Shirley
University of Alaska, Juneau
Juneau, Alaska
and
Albert K. Sparks and J. Frank Morado
National Marine Fisheries Service
Seattle, Washington

Abstract

Natural diseases within any animal population can be a factor in the overall cyclic nature of animal abundance. This is especially true in fishery stocks where management and resulting harvest pressures may unwittingly favor disease-causing organisms. Very little literature exists concerning specific diseases of Dungeness crab, *Cancer magister*. Conditions reviewed here include: 1) Chlamydia-like systemic infection (A.K. Sparks, J.F. Morado and J.W. Hawkes, in press); 2) metacercarial encephalomyeloneuropathy (Sparks and Hibbits 1981); 3) systemic ciliate disease (Armstrong *et al.* 1981; Sparks *et al.* 1982); 4) egg and larval mycosis (Armstrong *et al.* 1976; Armstrong and Fisher 1977); 5) epibiotic fouling of eggs (Wilson *et al.* 1975; Fisher and Wickham 1976); 6) shell disease (J.G. Chan *in* Sindermann 1977; C. O'Clair, unpublished data); 7) idiopathic granulomatosis (Sparks 1980).

Introduction

The cyclical nature in abundance of Dungeness crab (*Cancer magister*) comprising the Pacific Northwest fisheries has been well documented (Botsford and Wickham 1975; McKelvey *et al.* 1980). Such fluctuations in yearly catch have a nine year period in California and a twelve year period in Washington and Oregon. However, the increasing amplitude of the regular cycling pattern as the fishery has expanded suggests the possibility of an eventual crash (McKelvey *et al.* 1980). During the 1982-83 commercial season a total of 27.5 million pounds of Dungeness crab were landed collectively from California (4.7 million pounds), Oregon (4.1 million pounds), Washington (5.1 million pounds), British Columbia (1.8 million pounds) and Alaska (11.8 million pounds) (Pacific Fishing Yearbook 1984). From previous years, crab numbers have continued to decline in Oregon and

California fishing grounds. Washington has shown a slight improvement in total catch from the previous year (2.6 million pounds) and the British Columbia fishery remained low but stationary. The 1983 Alaska landings declined to a little over half of the 1982 harvest due to an increase in fishing effort by boats displaced from the depressed fisheries in the "lower 48" (Pacific Fishing Yearbook 1984). At this writing no statistics were available for the 1984 season. Although over-harvest would seem to be a major contributing factor in crab declines, past management experience by state and federal biologists emphasized that the reproductive capacity of the crabs should not be influenced by fishing effort. Female crabs have been protected as well as undersized males which have at least one opportunity to mate before entering the fishery. Consequently, there may be other factors influencing Dungeness crab abundance including such environmental factors as currents (Pacific Marine Fisheries Comm. 1965), upwellings (Petersen 1973), ocean temperatures (Wild 1980), density dependent biotic factors (Botsford and Wickham 1975, 1978; McKelvey *et al.* 1980) and possibly disease. It is the latter variable which is addressed in this review.

Naturally occurring diseases can be an underlying limiting factor in the cyclical growth, survival and recruitment success of any animal population. This is especially true when additional stressors such as human exploitation of stocks and/or pollution further enhance opportunistic disease causing organisms. At present there are very few diseases described in Dungeness crab, especially within the more vulnerable young-of-the-year and 1+ age classes. Those diseases which have been reported will be reviewed in two groups (Table 1): 1) diseases which are pathogenic and either cause or have potential of causing crab death; 2) diseases or lesions of unknown significance. The nemertean worm, *Carcinonemertes errans*, which is a commensal and egg predator of Dungeness crab will not be discussed in any detail.

Table 1. Reported Diseases of Dungeness Crab, *Cancer magister*.

Pathogenic Diseases	Reference
1. Chlamydia-like systemic infection	Sparks, Morado and Hawkes, in press
2. Metacercarial encephalomyeloneuropathy	Sparks and Hibbits 1981
3. Systemic ciliate disease	Armstrong *et al.* 1981; Sparks *et al.* 1982
4. Egg and larval mycosis	Armstrong *et al.* 1976; Armstrong and Fisher 1977
Diseases of Unknown Significance	
1. Epibiotic fouling of eggs	Nilson *et al.* 1975; Fisher and Wickham 1976; Fisher 1976; Wickham 1979
2. Shell disease	Chan cited in Sindermann 1977; C. O'Clair, personal communications
3. Idiopathic granulomatosis	Sparks 1980; Morado and Sparks, unpublished data

Pathogenic Diseases

Chlamydia-like systemic infection (A.K. Sparks, J.F. Morado and J.W. Hawkes, in press).

Mortalities of feral adult Dungeness crab within pots and commercial holding facilities in Willapa Bay and northern Puget Sound, Washington, have been associated with an intracellular chlamydia-like agent infecting crab tissues. The gram negative organism reaches a maximum prevalence of 10% in Dungeness crab during winter cold water temperatures beginning in December and continuing through March. This disease is systemic involving different cell types within many organ systems, but targets upon connective tissue cells, especially within the hepatopancreas and bladder. The histologic appearance of infected host cells is characterized by marked hypertrophy and large, basophilic cytoplasmic microcolonies of the causative agent. Such cells become necrotic and severe infections result in replacement of normal tissue architecture with large monotonous fields of the organism making identification of tissue type difficult. Transmission electron microscopy of infected host cells has shown the microcolonies to be comprised of a prokaryotic organism having some forms resembling previously reported chlamydia or chlamydia-like organisms in vertebrate (Storz, 1971) and invertebrate (Harshbarger *et al.* 1977; Meyers 1979) animals. However, this is the first *chlamydia-like* agent reported in a decapod crustacean (A.K. Sparks, J.F. Morado and J.W. Hawkes, in press). Although the organism has not been cultured *in vitro*, it has been maintained *in vivo* by laboratory passage from *crab to crab*. Infected crabs *become lethargic*, contain minute bodies of the organism within their hemolymph and eventually die. Consequently, the virulence of this pathogen for Dungeness crab is unequivocal, but its impact on limiting recruitment in feral crab populations needs further investigation. It is entirely speculative, but the mass mortalities of nearly 9,000 older female Dungeness crabs (140 mm carapace width) observed on Washington and Oregon beaches during 1979 and 1981 may have been associated with this chlamydia-like agent. Preliminary histological examination of some of these crab mortalities indicated a systemic bacterial infection, but the true etiology was never substantiated (Stevens and Armstrong 1981). Those crabs observed were probably only a fraction of the total mortality, possibly representing a significant loss of a reproductively important age group from those commercial fisheries (Stevens and Armstrong 1981).

Metacercarial encephalomyeloneuropathy

Metacercariae of an unidentified trematode species were found encysted within histologic sections of nervous tissues from 4.3% (8/188) of Dungeness crab randomly collected from northern Puget Sound and Willapa Bay, Washington (Sparks and Hibbits 1981). More recently, other cases of parasitized Dungeness crab have been observed in the same areas as well as in Alaskan waters (J.F. Morado and A.K. Sparks, personal communication). Nervous tissues affected included major peripheral nerves, brain, thoracic ganglion and the lamina ganglionaris of the eye. In most parasitized crabs only a single metacercaria is observed in sections of individual nervous tissues. Exceptions do occur in which crabs have many of their major nerves encysted with metacercariae. In the less severe cases, parasitized crabs show no clinical signs of disease. However, heavily parasitized crab are clearly ataxic. Histopathological findings in all specimens examined indicated compaction and/or necrosis of surrounding nervous tissues containing trematode cysts. This parasite has the potential to debilitate and possibly kill Dungeness crab hosts, but only if encysted metacercariae reach high numbers. Such a condition may cause disruption of nervous innervation to major organ systems and certainly limbs as indicated by ataxic crabs (Sparks and Hibbits 1981). The initial low prevalence of the parasite is considered conservative since serial sectioning of the entire nervous system was not feasible. Encysted worms were not visible at gross necropsy, consequently no fresh material was available for taxonomic identification. All trematode metacercariae previously reported in marine crabs have belonged to the family Microphallidae, and none were found exclusively within nervous tissues (Sparks and Hibbits 1981). Sections of the Dungeness crab metacercariae resembled *Microphallus carcini*, in *Carcinus maenas* from Great Britain (Stanier *et al.* 1968) and *M. similis* in the same host from Woods Hole, Massachusetts (Stunkard 1957), except the typical microphallid anterior spines were not apparent (Sparks and Hibbits 1981). Similar metacercariae have also been observed exclusively within the nervous tissue of shrimp (*Crangon alaskensis*) from Washington (Morado and Sparks 1983).

Systemic ciliate disease

Paranophrys maggii, a holotrichous ciliated protozoan, has been reported as a facultative pathogen of marine crustacea including *Carcinus maenas* on the Brittany coast (Poisson 1930) and Dungeness crab from Oregon (Armstrong *et al.* 1981). *Paranophrys* sp. has also been described in Dungeness crab from Washington (Sparks *et al.* 1982) and from the marine isopod, *Gnorimosphaeroma oregonensis* near Afognak Island, Alaska (Hibbits and Sparks 1983). In addition, a *Paranophrys*-like ciliate has been observed within the hemolymph and tissues of a moribund captive golden king crab (*Lithodes aequispina*) collected near Haines, Alaska (T.R. Meyers, unpublished data). *Paranophrys* sp. is generally considered a secondary invader requiring a primary portal of entry into the host through injury of the exoskeleton. Thus, the disease can be a problem among captive crabs in overcrowded conditions, especially if injured by handling or by each other. The ciliate becomes systemic by invasion of the host circulatory system where it multiplies and spreads to other organs while consuming hemocytes as well as other tissue cells. Death of the crab host probably results from massive destruction and dysfunction of major organ systems (Sparks *et al.* 1982). In captive Dungeness crab at least 40% have succumbed to this disease which exhibits a prepatent period of 9 to 26 days following injury (Armstrong *et al.* 1981). Infected crabs show progressive clinical signs of lethargy, anorexia and ataxia before death. Diagnosis can be made by examining hemolymph from infected crabs for the motile ciliates. Histopathological features in moribund Dungeness crab infected with *Paranophrys* sp. include almost complete destruction of circulating and tissue hemocytes accompanied by severe systemic necrosis of major organs and myriads of ciliates within the tissues (Sparks *et al.* 1982). Although the transmission and perpetuation of this parasite is favored by crowded artificial holding facilities, the disease has been observed in one field case of Dungeness crab (Sparks *et al.* 1982) and in feral *Carcinus maenas* (Poisson 1930). At this writing two of the authors (Morado and Sparks) have passaged *Paranophrys* sp. in Dungeness crab for about 1 1/2 years by injections of infected crab hemolymph.

Egg and larval mycosis

The fungus, *Lagenidium* sp., is a reported pathogen in eggs and larvae of laboratory *reared Dungeness* crab in Oregon (Armstrong *et al.* 1976; Armstrong and Fisher 1977). As much as 5-10% of the *total* egg mass about the periphery of the sponge in individual female crabs may become infected. Such areas appear discolored and cotton-like and are comprised of necrotic eggs. Fungus infection in Dungeness crab larvae may result in mortalities of up to 40% within 24 hours (Armstrong *et al.* 1976). Clinical signs of diseased larvae include *settlement to* the bottom of the rearing vessel, progressive opacity of the tissues and a similar cotton-like appearance occurring after death as in infected eggs. Egg and larval tissue opacities result from rapidly growing mycelial masses of septate (sparingly) hyphae and accompanying tissue necrosis. The cotton-like appearance is caused by hyphae penetrating to the exterior of egg shells or larval exoskeletons. Discharge vesicles, formed by emergent hyphae, release infective, motile biflagellated zoospores which penetrate uninfected eggs and larvae to perpetuate the disease. Nauplii of the brine shrimp, *Artemia salina*, which may be used as food for crab larvae can also *become infected* with the fungus and transmit the disease. Once infected, crab larvae do not respond to treatment although transmission of the disease may be reduced by pesticides such as trifluralin (0.005 mg/L) and captan (0.06 mg/L) (Armstrong *et al.* 1976). During an epizootic, control of the disease can *only be* accomplished by discarding infected crab larvae, disinfection of rearing containers and starting over with uncontaminated water and animals. Continued good cultural hygiene including removal of detritis, uneaten food and dead larvae, will reduce the possibility of future epizootics.

Lagenidium callinectes, a similar or possibly identical fungal pathogen, *causes the same* disease syndrome in eggs of feral blue crab, *Callinectes sapidus*, and in laboratory reared blue crab larvae (Couch *1942; Sandoz et al.* 1944; Rogers-Talbert 1948; Bland and Amerson 1974). This *same fungus* has also occurred on the eggs of other feral crabs such as *Panopeus herbstii* and *Libinia dubra* (Bland and Amerson 1974) and on *the eggs of the barnacle, Chelonibia patula* (Johnson and Bonner 1960). *Lagenidium* sp. is also *a severe pathogen* in egg and larval culture *of penaeid* shrimps (Cook 1971; Lightner and Fontaine 1973; Barkate *et al.* 1974; Lightner 1977) and lobster, *Homarus americanus* (Nilson *et al.* 1976) where some success in fungal *treatment has been* achieved *with* malachite green (Fisher *et al.* 1978). A freshwater *Lagenidium*-like fungus has also been *responsible* for impacting yearly *recruitment* of the copepod *Diaptomus novamexicanus* in an alpine California lake (Redfield and *Vincent 1979*).

Lagenidium sp. is apparently ubiquitous in the aquatic environment. *It may be* a normal epibiotic saprophyte on shrimp (Lightner 1976) which may be the case for other crustacea as well. It is clear that *Lagenidium* sp. is an important egg and larval pathogen of many *crustacea in rearing* facilities and it can affect egg survival in wild blue crab and the recruitment of feral freshwater copepods. At present, there is no evidence to indicate that this fungal agent is an important pathogen affecting feral Dungeness crab populations.

Diseases of Unknown Significance

Epibiotic fouling of eggs

Epibiotic fouling of eggs in wild Dungeness crab was first reported by Fisher and Wickham (1976). Organisms involved included those resembling the blue green algae *Oscillatoria* and *Rivilaracea*, the bacteria *Leucothrix*, the gliding bacteria *Beggiatoa* and *Vitreoscilla* and vorticellid stalked protozoans (Nilson *et al.* 1975; Fisher and Wickham 1976). Egg mortalities in wild crabs, particularly occurring at the edges of clutches and in older more developed embryos, were correlated with the presence of some of these epibionts. The cause of embryo death was postulated as suffocation due to thick epibiont growth and subsequent trapping of detritis. Laboratory studies seemed to corroborate a proportional cause and effect relationship of epibiont densities with egg mortality (Fisher 1976). It was further suggested that these fouling organisms were a contributing factor in the decline of the San Francisco area Dungeness crab fishery (Fisher and Wickham 1976). Previous literature regarding fouling of crustacean eggs indicated that direct embryo death only occurred in situations involving fungal organisms able to penetrate the egg shell (Rogers-Talbert 1948; Anderson and Conroy 1968). In reality, epibiotic fouling organims are ubiquitous on all life stages of many other crustaceans, being noticed particularly in reared species including lobster, the prawn *Pandalus platyceros*, various penaeid shrimps and crayfish (Overstreet 1973; Barkate *et al.* 1974; Nilson *et al.* 1975; Couch 1978; Fisher *et al.* 1978). Mortalities due to fouling have been significant in penaeid shrimp culture when thick mats of filamentous and non-filamentous epibionts colonize gill surfaces (Barkate *et al.* 1974; Lightner *et al.* 1975) or entangle larvae and postlarvae, thus, interfering with behavior and molting (Nilson *et al.* 1975; Lightner and Supplee 1976).

Wickham (1979) later reported that epibiont fouling in wild Dungeness crab eggs indirectly resulted from the feeding activities of the nemertean predator, *Carcinonemertes errans*. Worm feces and organic matter released from punctured crab eggs apparently provides a rich substrate promoting fouling organisms. Crab egg death was attributed directly to worm feeding and could be correlated with worm distribution rather than epibiont blooms resulting from nutrient rich effluents (Wickham 1979). Consequently, the true significance of fouling organisms in causing direct egg mortalities in wild Dungeness crab is not yet clear.

Shell disease

Although shell disease has not been described in Dungeness crab, there are unpublished reports from Washington (J.G. Chan cited in Sindermann 1977) and Alaska (C. O'Clair, personal communication). The latter observation involves a blackened erosive condition of the distal leg segments in crab inhabiting logging sites with large amounts of bark chips among the sediments. At present, no infectious agent has been implicated but rather a toxic cause is suspected.

In other crustaceans, shell disease is commonly caused by chitinoclastic bacteria infecting both natural and cultured decapod populations as reviewed by Johnson (1983). In wild crustacean populations shell disease typically has a low prevalence except in reports for Alaskan king crab, *Paralithodes camschatica* and *P. platypus* (Bright *et al.* cited in Sindermann and Rosenfield 1967), Oregon tanner crab, *Chionoecetes tanneri* (Baross *et al.* 1978) and crustacea including crangon shrimp and rock crabs, *Cancer irroratus*, from polluted sewage dump sites in the New York Bight area (Gopalan and Young 1975; Young and Pearce 1975). Captive populations of decapods, particularly lobsters, may also develop high prevalences of shell disease with accompanying high mortality rates (Taylor 1949). Disease develops following damage to the nonchitinous outer epicuticle by mechanical injury, microbial degradation (Baross *et al*. 1978; Cipriani *et al*. 1980) or possibly by chemical pollution (*Young* and Pearce 1975). The underlying chitinous cuticle then becomes colonized by chitinivorous bacteria causing erosion from secreted lipases. Additional bacterial secretions of chitinases and proteases cause progression of the shell lesion to underlying soft tissues (Cipriani *et al*. 1980). Shell lesions are most common on ventral surfaces beginning as small white foci which become cratered, friable and blackened from melanization. The lesions coalesce often resulting in lost appendages as well as gill erosion (Hess 1937; Sawyer and Taylor 1949; Taylor 1949; Rosen 1970). If lesions progress to soft tissues molting cannot eliminate the disease, but continues to a fatal outcome. Adhesions of old and new cuticle caused by tissue necrosis prevent successful ecdysis (Fisher *et al*. 1976). Various bacterial genera have been associated with crustacean shell disease including *Vibrio*, *Beneckea*, *Pseudomonas*, *Alteromonas*, *Spirillum*, *Photobacterium* and unspecified myxobacteria (Hess 1937; Cook and Lofton 1973; Amborski *et al*. 1975; Anderson and Conroy 1968; Baross *et al*. 1978; Cipriani *et al*. 1980). Under captive conditions shell disease can be contact transmitted from animal to animal, but experimental inoculations have met with success as well as failure (Bright *et al*. cited in Sindermann and Rosenfield 1967; Malloy 1978; Cipriani *et al*. 1980). Predisposing factors of shell disease appear to include excessive organic substrates, chemical pollution, handling, overcrowding and warm water temperatures (Hood and Meyers 1974; Fisher *et al*. 1978).

The significance of shell disease in affecting the recruitment of Dungeness crab in feral populations is still completely unknown.

Idiopathic granulomatosis

Multiple granulomata have been described in histologic sections from several Dungeness crab (34%) collected from the Puget Sound area of Washington State (Sparks 1980). The granulomata typically occur in the connective tissues of the midgut wall and are of two types. Type one is smaller and more frequent; consists of a melanized center with few surrounding hemocytes and is located throughout the midgut wall, but is most numerous beneath the epithelial basement membrane. The second type is a larger granuloma with a central melanized core surrounded by a large collar of hemocytes. This latter lesion is uncommon and located in the deeper connective tissues of the midgut wall. Special stains have shown no evidence for the etiological nature of these lesions. It has been speculated that they are reactions to two different biologic foreign bodies based upon their differences in size, morphology and location in the midgut wall (Sparks 1980). Affected crabs were clinically normal otherwise, suggesting that these lesions may only be of academic interest regarding Dungeness crab health. Similar foreign body granulomata have been reported in as many as 100% of Alaska Dungeness crab examined from bark sediments in logging areas (J.F. Morado and A.K. Sparks, unpublished data). The toxic nature of these sedmiments is under investigation (C. O'Clair, unpublished data) and may have some relevance to the high prevalence of granulomata in Dungeness crabs from these habitats. Reports of idiopathic granulomata do exist for other crustacean species as well (Lightner and Redman 1977).

Summary

The various Dungeness crab fisheries in the Pacific Northwest and Alaska are presently declining, some more than others. Regardless of whether these declines are part of the cyclical nature of the fisheries, management programs should examine all relevant aspects of Dungeness crab biology including parasitism and disease. Superficially, the literature suggests that not many diseases occur in Dungeness crab. However, such an assumption may well be in error unless based upon more investigative effort than has been expended. Recent investigations of other decapod species within the Pacific Northwest and Alaska have revealed several new disease entities and/or information regarding previously described agents. These contributions may be of potential value for future comparative disease studies of Dungeness crab from the same areas. Such discoveries include the following: the mycotic black mat syndrome in tanner crab *C. bairdi* (Sparks and Hibbits 1979; Sparks 1982); microsporidian diseases of Alaskan king crab (A.K. Sparks and J.F. Morado, unpublished abstract, 17th Annual Meeting of the Society for Invertebrate Pathology, U.C. Davis, 1984), pink shrimp (*P. jordani*) (Olson and Lannon 1984) and sand shrimp (*Crangon franciscorum*) (J.F. Morado and A.K. Sparks, *loc. cit*); putative herpesvirus-like infections in Alaskan king crab (A.K. Sparks and J.F. Morado, *loc. cit*); rhizocephalan parasitism by *Briarosaccus callosus* in Alaskan king crab (A.K. Sparks and J.F. Morado, unpublished abstract, 16th Annual Meeting of the Society for Invertebrate Pathology, Cornell University, Ithaca, N.Y., 1983; Hawkes *et al.* in press); rickettsia-like infection of Alaskan blue king crab (Johnson 1984); systemic bacterial and ciliate diseases of Alaskan king crab (T.R. Meyers, unpublished data).

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Condition of Dungeness crabs, *Cancer magister,* at a benthic deposit of decomposing bark: Physical trauma and reduced reproductive success

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Lincoln Freese and Charles E. O'Clair
National Marine Fisheries Service
Auke Bay, Alaska

Abstract

Logs harvested in southeastern Alaska are usually rafted to mills and shipping ports. Logs enter the stream at log transfer facilities (LTF's) where deposits of decomposing bark accumulate on the bottom. Depths of these deposits range from a few cm to 1 m. Though considered epibenthic organisms, Dungeness crabs (Cancer magister) frequently burrow into benthic sediments. Alterations in substrate composition or interstitial water chemistry where bark deposits impinge on crab habitat could cause deleterious changes in resident crabs. We report here the results of a field study designed to determine the nature of the responses of adult female Dungeness crabs to marine benthic bark deposits.

We compared crab populations at or near LTF's with those at nearby control sites in six bays in southeastern Alaska. The bays used in the study included Freshwater Bay and Corner Bay, Chichagof Island; Saook Bay and Appleton Cove, Baranof Island; Rowan Bay, Kuiu Island; and Traitors Cove, Revillagigedo Island. SCUBA divers hand collected 787 adult female Dungeness crabs at the study sites in March 1982 (Traitors Cove), April 1982 (Corner Bay), May 1982 (Freshwater Bay, Appleton Cove, Saook Bay, and Rowan Bay), and April 1983 (Rowan Bay). Crabs were generally rare at LTF's and were never seen burrowed into the bark, except at Rowan Bay. Crabs were common at the Rowan Bay LTF and were often seen burrowed into the bark deposit there. All crabs collected at Rowan Bay were from the bark deposit; all crabs from other LTF's were collected outside of the bark deposits, at distances ranging from 3 to 300 m.

Immediately after each dive, the reproductive condition (ovigerous over non-ovigerous) and the number of missing leg segments were noted for each crab. The left rear pleopod with attached eggs was then

removed from each crab. This sample was used to estimate relative fecundity, egg mortality, and density of Carcinonemertes errans in crab egg clutches. Carcinonemertes is a nemertean that preys on crab eggs.

Concentrations of sulfide and ammonia (products of anaerobic organic decomposition) were measured in interstitial water collected from the bark deposits at LTF's and from sediments at control sites.

Rowan Bay was the only site where crabs were found burrowed into the bark; therefore, Rowan Bay data were treated separately in the statistical analyses. Statistical tests included two-way analysis of variance (ANOVA) and two-way analysis of covariance (ANCOVA) for normally distributed data. Wilcoxon's signed-ranks test was used for data not meeting the assumptions of ANOVA or ANCOVA. The G-test for independence was used for binomial data.

Sixty-six percent of the 787 female crabs collected were ovigerous. The percentage of ovigerous crabs at the Rowan Bay LTF was significantly (G-test; $P < 0.001$) lower than at its control site in both 1982 and 1983 (30.4% vs 85.7% in 1982; 36.4% vs 66.5% in 1983). At bays other than Rowan Bay, ovigerous crabs always outnumbered non-ovigerous crabs near the LTF's. The percentage of ovigerous crabs was significantly higher near the LTF's at Corner Bay ($P < 0.001$), Freshwater Bay ($P < 0.05$), and Appleton Cove ($P < 0.05$) than at the control sites. No significant differences in the percentage of ovigerous crabs were found between treatments at Traitors Cove or Saook Bay.

ANCOVA (factors = treatment X year; covariate = crab width) indicated significant effects due to treatment ($P < 0.001$) and year ($P = 0.001$) on relative crab fecundity at Rowan Bay. Fecundity of crabs at the Rowan Bay LTF averaged 44% of that at the control site. ANCOVA (factors = treatment X location; covariate = crab width) with data from other study sites failed to show a significant effect due to treatment on fecundity; between bay differences in fecundity were significant ($P = 0.006$).

ANCOVA (factors = treatment X year; covariate = egg developmental stage) showed significant effects due to treatment ($P = 0.002$) and year ($P = 0.002$) on crab egg mortality. Egg mortality at the Rowan Bay LTF averaged twice that at the control site. Egg mortality at LTF's other than the Rowan Bay LTF did not differ from the controls but did vary significantly (ANCOVA; $P = 0.001$) between bays.

The mean density of C. errans (expressed as number of worms plus number of worm egg strings per 1,000 crab eggs) in crab egg clutches at the Rowan Bay LTF was twice as high as that at the control site in both 1982 and 1983. The ANCOVA (covariate = egg developmental stage) showed a significant ($P = 0.014$) treatment effect on this variable; the effect of year was not significant. Worm density at other sites differed significantly (ANCOVA; $P = 0.029$) between bays but not between treatments. Worm density and crab egg mortality were highly correlated ($r = 0.94$; $P < 0.001$).

Crabs at the Rowan Bay LTF averaged four more missing leg segments than did control crabs. These differences were significant (ANOVA; $P < 0.05$) over four sample periods (May 1982, July 1982, November 1982, and April 1983). No consistent pattern of differences was observed at the other study sites.

Significantly higher levels of sulfide (Wilcoxon's signed-ranks test; $P < 0.05$) and ammonia (ANOVA; $P < 0.05$) were found in interstitial water at LTF's than in interstitial water in control sediments. Differences in sulfide concentrations between LTF's and controls ranged from 1.1 X higher (Saook Bay) to 37.7 X higher (Appleton Cove). Differences in ammonia concentrations between LTF's and controls ranged from 1.05 X higher (Saook Bay) to 8.2 X higher (Appleton Cove).

Comparison of crab populations at the LTF vs control site at Rowan Bay indicate that LTF's can alter the benthic substrate in such a way as to cause somatic and reproductive abnormalities in Dungeness crabs. The most likely effect of LTF's on Dungeness crabs is the localized obliteration of suitable benthic habitat. Ovigerous crabs burrow deeply into sediments, probably to protect themselves or their eggs from predators. Crabs that burrow into coarse woody debris to oviposit (as observed at Rowan Bay) could lose eggs, before cementation of eggs to the setae is complete, because of large interstices between individual pieces of woody substrate.

Chemical changes associated with the decomposing bark, rather than textural changes, are more likely to have caused the reproductive abnormalities in the crabs at the Rowan Bay LTF. Levels of products of anaerobic organic decomposition (sulfide and ammonia) in the bark deposit at the Rowan Bay LTF were higher than those found in control sediments. These toxic compounds may have directly or indirectly caused the reproductive abnormalities.

Responses of Dungeness crabs, *Cancer magister,* exposed to bark debris from benthic deposits at log transfer facilities: Survival, feeding, and reproduction

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Charles E. O'Clair and Lincoln Freese
National Marine Fisheries Service
Auke Bay, Alaska

Abstract

Dungeness crabs associated with the benthic bark deposit at a log transfer facility (LTF) in Rowan Bay, Kuiu Island, Alaska, have shown somatic and reproductive abnormalities. Crabs in other bays in southeastern Alaska which contain LTF's appear to avoid bark deposits (Freese and O'Clair, this volume). We attempted to determine whether bark from other LTF's in southeastern Alaska could also cause deleterious changes in Dungeness crabs with a 90-day laboratory experiment in which recently molted female crabs were exposed to bark substrates. Our main objective was to determine the success of egg extrusion of the crabs on bark substrates, but we also studied other aspects of reproduction, survival, and feeding.

Crabs were hand collected at two sites without bark deposits (Freshwater Bay, Chichagof Island; and Saint James Bay) in Alaska. Bark debris was collected at two active (Rowan Bay; Kennel Creek, Chichagof Island) and two inactive (Corner Bay, Chichagof Island; Appleton Cove, Baranof Island) LTF's. Crabs were randomly placed in living stream tanks (inside dimensions, 208 cm x 54 cm x 56 cm; 10 crabs/tank), the bottom of which was covered with 10 cm of bark or clean sand (control tank). The crabs were held in flowing seawater in the treatment tanks throughout the experiment. Each treatment was run in triplicate. Temperature, salinity, dissolved oxygen, pH, and turbidity were measured in the water above the substrate in each tank. Concentrations of ammonia and sulfide were measured above and in the interstitial water below the surface of the substrate. Statistical tests were the G-test of independence for binomial data, the Kruskal-Wallis test for data not meeting the assumptions of the analysis of covariance (ANCOVA), and one-way ANCOVA with crab width as the covariate for normally distributed data. Scheffé's test was used for *a posteriori* comparisons.

The concentration of sulfide in the interstitial water of the bark in three of the four bark treatments was significantly greater (11-64 times greater than control concentrations; Kruskal-Wallis test, $\underline{P}$ <0.001) than that in the control sand. There was no difference in interstitial sulfide concentrations between the Corner Bay treatment and the control. The bark in the Corner Bay treatment contained more large pieces and fewer fines creating larger interstices between particles and probably promoting faster diffusion of sulfide into the overlying water. Because crabs are ammonotelic, the concentration of ammonia in the control sand as well as that in the bark treatments increased rapidly. The concentrations of ammonia in the interstitial water of the bark from Rowan Bay exceeded (twice the control concentrations) that in the sand substrate of the control tanks (Kruskal-Wallis test, $\underline{P}$ <0.005), but concentrations of ammonia in the interstitial water of the other bark treatments were similar to those in the control tanks.

Crabs exposed to bark from the Appleton Cove LTF had 10 times greater mortality than did control crabs (G-test, $\underline{P}$=0.004). Mortality of crabs in the other bark treatments was not significantly different from the control crabs ($\underline{P}$ >0.05).

Crabs were fed clean squid mantles replenished daily. Feeding rates (g squid/crab/hr) were measured every other day. Feeding rates generally declined in the first half of the experiment during which time the rates of control crabs were similar to those of crabs in the bark treatments (ANCOVA, $\underline{P}$ >0.05). However, in the second half of the experiment, rates tended to stabilize at which time feeding rates of control crabs exceeded those in the bark treatments (ANCOVA, $\underline{P}$ <0.001). The difference in rates was attributed to the Appleton Cove treatment where feeding rate was reduced to less than half of the control crabs (Scheffé's test, $\underline{P}$ <0.01).

Fecundity was estimated by calculating the mean individual egg weight from samples of 300 eggs taken from each crab and dried (at 70°C) to a constant weight. The number of eggs in each clutch was estimated by dividing the mean individual egg weight into the total dry weight of the clutch. Forty-nine of the 150 experimental animals extruded eggs. The proportion of crabs extruding eggs was similar between treatments (G-test, $\underline{P}$=0.19) averaging 40%. However, the egg clutches of those crabs in the Rowan Bay and Corner Bay treatments were significantly (Scheffé's test, $\underline{P}$ <0.001) smaller (37% and 35%, respectively, of the control fecundity) than were those of the control crabs.

Ovarian indices were determined for crabs which did not extrude eggs during the experiment. The ovaries were removed from these crabs and dried (at 80°C) to a constant weight. Total tissue weight excluding the ovaries was determined by drying (at 80°C) and weighing the crab (without ovaries), digesting the crab tissue in 10% potassium hydroxide, and then drying the remaining shell to a constant weight. Tissue dry weight was obtained by subtracting shell dry weight from crab dry weight (excluding ovaries) before digestion. The quotient resulting from the division of ovary dry weight by total tissue dry weight (excluding ovaries) was multiplied by 100 to obtain the ovarian index. There was no difference between the ovarian indices of crabs in the bark treatments compared with control crabs (ANOVA, $\underline{P}$ >0.05).

We conclude that Dungeness crabs exposed to bark from LTF's other than Rowan Bay can suffer reduced survival, inhibited feeding, and reduced fecundity. The deleterious effects are not necessarily induced by recently deposited bark alone. The Appleton Cove LTF had been inactive for 17 years prior to the time we collected bark there for the experiment. Our results indicate that Dungeness crabs burrowed into bark can extrude smaller clutches than crabs in natural substrates, but that exposures of three months are not sufficient to cause obvious changes in ovarian condition. Sulfide appears to play a more important role than ammonia in contributing to the deleterious changes in crabs. However, the synergistic effects of high concentrations of sulfide and ammonia and other factors not measured in this study such as large populations of anaerobic bacteria in the interstitial water should be considered in future studies of the effects of large accumulations of decomposing organic material on Dungeness crabs.

A recent history of the Orca Inlet, Prince William Sound Dungeness crab fishery with specific reference to sea otter predation

Al Kimker
Alaska Department of Fish and Game
Cordova, Alaska

INTRODUCTION

Orca Inlet is located in Prince William Sound adjacent to the community of Cordova in the north Gulf of Alaska (Figure 1). Water depths range from intertidal bars to approximately 30 fathoms in Nelson Bay. Most of the Inlet is less than 5 fathoms in depth including some of the main channels. Orca Inlet is approximately 20 miles long and 2 miles wide.

Historically Orca Inlet has contributed a significant poundage of Dungeness crabs (Cancer magister) to the commercial fishery in the Prince William Sound Management Area (Table 1). It has also provided crabs for subsistence use by the residents of the Cordova area.

A decline in abundance of crabs became noticeable within a few years after the 1964 earthquake, which caused a major uplift of 6 to 7 feet in Orca Inlet. This resulted in loss of habitat for both the Dungeness crab and one of its dominant prey species, the razor clam (Siliqua patula). The crab population began to stabilize, external of normal fluctuations in abundance, in the early 1970's. The second decline in abundance, which began in 1979, correlates with the arrival of a large number of sea otters (Enhydra lutris) in the area (Garshelis 1983). This was followed by three years of no fishing due to lack of abundance as identified by the Department's test fishing program.

The Department has conducted annual test fishing for Dungeness crab since 1977 for two reasons: to estimate abundance of legal males (6.5 inches, 165 mm, in carapace width) for commercial harvest, and to ascertain whether or not the shell condition of the crabs is sufficiently hard to warrant opening the commercial fishery. If the crabs are in a softshell condition, the test fishing continues periodically until results of the shell condition sampling justify a fishery.

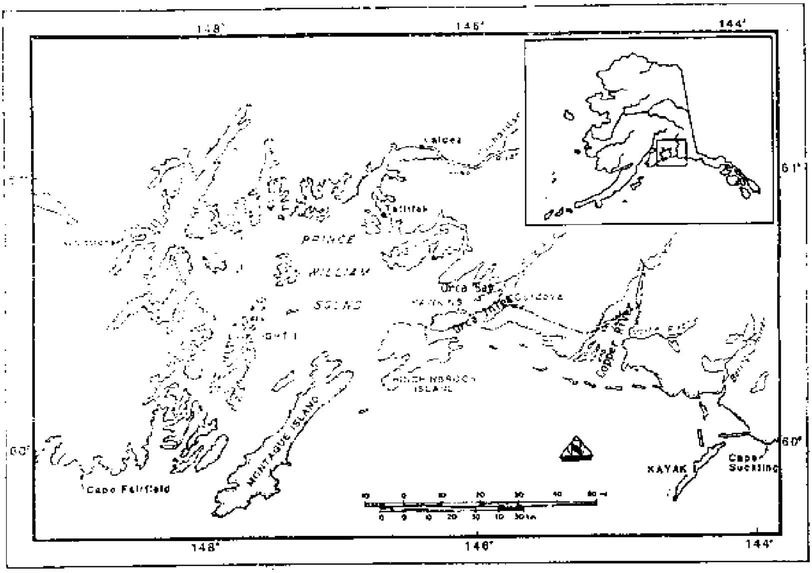

Figure 1. Prince William Sound, Gulf of Alaska.

Table 1. Prince William Sound Area Dungeness crab catch, 1960-84.

Year	Copper River Pounds	Vessels	Orca Inlet Pounds	Vessels	Total Catch Pounds
1960			1,524,326		
1961			990,242		
1962			1,353,190		
1963			1,216,846		
1964			1,290,929		
1965			1,240,372		
1966			999,341		
1967			No data available		
1968			579,279		
1969	333,696		541,822		878,696
1970	78,223		660,411		738,634
1971	78,848		430,976		509,824
1972	437,865		286,808		724,673
1973	458,613		347,764		806,377
1974	290,149		269,015		559,164
1975	654,410		163,631		818,041
1976	254,933	4	35,399	3	290,332
1977	506,751	4	228,858	23	735,609

Year	Copper River Pounds	Vessels	Orca Inlet Pounds	Vessels	Northern District Pounds	Vessels	Total Catch
1978	1,319,451	12	684,439	34	49,571	17	2,053,461
1979	504,770	19	123,245	32	20,924	16	652,924[1]
1980	659,667	10	No fishing		31,152	5	690,819
1981	1,503,574	18	No fishing		5,683	5	1,509,257
1982	757,911	16	No fishing		4,221	2	762,132
1983	379,094	9	No fishing		511	2	379,605
1984	826,788	10	No fishing		150	1	826,938[2]

[1] Includes 3,985 pounds taken incidentally during the calendar year 1979 portion of the 1978-79 Tanner crab season.

[2] Preliminary.

METHODS

Six stations, chosen systematically within the Orca Inlet area, were utilized for the annual test fishing program. A systematic approach was used in selecting the sites due to the very shallow waters of Orca Inlet and the resultant limitations put on the Department's research vessel Montague.

Five commercial type Dungeness crab pots were spaced in line 0.25 miles apart at each station. The two 4 3/8 inch escape rings were closed on each pot to allow for greater chance of retention of small crabs. Each pot contained one bait box filled with chopped herring. The soak time was 24 hours.

All crabs caught were sexed, shell aged, and the carapace width was measured to the nearest millimeter. Egg bearing condition of all females was recorded. Other fish and crabs captured were noted. All halibut were measured to the nearest centimeter, and condition of all groundfish including halibut was recorded.

This year the survey was conducted on August 21 and 22. The survey is normally conducted in latter August, as this gives the most timely results relative to the earliest possible regulatory opening date for the commercial fishery, which is September 1.

RESULTS

A total of 321 crabs, consisting of two legal males, 239 sublegal males, and 80 females, were caught in 29 pot lifts. As only two legal males were caught, the number of legals caught in the index remained at the extremely low level of 0.07/pot (Table 2). The average number of pre-recruits declined from 4.8 in 1983 to 2.0 in 1984; however, the males smaller than pre-recruits (less than 140 mm) increased from 2.9 to 6.2/pot. The average number of females caught per pot increased from 0.5 in 1983 to 2.8 in 1984. This gain was due to the large number of females caught in the Mud Bay station. The overall catch per pot of all crabs increased from 8.2 to 11.1. The gain was due to the increase in small females and small males caught in the Mud Bay station. Catch by individual station varied from a high of 36.4 total crabs/pot in Mud Bay to a low of 0.4 crabs/pot at Shepard Point (Table 3).

Thirty nine percent of the males captured were soft shelled. Forty six percent of the females were in a soft shelled condition. None of the 80 females captured were bearing eggs. Of the two legal males taken, one was a newshell and one was an oldshell. Of the females, 37 were soft shells, 39 were newshells, 3 were oldshells and 1 was very old. The size of the two legal males was 165 and 167 mm, while the average size of the females was 111 mm. The average width of the 58 pre-recruits (140-164 mm) was 149 mm, while the average width of those 181 males less than 140 mm was 119 mm. The smallest male captured was 72 mm and the smallest female was 91 mm.

Ten halibut (Hippoglossus stenolepis) were caught, two of which were dead. This was identical to the number of halibut caught in 1983, but was a decline in number of halibut from the 1980, 1981 and 1982 levels of 29, 23, and 17 respectively. The average size of the halibut caught

Table 2. Results of the annual Orca Inlet Dungeness crab surveys, 1977-84.

Year	Avg. No. Legal[1] Males/Pot (Index Number)	Avg. No. Pre-[2] Recruits/ Pot	Avg. No. Other[3] Males/ Pot	Avg. No. Females/ Pot	Total Avg. No. Crab/ Pot	No. Pots Pulled	Commercial Catch (lbs.)
1977	11.9	5.7	0.01	3.4	21.0	29	228,858
1978	27.8	2.7	0.3	3.0	33.3	27	684,439
1979	7.2	10.7	0.6	4.6	23.0	30	123,245
1980	3.0	4.1	0.1	0.5	6.5	29	No fishing
1981	1.1	2.5	0.2	0.7	4.5	30	No fishing
1982	0.03	0.8	1.1	0.7	2.7	29	No fishing
1983	0.03	4.8	2.9	0.5	8.2	29	No fishing
1984	0.07	2.0	6.2	2.8	11.1	29	No fishing

[1] Legal males are equal to or greater than 6.5 inches (165 mm) in carapace width.

[2] Pre-recruits are males greater than or equal to 5.5 inches (140 mm) and less than 6.5 inches (165 mm) in carapace width.

[3] Others are males less than 5.5 inches (140 mm) in carapace width.

Table 3. Results of the 1984 Orca Inlet Dungeness crab survey by station.

Station	Avg. No. Legal[1] Males/Pot	Avg. No. Pre- [2] Recruits/Pot	Avg. No. Other[3] Males/Pot	Avg. No. Females/Pot	Total Avg. No. Crab/Pot[4]
3 Mile Bay	0	0.4	0.4	0.0	0.8
Mud Bay	0	0.2	23.0	13.2	36.4
Grass Island	0	1.0	9.6	1.0	11.6
Deep Bay	0.3	10.0	2.8	2.3	15.3
Shepard Point	0	0.5	0.0	0.0	0.4
New England	0.2	1.8	0.8	0.0	2.8
Total	0.07	2.0	6.2	2.8	11.1

[1] Legal males are equal to or greater than 6.5 inches (165 mm) in carapace width.

[2] Pre-recruits are males greater than or equal to 5.5 inches (140 mm) and less than 6.5 inches (165 mm) in carapace width.

[3] Others are males less than 5.5 inches (140 mm) in carapace width.

[4] 5 pots were pulled for each station except in Deep Bay where 4 pots were pulled (one was lost).

was 463 mm with a range of 420-610 mm. Pot tunnel size restricts entry of larger halibut, which do exist in the Inlet.

Incidental catch of other fish included 59 yellowfin sole (*Limanda aspera*), four starry flounder (*Platichthys stellatus*) and two rock sole (*Lepidopsetta bilineata*).

A linear regression analysis was run on the index number (x) and the commercial crab catch (y) for the years 1977-79 ($y = 12{,}068x - 24{,}070$ and $r = .99$). The commercial catch figures, which are in pounds, were converted to crabs. The regression values are in number of crabs.

Applying the 1984 index number of 0.07 crab per pot to the regression equation yields an estimated harvest of -23,225 crabs with a 95 percent confidence interval of -51,781 crabs to 5,331 crabs. The confidence interval for the regression coefficient (slope) at the 95 percent level is 10,465 crabs to 13,671 crabs.

DISCUSSION

As was the case for the past three years, the 1984 estimated abundance of crabs did not warrant the opening of either the commercial or subsistence fisheries in Orca Inlet. Although the regression analysis estimated an unlikely negative quantity of crabs for a 1984 harvest, the data sufficiently shows a very linear relationship between the index numbers and commercial harvests. Even with the regression results as they are, a downward trend in abundance is clearly evident.

The severe reduction in abundance of the Orca Inlet Dungeness crab is explained by the arrival of the sea otter in Orca Inlet in 1979 (Garshelis 1983). Garshelis cites numerous publications which document the impact on shellfish populations which have declined due to otter predation. Garshelis's own observations in 1980 and 1981 of the otters in Nelson Bay, in the northern portion of Orca Inlet, yielded an annual consumption estimate by sea otters of 370,000 Dungeness crabs. Through direct observation Garshelis observed that sea otters were capable of eating 14 Dungeness crabs per day in the Nelson Bay portion of Orca Inlet.

In 1983 the number of sublegal crabs caught increased fourfold over the number captured in 1982 (Table 2). Taken at face value this increase may be construed as the beginning of a recovery in Orca Inlet. These sublegal crabs move into the desirable habitat of Orca Inlet from the deeper waters of Orca Bay. This movement occurs during the summer months after the spring molt. Summer vessel traffic reduces the numbers of sea otters in much of the area occupied by Dungeness and the index stations in Orca Inlet; therefore reducing summer predation in portions of the Inlet (Garshelis 1983). However, as the vessel traffic is significantly reduced in the fall due to the end of commercial salmon fishing, the otters once again disburse throughout the Inlet for feeding purposes. Based on Garshelis's previously mentioned feeding observations, it appeared improbable that the 1983 sublegal Dungeness would have survived to become legal sized in 1984. This is precisely what occurred. Survival of the pre-recruits as measured by the 4.8 index number in 1983 was 0.07, the legal index number in 1984 (Table 2).

Figure 2 a and 2b show histograms of the size frequencies of all males captured in the 1983 and 1984 indices respectively. The large year class of pre-recruits in 1983 under normal conditions would have yielded a significant amount of legal crab in 1984; the figures graphically illustrate that this was not the case.

The Orca Inlet Dungeness Fishery will remain closed to commercial and subsistence fishing until the abundance of legal males shows a significant increase coupled with a stabilization in abundance of the sublegals and females. Both David Garshelis and the author believe this situation is an unlikely occurrence without a major change in the otter population. Garshelis and the author believe that the Orca Inlet Dungeness crab population is at such a depressed state that even if the current otter population in the Inlet was reduced by nearly 100 percent, the Dungeness would not recover as continued recruitment of otters into the Inlet would be sufficient to keep the crab population at a depressed level.

Since arrival of the sea otter in Orca Inlet, the Deep Bay station has usually had the largest annual index number (Table 4). This year however, Deep Bay was second to Mud Bay in total crab number as Mud Bay had an unusually large amount of small females and males below the pre-recruit size (Table 3). Deep Bay has maintained on of the highest annual index catches due to immigration into Orca Inlet by newly molted crabs from the deeper waters of Orca Bay which is immediately adjacent to Deep Bay (Figure 1). The presence of a relatively large amount of sublegal Dungeness crabs in Orca Bay was documented in 1983 and to a lesser extent in 1984 by the Prince William Sound Tanner crab surveys. The Dungeness are protected from otter predation in Orca Bay as most of the bay is deeper than the 97 meter (318 feet) maximum depth at which an otter has been found (Newby 1975).

Immigration of relatively large numbers of crabs into Orca Inlet from Orca Bay is symptomatic of strong year classes in Orca Bay. These strong year classes cannot last. In fact, that part of the 1984 Tanner crab survey conducted in Orca Bay showed a decline in Dungeness catch from 1983. Once the available food supply in Orca Inlet diminishes the otters will move elsewhere in search of food. The likely area of immigration would be the Copper River/Kayak Island area (Figure 1) where there currently is a large population of Dungeness crabs (Table 1) and razor clams. In the Aleutians a similar situation occurred where otters emigrated to sparsely populated islands with abundant food (Kenyon 1969). The emigration out of Orca Inlet to the Copper River/ Kayak Island area is already occurring according to observations by commercial fishermen, the author, and an otter count by the U.S. Fish and Wildlife Service in August of 1983 (Schmidt 1983).

In summation, Garshelis (1983), Julius Reynolds (ADF&G Area Game Biologist), and the author believe that the commercial Dungeness crab fishery in Orca Inlet is unlikely to be resumed in the near future. Management of sea otter may be necessary and should focus upon the pending conflict in the Copper River/Kayak Island area.

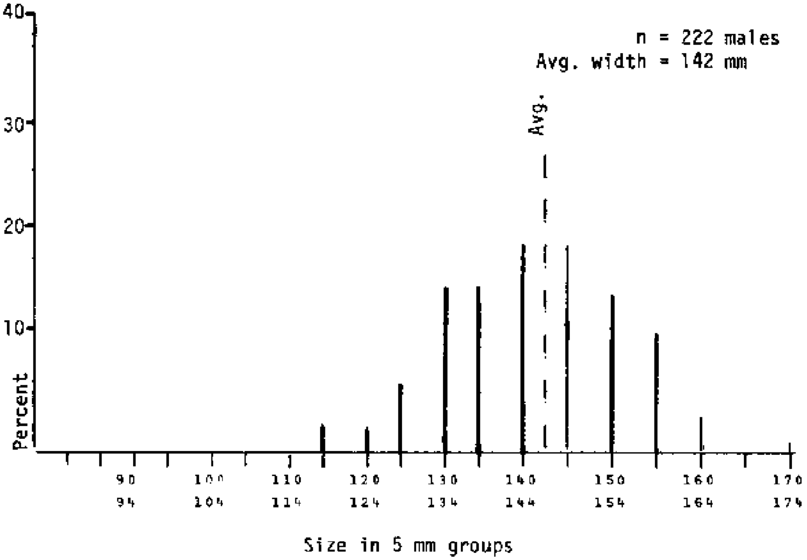

Figure 2a. Size frequency distribution of male Dungeness crabs caught in the 1983 Orca Inlet Index.

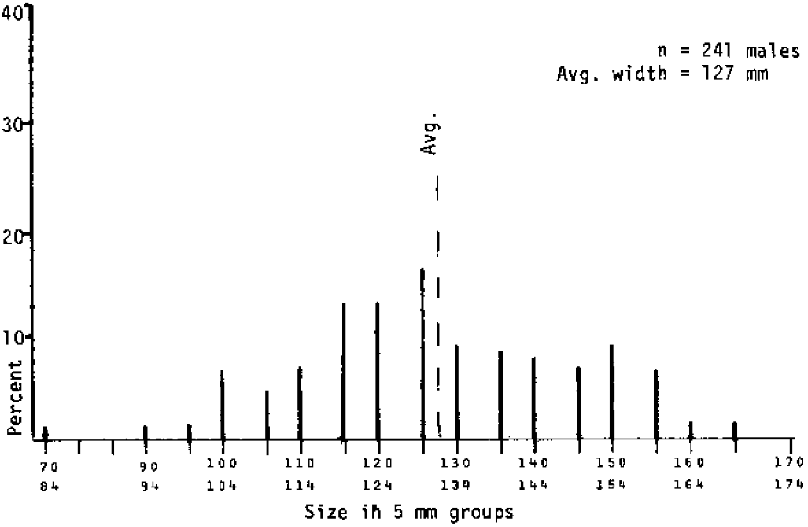

Figure 2b. Size frequency distribution of male Dungeness crabs caught in the 1984 Orca Inlet Index.

Table 4. Total crab[1] index values, Orca Inlet Dungeness crab survey, 1977-84.

Station	Survey Year 1977	1978	1979	1980	1981	1982	1983	1984
3 Mile Bay	19.0	27.0	29.1	23.4	3.4	1.8	8.6	0.8
Mud Bay	19.0	27.5	14.0	2.8	0.8	0.4	0.6	36.4
Grass Island	30.8	31.6	21.4	1.6	2.6	0.2	6.4	11.6
Deep Bay	20.8	32.6	31.3	4.6	15.0	9.0	20.6	15.3
Shepard Point	17.8	45.6	18.0	4.8	0.6	2.6	3.0	0.4
New England	20.2	32.0	22.6	8.4	4.4	1.8	10.2	2.8
Total	21.0	33.3	23.0	6.5	4.5	2.7	8.2	11.1

[1] Total crabs including both sexes and all sizes.

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Session IV

Population Dynamics

Dynamics of Dungeness crab, *Cancer magister,* larvae off central and northern California

Paul N. Reilly
California Department of Fish and Game
Menlo Park, California

INTRODUCTION

The Dungeness crab, *Cancer magister,* passes through five zoeal stages and one megalopal stage after hatching from eggs carried on the abdominal pleopods of the female (Figure 25). A pre-zoeal stage of approximately 10 to 15 min duration has been observed in the laboratory and, although it has not been collected in the field, is considered a normal developmental stage (MacKay 1934; Buchanan and Milleman 1969). The zoeae are entirely planktonic. The megalopa, the final larval stage, is planktonic until settling to the bottom and molting to the first post-larval instar. The larval stages range in length (tip of rostral spine to end of telson) from approximately 2.5 mm for stage I zoeae to 11.0 mm for megalopae (Poole 1966).

Several field studies report on the occurrence of Dungeness crab larvae. Various observations in the Gulf of the Farallones off San Francisco are recorded in California Department of Fish and Game research cruise reports between 1956 and 1970. Dungeness crab larvae were recorded at a Gulf station during a pre-design study on marine waste disposal (Brown and Caldwell 1973). Wickham (1979b) collected megalopae in plankton tows and on the hydroid *Velella velella* in ocean waters near Bodega Head, California. Lough (1974 and 1976) found all zoeal stages and megalopae in Oregon waters in 1970 and 1971. Mayer (1973) reported the occurrence of megalopae in Similk Bay, Washington. On the east coast, Sandifer (1973 and 1975), in a study of decapod crustacean larvae in and near Chesapeake Bay, reported on the occurrence of rock crab, *C. irroratus,* larvae and discussed transport and recruitment of larval stocks. Nevertheless, Dungeness crab larval dynamics and life history were not well understood when we began our study.

The purpose of our study was to investigate Dungeness crab larval life history and relate field observations of distribution, relative abundance, and behavior to possible mechanisms associated with the decline and continued low level of the crab resource in central California. Our studies were conducted from 1975 to 1980.

METHODOLOGY

We initiated our larval sampling having limited past experience with methods and equipment necessary to achieve our objective. As a result, we frequently altered procedures during the study after considering factors such as efficient use of vessel time, experimental gear, probable larval stages we would encounter during a cruise, and knowledge gained from previous cruises.

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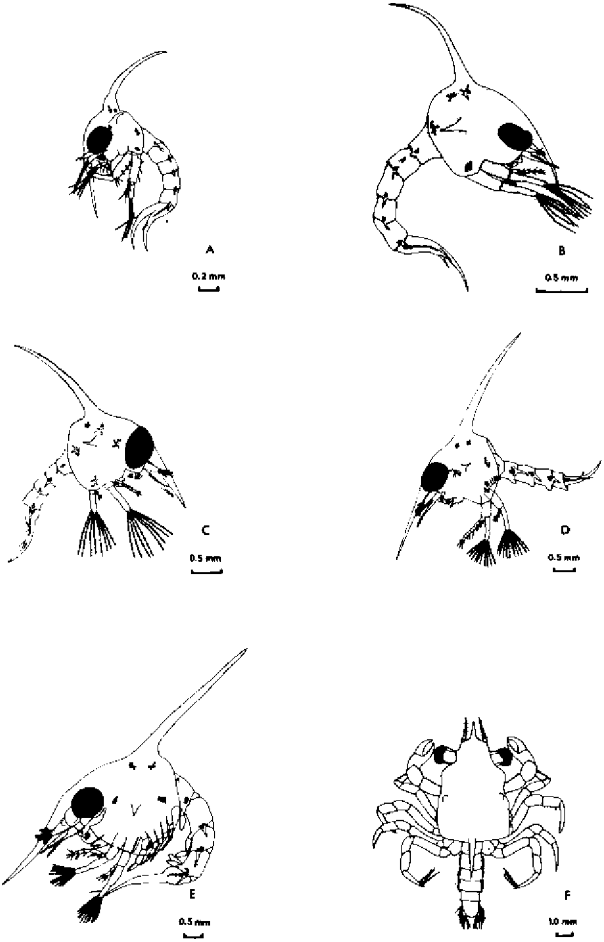


FIGURE 25. Zoeal stages I–V and megalopa of the Dungeness crab; A. Zoeal stage I, B. Zoeal stage II. . . (from Poole 1966).

Field Sampling

In 1975, the majority of our plankton sampling in the Gulf (Figure 11) consisted of horizontal, discrete-depth tows at the surface and at depths of 5, 15, and 25 m (where possible) using a 0.5-m diameter, 0.505-mm mesh plankton net with opening and closing capabilities. Several bottom to surface oblique tows were conducted at shallow stations (less than 15 m) with a 0.5-m, 0.343-mm mesh net. This same net was used for all surface and oblique tows in San Francisco-San Pablo Bay (Figure 12) that year. From December 1975, we routinely included one oblique tow at each plankton station.

A series of 1-day cruises was conducted in the Gulf and the Bay using the 0.343-mm mesh net from December 1975 to March 1976. After these cruises, we discontinued sampling with this mesh size because of problems with clogging during a phytoplankton bloom in the Gulf. The 0.505-mm mesh proved adequate for retaining stage I zoeae. During major cruises in March and April–May 1976, one oblique and four discrete-depth tows were conducted at each Gulf station. For the May–June cruise of that year, plankton sampling at Gulf stations was reduced to surface and oblique tows to allow for trawling operations at a time when we expected to find early post-larval instars.

During a major cruise in January–February 1977, sampling procedures were similar to the previous spring. However, 97 of 137 discrete-depth tows in the Gulf were made with a 12-inch (0.305-m) diameter, 0.505-mm mesh, opening-closing Clarke-Bumpus sampler which was equipped with a flowmeter to measure the volume of water filtered. The small mouth diameter and high flow impedance at normal towing speed (approximately 2 knots) made its use impractical, particularly at offshore stations where brachyuran larval densities were low. This sampler was no longer used after a 3-day cruise in mid-March when we began to use digital flowmeters attached to the 0.5-m opening-closing and other 0.5-m diameter, 0.505-mm mesh nets. Prior to the use of flowmeters, volume of water filtered had been calculated using towing speed of the vessel, duration of tow, and area of the mouth of the net.

In January 1977, we began conducting some plankton tows at night to investigate vertical migration of Dungeness crab larvae. In April 1977, 12 stations were sampled once during the day and once at night to compare day versus night catches of megalopae in surface and oblique tows. All surface and oblique tows were conducted with the 0.5-m, 0.505-mm mesh net during this cruise. For Bay work in May 1977, we attached a 0.5-m diameter, 1.0-mm mesh net to a towing sled (Figure 26) to sample plankton within 1 m of the bottom. This larger mesh size retained all Dungeness crab larval stages except possibly stage I zoeae. However, we used it only when we expected to find late-stage (IV and V) zoeae and megalopae.

Our sampling routine for early-stage zoeae during the January 1978 cruise was similar to previous years, although many oblique and discrete-depth tows in the Gulf were conducted at night to determine vertical distribution of stage I zoeae. We also made replicate tows at three stations to estimate sampling variability of stage I densities. A 1-day, eight-station transect from the Golden Gate to the Farallon Islands was sampled three times from December 1977 to February 1978 during the 1978 larval season. On major cruises in March and April 1978, bottom tows were made with the sled to determine if late-stage zoeae were associated with the ocean bottom. Routine oblique and discrete-depth tows also were conducted during the spring cruises.

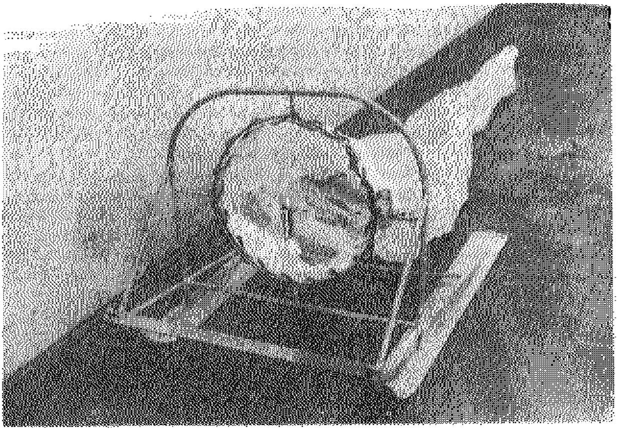


FIGURE 26. Towing sled and net used to sample plankton at ocean bottom. Photo by Paul W. Wild.

We completed three transects to the Farallon Islands between December 1978 and March 1979, the last on a chartered commercial salmon troller. In 1979, we concentrated our efforts on late-stage zoeae and megalopae. During the March 20–29 cruise aboard the R/V OCONOSTOTA, chartered from Moss Landing Marine Laboratories, we extended our sampling out of the principal study area north to Cape Mendocino and to 185 km from shore (Figure 16). We made oblique tows with the 1.0-mm mesh net to 100-m depth or the bottom at shallower stations. Discrete-depth plankton samples were taken at selected stations. The April–May 1979 cruise in the Gulf and Bodega Bay area (Figure 17) consisted of surface and oblique tows with the 1.0-mm mesh net.

As we determined the minor importance of the Bay relative to Dungeness crab larval dynamics, we reduced our effort there. We conducted 65 Bay plankton tows in 1975, 77 in 1976, 50 in 1977, 29 in 1978, 23 in 1979, and 0 in 1980.

Limited sampling during the 1980 larval period began with three transects to the Farallon Islands between late December 1979 and late January 1980, all of these aboard a chartered commercial crab boat. In early April, we chartered a commercial salmon troller from Fort Bragg (Figure 18) and the R/V CAYUSE from Moss Landing Marine Laboratories to obtain additional data on the distribution of megalopae in northern and central California. Surface and oblique tows were conducted with the 1.0-mm mesh net, and discrete-depth tows with the opening-closing net were made in the Bodega Bay area.

We obtained additional data on distribution and abundance of larvae in northern California (Figure 15) by sampling along transects off Eureka in February and April 1977, March 1978, March 1979, and January 1980.

We occasionally used methods other than plankton tows to sample megalopae. In June 1977, April 1978, April–May 1979, and April 1980, we dipnetted *V. velella* from ocean surface waters to examine for presence of megalopae. We also dipnetted megalopae which were attracted to a nightlight suspended over the water from our anchored vessel at various Gulf locations during our April–May 1979 cruise.

All plankton samples were preserved in 10% buffered formalin upon collection. The following data were recorded for each sample: date; cruise, station, and accession numbers; station depth; tow type (horizontal or oblique), time, depth, and duration; and volume of water filtered. We calculated tow depth after measuring wire angle and amount of wire out.

Laboratory Operations

Cruise Samples

Plankton samples were returned from the field to the Menlo Park laboratory where they were inspected and settled volume was measured. We used a Folsom wheel to split samples in which brachyuran densities were high (generally those samples collected in the Bay and at nearshore coastal stations) or those in which the settled volume exceeded 200 ml. A series of 2-ml aliquots, taken with a Stempel pipette, was analyzed if densities remained high after splitting. We examined the entire sample, or all of one of the split portions, with a binocular microscope. Brachyurans were removed, identified to family or, for *Cancer* larvae, to species and stage, and enumerated. Densities of brachyurans (no./m^3 of water filtered) were recorded on standardized computer forms which were keypunched and stored. Selected morphological measurements of all *Cancer* larval stages were recorded. Larvae were identified by using published and unpublished manuscripts and samples of larvae cultured at the Department's Marine Culture Laboratory near Monterey.

CalCOFI Samples

CalCOFI (California Cooperative Oceanic Fisheries Investigations) cruises have collected plankton samples off the California and Baja California coasts since 1949. These samples are curated by Scripps Institution of Oceanography, La Jolla, California. We examined samples taken between 1949 and 1975 along transects perpendicular to the coastline between the Oregon border and Pt. Santa Cruz and to approximately 320 km seaward (Figure 27). No samples were collected north of Pt. Santa Cruz in 1955, 1957, 1967, 1970, 1971, 1973, and 1974. Only in 1949, 1950, 1958, and 1960 were samples collected north of Pt. Reyes. We analyzed samples taken from January to early May for presence of brachyuran larvae. The number of samples examined from any one year ranged from 6 to 74. Although spaced widely in distance and time, they provided some historical data on occurrence and distribution of Dungeness crab larvae off California. Data recorded for each sample included the following: date; cruise and station number; station depth and distance from shore; time, depth, and duration of tow; and volume of water filtered. Brachyuran larvae were identified and enumerated by the methods discussed previously.

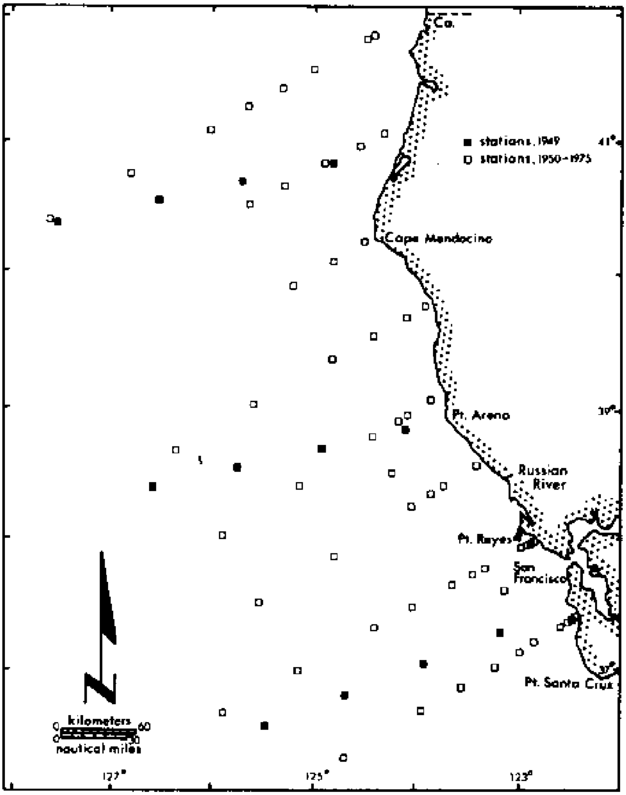


FIGURE 27. Central and northern California CalCOFI stations, 1949–1975.

RESULTS

From April 1975 through April 1980, we collected 1,914 plankton samples; 1,670 were from ocean stations and 244 from Bay stations. Routinely recorded plankton station data are summarized in Appendices IV and V. In addition, we examined 404 CalCOFI samples, all from ocean stations. Our samples yielded 11,560 Dungeness crab larvae and 1,910 were found in CalCOFI samples (Table 5); only two zoeae and 97 megalopae came from Bay stations.

Table 5. Numbers of Dungeness Crab Larvae by Stage Collected from Program and CalCOFI Samples.

Stage	*Program samples*	*CalCOFI samples*
Zoea I	8,782	733
Zoea II	426	548
Zoea III	266	270
Zoea IV	153	106
Zoea V	707	110
Megalopa	1,226	143
Total	11,560	1,910

Timing of Larval Occurrences

The initial appearance of Dungeness crab larvae by stage in our studies and CalCOFI samples ranged from mid-December for stage I zoeae to early March for megalopae (Table 6). Mel Willis (Calif. Dep. Fish and Game, unpublished data) found stage I zoeae in the Gulf in late November 1969. We found stage I zoeae at low densities as late as mid-May.

TABLE 6. Range and Earliest Date of First Occurrences of Dungeness Crab Larval Stages in Program and CalCOFI Samples.

Stage	*Range of first occurrences*	*Date of first occurrence*
Zoea I	Mid-Dec–early Jan	Dec 12
Zoea II	Early Jan–late Jan	Jan 6
Zoea III	Early Jan–mid-Feb	Jan 6
Zoea IV	Late Jan–late Feb	Jan 23
Zoea V	Mid-Feb–mid-Mar	Feb 15
Megalopa	Early Mar–mid-Apr	Mar 6

We found ovigerous (egg brooding) female Dungeness crabs in the Gulf as early as late September, although most apparently spawn during October and early November; most of the larvae hatch by late January. We estimated time of hatching from changes in density of stage I zoeae and time of first occurrence of stage II zoeae or, as in 1975 and 1977, we inferred it from first occurrences of late-stage zoeae. Onset of hatching was early when Gulf water temperatures during late fall and early winter were warm and later when they were cool. Each year there was apparently one peak hatching period in the Gulf of 1 to 2 weeks duration (Table 7) although a small amount of hatching occurred earlier and (or) extended well into the spring.

The January 6, 1978 appearance of a stage III zoea occurred in the same larval period in which we found stage I zoeae on December 12, 1977 (Table 6). We did not sample between these dates, but some stage II zoeae most likely were present in late December that year.

Based on the first appearance of post-larval crabs each spring in the study area (Tasto, Chapter 9), I estimate the length of the larval period (time for development of individual larvae) in central California to be approximately 105 to 125 days; approximately 80–95 days are required to complete the five zoeal stages and the remaining 25–30 days are spent in the megalopal stage.

TABLE 7. Estimates of Peak Hatching Periods for Dungeness Crabs and Mean December-January Sea Surface Temperatures in the Gulf of the Farallones for Larval Seasons 1975–1980.

Larval season	*Mean surface temp. (C) December–January* *	*Estimated peak hatching period*
1975	11.8	Jan 1–10
1976	10.6	Jan 11–20
1977	12.8	Dec 26, 1976 to Jan 4, 1977
1978	13.1	Dec 21–30, 1977
1979	11.1	Jan 1–10
1980	12.9	Dec 21–30, 1979

* December readings are for the year prior to the assigned date for the Larval season.

Although no CalCOFI samples were collected north of Pt. Reyes in early January, we collected some data to compare relative timing of larval development in central and northern California. In January 1980, we sampled transects 1 day apart in the Gulf and off Eureka. Zoeal stages I and II occurred in both areas in approximately equal proportions. In mid-February 1977, we found stage IV zoeae off Eureka. They occurred in CalCOFI samples from northern California as early as January 24 in 1960, while stage V zoeae and megalopae were present as early as February 15 and March 8, respectively, similar to results from central California.

However, during our late March 1979 cruise, stage III zoeae occurred at densities similar to stage V zoeae in oblique tows off Eureka, but were scarce in central California. Ten days previously, samples off Eureka yielded relatively high densities of stage II and III zoeae during a time when we expected to find primarily late-stage zoeae. Thus, these data indicate that the major hatching period appears to be longer in northern California which would result in a longer larval season for the northern California population as a whole.

Distribution of Larvae in Bay and Gulf

Zoeae

We never found ovigerous female Dungeness crabs in San Francisco Bay east of the Golden Gate Bridge nor any other evidence that the larvae hatch there. In 244 plankton tows in the Bay, the only Dungeness crab zoeae we collected were one stage I and one stage II, both on February 13, 1976 in central San Francisco Bay. Hatching of other *Cancer* larvae does occur in the Bay, and we collected ovigerous females and early-stage zoeae of the red crab, *C. productus,* slender crab, *C. gracilis,* rock crab, *C. antennarius,* and yellow crab, *C. anthonyi,* there during our study.

During the 5 years of the study, we found stage I Dungeness crab zoeae at most of our routinely sampled Gulf stations (Figure 28). Relatively high oblique tow densities of stage I zoeae were found at Gulf stations with bottom depths of 30 to 70 m. On 26 occasions, stage I zoeae were collected in these tows at densities greater than 20/100 m^3; only one of these occurred at a station not within this depth range. During the January 6–12, 1978 cruise, stage I zoeae were absent at many stations within 5 km of shore and in the outer reaches of the Gulf (Figure 29).

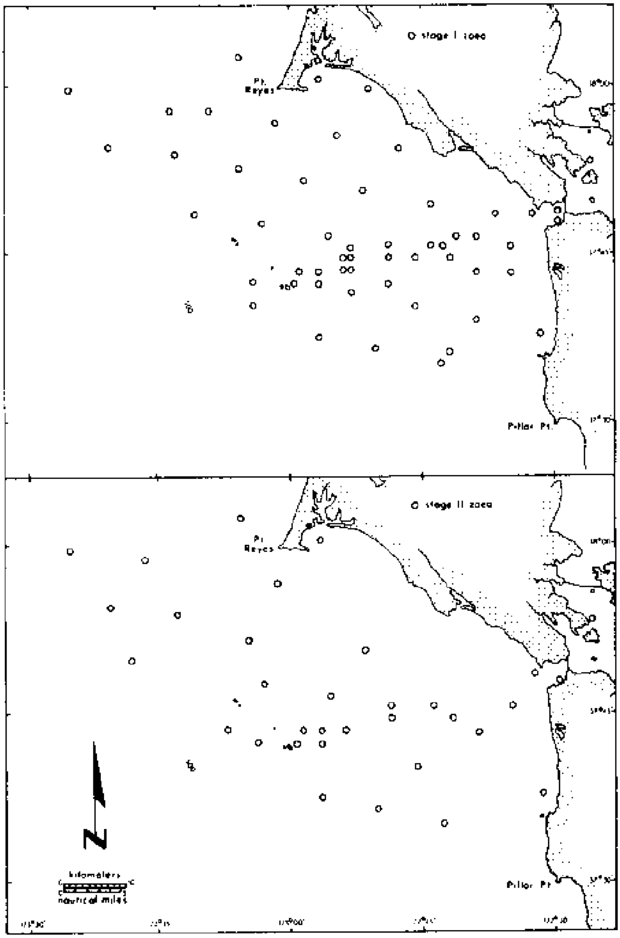


FIGURE 28. Distribution of Dungeness crab stage I and II zoeae in the Gulf of the Farallones, 1975–1980.

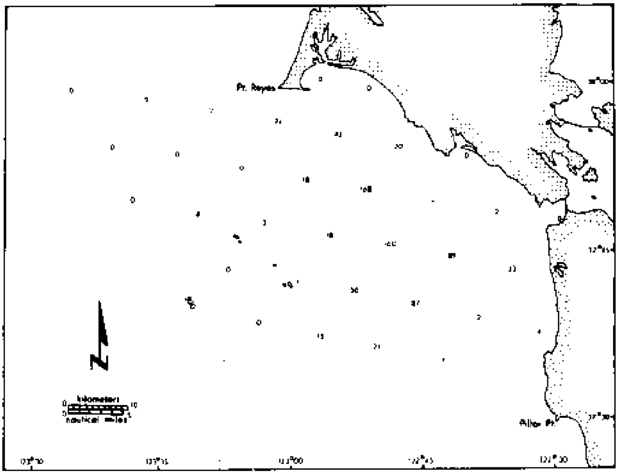


FIGURE 29. Oblique tow densities (number/100 m^3) of Dungeness crab stage I zoeae in the Gulf of the Farallones, January 6–12, 1978.

Our data suggest that Dungeness crab larvae occupy a unique niche among larval brachyurans in the Gulf. At most stations greater than 30-m depth, Dungeness crabs were the most common brachyuran stage I zoeae in our January samples, usually occurring at far greater densities than any other species. Occasionally, they co-occurred with stage I *C. productus* and *C. oregonensis*, but these species have a longer hatching season in central California, particularly *C. productus*.

Diel vertical migration of Dungeness crab stage I zoeae was evident in day and night samples collected from discrete depths during the January 6–12, 1978 cruise. The zoeae were more abundant at the surface by night and at 15- and 25-m depths by day (Table 8); using the multi-way contingency table method, day versus night densities at these levels were significantly different ($P = 0.01$).

Horizontal dispersal was evident during the early zoeal stages. On the Farallon Islands transect on January 14, 1976, all stage I zoeae were found between 13 and 26 km from shore. Two weeks later they occurred from 1 to 42 km from shore, although densities within 13 km were low.

Our March 1978 cruise was conducted after a large plume of estuarine water had entered the Gulf (Figure 22). At this time, we found only stage I and II zoeae in Gulf samples, all at low densities. All stage II zoeae were associated with water in which surface salinity was greater than 32 ppt, even though approximately 50% of the Gulf surface water ranged in salinity from 23.2 to 31.7 ppt. In laboratory studies, salinities within this range did not adversely affect larval survival (Reed 1969). Thus, low salinity probably did not cause mortality in the

Gulf, but advancement of estuarine water apparently aided offshore movement of zoeae.

TABLE 8. Densities (No./100m^3) of Dungeness Crab Stage I Zoeae in the Gulf of the Farallones, January 6–12, 1978.

	Day samples				
Station no. (Figure 14)	*Surface tow*	*5-m tow*	*15-m tow*	*25-m tow*	*Oblique tow*
917	1	–	2	0	2
1007	0	1	22	24	30
1116	0	3	95	–	89
1165	10	14	544	486	160
1216	3	3	22	8	18
1241	0	0	0	0	0
1414	4	17	225	16	171
1639	0	0	0	0	0
1709	128	92	189	70	74
1757	3	32	52	16	2
1804	0	0	0	0	0
1851	0	0	0	0	0
	Night samples				
784	26	1	3	7	7
824	3	4	3	6	21
864	12	2	3	4	15
874	22	5	0	–	4
906	0	0	0	0	0
961	169	28	2	24	87
1053	0	1	0	0	1
1068	30	2	0	–	20
1100	0	0	0	0	0
1299	0	2	0	–	0
1332	0	1	0	5	8
1357	217	15	18	26	–
1390	0	0	0	0	0
1472	31	13	16	1	18
1529	0	0	0	0	0
1552	0	0	0	–	0
1584	0	0	0	0	0
1607	5	11	1	–	20
1660	9	9	9	56	43
1819	1	0	0	7	0
1865	6	0	1	–	0
1274	1	0	0	0	3

We observed similar results during December 1979 and January 1980 when substantial rainfall and Delta outflow caused an extensive plume of estuarine water in the Gulf (Reilly, Chapter 5). On the December 27, 1979 transect to the Farallon Islands, no stage I zoeae were found within 20 km seaward of the Golden Gate Bridge but maximum densities occurred 25 to 35 km seaward. The plume extended into the Gulf approximately 15 to 20 km. On January 21, 1980, the plume had advanced to 40 km seaward. Stage I densities had decreased from 32 to 56/100 m^3 to 3 to 8/100 m^3; most of the zoeae probably had molted to stage II by then. We only collected stage II zoeae seaward of the plume at our most distant station.

Continued movement of zoeae out of the Gulf was evident as the stages progressed (Figure 30). During the entire study, we collected only 65 stage III, 26 stage IV, and 10 stage V zoeae inshore of the 500-fm (915-m) depth contour which lies approximately 10 km seaward of the Farallon Islands. No stage V zoeae were found within 36 km of shore. On March 3, 1979, at a station 4 km seaward of the Islands, densities of stage I, II, III, and IV zoeae were 4, 13, 15, and 5/100 m^3, respectively.

To determine whether scarcity of late-stage zoeae in our Gulf samples could be due to zoeae descending to the ocean floor, which previous plankton tows probably had not sampled adequately, we conducted 27 bottom tows with the plankton sled during March and April 1978 cruises and one additional tow in April 1980. Although *Cancer* larvae occurred in these tows at densities as high as 2,090/100 m^3, no Dungeness crab larvae were found. No late-stage Dungeness crab zoeae were collected in any plankton tows in the Gulf in 1978 and 1980. Thus, we could not compare bottom and oblique tows. In fact, late-stage zoeae were absent from Gulf waters during most of our sampling.

Megalopae

Although late stage zoeae were most abundant offshore, we frequently collected megalopae at routinely sampled Gulf stations from April to June (Figure 30). In 1976, 14 megalopae were captured in the Gulf, all in the northern section. In April 1977, we captured 366 megalopae. The highest densities occurred in the Gulf within 15 km of Pt. Reyes. Surface isotherms during the same period showed colder water entering the Gulf from the north (Figure 21). It is possible that megalopae were transported into the Gulf with it. In May 1977, and April and May 1978, our total catch of 20 megalopae again came from the northern Gulf. In June 1977, we dipnetted more than 500 *V. velella* from Gulf surface waters. Although these coelenterates occurred throughout the Gulf, those carrying megalopae were only found north of the entrance to San Francisco Bay and within 20 km of shore. During the April–May 1979 cruise, which extended to the Bodega Bay area in the northern Gulf, relatively high densities of megalopae again occurred within 15 km of Pt. Reyes. Megalopae also occurred at relatively high densities north of Pt. Reyes within 10 km of shore. One station yielded 306 megalopae in a 10-min surface tow (139/100 m^3). Few or no megalopae were found at stations farther seaward. During the April 1980 cruise, we sampled stations to 50-km seaward of Bodega Bay and megalopae occurred only within 31 km of shore.

In April 1979, we conducted a series of night-light stations from our research vessel. In Drakes Bay (Figure 17) the light attracted an estimated 100,000 megalopae within an hour's time on each of two successive nights. Smaller numbers were attracted in Bodega Bay and central San Francisco Bay and a few were observed near Southeast Farallon Island.

In the southern Gulf, station 961 (Figure 14), 24 km from shore, yielded good catches of megalopae on three occasions. Surface tow densities during the April 1977 and April–May 1979 cruises were 14 and 21/100 m^3, respectively. We also dipnetted 100 *V. velella* at this station on April 30, 1979 and found 50 megalopae, the highest ratio of megalopae to *V. velella* we observed during the study. However, most southern Gulf stations generally yielded few or no megalopae.

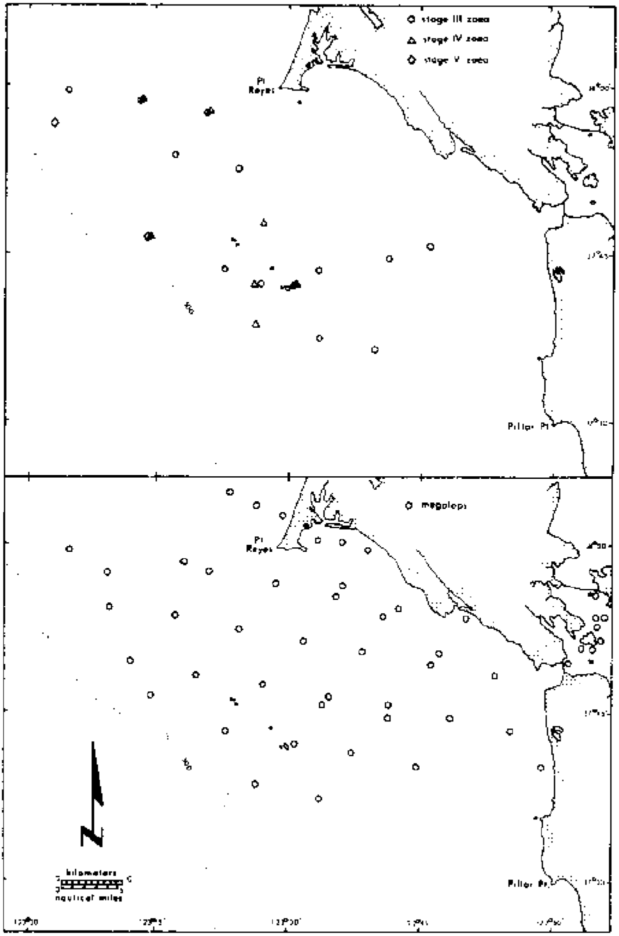


FIGURE 30. Distribution of Dungeness crab stage III, IV, and V zoeae and megalopae in the Gulf of the Farallones, 1975–1980.

Day vs. Night Distributions. Thirty-four Gulf stations were occupied during the April 1977 cruise when 366 megalopae were collected. We sampled 12 stations, once by day and once by night, to determine vertical distribution of megalopae. We statistically compared megalopal densities for day versus night surface and oblique tows (Table 9) using Student's t-test. Day and night surface tow densities were not significantly different, nor were day and night oblique tow densities. However, day surface tow densities were significantly greater than day oblique tow densities ($P = 0.05$) and night surface tow densities were significantly greater than night oblique tow densities ($P = 0.01$). In April 1980, at a night station 4 km west of Bodega Bay, a series of discrete-depth tows at the surface, 5 m, 15 m, 25 m, and an oblique tow yielded megalopal densities (no./100 m^3) of 3.7, 15.8, 5.6, 0.0, and 2.5, respectively. These data show that megalopae occur more frequently in the upper 15 m of the water column. Their vertical distribution differs from that of stage I zoeae in that relatively high densities of megalopae occur in the upper 15 m during both day and night.

TABLE 9. Densities (No./100 m^3) of Dungeness Crab Megalopae in the Gulf of the Farallones, April 6–11, 1977.

	Day		*Night*	
Station	*Surface*	*Oblique*	*Surface*	*Oblique*
784	0	0	0	0
864	0	0	1	1
961	14	4	0	0
1053	0	0	1	1
1165	9	0	1	5
1274	1	1	0	1
1390	1	1	0	0
1529	22	0	33	6
1639	1	1	2	0
1660	43	3	13	1
1757	0	1	26	4
1851	0	0	0	0

As megalopae approach the molt to the juvenile stage, they settle to the bottom. Although megalopae were found throughout the Gulf, they were found at the bottom primarily in the nearshore zone and occasionally in the Bay. Although their presence in stomachs of demersal fishes indicates that settling occurred to a maximum bottom depth of 60 m (Figure 31), of 995 megalopae taken from demersal fish stomachs outside the Bay, 965 occurred at stations with depths less than 25 m, including samples from the Pt. Reyes–Bodega Bay area.

We collected 97 megalopae in plankton tows in central San Francisco Bay between the Golden Gate Bridge and the Richmond-San Rafael Bridge. One megalopa in the stomach of a Pacific staghorn sculpin, *Leptocottus armatus*, collected near Pinole Point in San Pablo Bay represents the maximum penetration into the Bay in our samples. We did not have sufficient data to determine the statistical significance of megalopal densities in surface and oblique tows in the Bay. However, on May 6, 1979, at a station near the Golden Gate Bridge, an oblique tow yielded 44 megalopae compared to only four megalopae in a surface tow of similar duration. This suggests that megalopae may be carried into

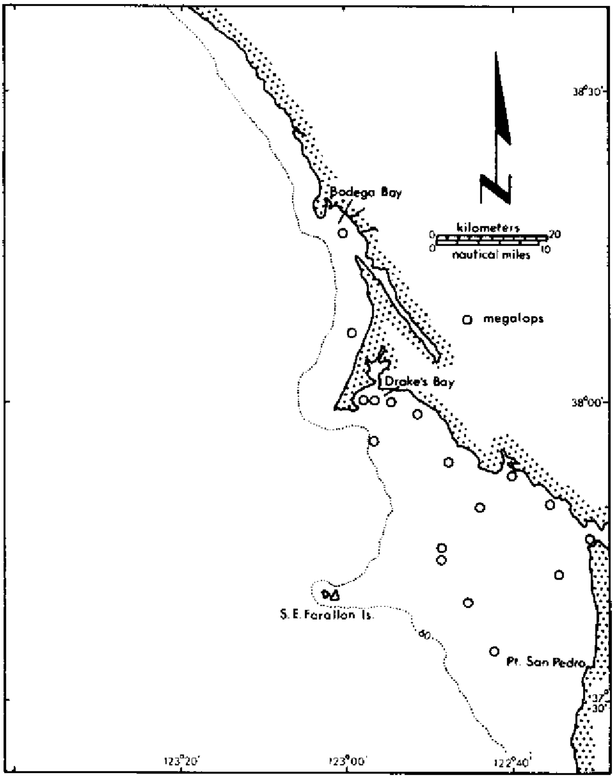


FIGURE 31. **Distribution of newly settled Dungeness crab megalopae from Bodega Bay to Pt. San Pedro, based on fish stomach analysis, 1975–1979.**

the Bay by bottom currents after settling in the Gulf or that they descend from surface waters as they enter the Bay.

Distribution of Larvae From the Gulf to Northern California

One cruise conducted in March 1979 (Figure 17) provided much of the data from which distributions of various stages in northern and central California were determined. This cruise, conducted from the Gulf to Cape Mendocino and to 100 nautical miles (185 km) seaward, collected all Dungeness crab larval stages including 11 stage I, 19 stage II, 129 stage III, 103 stage IV, and 681 stage V zoeae, and 18 megalopae. Before 1979, we did not encounter any stage V zoeae in the Gulf study area. The March 1979 cruise extended farther offshore and apparently coincided with a peak occurrence of stage V zoeae in California.

Zoeae

Offshore Dispersal. The pattern of larval distribution demonstrated substantial offshore dispersal as zoeal stages progressed (Figures 32 and 33). All stage I and II zoeae were found within 50 km of shore while stages III–V extended to 185 km from shore. Maximum offshore dispersal was apparent during stage III. We collected stage II and III zoeae at relatively high densities off Cape Mendocino at one station over the continental shelf where we observed a well-defined color change in the surface water. The salinity inshore of the boundary was 0.5 ppt less than that immediately seaward. This may have been the boundary of coastal water diluted by winter rain and runoff; early-stage zoeae occurred seaward of it. Stage V zoeae were collected at stations 24 to 186 km from the coast but were most abundant from 40 to 150 km. They occurred farther from shore off Cape Mendocino and Pt. Arena than in the vicinity of the Gulf.

Relative age of stage V zoeae on this March 1979 cruise, as determined by readiness to molt also suggests continual offshore dispersal of zoeae. Readiness to molt was determined by examination for withdrawal of tissue from the exoskeleton, particularly in dorsal and rostral spines and the telson. Larger percentages of stage V zoeae close to molting were found farthest from shore (Table 10).

TABLE 10. Percentages of Dungeness Crab Stage V Zoeae Close to Molting, March 20–29, 1979.

	Distance from shore (km)			
	0–50	*51–100*	*101–150*	*> 151*
Number collected	40	550	74	17
Percentage (%) close to molting	17.5	18.7	40.5	35.3

Of 168 stage V zoeae collected in oblique tows during this cruise, 98.8% occurred at stations with depths in excess of 500 fm (915 m), while 72% of the stations sampled had depths greater than this. A step-wise multiple regression analysis was performed with stage V zoeal density as the dependent variable and station depth, latitude, distance from shore, time of day, surface temperature, surface salinity, 25-m temperature, and 25-m salinity as independent variables. A coefficient of multiple determination (r^2) of 0.18 was obtained with all independent variables included in the regression. Among the independent variables, depth contributed most to the overall r^2 ($\Delta r^2 = 0.11$), followed by latitude ($\Delta r^2 = 0.04$). However, the overall low r^2 indicates that very little (18%) of the variation in offshore dispersal is explained by these variables.

Limited data from stations sampled off Eureka (Figure 15) from 1977 to 1980 also indicate offshore dispersal of larvae. In March 1978, for example, all stage V zoeae occurred seaward of the continental shelf, over the continental slope (depth 200 to 1,000 m). However, the Eureka transects extended only 53 km seaward, and it is likely that we sampled only part of the offshore range of the

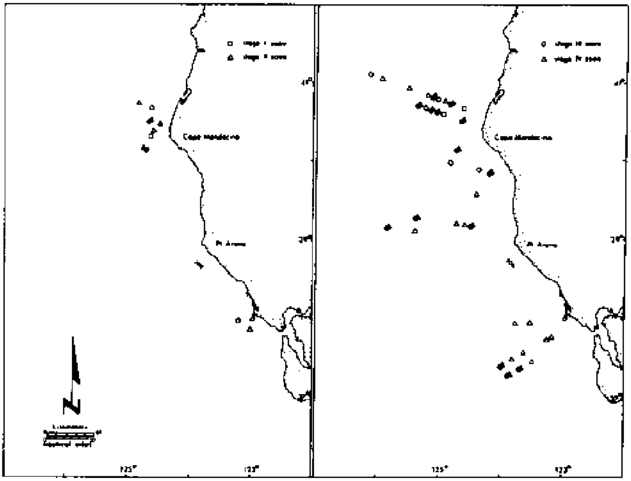


FIGURE 32. Distribution of Dungeness crab stage I, II, III, and IV zoeae in central and northern California, March 20–29, 1979.

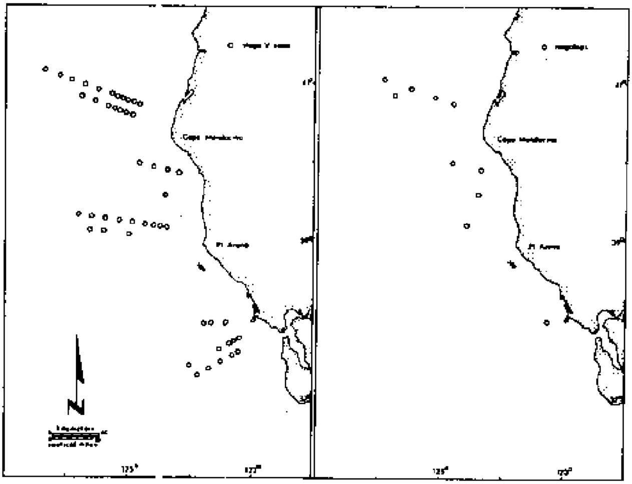


FIGURE 33. Distribution of Dungeness crab stage V zoeae and megalopae in central and northern California, March 20–29, 1979.

late-stage zoeal population in that area.

The fact that nearly all stage V zoeae were collected seaward of the continental shelf does not imply a causal relationship with water depth, but is most likely a result of dispersal by ocean currents.

Diel migration. Night surface tows were conducted at 25 stations during the late March 1979 cruise. Densities of stage V zoeae at two of these stations, one 75 km seaward of Pt. Arena and the other 74 km seaward of Cape Mendocino, were 374 and 154/100 m^3, respectively. Only four daytime surface tows were conducted at stations within the range of occurrence of stage V zoeae and no larvae were found. At one night station in which stage V zoeae were collected at the surface (9/100 m^3), none were found in tows at 5, 15, and 25 m. The highest densities of stage III (45/100 m^3) and IV (34/100 m^3) zoeae observed during the study also occurred in night surface tows. Although we did not have sufficient data to test statistically for vertical migration, it appears that late-stage zoeae exhibit similar diel behavior as stage I zoeae in that they occur more frequently in surface waters by night than by day.

Megalopae

All 18 megalopae collected during the March 1979 cruise had molted recently, as evidenced by soft exoskeletons. Megalopae were more abundant in surface than in oblique tows and occurred from 34 to 148 km from the coast. By contrast, 1 month later we found megalopae aggregated nearshore.

CalCOFI Samples

Results from the CalCOFI collections must be considered in the context of their sampling plan, which was designed as a fish egg and larval survey that extended more than 1,000 km from the coast, and in which collection efforts were less intense in the nearshore zone than in our study. Nevertheless, CalCOFI results support our observations. Most Dungeness crab larvae (>98%) occurred within 200 km of shore and distribution of the larvae provides further evidence of offshore drift during zoeal development with subsequent inshore movement of the megalopae (Figures 34, 35, and 36). Only 10 of 733 stage I zoeae were collected seaward of the 500-fm (915-m) depth contour, while 109 of 110 stage V zoeae were found in this range. Substantial drift offshore, to 143 km, was observed for zoeal stage II. The occurrences of one stage III zoea 235 km seaward and one megalopa 296 km from shore exemplify the potential offshore drift that may occur during larval development. By contrast, only one of 57 megalopae collected in March was found within 90 km of shore, while 77 of 82 megalopae occurred there in April.

Relative Abundance of Larvae

Maximum Densities by Stage

The terms "low" and "high" have been used frequently in this chapter to describe larval densities. A summary of maximum densities from oblique tows for each larval stage (Table 11) may serve to define the above terms and allow comparisons between years and with other studies. The maximum oblique tow density (896/100 m^3) of stage I zoeae in 1976 (Table 11) was the highest density

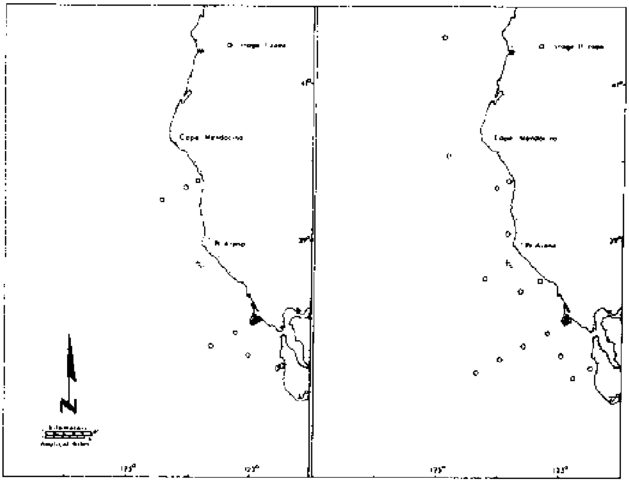


FIGURE 34. Distribution of Dungeness crab stage I and II zoeae in central and northern California from CalCOFI samples, 1949–1975.

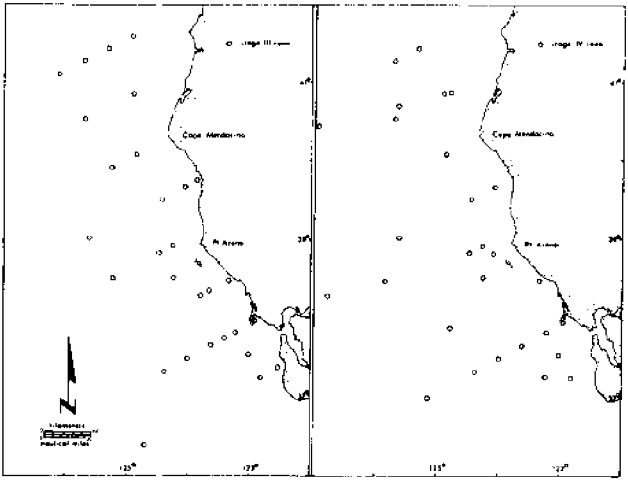


FIGURE 35. Distribution of Dungeness crab stage III and IV zoeae in central and northern California from CalCOFI samples, 1949–1975.

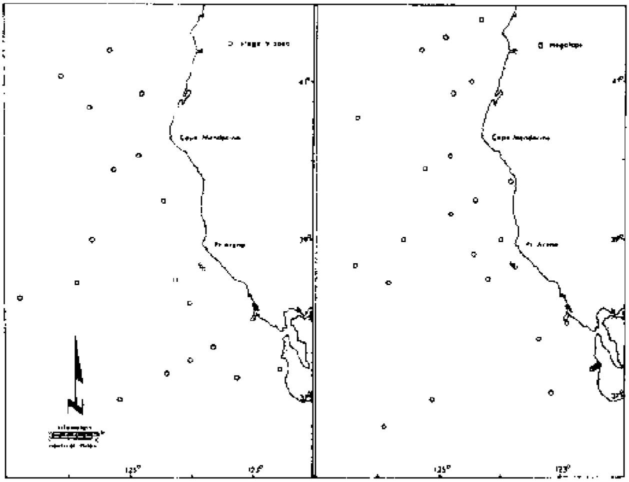


FIGURE 36. Distribution of Dungeness crab stage V zoeae and megalopae in central and northern California from CalCOFI samples, 1949–1975.

of Dungeness crab larvae we collected. However, a 15-m tow in January 1978 yielded stage I zoeae at a density of 544/100 m^3.

Discrete depth tows at times resulted in considerably higher densities than oblique tows, reflecting vertical distribution of larvae. For example, maximum densities of stage V zoeae and megalopae, observed in surface tows in 1979, were 374 and 139/100 m^3, respectively, compared to 14 and 16/100 m^3 in oblique tows in 1978 and 1979, respectively (Table 11).

Sampling Variability

The distribution of planktonic organisms is non-random and usually patchy (Cushing 1962; Barnes and Marshall 1951) and considerable variability often occurs in plankton samples. To analyze for variability in our samples, five replicate oblique tows were taken at each of three stations during the night of January 12, 1978. The tows were conducted sequentially at 10-min intervals while the ship circled. A normalizing logarithmic transformation was performed on the data and 95% confidence limits were determined for mean densities of stage I zoeae in the tows (Table 12). The unusually high standard deviation in our data from station 1165 resulted from the absence of stage I zoeae in one of the tows. Subsequent analysis indicated that zoeae occur more abundantly in surface waters at night and, thus, oblique tows would have a greater probability of missing surface "patches" of zoeae than surface tows. However, results from

TABLE 11. Maximum Densities (No./1000m³) of Dungeness Crab Larval Stages Collected by Oblique Plankton Tows (GF= Gulf of Farallones; EK= Eureka Area; SF= San Francisco Bay Complex; PA= Pt. Arena; BB= Bodega Bay Area).

	Zoeal stage I		*Zoeal stage II*		*Zoeal stage III*		*Zoeal stage IV*		*Zoeal stage V*		*Megalopa*	
	Density	*Area*	*Density*	*Area*	*Density*	*Area*	*Density*	*Area*	*Density*	*Area*	*Density*	*Area*
1975	NS *		NS		NS		NS		NC †		1	GF
1976	897	GF	44	GF	1	GF	1	GF	NC		4	GF
1977	NS		NS		11	EK	5	EK	NC		10	GF
1978	171	GF	6	GF	4	GF	2	EK	14	EK	2	GF,EK
1979	447	GF	51	EK	30	EK	5	GF	5	EK	16	SF
1980	290	EK	NS		NS		NS		NS		3	BB
CalCOFI	78	GF	165	GF	18	GF	3	GF	3	PA	5	GF

* NS= Primary larval period not sampled.
† NC= None collected.

stations 1068 and 1116 are within the range of variability for individual crustacean species reported by other workers, as summarized by Wiebe and Holland (1968). Our sampling effort proved adequate to show differences of at least one order of magnitude.

TABLE 12. Sampling Variability of Stage I Zoeae from Replicate Oblique Plankton Tows in the Gulf of the Farallones, January 12, 1978 (x = No./100 m^3; $y = \log_{10} x$).

	Station 1068		*Station 1116*		*Station 1165*	
Tow number	*x*	*y*	*x*	*y*	*x*	*y*
1	32.7	1.515	5.9	0.771	1.0 *	0.000
2	17.1	1.233	8.7	0.940	29.1	1.464
3	16.5	1.217	9.0	0.954	22.8	1.358
4	17.6	1.246	8.9	0.949	28.6	1.456
5	14.7	1.167	5.6	0.748	22.3	1.348
Sum	98.6	6.378	38.1	4.362	103.8	5.626
Mean	19.72	1.276	7.62	0.872	20.76	1.125
SD		0.137		0.103		0.665
95% CL		41.6–240%		51.8–193%		1.43–6998%

* Due to zero density in this tow, the transformation of log (x + 1) was used for all tows at station 1165.

Relationship to Water Temperature

An inverse relationship was observed between relative abundance of stage I zoeae in the Gulf and water temperature. The highest density of stage I zoeae we collected occurred in January 1976 when Gulf temperatures during December 1975–January 1976 (Table 7) were colder than any other December–January period during the study. Gulf temperatures during December 1976–January 1977 were warm and, although we began sampling in January, we missed the peak stage I zoeal period which was early that year. The 1979 larval year class, the strongest during our studies, also hatched in relatively cold water, while the 1978 and 1980 year-class hatches occurred during warmer conditions and resulted in lower larval production. Student's t-test was used to compare mean densities of stage I zoeae from oblique tows taken on Golden Gate-Farallon Islands transects from 1976 to 1980 using the transect that produced the best catch each year. There was considerable variability in individual samples and the only statistically significant difference was that mean density for 1976 was greater than that for 1980 (P=0.05, t=2.35, d.f.=10).

Central California vs. Northern California

On January 22, 1980, stage I zoeae occurred at a maximum density of 290/100 m ^{3} off Eureka, while the highest density in the Gulf for the 1980 larval year class was 56/100 m^3 on December 27, 1979. In March 1979, transects (20 to 30 stations each) to 185 km seaward off Cape Mendocino, Pt. Arena, and the Gulf yielded average densities of stage V zoeae in oblique tows of 1.3, 0.7 and 0.4/100 m^3, respectively. These data suggest that zoeal abundance may be directly related to the magnitude of the spawning stock which presumably is larger in northern California.

Stage I Zoeae vs. Megalopae in the Gulf

The relative abundance of stage I zoeae and megalopae in the same year class in the Gulf were not consistently related. We sampled too late in 1975 and 1977 larval seasons to estimate adequately stage I zoeal densities. In 1976, stage I zoeal densities were high, but the catch of megalopae was poor. In 1979, stage I zoeae and megalopae were relatively abundant, while in 1978 and 1980 densities of both were low.

Megalopae vs. Juveniles

The relative abundance of megalopae was consistently related to strength of the new year class of post-larval crabs in the Gulf and the Bay (Tasto, Chapter 9; Reilly, Chapter 10). Juvenile year classes in 1976 and 1978 were relatively weak and catches of megalopae also were poor in both years. Stronger juvenile year classes occurred in 1977 and 1979 when megalopal abundance also was high. During the peak megalopal period (estimated from highest catches), the average density for surface tows in the Gulf was 4.1 and 0.1/100 m^3 in 1977 and 1978, respectively. In the Pt. Reyes-Bodega Bay area the average density for surface tows during April–May 1979 was 18.6/100 m^3. Limited data suggest that the 1980 year class of megalopae was weak; average surface tow densities during our April 1980 cruises in the Fort Bragg and Bodega Bay-Pt. Reyes areas were 0.3/100 m^3 and 0.5/100 m^3, respectively.

CalCOFI Samples

Data from CalCOFI samples (Table 5) were sparse when considered in the context of time and geographical area. Thus, no definite conclusions could be reached concerning pre- and post-decline years or geographical variations in abundance.

DISCUSSION

Timing of Larval Occurrences

We observed the peak hatching period of Dungeness crab larvae in the Gulf of the Farallones to vary from late December to early January. Hatching was early when temperatures during the December–January period were warm and later when they were cool. Laboratory studies with ovigerous Dungeness crabs verify this inverse relationship between water temperature and both egg development and hatching times (Wild, Chapter 16).

Larval development time also has been shown to be inversely related to water temperature (Poole 1966; Reed 1969). Reed (1969) reported a development time of approximately 90 days to the megalopal stage at 10 C and 25 to 30 ppt salinity. Complete larval development time in Poole's laboratory studies with water temperature constant at 10.6 C was 111 days. However, only one of his larvae reached the first post-larval instar. Gaumer (1969) found that 109 days were needed at 11 C to complete larval development. Lough (1974) observed the peak appearance of stage I zoeae in mid- to late January in Oregon waters. He estimated length of the larval period to average approximately 130 days. Because winter temperatures in central California generally are 2 to 3 C warmer than in Oregon waters, my estimate of the length of the larval period (105 to 125 days) appears to be reasonable.

Distribution

Horizontal Dispersal

Most Dungeness crab larvae in central California hatch and complete their early zoeal development during the Davidson Current period when the general pattern of circulation along the coast has a net northward movement (Reid and Schwartzlose 1962; Pirie and Steller 1977). We were not able to discern northward or southward (alongshore) drift of larvae in our samples; however, Lough (1976) concluded that northward larval transport, based on the average speed of the Davidson Current in Oregon waters, could be up to 150 miles (280 km) per month.

We found that considerable offshore movement of larvae occurs during zoeal stages II-V. The larvae appear to be transported seaward from the onset of hatching, but most molt to the second zoeal stage before reaching the continental slope. Offshore movement of zoeae appears to be aided by estuarine runoff and possibly also by upwelling, especially for late stages in the Pt. Arena and Cape Mendocino areas. Geostrophic flow offshore may occur throughout the year in central California north to Cape Mendocino (Richard Parrish, NMFS, pers. commun.).

The factors influencing larval distribution north of Cape Mendocino are less clear. We found zoeae to be farther from shore in northern than in central California, yet onshore flow occurs during January and February north of Cape Mendocino (Richard Parrish, NMFS, pers. commun.). It seems possible that some larvae occurring in northern California waters in March could have hatched in central California and were transported offshore by estuarine runoff and carried northward by the Davidson Current. Caumer (1971) theorized that larvae hatching in northern California in December could be carried northward to British Columbia by the time they settled out.

Studies of larval distribution in Oregon contrast in part with results of our study. Peterson et al. (1979) concluded that surface waters are transported northward and onshore from October to March in Oregon. Lough (1976) found the majority of early stage Dungeness crab larvae within 10 miles (16 km) of shore and attributed this to retention by an onshore component of the Davidson Current. However, Lough (1974) found stage III-V zoeae and megalopae at stations 45 to 60 miles (72 to 96 km) from shore which also suggests offshore drift similar to results from our study. Lough did not capture any Dungeness crab stage V zoeae within 16 km of shore. He reasoned that the volume of water filtered at inshore stations was inadequate and that late-stage zoeae may be associated with the ocean bottom. We did not collect any Dungeness crab larvae in bottom tows with the plankton sled in the Gulf in March and April 1978 or April 1980.

Our results demonstrate the recruitment of megalopae to nearshore ocean waters of central California following a period in which stage V zoeae were generally absent within 40 km of shore. Lough (1974) observed large numbers of megalopae within 10 miles (16 km) of the Oregon coast during April and May in 1970 and 1971. In 1975, Wickham (1979b) dipnetted *V. velella* seaward of Bodega Bay to 24 km and found megalopae only on those within 10 km of shore. In May 1976, Wickham (1979b) observed two distinct bands of megalopae in surface waters 1 and 8 km offshore of Bodega Bay with an estimated average density of $1/m^2$. More recently, aging of megalopae by intermolt staging (Hatfield, Chapter 7) has provided further evidence of inshore transport. Megalopae that were more advanced in their development occurred closer to shore and in San Francisco Bay in central California.

We were unable to determine the mechanism for inshore transport of megalopae which occurs at a time when offshore Ekman transport of surface waters induced by northwesterly winds is common. Studies by Bourke et al. (1971) off Oregon, indicate that wind-driven water motion may extend to a depth of 10 m and that flow in the Eckman surface layer is offshore. Hachey and Fothergill (1953) found that winds greater than 10 mph will influence the magnitude and direction of surface currents, but that a given surface current is a complex mixture of wind current, tidal current, and semi-permanent current. In central California, the arrival of megalopae in nearshore waters generally occurs in April after the onset of predominantly northwest winds in March (Figure 24). From April to June, winds blow predominantly from the northwest with Ekman transport directed offshore which makes it difficult to understand how megalopae become aggregated nearshore. The formation of counter-clockwise eddies in the vicinity of headlands during the upwelling period is a possible explanation.

Northwesterly winds blowing toward the coast in the spring cause rafts of *V. velella* to wash ashore in central California (Wickham 1979b); megalopae are often found attached to them. We have found the occurrence of these hydroids in central California to be sporadic. Therefore, although they occasionally may be of importance as inshore transporters, they could not account for the annual recruitment of megalopae. Recruitment from the north could explain the presence of megalopae in the Gulf in June 1977 after a major period of settling and molting to the juvenile stage had occurred in early April. Dipnetting of *V. velella* in June yielded an average of 1 megalopa/10 *V. velella* in the northeastern section of the Gulf, an area of approximately 1×10^9 m^2. Although we did not estimate the average density of *V. velella*, a conservative value of $1/100$ m^2 would indicate that almost 1 million megalopae were present on *V. velella*. At a maximum speed of 20 km/day (Schwartzlose and Reid 1972), the California Current could transport megalopae from the Oregon border to Pt. Reyes during an average 25-day megalopal period. Temperatures south of Cape Mendocino during the spring of 1977 were colder than in any other year of the study; this would prolong development and extend southerly transport.

Larvae of the anomuran sand crab, *Emerita analoga*, frequently co-occurred with Dungeness crab larvae in offshore samples from the CalCOFI collection and our study (Hatfield, Chapter 8). Efford (1970) discussed several aspects of the planktonic life history of *E. analoga* which closely parallel those of the Dungeness crab. Development time from hatching to settling is approximately 4 months and megalopae begin to arrive on California beaches in large numbers by April. He proposes a hypothesis in which larvae drift from one current to another and back again via interconnecting eddies. In this manner many would be retained nearshore. No evidence, however, is presented from plankton samples to support this concept.

Mayer (1973) related the recruitment of megalopae into Similk Bay, Washington to tidal and density currents. The megalopae that occasionally enter central San Francisco and San Pablo Bays most likely are transported by density currents of high-salinity bottom water. The vertical extent of these currents is not known, but we observed a halocline at approximately 5 m in the Gulf near the Golden Gate during periods of high Delta outflow. Conomos et al. (1970) found that seabed drifters released within 25 km of the Bay entrance moved into the Bay.

Sandifer (1973 and 1975) noted that many species of decapod larvae in Chesapeake Bay were more abundant in the lower layer of the water column where net transport is upstream. This distributional adaptation would retain them in the estuary. *C. irroratus* larvae were occasionally found in low concentrations in the Bay. However, he found no tendency for *C. irroratus* larvae to concentrate near the bottom; surface and bottom concentrations were 44.3% and 55.7%, respectively. No megalopae or stage V zoeae were collected. Apparently most *C. irroratus* larvae hatch offshore and some are retained within the Bay by chance only. Sandifer concluded that the Chesapeake Bay population is apparently restocked by migration of animals from the inner-shelf area. Bigford (1979) speculated that passive migration of *C. irroratus* stage V zoeae, megalopae, and juveniles, aided by bottom currents, is a major factor in recruitment to Chesapeake Bay. We found high densities of Dungeness crab stage V zoeae in night surface tows offshore and aggregations of megalopae in the upper layer of the water column nearshore and occasionally in San Francisco Bay.

Vertical Migration

Analysis of our field data shows that stage I Dungeness crab zoeae undergo diel vertical migration; they were captured more frequently near the surface by night and at 15- and 25-m towing levels during the day. The data also suggest that later zoeal stages have a similar diurnal distribution. These behavioral adaptations may be related to observed patterns of dispersal and aggregation. During early zoeal development in winter, nights are longer than days and larvae would thus spend more time in surface waters. They would then be influenced more by estuarine runoff and would be transported offshore. In contrast, we observed the highest densities of megalopae in the upper 15 m both day and night in the nearshore area. It is unclear how this change in vertical orientation affects their horizontal distribution.

In laboratory studies, Gaumer (1971) reported that Dungeness crab zoeae and megalopae displayed positive phototaxis to light intensities of 25 and 240 ftc and a negative response to 990 ftc. Megalopae exhibited the strongest negative response to the water surface or light. He predicted that larvae in the ocean would approach the water surface at night and the opposite response should be expected during daylight hours. However, he implied that the megalopal response may be a trait of cultured megalopae and reported field observations of megalopae actively swimming on the surface in Yaquina Bay, Oregon during the day.

Jacoby (1980) tested responses of Dungeness crab larvae to light intensities of 4, 20, 90 and 4500 ftc. The latter corresponds to full sunlight at the ocean surface in central California. Stage III, IV, and V zoeae moved toward brighter light than stages I and II, but megalopae moved only toward the dimmest light unless pressure was increased. However, megalopae never moved toward the brightest light.

Jacoby found that all Dungeness crab larval stages could detect gravity and pressure changes but that their responses were too inconsistent to predict field behavior. Bigford (1977 and 1979) reported that stage I and III *C. irroratus* were geonegative and stages II, IV and V were geopositive without directional light or increased pressure. Megalopae remained on the bottom of the experimental chamber. He observed a "pre-megalopal" behavior pattern as the fifth stage progressed in which depth maintenance by swimming was reduced gradually.

Larval Abundance and Sampling Variability

I did not find a consistent relationship between larval abundance and subsequent recruitment to the commercial fishery for a given year class. We began sampling stage I zoeae in January 1976. This relatively strong zoeal year class, which was followed by weak megalopal abundance, contributed to the fishery during the 1978–79 and 1979–80 seasons; the 1977 larval year class with highest megalopal abundance contributed to the fishery in 1979–80 and 1980–81, assuming 3 and 4-year lag times. Landings were above average for northern California and remained low in central California (Figure 10). Gregory Lough (Oregon State University, unpublished manuscript) could not relate Dungeness crab larval abundance in 1970 and 1971 to commercial landings in Oregon. Mean abundance of early-stage zoeae at four inshore stations in Lough's study was 680 and 190/100 m^3 in 1970 and 1971, respectively. These are in the same order of magnitude as maximum stage I zoeal densities in 1976 and 1979 in the Gulf. Lough found that Oregon crab landings in 1974 and 1975 were extremely low and similar for these 2 years. Compounding our problem is lack of knowledge of the ultimate destination of larvae produced in the Gulf. If larvae return to the area of hatching, then comparisons of stage I zoeal densities between areas may be valid. On the other hand, larval production in the Gulf may contribute to recruitment in northern California and (or) some may be lost by offshore drift.

We attempted to minimize sampling variability by using larger mesh for collecting late-stage zoeae and megalopae, thereby reducing avoidance, using flowmeters to determine the amount of water filtered, and sampling frequently to minimize effects of non-random spatial distribution of larvae. Variability in our sampling results was small enought to enable us to discern differences in average larval densities of at least one order of magnitude. Lough (1974) conducted six replicate tows at one station in Oregon waters and reported 95% confidence limits of 4 to 2484% for seven species of brachyurans. He attributed this wide range to the low number of larvae collected. No Dungeness crab larvae were found in these tows. Series of duplicate tows the same year yielded more narrow limits (e.g. 44 to 230% for *C. oregonesis* stage II zoeae), although the range for Dungeness crab megalopae, 3 to 3227%, was high. Confidence limits for single observations for individual crustacean species, summarized by Wiebe and Holland (1968), ranged from 14.3–698% to 59–169%. Confidence limits for two of our three sets of replicate tows for stage I Dungeness crab zoeae (Table 12) were within this range.

We found a direct relationship between stage I zoeal production, relative abundance of megalopae, and resultant strength of year classes of juvenile crabs in 1978 and 1979, but in 1976, zoeal production was high and recruitment of megalopae and juveniles to the Gulf and Bay was low. However, Wickham (1979b) found megalopae to be abundant in waters off Bodega Bay in 1976. It is possible that large numbers of megalopae were transported from the north to the Bodega Bay area but did not penetrate farther south into the Gulf, or that our sampling missed the major period of recruitment of megalopae in the Gulf that year. However, results of stomach content analysis of demersal fishes (Reilly, Chapter 10) indicate that our sampling effort did not miss the major period of recruitment into the Gulf; very few young-of-the-year juvenile crabs were found in the stomachs of fishes collected in the Gulf and Bay that year.

Several other studies have investigated relationships between larval production of commercially important Crustacea and spawning stocks. For example, Scaratt (1964) sampled American lobster, *Homarus americanus*, larvae in coastal Canadian waters from 1949 to 1961 and could find no conclusive relationship between larval and subsequent stock abundance, although he concluded that there was a possible direct relationship between abundance of stage I larvae and parent stock density. An estimate of total abundance of stage I larvae of the lobster *H. gammarus* was calculated by Nichols and Lawton (1978) for a portion of coastal England. Their estimate was extremely low when compared with the potential from the available breeding stock (ovigerous females) for that year.

CONCLUSIONS

Our primary goal was to identify life history stages of the Dungeness crab that are critical to high recruitment and survival in the Gulf of the Farallones and San Francisco Bay. These areas provide habitat for crabs which are recruited into the San Francisco area commercial fishery. We consider a "critical" stage to be one during which a year class of crabs suffers sufficient mortality or displacement so that relative abundance of subsequent stages results in a small population and low fishery landings.

The most consistent relationship we observed during the study was that the relative abundance of megalopae was directly related to the subsequent year class of juvenile crabs. Most of the megalopae we collected nearshore were in advanced stages of development (Hatfield, Chapter 7). Thus, if a relatively large number of larvae reach the late megalopal stages, a good year class of juvenile crabs should result. Therefore, the late megalopal to early juvenile instar period does not appear to be a "critical stage". One indication of the potential recruitment of megalopae to nearshore areas was an observation by Lough (1974) of an oblique plankton tow density of 800/100 m^3 in Oregon waters. This is 50 times greater than the maximum density we found in any oblique tow in our study area. It is possible that present recruitment levels of megalopae, although varying substantially during the study, are still one or more orders of magnitude below that necessary to sustain the commercial fishery at historic levels in central California.

We did not find a consistent relationship between relative abundance of stage I zoeae in the Gulf of the Farallones and subsequent relative abundance of megalopae of the same year class. Therefore, survival or displacement during zoeal stages and early megalopal development apparently are "critical" to the strength of a year class of juvenile crabs. The sampling procedures did not allow us to define more precisely which early life stages are the most critical.

Fine scale spatial distribution of *Cancer magister* megalopae and its relevance to sampling methodology

J. Booth, A. Phillips and G. S. Jamieson
Department of Fisheries and Oceans
Nanaimo, British Columbia

Abstract

The vertical and horizontal spatial patterns of Cancer magister megalopae in Dixon Entrance in northwestern British Columbia were found to be non-random. Megalopae were most abundant in the upper 25 m of the water column, concentrating in the neuston layer at dawn and dusk. The vertical pattern is probably consistent between areas. Precise quantitative sampling of C. magister megalops requires the concurrent use of a neuston tow and a bongo net undulated vertically through the upper water column.

The horizontal spatial pattern of megalopae was found to be overdispersed along transects run perpendicular to the shore and tidal currents, with a patch dimension of about 2-4 km.

Horizontal patch size and distribution are probably site and time specific, making it impractical to recommend a standard sampling design for all situations.

Introduction

The Dixon Entrance - Hecate Strait region around the Queen Charlotte Islands is a major Dungeness crab (Cancer magister) fishing area in British Columbia (Jamieson, this symposium). This fishery, like other Dungeness crab fisheries, is characterized by fluctuations in catch which are generally thought to reflect variable recruitment. One factor which may influence year-class strength is larval survival. "Larval wastage", defined here as the transport of the larvae away from the adult population into areas unsuitable for survival, has received much attention as a possible cause of variability in larval survival (Lough 1976; Reilly 1983; Johnson et al., this symposium). Studies of larval spatial patterns off the central and northern California coast (Reilly 1983) and the Oregon coast (Lough 1976) indicate that the zoeal stages drift offshore; however on molting to the megalops stage the larvae apparently return inshore by some yet unknown mechanism. The ocean circulation patterns in the Queen Charlotte Islands region differ from those along the open west coast of California and Oregon. Thus *C. magister* larval distribution patterns and transport mechanisms may also be quite different.

As part of a larger investigation of the distribution and larval survival of *C. magister* in Dixon Entrance (Booth unpub. data), this study discusses factors affecting sampling methodology for *C. magister* megalopae. Earlier plankton work in Dixon Entrance 1982 and 1983 indicated three major concerns in designing an effective larval sampling strategy:

1. A non-random horizontal and vertical distribution.
2. Pronounced diel migrations.
3. Inherent bias in gear performance and tow techniques.

Study of the fine-scale temporal and spatial patterns of distribution of the megalops stage was initiated in July 1984 in Dixon Entrance to address these issues.

The megalops stage was chosen for study for three reasons. Because of its relatively large size, coarse-mesh nets can be used which reduce the problem of net drag and clogging. Because the large megalopae can be easily picked out of samples, sample analysis is rapid and an interactive sampling strategy is possible. Finally, the biology of the megalops stage was perceived to be particularly important as individuals in this life stage must locate a suitable location for settlement and subsequent survival. The spatial distribution of megalopae and their use of physical oceanographic transport mechanisms might be of primary importance in understanding causes of year-class flucations in abundance.

Methods

The study was conducted from July 6 to 17, 1984 in Dixon Entrance from the 45 m R/V G.B. REED. The weather was calm and overcast throughout the 11 day period.

Plankton tow methods.

Two types of nets were used: An otter neuston sampler (Sameoto and Jaroszynski 1969; Mason and Phillips, in press) and standard bongo nets. Both gear types had black net frames to reduce avoidance behaviour by the megalopae. General Oceanic flowmeters mounted inside and 0.5-1.0 mm black nitex nets with solid PVC codends. The cross sectional areas of the neuston and bongo nets were 0.21 m^2 and 0.25 m^2 respectively. All tows were made off the starboard side of the vessel at tow speeds of 1.5-2.0 $m \cdot s^{-1}$.

A 5-minute neuston tow sampled a distance of approximately 650 m, or 150 m^3 of water from the surface to 0.41 m depth. Towing distance was varied depending on the density of megalopae. Bongo gear was towed in 3 different ways: the first, referred to as an 'undulating bongo tow' consisted of repeatedly lowering and raising the bongo gear at a speed of 0.3 $m \cdot s^{-1}$ while the ship steamed forward at 1.0-1.5 $m \cdot s^{-1}$ thus causing the net to undulate between the desired depth strata. In this way a minimum flow volume of 300 m^3 through each net was achieved. Two depth strata could be sampled simultaneously by adding a second set of bongo gear at a fixed distance above the first set. For instance, with two sets of gear separated by a vertical distance during towing of 25 m, the upper set could be undulated between 0 and 25 m while the lower set sampled between 25 and 50 m. The two other ways in which bongo nets were towed included, oblique bongo tows between the surface and 3 m off the bottom and surface bongo tows. Undulations were achieved by repeatedly lowering and raising the bongo net over the coarse of one tow.

Vertical sampling design:

The diel pattern of vertical distribution of C. magister megalopae was documented over a 48 hour period at two stations; Station 1 at 55 m depth and Station 2 at 27 m depth (Figure 1). Three other stations were occupied for shorter periods to measure the vertical movement of megalopae at dawn and dusk when it was predicted to be most pronounced (Stations 3, 4, 5; Fig. 1). At the two 48-hour stations (Stations 1 and 2), an undulating bongo tow with two nets in tandem and a neuston tow were made every 2 hours with more frequent tows during dawn and dusk. The two nets of the undulating bongo tow were separated by a

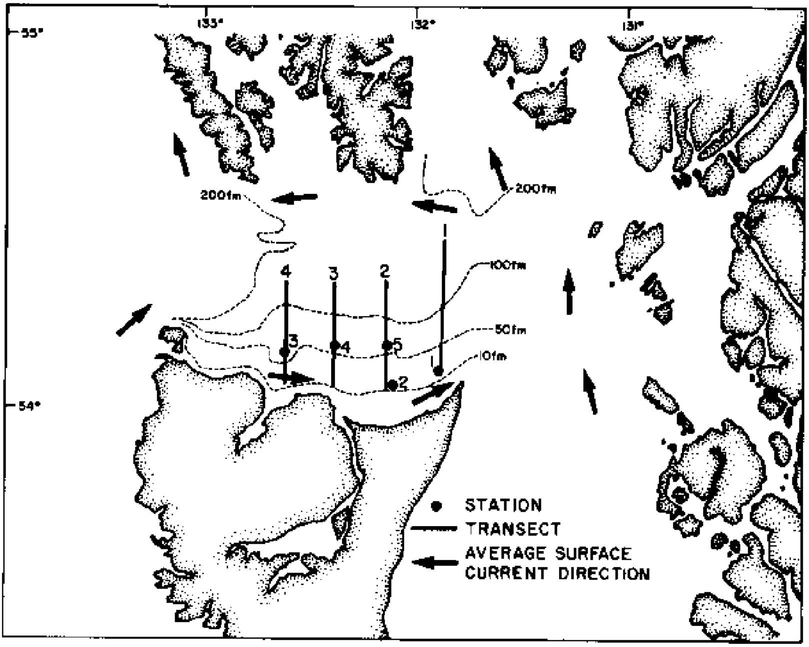


Figure 1. Transect and station positions in Dixon Entrance, July 1984.

distance of half the mixed layer depth which was determined using an Applied Microsystems CTD. Thus the entire mixed layer depth was sampled. At the other three stations, only neuston tows at 5 to 10 minute intervals during the dawn and dusk periods were made.

The data from stations 1 and 2 were combined in a one-way analysis of variance of the rank value of the density of megalopae over time for each depth stratum, nested by station. The data were combined into 4 hour time-of-day periods for statistical analysis.

Analysis of net bias.

Comparisons of the relative efficiency of three sampling techniques were made. These included:

1. Surface neuston to oblique bongo tows at dusk.
2. Single deep undulating bongo to oblique bongo tows during the day.
3. Surface neuston to surface bongo tows during both the day and night.

Four tows of each type were made for the neuston/oblique bongo and deep undulating bongo/oblique bongo tow comparisons. The surface bongo tow was used concurrently with the neuston tow on all of the transects occupied during the fine scale horizontal spatial pattern survey.

Horizontal sample design.

The fine scale (<1000 m) horizontal spatial pattern of megalopae was measured along four transects which ran perpendicular to the predominantly eastward tidal current along the north shore of Graham Island (Crean 1967) (transects 1 to 4; Fig. 1). Consecutive 5-minute (650 m) neuston tows were made along the transects. Tows were made throughout a 24-h period except at dawn and dusk, when the fixed stations were occupied. Although a 'time of day' bias was present along the transects, adjacent stations were sampled at similar times and thus fine scale horizontal patterns could still be detected.

Plots of the estimated densities of megalopae in the tows along the transects, analysis of the frequency distribution of these densities and autocorrelation analysis were used to describe the nature of the horizontal spatial pattern of megalopae.

Results

The pattern of megalopae distribution varied with time of day at both Stations 1 and 2 (Fig. 2 and 3). The occurrence of megalopae varied significantly between time of day in each depth stratum (Table 1). The density of megalopae was greatest between 1600 and 1800 h in both the upper and lower portion of the mixed layer. In the neuston layer however, densities were greatest at dawn (0400 to 0800 h) and dusk (2000 to 2400 h) with the average density of the megalopae in the neuston layer two orders of magnitude greater than that in the water column below it. The time period with the next highest density in the neuston layer was the period between dawn and dusk (0000 to 0400 h). Scheffe's multiple-comparison of means procedure failed to show a significant difference between any two mean ranks in any of the depth strata.

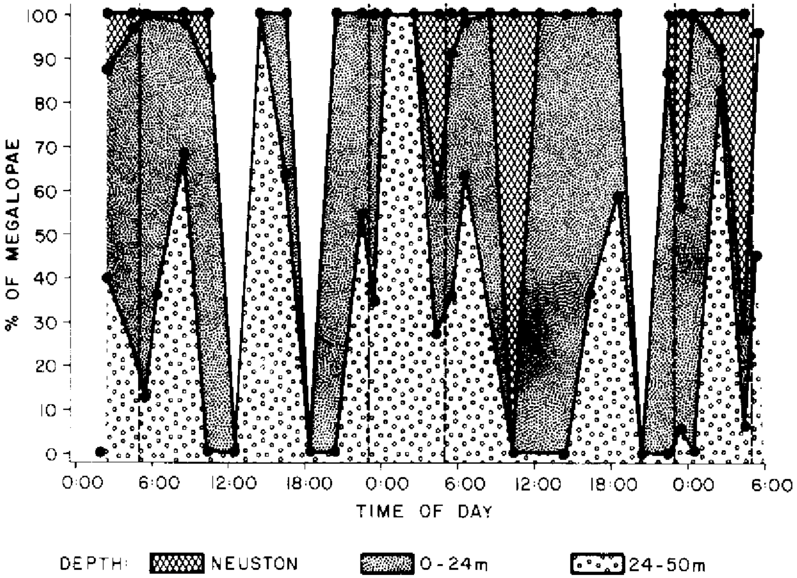


Figure 2. Relative number of _Cancer magister_ megalopae in the neuston and upper and lower halves of the mixed layer at Station 1, July 11-13, 1984.

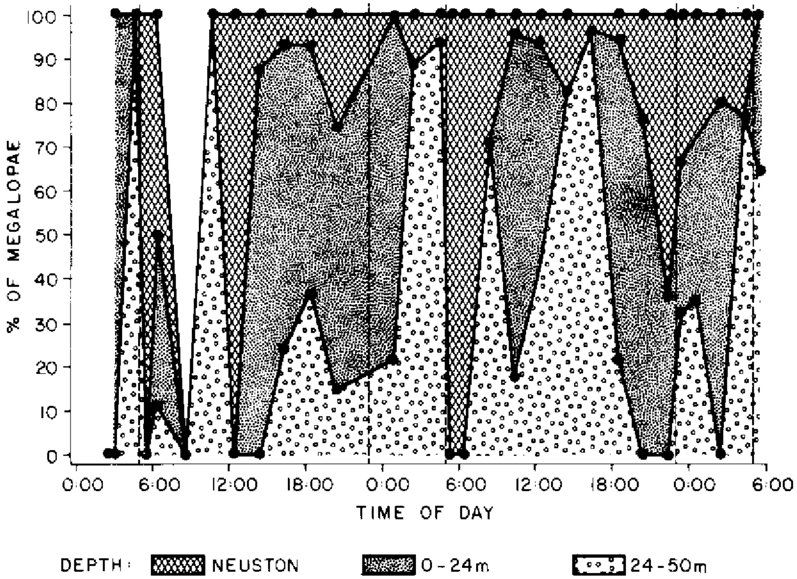


Figure 3. Relative numbers of _Cancer magister_ megalopae in the neuston and upper and lower halves of the mixed layer at Station 2, July 8-10, 1984.

Table 1. Friedman's two way analysis of variance blocked by station with Sheffe's multiple range test for density of megalopae in the neuston layer, and upper and lower halves of the mixed layer during 4 hour time of day periods at Stations 1 and 2, July 1984, Dixon Entrance.

	Source of variation	df	SS	MS	F
Neuston layer (neuston tow)	Time of day period	6	12657.37	2109.56	28.68*
	within time of day period	57	4192.13	75.55	
	total	63	16849.50		
Upper half of mixed layer (undulating bongo tow)	Time of day period	6	17156.21	2859.37	35.72*
	within time of day period	57	4563.29	80.08	
	total	63	21719.50		
Lower half of mixed layer (undulating bongo tow)	Time of day period	6	18433.78	31072.30	42.50*
	within time of day period	58	4192.72	72.29	
	total	64	22626.50		

Depth Strata	Neuston layer		Upper half of mixed layer		Lower half of mixed layer	
Time period	Mean rank	N	Mean rank	N	Mean rank	N
0000-0400	13.41	11	13.21	12	14.36	11
0400-0800	14.89	18	16.75	18	18.03	19
0800-1200	13.31	8	12.38	8	15.88	8
1200-1600	9.75	8	16.43	7	11.69	8
1600-2000	13.13	8	20.56	8	25.31	8
2000-0000	17.70	10	18.75	10	13.25	10
Minimum sign diff. in rank	9.65		14.15		13.3	
Maximum range of ranks	7.95		8.19		13.62	

*$p \leq 0.0001$

In general *C. magister* larvae were more abundant in the upper half of the mixed layer than in the lower half. At the deeper of the 48 hr stations, Station 1 (55 m) the mixed layer was approximately 40-50 m deep. The average density of megalopae between 0 and 24 m was greater than or equal to that between 24 and 50 m in all but two of the 30 tows. In shallower water, at Station 2 (27 m), where the mixed layer extended to 20-25 m, the average density between 0 and 12 m was greater than or equal to that between 12 and 24 m in 23 of the 32 tows.

At all stations the diel changes in surface densities were clearly defined (Figures 4a and 4b). A Friedman's test of the hourly variation in neuston megalopae density by station was significant ($p<0.0001$).

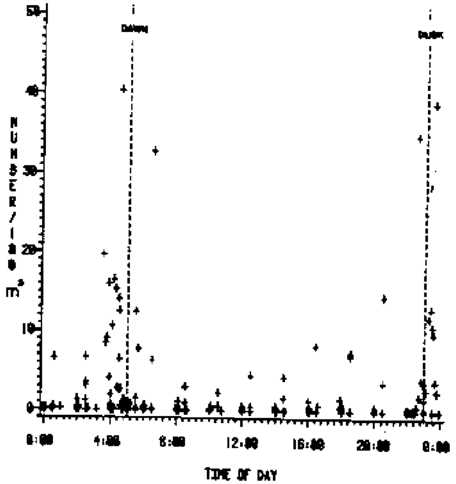


Figure 4a: Diel pattern of *Cancer magister* megalopae in the neuston layer at Stations 1–4. July 1984, Dixon Entrance.

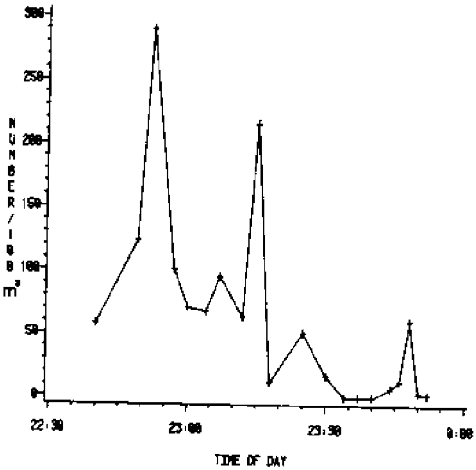


Figure 4b: Pattern of density of *Cancer magister* megalopae in the neuston layer around dusk at Station 5,July 1984, Dixon Entrance.

The comparisons between the neuston tow and oblique bongo tow and the deep undulating bongo tow and oblique bongo tow did not show significant differences between the mean estimated megalopae densities calculated from the different sampling methods. In both comparisons, however, estimated density from the oblique bongo tow was always the lowest and occasionally this net caught no megalopae in instances when other methods showed their presence (Table 2).

Table 2. Comparison of neuston and deep undulating bongo tow methods with oblique bongo tows by one-way ANOVA.

Date	Time of day	Tow type	Number of tows	Mean number of megalopae per 100 m^3	S^2		
July 17	0136-0605	Neuston	4	22.01	478.97	$F_{1,6}=3.01$	$p=0.13$
		oblique bongo	4	0.075	0.006		
July 16	0900-1100	Deep undulating bongo	4	0.56	0.02	$F_{1,4}=1.88$	$p=0.25$
		oblique bongo	4	0.30	0.05		

A difference in net efficiency was also observed when the surface bongo tows were compared to the concurrently made neuston tows. The bongo tows always caught fewer megalopae then the neuston tows. This may be attributable to proximity of the bongo net to the ship's hull. The bongo net was always less than 2 m from the ship's hull. The megalopae had 11-18 sec to move away and avoid the bongo net. The neuston net was towed 20-25 m from the ship's hull and megalopae were less likely to be influenced by the ship's presence. The bongo net with its 200 kg weight and central bridle may also have been more conspicuous, thus increasing avoidance behaviour.

The distribution of *C. magister* megalopae in the neuston layer along transects perpendicular to the tidal current and shore was highly variable and was complicated by differences in the time of day when tows were made. Transect 1, which met Graham Island at Rose Spit, was sampled between 0200 and 0800 h to 54°25' N on the offshore leg. The offshore leg north of 54°25'N and the inshore leg were sampled during the day, which explains the lower abundance of megalopae. Day-night differences in megalopae density at the surface were apparent along all transects (Fig. 5).

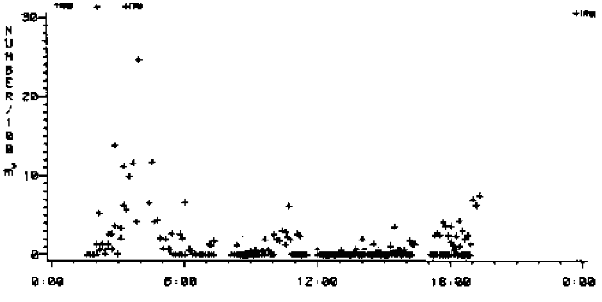


Figure 5. Effect of time of day on the surface distribution of *Cancer magister* megalopae on north-south transects, July 1984, Dixon Entrance.

Horizontal variation in density was evident despite the 'noise' created by diel vertical migration (Fig. 6). The density of megalopae along the transects was patchy and had a negative binomial frequency distribution. The mean density along transect 1 when daytime tows were included in the analysis (Table 3), was 11 times less than the variance, with 50% of the tows having no megalopae in them.

Table 3. Descriptive statistics for Cancer magister megalops abundance continuously sampled along north-south transects using 5 minute (- 650 m) neuston tows.

Time of day	Transect	Number of tows	% Tows with megalopae present	Mean density of megalopae per 100 m^3	$\hat{S}^2$	$\hat{S}^2/x$	Maximum density of megalopae per 100 m^3
Day/night							
0154-1911	1	137	50.4	1.64	18.11	11.04	36.82
0136-0906	3	49	53.1	1.43	7.64	5.34	13.81
Day only							
1034-1825	2	69	34.8	0.36	0.44	0.82	2.62
0831-1847	4	88	29.5	0.41	0.99	2.41	13.81
Night only							
0154-0800	1	37	67.56	3.95	54.40	13.77	36.82
0136-0800	3	27	44.4	2.05	11.97	5.81	13.81

Autocorrelation analysis of the log transformed densities of megalopae along the portions of transects 1 and 3 sampled during the night showed a rapidly decreasing correlation as intertow spacing was increased from 1 to 3 tow lengths (0.65-1.95 km) (Fig. 7). Autocorrelation decreased again with intertow spacings of greater than 6 tow lengths (3.9 km) and was non-significant ($p<0.01$) at spacings of 9 tow lengths (~6 km). This suggests that under calm weather conditions C. magister megalopae concentrations are about 2-4 km in size perpendicular to the current. If the intertow distance is increased beyond 4 km it becomes possible to completely miss sampling a concentration of megalopae. This is demonstrated by the changes in estimated mean abundance and standard deviation along transect 1 with variable tow spacings (Fig. 8). As the intertow spacing was increased to 3.25 km (i.e. only the results from every 6th tow were used), the mean density estimate and standard deviations tended to decrease.

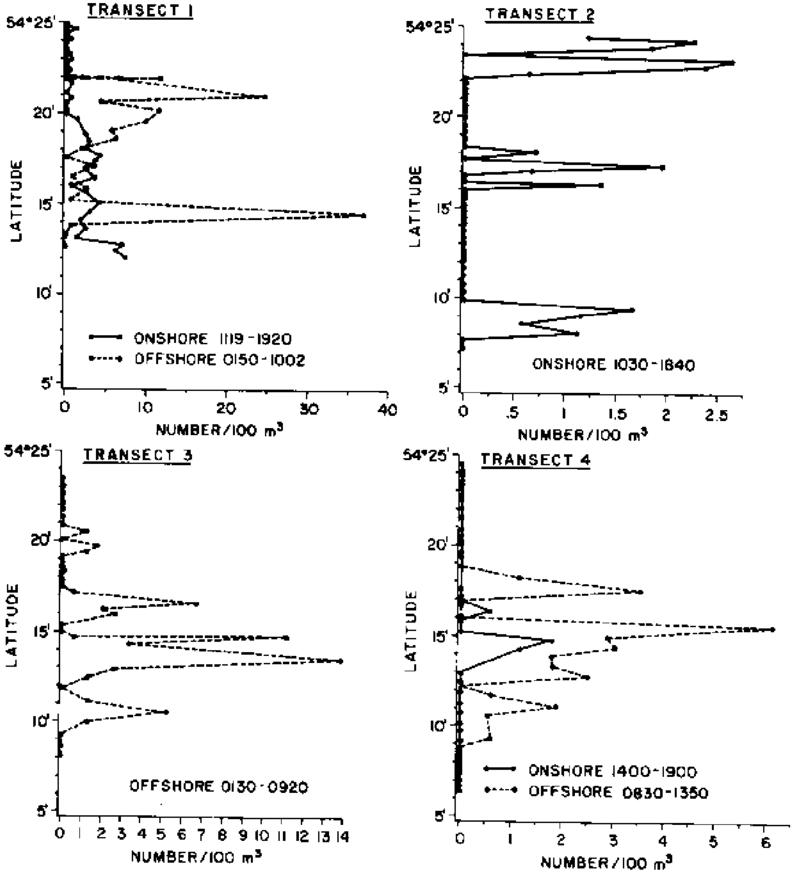
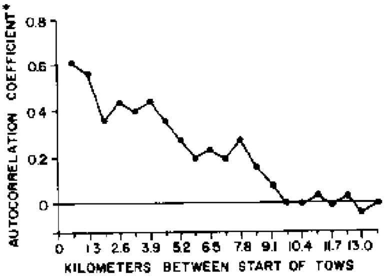


Figure 6. Distribution of Cancer magister megalopae along transects 1-4, July 1984, Dixon Entrance.



*p(r≥0.228)≤0.01, n=141

Figure 7. Autocorredlation of log transformed density of Cancer magister megalopae sampled in 5 minute (650 m) neuston tows along transect 1, 131 45'W, July 1984.

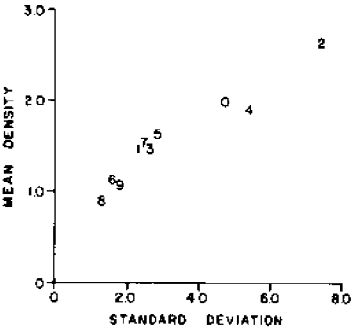


Figure 8. Effect of distance between tows on the estimate of mean density and its standard deviation in the neuston along transect 1 Dixon Entrance, July 1984. Number on plot is number of towlengths (650 m) between end of one tow and the start of the next neuston tow.

Discussion

The vertical distribution of megalopae observed in this study is consistent with the results of laboratory behavioural experiments reported by Jacoby (1982) and Gaumer (1973). Both studies found the phototaxis of C. magister megalopae to be positive at low light intensities but negative at high light intensity. This could account for the upward movement of megalopae at dawn and dusk; times of low light intensity at the surface. In the absence of light, the megalopae may maintain themselves in the upper water column by negative geotaxis which is activated by the increased pressure they encounter as they sink to lower depths. Such a response has been demonstrated in laboratory studies for the fifth zoeal instar (Jacoby 1982). This behavioural basis for depth regulation suggests that the vertical distribution of C. magister megalopae observed in Dixon Entrance would also be found in other areas. Some variability in depth distribution may be accounted for by behavioural changes with intermolt stage development (Hatfield 1983). Strong mixing from wind or tidal currents may temporarily disrupt these patterns.

To maximize sampling efficiency it is suggested that only the upper 25 m be sampled. The lower sampling depth should be deeper when strong surface mixing occurs. An undulating bongo tow is the recommended technique for sampling megalopae. It does not, however, efficiently sample the neuston layer and so a neuston tow should be made concurrently, especially during the hours around dawn and dusk.

The 'patchy' horizontal spatial pattern of C. magister megalops may have resulted from the action of fine scale physical processes. The patchy nature of zooplankton spatial patterns is a well recognized phenomenon (e.g. Hardy 1936, Cassie 1963, Wiebe 1970, Smith et al. 1976). Physical mechanisms which have been proposed as causative forces for patch formation are convergent zones resulting from tidally forced internal waves (Kamykowski 1974; Zeldis and Jillett 1982; Cobb et al. 1983; Levasseur et al. 1983; Shanks 1983), Langmuir cells (Stavn 1971), oceanic fronts (Zeldis and Jillett 1982) and mesoscale eddies (Gower et al. 1980). As with vertical distribution patterns, patches are susceptable to disruption by surface mixing (Levasseur et al. 1983). The dominant components of the physical circulation differ between areas, and so the characteristics of the horizontal distribution of C. magister megalopae will also likely vary. Optimal horizontal tow spacing will thus have to be established for each new study. The vertical sampling strategy, however, should be applicable to all areas where vertical currents can be overcome by the megalopae.

Acknowledgments

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Modeling a fishery characterized by uncertain resources and a multipurpose, heterogeneous fishing fleet—the Eureka Dungeness crab fishery

J. J. Fletcher
Purdue University
West Lafayette, Indiana
and
W. E. Johnston and R. E. Howitt
University of California
Davis, California

Abstract

The principal goal is to develop a method to analyze the economic effects of fishery management policies when: (1) the biological dynamics of the fish stocks are not known; (2) the fishing fleet is multipurpose (i.e., capable of fishing in more than one fishery each year); and (3) the fishing fleet is heterogeneous (i.e., composed of a mixture of vessel types and configurations with differing cost structures). The methodology is developed in an application to the Eureka Dungeness crab fishery on the northern California coast.

Fisheries economics has been dominated by the application of the cannonical model of a renewable resource with suitable bioeconomic growth relations assumed known or estimable. However, growth relationships have not been quantified for many species of interest, and the data necessary to do so do not appear to exist today. Additionally, most models include a single species harvested by a homogeneous fleet, while commercial fishing fleets are often composed of a variety of vessels. Their operations are better described as multispecies (harvesting a number of species simultaneously), multipurpose (harvesting different species at different times of the year), or both.

Problems with theoretical models do not alter the necessity of formulating management policies for fisheries, nor do they diminish the need for economic input into this process. What is necessary is recognition of both the limitations of the traditional approach and the need to develop alternative approaches that are applicable using the data now available.

We present an approach to quantitative economic analysis of commercial fisheries useful for policy modelling given current limitations. A simulation model of the behavior of the Eureka crab fleet is developed incorporating interseasonal dynamics of the biological population derived from a multiple time series model and intraseasonal dynamics based on a behavioral model of fleet behavior. In the absence of adequate bioeconomic models, a multivariate, linear, time series model of the Box-Jenkins type can provide adequate intertemporal relationships for certain policy evaluations. The intraseasonal behavior of a commercial fishing fleet in an open-access fishery under the broader set of assumptions is explained and combined with the interseasonal time series output in a Monte Carlo simulation of the Eureka Dungeness crab fleet in order to assess the effects of alternative management policies.

The effects on the simulation outcomes provide insight into the reactions of the fleet to management decisions. Results for each scenario are compared to results of a base run made under the current structure of the industry. The changes in outcomes for each scenario from the base run are interpreted as the estimated effects of management policy.

Introduction

The abstract of this paper describes the general thrust of work reported in the senior author's dissertation (Fletcher 1980) and more recently, in a more succinct form (Fletcher et al. 1984). The present proceedings paper also reflects the research attempt to summarize revenue, cost, and other vessel characteristics of the Northern California or Eureka Dungeness crab fleet (Fletcher and Johnston 1980, Fletcher and Johnston 1984).

Two important characteristics of this fleet are, first, that it is multipurpose in the sense that vessels in that fleet report landings of crab, salmon, and albacore at California ports and, in addition, land salmon and albacore in Oregon. Thus, vessels participating in the Eureka Dungeness crab fishery often operate in two or more fisheries each year. The second characteristic of the fleet is its heterogeneous nature which affects vessel efficiency in alternative fisheries via capacity and configuration characteristics. For example, the percentage distribution among the three fisheries varies considerably by vessel class in an average year of harvest:

	Days of fishing (average year)		
	Crab	Salmon	Albacore
	percentage		
Vessel size:			
39 foot, and smaller	54	40	24
40 to 49 foot	38	33	28
50 foot, and larger	8	27	48

The interaction of these two characteristics manifests itself in the apparent higher specialization of smaller vessels on Dungeness crab and on salmon. Furthermore, fleet behavior is also influenced by relative shifts among the three fisheries to the extent permissable, by capacity, configuration and other vessel constraints in years of below or above average harvests. Total days fishing, as reported by Eureka vessel operators, on the three fisheries in the aggregate, were:

	Days of fishing		
	Below-average Year	Average Year	About-average Year
Vessel size:			
39 foot, and smaller	60 days	100 days	140 days
40 to 49 foot	90 days	135 days	180 days
50 foot, and larger	100 days	140 days	180 days

Additionally, there is considerable variation in fleet size in absolute numbers [the Eureka crab fleet was defined to include only vessels landing at least 1,000 pounds of crab at north coast ports over the season, based on California Department of Fish and Game (CDFG) data]. The number of vessels identified in the fleet over the past two decades has varied from a low of only 20 vessels in 1974 to a high of 181 in 1977, only three years later.

In an important way, cycles in abundance among the three fisheries influence fishing effort via landings (and often inversely-related prices and/or expected revenues). For example, the senior author early observed apparent correlations among Dungeness crab and king and silver salmon landings; acceptable biological models to explain that behavior is not yet clearly known (Botsford *et al.* 1982). Thus, these interactions and the uncertain nature of the fisheries importantly influence harvests and the economics of the Eureka Dungeness crab fleet.

The paper proceeds with a section describing the fishery in more detail, followed by a general description of the analytical model utilized in simulating the fishery under open access and under several alternative management policies. The analysis differs importantly from that which would be logically proposed at a conference such as this where the typical participant is likely to be a biologically-oriented scientist or manager. It was our assessment that necessary biological models were not yet available with sufficient precision to provide a bioeconomic model of the fisheries. We use a statistical time series approach which combines all available information contained in data sets of biological and economic variables to provide short- to medium-run estimates of variables we identified as important for future policy decisions--namely, crab and salmon revenues and fleet size or capacity. The multiple time series approach used can be considered the "positive economic" analog to the usual bioeconomic approach, which if and when available with precision can displace this sort of analog in future policy analyses of management alternatives.

The Eureka Dungeness Crab Fleet

Characteristics of the fleet

As noted above, most vessels participating in the fishery are multiple-purpose vessels capable of operating in two or more fisheries, with the ability to participate in additional fisheries varying with size and configuration characteristics. The analysis simplifies the heterogeneous nature of the fleet by using two representative types of vessels. "Small" vessels represent vessels under 40 feet in length, typically crabber-trollers primarily active in the crab and salmon fisheries and, to a much lesser degree, in the albacore fishery when the migration passes close to shore. "Large" vessels in the 40 foot and larger class are of two distinct types: trollers and trawlers. The former are owned predominantly by albacore highliners--those who follow the albacore migration from southern California waters north along the coast from early summer to late fall. The trawlers are of two types: those dragging for groundfish and those trawling for shrimp. Most draggers participate in the crab fishery only during years of exceptional abundance, whereas shrimpers appear in the crab fishery most years.

The above classifications are rough characterizations of the types of vessels operating on the north coast. Because the number of trawl vessels that operate in the crab fishery are small, the study assumes that the activity of the crab fleet can be approximated by that of representative "small" and "large" crabber-troller vessels. More detailed information on the production patterns, revenues, and associated costs are given in Fletcher and Johnston (1984).

Landings, values, and exvessel prices of crab, salmon, and albacore for the period, 1946-1981

As defined in the study, the Eureka Dungeness crab fishery includes landings at Fields Landing, Eureka, and Trinidad on the north coast of California. Seasonal crab landings at these ports are characterized by a ten-year cycle. Similar cycles have been noted for other crab fisheries along the west coast from San Francisco to British Columbia. The change in landings from the low to high point in the cycle was especially evident in the 1974-77 period. Although price was a record high, both landings and value reached a postwar low during the 1974 season. Two years later the exvessel value peaked at nearly $8 million, a 26-fold increase. Landings set new records the following year when 11 million pounds of crab were landed during the 1977 season, up sharply from the 1974 season total of less than 200,000 pounds.

Landings, values, and exvessel prices for 1946 through 1981 are given in Table 1. Because of marked price changes over the period of study, all economic data are presented in terms of "real" 1980 dollars. "Real" 1980 dollars are obtained by dividing annual nominal prices by the Consumer Price Index (CPI) for that year. The number of vessels landing at least 1,000 pounds of crab at Eureka ports is also reported for the 1954-1981 period. Figure 1 depicts patterns over the period for landings, values, and vessel numbers. Note the general ten-year pattern in landings. Five or six years of above average landings are followed by four or five years of landings below average.

Table 1

Landings, Value, Price, and Numbers of Vessels for the Eureka Dungeness Crab, the Northern California Salmon, and California Albacore Fisheries, 1946-1981

Year	Eureka Dungeness Crab Fishery[a]				Northern California Salmon Fishery[b]			California Albacore Fishery[c]			Price Indices	
	Landings (millions of pounds)	Value[d] (millions of dollars)	Price[d] (dollars per pound)	Number of vessels[e]	Landings (millions of pounds)	Value[d] (millions of dollars)	Price[d] (dollars per pound)	Landings (millions of pounds)	Value[d] (millions of dollars)	Price[d] (dollars per pound)	CPI (1967=100)	CPI inflator (1980=1.0)
1946	2.94	1.55	0.53	n/a	4.54	4.03	0.89	16.07	15.13	0.84	58.5	4.22
1947	3.22	1.31	0.41	n/a	5.87	4.60	0.79	13.43	11.58	0.86	66.9	3.69
1948	3.62	1.30	0.36	n/a	4.03	3.74	0.93	37.62	37.72	1.00	72.1	3.42
1949	4.15	1.59	0.38	n/a	2.60	2.13	0.82	44.28	28.32	0.64	71.4	3.46
1950	2.84	1.10	0.39	n/a	2.22	1.79	0.81	66.12	42.98	0.65	72.1	3.42
1951	5.67	1.98	0.35	n/a	2.00	1.65	0.82	30.92	15.44	0.50	77.8	3.17
1952	4.41	2.03	0.46	n/a	2.49	1.86	0.75	49.80	26.78	0.54	79.5	3.10
1953	2.09	1.18	0.56	n/a	2.95	2.21	0.75	33.86	20.77	0.61	80.1	3.08
1954	1.53	0.71	0.46	66	3.93	3.67	0.93	26.11	16.09	0.62	80.5	3.07
1955	0.64	0.37	0.58	34	4.81	5.17	1.08	29.00	14.46	0.50	80.2	3.08
1956	4.06	1.79	0.44	69	6.31	6.76	1.07	37.06	19.20	0.52	81.4	3.03
1957	4.33	1.09	0.25	58	3.32	3.20	0.96	43.53	18.39	0.42	84.3	2.93
1958	4.63	1.52	0.33	70	1.60	2.02	1.26	27.19	15.87	0.58	86.6	2.85
1959	6.24	2.63	0.42	99	1.85	2.12	1.14	32.74	17.20	0.53	87.3	2.83
1960	5.30	2.52	0.48	110	2.44	3.67	1.51	35.11	14.40	0.41	88.7	2.78
1961	3.86	1.82	0.47	97	4.13	5.89	1.42	29.12	14.29	0.49	89.6	2.75
1962	1.21	0.71	0.59	89	4.19	6.67	1.59	36.62	16.45	0.45	90.6	2.72
1963	0.48	0.44	0.90	53	7.86	10.66	1.36	48.86	19.69	0.40	91.7	2.69
1964	0.34	0.31	0.93	42	5.42	7.07	1.30	42.55	17.48	0.41	92.9	2.66
1965	2.02	1.17	0.58	73	5.48	6.83	1.25	23.22	9.28	0.40	94.5	2.61
1966	5.12	2.04	0.40	89	6.94	8.65	1.25	18.19	8.53	0.47	97.2	2.54
1967	5.47	2.13	0.39	83	5.29	6.91	1.31	17.86	8.41	0.47	100.0	2.47
1968	6.17	2.80	0.45	97	4.06	5.18	1.27	15.08	7.08	0.47	104.2	2.37
1969	6.20	3.65	0.59	101	3.36	4.46	1.33	14.72	7.05	0.48	109.8	2.25
1970	7.42	4.03	0.54	118	3.95	6.14	1.55	29.92	16.65	0.56	116.3	2.12
1971	2.92	1.63	0.56	122	5.63	6.19	1.40	36.12	22.13	0.61	121.3	2.03
1972	1.44	1.11	0.77	99	3.37	4.61	1.37	21.00	13.56	0.65	125.3	1.97
1973	0.57	0.75	1.32	62	5.70	9.03	1.58	8.64	6.46	0.75	133.1	1.85
1974	0.20	0.31	1.53	20	5.13	7.27	1.42	11.81	7.09	0.60	147.7	1.67
1975	0.68	0.77	1.13	41	4.31	6.37	1.48	15.41	7.71	0.50	161.2	1.53
1976	8.38	7.96	0.95	118	4.84	9.24	1.91	27.76	18.42	0.66	170.5	1.45
1977	11.06[f]	6.97[f]	0.63[f]	181[f]	3.40[f]	9.14[f]	2.69[f]	15.91[f]	12.49[f]	0.79[f]	181.5	1.36
1978	6.85[f]	5.34[f]	0.78[f]	157[f]	3.98[f]	10.94[f]	2.75[f]	21.55[f]	17.96[f]	0.83[f]	195.4	1.26
1979	3.64[f]	3.52[f]	0.97[f]	149[f]	5.25[f]	14.72[f]	2.80[f]	8.00[f]	5.99[f]	0.75[f]	217.4	1.14
1980	6.56[f]	3.89[f]	0.59[f]	164[f]	3.13[f]	6.87[f]	2.20[f]	9.50[f]	7.70[f]	0.81[f]	246.8	1.00
1981	4.12[f]	2.60[f]	0.63[f]	159[f]	3.17[f]	6.77[f]	2.14[f]	18.00[f]	14.79[f]	0.82[f]	270.3	0.91

Source: Fletcher and Johnston, 1984.

[a] Includes all commercial landings at the Fields Landing, Eureka, and Trinidad ports. Data are for the crab season, December to August, referred by the later year.

[b] Includes all commercial salmon landings for all salmon species from Fort Bragg to the Oregon border. Data are for the Eureka statistical area defined by CDFG.

[c] Includes all commercial albacore landings made at Eureka ports.

[d] Dollar figures are in 1980.

[e] The number of vessels landing a minimum of 1,000 pounds of crab.

[f] Based on CDFG preliminary estimates.

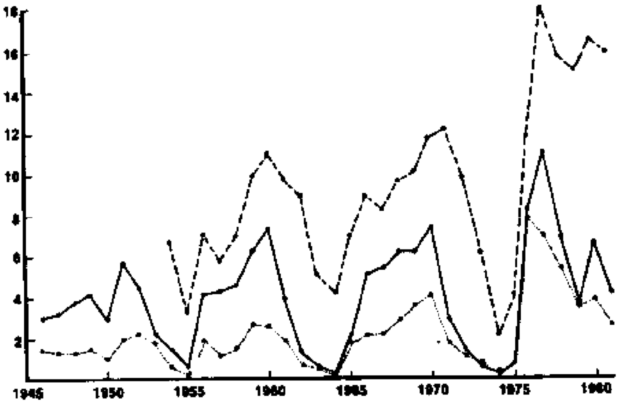

Figure 1. Eureka Crab Data

Number of crab boats (÷ by 10)

Crab landings (millions of pounds)

Exvessel value (millions of 1980 dollars)

Economically, value (price times total catch) is more important to individual operators in the fishery than are landings. The percentage change in value between high and low points in the cycle is less than the percentage change in landings. That is, the effect of changes in catch on gross income is moderated, since prices are high (low) in years of low (high) landings. If the change in price is large compared to the change in catch, value and catch may even move in opposite directions. For example, sharp price declines from 1976 to 1977 lowered the value 14 percent despite a 30 percent increase in catch.

The number of boats in the crab fishery follows the same general pattern as the landings and value data, but with peaks and troughs generally occurring one or two years later. The increase in the number of boats as value declines (e.g., between 1959 and 1960, 1970 and 1971, 1976 and 1977) may reflect the fishery's delayed response to economic factors.

The salmon data contained in Table 1 pertain to all commercial salmon landings from Fort Bragg to the Oregon border--the "Eureka Area" as defined in data reports of the California Department of Fish and Game. Landings and values, shown in Figure 2, closely track each other through the mid-1970s, when values increased sharply relative to landings due to substantial price increases.

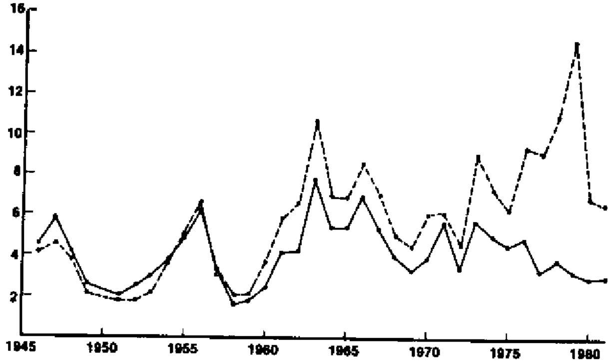

Figure 2. Northern California Salmon Data

———————— Salmon landings (millions of pounds)

– – – – – – – Exvessel Value (millions of 1980 dollars)

It is especially difficult to find data on the albacore fishery which are representative of the opportunities relevant to Eureka vessels. For smaller boats, the distance from shore during the summer migration has more effect on catch of albacore than has actual abundance. As distance increases, greater numbers of smaller boats are precluded from the fishery due to restricted fuel capacity and safety considerations. Thus, the California albacore data, contained in Table 1 are more generally applicable to larger vessels, often operated by highliners. Albacore landings reached a peak in 1950 and the landings have trended downward since. However, the decrease in landings since 1975 has been partially offset by gradually increasing prices as shown by the convergence of the value and landing lines in Figure 3.

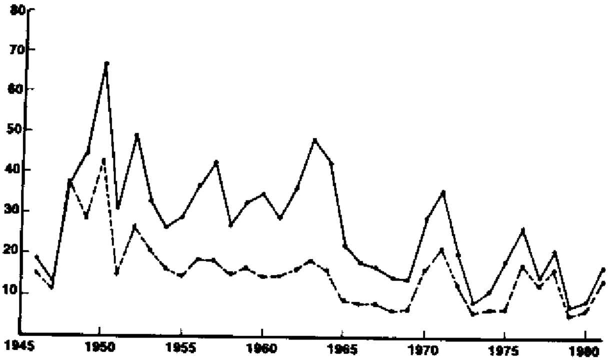

Figure 3. California Albacore Data

———————— Albacore landings (millions of pounds)

– – – – – – – Exvessel Value (millions of 1980 dollars)

Exvessel prices of crab, slamon, and albacore for the postwar years are depicted in Figure 4. Crab prices have followed a cyclical pattern, moving gradually upwards. Prices tend to be high when landings are low--most obvious during the 1973-75 period; then prices drop when landings increase, as happened in 1977. Salmon prices followed an upward trend through the early 1960s, leveled off until the mid-1970s, and then increased sharply, nearly doubling between 1975 and 1979. Note especially the increase in salmon prices relative to those of crab and albacore. Albacore prices were strong after the war, but dropped through the 1950s and remained rather constant through the 1960s. Prices trended generally upward during the 1970s except for reductions in the period 1974-76.

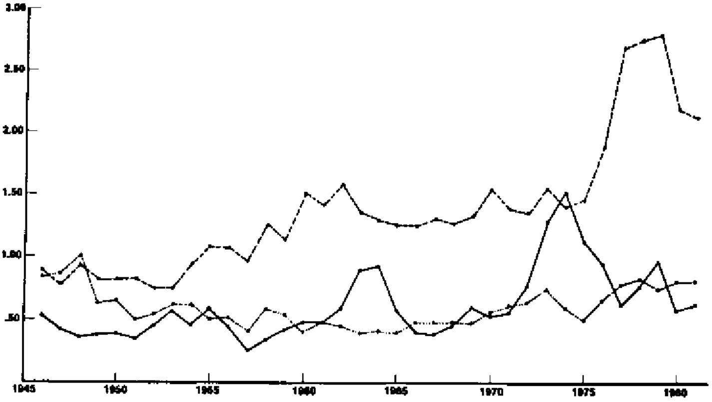

Figure 4. Exvessel Prices (1980 dollars per pound)

--------- Average exvessel salmon price

Average exvessel crab price

Average exvessel albacore price

Summary of the Analytical Model

While the proceedings of this symposium may reveal more precise knowledge of the causal dynamic relationships in the fisheries important to the Eureka Dungeness crab fleet--most importantly, the crab and salmon fisheries--our evaluation in the mid to late 1970s was that the basis for building reliable bioeconomic models for those fisheries was not at hand. We, thus, sought an alternative approach which might permit the modelling of fleet behavior and responses to management alternatives. The basic components reflect fleet dynamics resulting from the aggregate of individual vessel operator decisions--in our case that of representative "small" and "large" crabber-trollers--that include arguments for expected returns to participation in a fishery as a function of price, abundance, variable costs, and the total number of other participants.

The problem of modeling the dynamics of fleet entry and exit is central to the problem. One approach is to consider fleet behavior directly. Assume fishermen form their expectations of fleet size rationally. In the aggregate, expected fleet size, N_t^e, adjusts in proportion (ϕ) to the present value of expected returns, Y_t^e. When the cost of switching is small and the decision can be revised annually, a fisherman need only be concerned with the expected profitability each season:

$$N_t^e = N_{t-1} + (\cdot)\ Y_t^e = N_{t-1} + h\ (R_t^e\ ,\ N_t^e\ ,\ C_t^e\ ) \tag{1}$$

where R_t^e is the expected total revenue generated by the fishery during the season and
C_t^e is the expected cost of production.

Revenues depend on the expected fleet size, expected abundance of the resource, A_t^e, and expected price, P_t^e:

$$R_t^e = g(N_t^e,\ A_t^e,\ P_t^e) \tag{2}$$

These relations define a pair of implicit simultaneous equations in fleet size and revenue (variables that are embodied in the sought-for bioeconomic models) and a set of exogenous variables.

Entry and exit decisions by fishermen depend on revenue, not catch. Previous crab demand studies (Wix 1976; Erickson 1975) indicate that the price of King crab and personal income in California are significant in explaining the exvessel price of Dungeness crab. In the absence of a dynamic model describing these variables, a multivariate time series model is used in this study. It includes any past trends in a data series regardless of the cause. A reflection of underlying behavior relations including price variability is obtained using harvest revenues, rather than quantities. The analysis is based on the simultaneous modeling of three data series on (1) crab revenues, (2) salmon revenues, and (3) crab fleet capacity.

The time series on fleet capacity developed for this study corresponds to fleet capacity each year in terms of a standard measure of fishing effort (Hannesson 1978). Let S_t, Y_{st} and L_t, Y_{Lt} be, respectively, the number of vessels and the total landings, of the small and large subfleets each year. If the unit of effort is defined as a vessel fishing for a season, the catch-per-unit-effort (CPUE) is the average annual crab catch per vessel. The ratio of the CPUE of large boats to that of small boats defines the relative efficiency of large to small boats, RE_t. That is, the fleet capacity in small boat units each year, F_t, is given by:

$$F_t = L_t(Y_{Lt}/L_t)/(Y_{st}/S_t) + S_t = S_t(Y_{Lt}/Y_{st} + 1) \tag{3}$$

The average measure of relative efficiency over the 1954-1977 period was 1.25 (a one tailed test of equal average efficiencies was rejected at the 1 percent level). A regression of the natural log of the relative efficiency measure against time indicated no bias in technical efficiency gains. Thus, the effective fleet capacity in small boat units was calculated from subfleet data using the estimated relative efficiency of 1.25 for large vessels.

A joint model of the three revenue and capacity series failed to provide sufficiently accurate one step ahead forecasts of Eureka crab revenues. The difficulty was traced to an extreme jump in the crab revenue series between 1975 and 1976. Given that this change was an anomaly independent of the usual structure, intervention analysis (a dummy variable technique) was used, with a pulse variable equal to one in 1975 and zero elsewhere introduced into the model. As a consequence, the within sample forecasts over the 1968-1981 period were improved significantly. The empirical model is specified and discussed in more detail elsewhere (Fletcher 1982; Fletcher *et al.* 1984); its existence suffices for the purpose of this presentation.

Particular problems associated with multipurpose, heterogeneous fishing fleets have only recently been treated in the literature (Huppert 1979; Anderson 1980; Holt 1982; McKelvey 1983). The model used in the study has similarities to those of Holt and McKelvey. An implication derived from the model is that, in addition to the usual economic inefficiencies that arise under open access, there are also efficiency losses due to the heterogeneous composition of the fleet.

To model interseasonal fleet-behavior, one can abstract from the biological dynamics and concentrate on recruitment, R_j, and escapement, S_j, for each species. Escapement differs from recruitment only through total fleet harvest, H_j. All other interactions are relegated to the interseasonal model, which also takes as given any current regulation designed to protect the reproductive capacity of the stock, e.g., gear restrictions and season limitations. This framework is appropriate for fisheries such as the Dungeness crab where growth and reproduction occur primarily during the season closures.

Ignoring natural mortality, the stock of fish for each species, $x_j(t)$, decreases over the season as fish are harvested. The fishing season for each species has maximum length, T_j, either through regulation or natural availability. To avoid confusion, each fishing unit is referred to as a vessel. The catch rate per vessel, $h_j(t)$, is assumed proportional to the total stock by the catchability coefficient, q_j, so that $h_j(t) = q_j x_j(t)$.

Let N_i be the number of vessels in subfleet i. All N_i vessels fish for species j until switching time t_{ij}, where $t_{ij} \leq T_j$. The number of vessels active in fishery j at time t, $N_j(t)$, is represented by the step function:

$$N_j(t) = \sum_i N_{ij}(t) \qquad \begin{array}{ll} N_{ij}(t) = N_i & t \leq t_{ij} \\ N_{ij}(t) = 0 & t > t_{ij} \end{array} \tag{4}$$

$N_{ij}(t)$ thus represents the number of vessels in subfleet i fishing for species j at time t. The stock level decreases by the total fleet catch each day:

$$\dot{x}_j(t) = -q_j N_j(t) x_j(t) \qquad x_j(0) = R_j \text{ and } 0 < t < T_j \tag{5}$$

Total fleet fishing effort for any species up to time t, $F_j(t)$, is the total number of vessel-days fished to that point.

$$F_j(t) = N_j(t)t + \sum_{\{k|t_{kj}<t\}} N_k t_{kj} \tag{6}$$

Solving (5) for $x_j(t)$, the fish stock during the season and the escapement can be represented by:

$$x_j(t) = r_j e^{-q_j F_j(t)} \qquad 0 < t < T_j \tag{7a}$$

$$x_j(T_j) \overset{\Delta}{=} S_j \tag{7b}$$

This function is continuous, bounded, and differentiable at all but a finite number of points and therefore integrable on [0,T]. The exvessel price for each species, p_j, is assumed constant over the season. Each vessel from fleet i has annual fixed costs, I_i, and constant operating costs per day in fishery j, c_{ij}, which can include opportunity costs associated with alternative fisheries. Annual profit for a class i vessel is, thus, represented by:

$$\Pi_i = \sum_j \left[\int_0^{t_{ij}} P_j q_j R_j e^{-q_j F_j(s)} ds - c_{ij} t_{ij} - I_j\right] \tag{8}$$

Under open access, each fisherman seeks to maximize profits by choosing effort levels in each fishery, t_{ij}, given seasonal constraints, T_j, and the number of vessels in each subfleet, N_i. As the second order conditions are guaranteed by the functional forms, the first order Kuhn-Tucker conditions (FOC) represent conditions for a maximum:

$$p_j q_j R_j e^{-q_j F_j(t_{ij})} - c_{ij} - \mu_{ij} \leq 0 \tag{9a}$$

$$(T_j - t_{ij}) \geq 0 \tag{9b}$$

$$(\partial L/\partial t_{ij}) t_{ij} = (\partial L/\partial \mu_{ij}) \mu_{ij} = 0 \tag{9c}$$

$$t_{ij} \geq 0, \ \mu_{ij} \geq 0 \tag{9d}$$

Assuming a vessel participates in a *given* fishery, equation (9a) emphasizes that each vessel fishes *until* daily revenue is reduced to daily costs or the season ends. If the season ends first, μ_{ij} represents the profit rate at the end of the season for species j for a type i vessel, or equivalently, the amount a fisherman would pay to fish an additional day.

To this point, the number of vessel classes and species has not been specified and the FOC are applicable to any number of species and vessel types. Considering the diverse nature of the fleet active in fisheries such as the Dungeness crab, daily costs may be expected to vary substantially among participants. If daily costs include opportunity costs for both the vessel and the captain, the variation across the fleet increases. Considering the necessary conditions for profit maximization, the decrease in effort observed as the season progresses is seen as a reflection of rational decisions by participants to maximize profits. Vessels with high costs may fish for a given species for only a short time while those with low costs may continue to fish throughout the season.

The necessary conditions can also be used to show the relationships among daily cost, price, and escapement. Choose i to represent the vessel class with minimum daily costs in fishery j, say c_{ij}'. Solving the revenue for the last fishing day of a type i vessel on species j and using the complementary slackness conditions (9c), one gets:

$$s_j = \frac{c_{ij}' + \mu_{ij}}{p_j \, q_j} \geq \frac{c_{ij}'}{p_j q_j}. \qquad (10)$$

Escapement for any stock is then inversely related to price and fishing effectiveness (technological inputs) and directly related to daily variable costs of the most efficient vessel. If μ_{ij} is zero so that the season constraint is not binding (the usual case for many open-access fisheries), equality holds in (10) and escapement is determined by marginal profitability conditions. If the season constraint is binding, these conditions set a lower bound on escapement. If annual economic profits are zero for all vessels, the number in each subfleet is in equilibrium in the sense that there is no incentive for additional boats to enter or for any participant to either leave or invest in changing vessel characteristics.

Note that an equilibrium under open-access for a heterogeneous fleet implies an additional kind of inefficiency. Whereas loss of efficiency by a homogeneous fleet results from the operation of an excess number of vessels, an additional loss results from excess use of relatively inefficient vessels over at least a portion of the season. This can be easily seen by assuming that (10) is an equality, so that the most efficient vessel stops fishing before the season is finished. Less efficient vessels with higher variable costs would have quit earlier in the season, but would have still fished too long for social optimality. This follows because social costs could be reduced by restraining less efficient vessels so that the more efficient vessels could fish throughout the season. Consequently, costs could be reduced without a reduction in fleet size.

The simulation model was ultimately developed to aid understanding of the behavior of open access fishing fleets, to study the effects of a set of proposed management alternatives on fleet behavior and to evaluate the economic effects of these management alternatives on the fleet. The model simulates crab fleet capacity and crab revenues, capturing both intra- and interseasonal fleet behavior. The interseasonal dynamics are derived from the multivariate time series model. Intraseasonal behavior is based on the behavioral model modified to reflect characteristics reflected in the historical behavior of the fleet.

Characteristics peculiar to the Dungeness crab fishery are included to obtain a model adequate for policy analysis. For example, processors have often imposed restrictions or quotas on the quantity of crab purchased daily from individual fishermen during the first part of the season. The effective opening of the crab season was delayed by price negotiations at least one month for five of the eight seasons in the 1970-77. All vessels do not fish crab for the same length of time; some fish for a few weeks while others fish for crab throughout the season.

The salmon fishery is not a single stock of fish, but rather is a multispecies fishery composed of king and silver salmon. Each of these can be further divided by stream of origin. All of the fish do not enter the fishing grounds simultaneously, but arrive over an extended time. Thus, catch per vessel per unit time fishing is relatively constant over a substantial portion of the season and the salmon fishery does not seem to have exhibited the same crowding effect as the crab fishery during the period of analysis.

Crab fishing patterns vary according to characteristics of individual vessels. Since larger vessels have higher variable and opportunity costs (Fletcher and Johnston 1984), as catch declines over the season, they tend to quit fishing for crab sooner than smaller vessels. Differences in cost factors are captured by dividing the fleet into two subfleets for each year.

Fishermen still fishing crab when the salmon season opens have an additional decision to make. They not only consider the profitability of fishing crab versus not fishing, but must consider the relative profitability of continuing to fish for crab versus switching to salmon.

The dynamic "positive economic" model used in the absence of a bioeconomic model consists of a set of stochastic difference equations derived from the multivariate time series model. The difference equations provide the values for: (1) the initial capacity of the Eureka crab fleet each year in small-boat units, F_t; (2) a season total for crab revenues available from the Eureka fishery in 1980 dollars, TCR_t; and (3) the annual value of the northern California salmon harvest, TSR_t, also in 1980 dollars.

Intraseasonal behavior is a discrete time (monthly) version of the profit maximizing short-run models described by equations (9a-d). The main simulation routine consists of three nested loops. The <u>inner</u> loop is the model of intraseasonal behavior and performs a month-to-month simulation of the fleet capacity and size of each subfleet. Revenues for individual vessels, each subfleet, and the entire fleet are calculated given the initial data provided by the interseasonal model. The <u>middle</u> loop represents the interseasonal model and controls the simulation over a period of years. For each year to be simulated, the difference equations are evaluated and updated to provide forecasts of the seasonal crab revenues, annual salmon revenues, and the capacity of the crab fleet at the start of each season. The <u>outer</u> loop performs a Monte Carlo experiment on the output variables of the simulation model. The simulation over the entire time horizon is repeated and the statistics for various output variables are calculated for individual years and the entire simulation period.

Summary of Selected Simulation Results

The simulation model was used to examine the effects of landing restrictions and potential management policies on the fleet and the social benefits attributed to the Eureka crab fishery. Random simulations over the 1982-1991 cycle of the fishery were computed assuming alternative policy scenarios and compared to those of a run made under the then current institutional structure of the mid- to late 1970s. The alternative scenarios considered included the effects of uniform landing quotas for all vessels, of limited entry programs for the Eureka crab fishery, of a uniform coastwide January first season opening, and the effects of single species management policies on a multipurpose fleet. Empirical results are discussed in detail in Fletcher (1982) and in Fletcher *et al.* (1984); here we present qualitative summaries of the outcomes generated by Monte Carlo repetitions of the simulation model. These conclusions result from mean statistics from an average of 100 iterations of the simulation model over a ten-year period approximating the average length of recent cycles in the crab fishery.

Impacts of marketing restrictions

By the 1970s, the intensification of fishing effort on the Eureka crab stock resulted in large landings during the first few weeks of most seasons, with the consequence that the harvest capacity of the fleet surpassed the capacity of buyers to process and market the catch. In addition, the local bargaining unit negotiated crab and salmon prices to include a provision that processors were obligated to buy from all members of the unit, and the unit was to be open to all fishermen who wished to join! The agreement, thus, tended to exacerbate the problem of redundant capital by providing a ready market for all new entrants, and as fleet capacity increased, so did total landings during the first part of the season. Processors reacted by limiting the amount of crab they would buy from each fisherman each day.

The limits were primarily implemented as daily quotas per boat and were independent of boat capacity. The effects of such restrictions was considered by comparing simulation results under alternative relative efficiency assumptions for large vessels. The average efficiency ratio over the historical period was estimated to be 1.25, but observations on years of average landings when fewer restrictions were imposed indicated a value of 1.50.[1]

The simulation results imply that uniform landing restrictions on all vessels as imposed by processors in the past had a disproportionately adverse effect on larger vessels with higher costs and larger capacities. The varying effects on vessels types of the quotas used by processors to limit production causes distortions in the production

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[1] The effect of changing the assumed relative efficiency from 1.25 to 1.50 is significant. Simulations based on the continuation of historical, open-access fleet behavior were performed assuming a relative efficiency of 1.25 and 1.50. Net revenue per large boat per month increases by more than $1,200; this may be taken to be a reflection of the costs of restricting the productivity of large vessels.

patterns of heterogeneous fleets. Any policy based in quotas has the potential for substantial equity problems and management plans should recognize possible asymmetric effects of policies among participatns in a heterogeneous fleet.

By the 1980s, some operators have been able to establish new markets and are fishing without landing restrictions, thus reducing the effect of landing limits. To reflect the ability of larger boats to now fish more productively, the relative efficiency value of 1.50 is used for the remainder of the policy simulations.

Limited entry programs

Several Monte Carlo simulations were run to examine the effect of maximum fleet size (capacity) on revenues. In the open-access fishery where there were no maximum fleet size specified, net revenues for both large and small boat classes were negative indicating entry in excess of the open access equilibrium, implying that revenues were not sufficient to cover all of the long-run costs--variable and fixed costs.

The effect of lowering the capacity constraint is not large until the level of 100 units of small-boat capacity is reached. As the capacity constraint is lowered further, remaining vessels fish longer. For limits of 60 units or less, the average season length approaches the legal limit of eight months showing greater capital utilization. At the same time, the average total fleet revenue decreases since fewer boats catch slightly fewer crab. Net revenues for the fleet increase until the capacity reduction effect exceeds the cost savings. At first, the loss in value to the consumer is smaller than the gain in net revenue. The decrease in catch is more than offset by the cost savings, so the increase in producers' surplus must exceed any loss in consumers' surplus. To this point, the change in social welfare from management is positive. The gain exceeds the loss until the fleet size is reduced to 50 units. The model indicates a gain in net revenue of over $850,000 per year from a policy limiting capital to 50 units compared to the open-access fishery. Since total revenues decrease by only $187,000, the fleet size of 50 units would appear to be socially preferred among the alternatives compared.

Thus, the analysis of the historical profit structure of the Eureka crab fleet indicates that entry into that fishery has been in excess of the open-access equilibrium. Assuming the open-access framework continues, the simulation results for the next ten years indicate the problem of excess capacity will remain but that total fleet capacity is likely to decrease moderately from current levels. Substantial benefits can be obtained by limiting (and reversing) capital investment in the fishery.

Uniform coastwide crab season opening

The possibility of changing the opening date of the crab season to provide a uniform coastwide opening date has been discussed in the recent tri-state-federal study (Pacific Marine Fisheries Commission, 1978). The effects of changing the opening date can be simulated within the model by delaying the north coast opening until January first. The policy was then considered for the traditional open-access fishery and in conjunction with the limited entry outcome of constraining the fleet to 50 units.

It is obvious that in order to maintain the same annual landings for a shorter season, a larger fleet would be required. Net revenues must, as a consequence, decline. A coast-wide January 1 uniform season opening for the Dungeness crab fishery would have little impact under open-access. Under restricted entry, a shorter season would require a larger fleet to maintain the same harvest levels. And when capacity is limited, an additional cost must be added to the impact of changing season lengths in the analysis. Interactive effects of the two policies cannot be ignored. There are, thus, real costs to changing the starting time of the season if the fleet capacity were approximately optimal.

Cross effects of salmon management on the crab fishery

It was hypothesized that economically important interaction effects occur when simultaneously available species are harvested by a multipurpose fishing fleet. For the majority of Eureka Dungeness crab fleet effort, the most common alternative species harvested is salmon. The simulation model can be used to examine some of the possible cross effects of implementing single species management policies on complementary fisheries harvested by a multipurpose fleet. Such were considered in several salmon-crab interaction examples, but results were such that cross effects were not significant.

The legal seasons for crab and salmon have historically overlapped from the April 15 start of the salmon season until the end of the crab season. However, few of the crab vessels were normally active in the salmon fishery prior to May 1. The initial hypothesis that interactions are important was, thus, not substantiated by the simulation results, and not surprisingly, given the lack of substantial actual simultaneous fishing for crab and salmon. Under open-access, the crab season is over before the salmon season begins. When a capital limiting policy is imposed on the crab fishery but the salmon fishery remains open-access, crab are so profitable that salmon are ignored as a more attractive economic alternative.

Since the opening of the salmon season has often been delayed by fisheries managers over the past few years, an obvious test was to consider the impact of such closures on the Eureka crab fleet. Again, there was none, given recent fishery patterns of the north coast fleet. Historically, the crab fishery is already terminated for much of the effort before the salmon season is opened. Results are identical for both the open-access and limited entry scenarios.

The Research Agenda

This paper develops an approach perhaps useful in assessing the impacts of alternative management policies. The application to a heterogeneous, multipurpose fleet with stock uncertainties is a novel approach using a "positive economic" analog to the more desirable bioeconomic approach. The insufficient precision of existent bioeconomic models for these fisheries make the particular approach taken both feasible and of sufficient long-tern validity to warrant further modification and development leading to clearer evaluation of management alternatives. We, of course, would applaud the concomitant development of improved bioeconomic models as well.

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Proposed explanations for fluctuations in abundance of Dungeness crabs: A review and critique

David G. Hankin
Humboldt State University
Arcata, California

Introduction

Dramatic fluctuations in commercial landings of Dungeness crabs (Cancer magister) have occurred throughout the Pacific Northwest for the past several decades (Figure 1). These fluctuations have frustrated fishery managers, commercial fishermen, fish processors and consumers. Mangers feel they have little, if any, control over fisheries; commercial fishermen are faced with substantial year-to-year variation in crab abundance and fishing effort, "invasions" of fishermen from neighboring areas having poor catches, and widely varying market prices; processors have found it difficult to expand markets for a product with unreliable supply, and are often forced to freeze a large portion of catches (thus significantly decreasing product quality); consumers are baffled by striking within and between year variation in the price they must pay for Dungeness crab and in availability of fresh crab. However, despite the "misbehavior" of the resource, Dungeness crabs support important and apparently fully exploited fisheries in California, Oregon, Washington and British Columbia, and there is increasing exploitation of Dungeness crabs in Alaska, resulting in part from serious declines in king crab abundance.

Fishery research scientists, in contrast to those user groups with serious personal stakes in this resource, have been intrigued rather than frustrated by the dramatic fluctuations in crab landings. Many fishery scientists have been unable to resist the temptation to "explain" these fluctuations (including the author!). Early attempts at explanation concluded that fluctuations reflected market conditions rather than actual crab abundance (Clark and Bonnot 1940). However, Cleaver (1949) found that fishing effort remained fairly steady throughout extreme Washington landings fluctuations and he concluded that landings therefore reflect real fluctuations in crab abundance. Many subsequent studies have presented alternative "explanations" for landings fluctuations and there has been complete agreement on just a single point; namely, that landings fluctuations do indeed, however crudely, reflect real and substantial variation in abundance of Dungeness crabs. In addition, there has been misplaced, but nearly unanimous, agreement that landings fluctuations are a direct reflection of fluctuations in crab year class strength.

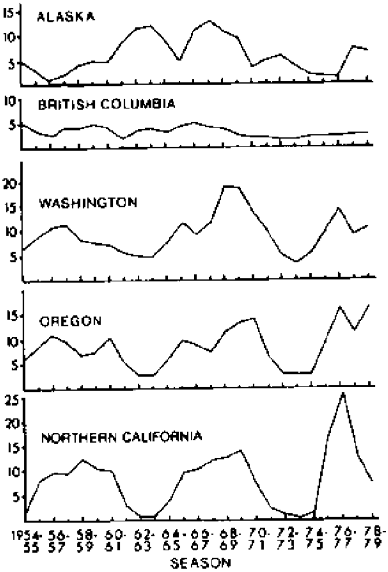

Figure 1. Commercial landings of Dungeness crabs from Alaska through northern California. Reproduced from Wild (1983).

For most species of fishes or crustaceans, year class strength is determined during early life stages, egg or larval. These stages are most sensitive to fluctuations in environmental conditions and/or predator abundance, and survival rates during these early life stages are usually extremely low (10^{-3}-10^{-6}). Very small changes in mortality rates through these life stages can thus give rise to very substantial fluctuations in survival rates and resulting year class strength. For example, an average adult female Dungeness crab may produce 10^6 eggs per year. Of these, a very rough average of two must survive to become adult to ensure population replacement. Hence, mortality from egg to adult would be 0.999998; almost all of this mortality would take place during egg and larval stages. If mortality rates were just 99.99% of this figure for a particular year class, the resulting mortality rate would be 0.999898. This very small change in mortality rate, however, would change the resulting survival rate from about 10^{-6} to 10^{-4}; in this manner year class strength might easily fluctuate over two orders of magnitude. This kind of simplistic, but compelling, calculation has led most researchers to focus on early life stages of Dungeness crabs in their searches for possible explanations for fluctuations. Cleaver (1949), PMFC (1964), Wickham (1979), Wild (1980, 1983) and McKelvey et al. (1980) have all concluded, using very different arguments, that year class strength must be determined during egg and/or larval stages.

However, year class strength need not be determined during sensitive early life stages. Forney (1976) showed that walleye year class strength in Oneida Lake, New York, was principally determined by (a) predation by yellow perch, and (b) cannibalism by adult walleye on walleye juveniles; year class strength was not determined until well after early life stages. Hankin (1980) showed that cannibalism by juveniles on newly born fry could have major effects on recruitment in laboratory fish populations. Botsford and Wickham (1978) indeed proposed that cannibalism was the principal cause of Dungeness crab fluctuations, thus implying that year class strength must be determined after metamorphosis of larvae and settling of juvenile crabs. Peterson (1973) speculated that fluctuations in landings arose not from fluctuations in early life survival, but from fluctuations in survival rates and/or molting success of sub-legal adult male crabs.

This paper reviews and critiques six of the more recent and/or more controversial of the proposed explanations for Dungeness crab fluctuations. Primary attention is placed on the northern California fishery because the author's research has concentrated on this fishery (McKelvey et al. 1980; McKelvey and Hankin 1981; Hankin et al., and Diamond and Hankin, this Symposium) and because fluctuations in northern California landings have been more dramatic and more regular than in other Northwest fisheries. Critique of the proposed explanations consists of subjecting each of them to two tests, one biological in nature and one statistical in nature. None of the proposed explanations convincingly pass both tests. But two of the six ((1) Wild 1980, 1983, and Wild et al. 1983; and (2) McKelvey et al. 1980) convincingly pass one test and cannot be rejected by the remaining test. These two explanations are complementary, rather than conflicting, and both suggest that year class strength must be determined during early life stages, prior to metamorphosis and settling of juveniles.

Six Proposed Explanations

Proposed explanations have been classified according to whether the principal hypothesized causes for fluctuations are density-independent (environmental factors) or density-dependent (usually internal biological controls). Density-independent environmental factors have been implicated by:

(1) Peterson (1973): upwelling-induced effects on molting success and/or survival rates of sub-legal adult male crabs;
(2) Love and Westphal (1981): sunspot activity and its statistical correlation with crab landings data; and
(3) Wild (190, 1983) and Wild et al. (1983): fluctuations in ocean water temperatures and their effects on egg survival.

Density-dependent controls have been proposed by:

(4) Wickham (1979): density-dependent egg mortality resulting from a predatory nemertean worm, *Carcinonemertes errans*;
(5) Botsford and Wickham (1978): density-dependent juvenile survival resulting from cannibalism by older crabs; and
(6) McKelvey et al. (1980): density-dependent egg/larval survival mediated through fluctuations in the total egg production of the unexploited female stock.

Two Minimal Tests

The relative merits of each of the above hypotheses were evaluated by subjecting each hypothesis to the two tests described below. Proposed explanations that failed one or both tests were rejected as lacking minimally adequate support. Those explanations that could not be found to fail one or both tests were judged most plausible.

Test 1: Biological.

A proposed explanation should be:

(a) supported by and must certainly not conflict with existing biological knowledge concerning Dungeness crabs; and

(b) judged "plausible" from an ecological perspective.

In applying the biological test, (a) required a direct and straightforward comparison of an explanation with existing biological data, but (b) required qualitative and subjective judgements which are, however, routinely made of necessity in fisheries research.

Test 2: Statistical.

For explanations involving an environmental factor, there must be (a) a statistically significant correlation between that factor and fishery data, and (b) analyses used to generate that correlation(s) must appear free of apparent bias. For mathematical models of density-dependence, (a) models must be capable of roughly matching empirical fishery time series (especially the observed period of apparent fluctuations), and (b) there should be a significant statistical "fit" of the model to empirical fishery data. (See Botsford (1981) and McKelvey and Hankin (1981) for a detailed consideration of this second test in the context of mathematical models.)

Landings Versus Year Class Strength

Almost all studies of Dungeness crabs have assumed that annual landings data provide a suitable proxy for year class strength. This assumption appears to have originated from Cleaver's (1949) early research and was first contested by Gotshall (1978), then McKelvey et al. (1980), and most recently by Methot and Botsford (1982). McKelvey et al. argued that the striking fluctuations in northern California fishing effort (Figure 2) should have produced significant fluctuations in exploitation rates. If this were true, then landings data would include contributions from two or more year classes of crabs and would not be a direct simple reflection of year class strength.

McKelvey et al.'s arguments were based on classical fishery mortality models (Ricker 1975), but also on some previously unpublished analyses of the northern California fishery which are reproduced here graphically as Figures 3 and 4. Figure 3 shows that the statistical correlation between a season's commercial landings and an index of pre-season abundance (number of legal males per trap) was quite weak. However, when the pre-season index was multiplied by fishing effort (measured as total pots fished), a remarkably good statistical relation was achieved between actual landings and this combined measure of initial abundance and fishing effort (Figure 4). Unexplained variation in landings was reduced from 45% (Figure 3) to just 15% (Figure 4); this occurred despite the fact that the pre-season index was measured as numbers of crabs whereas landings were measured as pounds of crab. The clear implication of these figures was that fishing effort must indeed exert an important influence on annual exploitation rates, at least in northern California.

Methot and Botsford (1982) recently concluded that exploitation rates had indeed varied significantly in the northern California fishery, but they discounted the earlier analyses of McKelvey et al. In particular, they challenged McKelvey et al.'s contention that exploitations rates had generally increased over time in the northern California fishery.

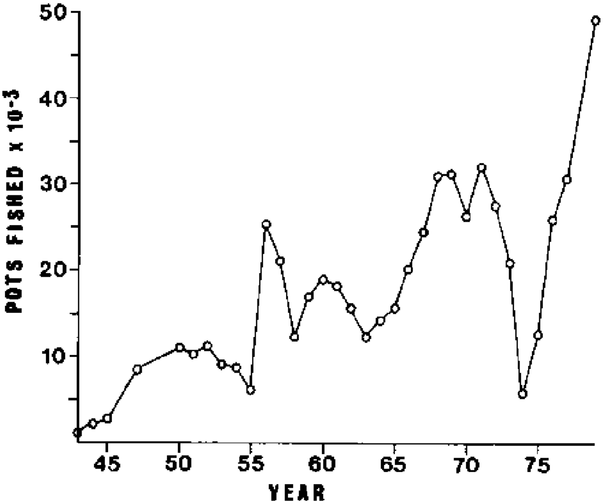

Figure 2. Estimated number of pots fished in the northern California fishery, 1943-1978.

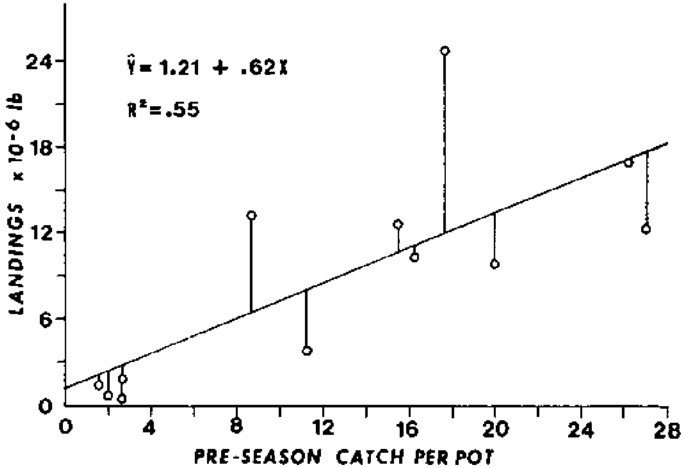

Figure 3. Northern California commercial Dungeness crab landings plotted against pre-season catch per pot (measured as number of legal males) for the period 1962-1977. Vertical lines indicate deviations of landings data from the indicated predictive regresion line. Data from R. Warner, California Fish and Game.

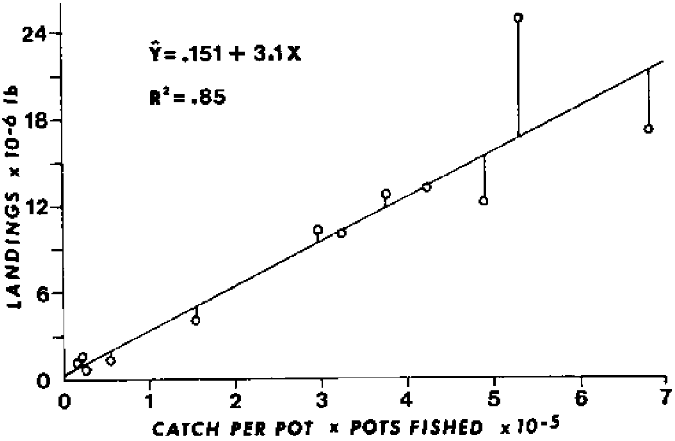

Figure 4. Northern California commercial Dungeness crab landings plotted against a combined measure of pre-season catch per pot and fishing effort (number of pots fished). Same data as for Figure 3. Vertical lines indicate deviations of landings data from the indicated predictive regression line.

Figure 5, however, shows that exploitation rates estimated by the two groups of researchers, using independent methods, are in rather remarkable agreement. Difference in interpretation regarding the existence of a generally increasing trend in exploitation rates appears to hinge on the longer times series employed by McKelvey et al. (1980) as compared to that used by Methot and Botsford (1982) and seems a rather minor point.

Studies by McKelvey et al. (1980) and Methot and Botsford (1982) are thus in substantial agreement that exploitation rates have not remained constant in the northern California fishery, nor have they remained high enough so that virtually all legal males are harvested each season (as has been assumed by most fishery scientists). As a consequence, fluctuations in landings may give a misleading and erroneous picture of real fluctuations in year class strength. Hence, any study that relies solely on the statistical correlation between landings and some factor (density-dependent or density-independent) must be viewed with skepticism. Thus far, only McKelvey et al. (1980) have attempted extraction of year class strength from landings data. Their extracted estimates of year class strength, although crude, suggest real cyclic fluctuations in year class strength with a period of 9-10 years in northern California. Although analyses similar to those presented by McKelvey et al. and Methot and Botsford have not been made for other West Coast fisheries, it seems likely that exploitation rates have varied significantly in all crab fisheries. Crab landings data are probably a very poor proxy for year class strength in all fisheries.

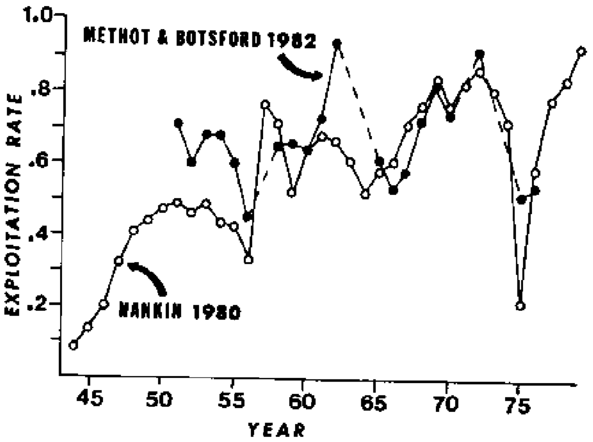

Figure 5. Estimated exploitation rates in the northern California Dungeness crab fishery, 1944-1979. Methot and Botsford's estimates were based on comparing actual landings with Leslie estimates of initial abundance of harvestable crabs. Hankin's estimates were based on classical fishery mortality models (see McKelvey et al. 1980 for explanation).

Critique of Proposed Explanations

1. Upwelling. Peterson (1973) investigated the statistical correlations between summed summer upwelling indices and crab landings from northern California, Oregon and Washington. By manipulating lag-times, he found that upwelling was significantly and positively correlated with crab landings in northern California and Oregon at a 1.5 year lag, and in Washington at a 0.5 year lag. Based on these findings, he argued that upwelling, through its effect on food availability, must have a significant impact on survival rates and/or molting success of sub-legal adult male crabs.

Although Peterson's hypothesis passes the statistical test, Botsford and Wickham (1975) showed that although crab landings were cyclic, upwelling time series were not; they thus rejected the upwelling hypothesis in favor of density-dependent internal controls. However, Peterson's hypothesis may be more seriously challenged on biological grounds. There are no biological data which support an hypothesis of strong upwelling effects on survival and/or molting success of sub-legal adult male crabs, and there are data which conflict with this hypothesis. The upwelling hypothesis would require that landings are largely independent of year class strength (in the sense that upwelling effects among sub-legal adult males would mask any earlier-established year class strength) and thus that upwelling must produce nearly 50-fold variation in survival rates and/or molting success (northern California landings have ranged from about 0.5 - 25 x 10^6 pounds). Although research has shown that some adult male crabs may miss molts, the vast majority do not. Poole (1967) stated that up to

10-15% may miss molts, whereas Warner (pers. comm.) has found, on the basis of mating marks, that from 0-25% may miss molts. Variation in adult male molting success seems far to small to account for any but a very minor part of the required variation; hence, the primary effect of upwelling would have to be on adult survival rates. This is contradicted by Warner's (pers. comm.) studies of northern California Dungeness crab. Over a five year period, Warner found that relative abundance of several year classes of crabs could be readily tracked through trawl data series. According to Peterson's hypothesis, the effect of upwelling would be so strong that one would not expect the relative abundance of a cohort to remain fairly constant over a period of years. Upwelling-induced variation in survival rates would mask any direct relation between year class strength at age three and subsequent availability of age four and five crabs. Finally, it is biologically implausible to expect such pronounced upwelling effects on crab life stages which are a priori far less sensitive to such effects than are early life stages.

2. **Sunspot Activity.** Love and Westphal (1981) proposed that fluctuations in total annual West Coast landings of Dungeness crabs reflected fluctuations in mean annual sunspot number. They freely admitted that they had no direct biological connection in mind and it is thus impossible to subject their proposed explanation to the biological test. However, it is possible to subject their hypothesis to the statistical test, in particular as regards possible bias of analysis methods.

Love and Westphal summed landings from all Pacific Coast areas in their analyses, thus deriving landings data which are of uncertain quality. Figure 1 shows that landings fluctuations of Dungeness crabs are not strictly synchronous in all areas; in fact, Botsford and Wickham (1975) found that period of apparent fluctuations ranged from about 9 years in California to 12 years in Oregon and Washington. Because periods of sunspot activity appear to follow an 11 year cycle, summation of landings could easily be regarded as a thinly disguised method to achieve an approximate period of landings fluctuations of about 11 years and to thereby generate a significant correlation between summed landings and sunspot activity. Love and Westphal did not justify their summation of landings data, nor did they present results of correlation analyses separately applied to regional fisheries.

A more serious objection may be raised concerning Love and Westphal's analyses of these summed landings data. Figure 6 reproduces their plot of total crab landings and sunspot numbers. For again unjustified reasons, they treated each of the first two "cycles" (1955-1964, 1965-1975) independently and thereby generated substantial positive correlations (0.90, 0.87) between sunspot activity and landings; they chose to ignore remaining data. They then found that lags of 5 years resulted in largest significant negative correlations for the two cycles; these results were to be expected, because 5 years was as close to half a period out of phase as was possible, and were not independent of the previous results. One must ask: Why did they not compute the correlation between the two variables over the entire 1955-1980 period for which they had data? Inspection of Figure 6 suggests the answer: they would have found a far smaller correlation. Reading data crudely off of Figure 6, the computed linear correlation between the two variables over the entire data set was about 0.5; sunspot activity could thus account for about 25% of the variation in total crab

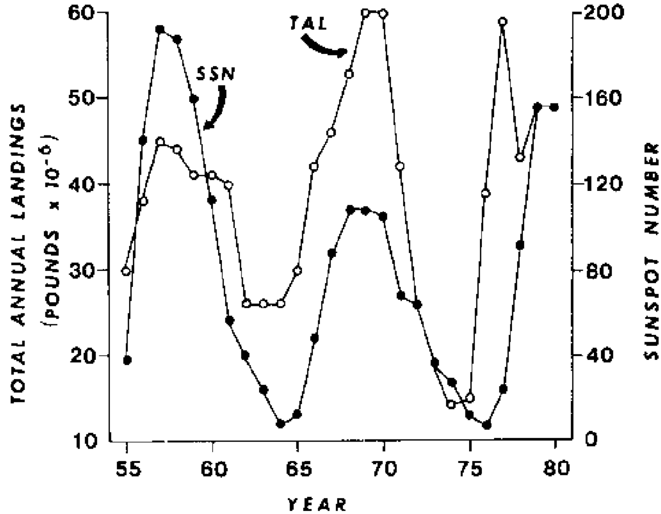

Figure 6. Total annual West Coast Dungeness crab landings and mean annual sunspot numbers for the period 1955-1980. Redrawn from Love and Westphal (1981).

landings throughout the West Coast. Although statistical tables will verify that this correlation is indeed statistically significant, it is hardly "such stuff as dreams are made on". Also the residual pattern for the entire period indicates serious lack-of-fit (see Draper and Smith 1981).

To summarize, Love and Westphal's proposal lacks any biological basis and statistical correlation analyses employed in their study are not clearly free of bias. One hopes that their paper was intended as a tongue-in-cheek satirical commentary on the controversy surrounding the various proposed explanations for fluctuations in crab abundance and that the editorial staff of Fishery Bulletin was well aware of the satirical nature of the piece. If this was not the case, then the paper is a sad commentary on existing peer review standards for Notes in what otherwise is a solid publication of fisheries research.

3. Ocean Water Temperatures. Wild (1980) first proposed that fluctuations in ocean water temperatures during the egg brooding period were responsible for the "crash" of the central California fishery and at least partially responsible for fluctuations in northern California crab landings; this proposal has been more recently restated in Wild (1983) and Wild et al. (1983). The proposal was based on two different lines of evidence. First, plots of crab landings and ocean water temperatures during egg brooding periods were not inconsistent with this hypothesis for the central and northern California fisheries (Figures 7 and 8). The dramatic decline and "collapse" of the central California fishery coincided with a dramatic increase in ocean water temperatures to near 16°C three years previous during egg brooding stages.

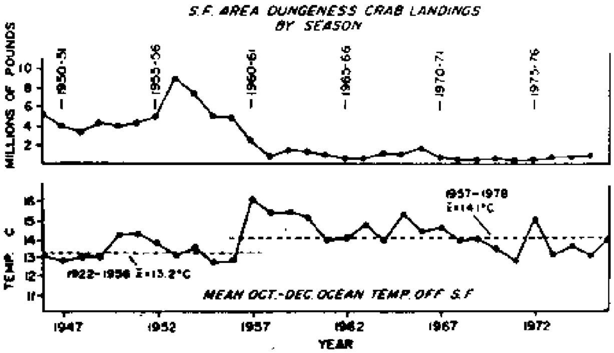

Figure 7. Central California Dungeness crab landings and mean ocean water temperatures three years previous during egg brooding periods. Reproduced from Wild et al. (1983) with permission.

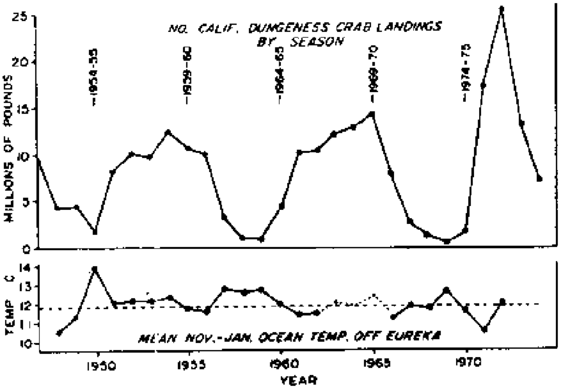

Figure 8. Northern California Dungeness crab landings and mean ocean water temperatures four years pervious during egg brooding periods. Reproduced from Wild et al. (1983) with permission.

In northern California, peak landings in the 1975-76 (and 1976-77) season(s) coincided with unusually low temperatures during egg brooding periods four years previous. Lag-times for these figures seem appropriate for the delay between brooding of eggs to fishery recruitment in the two areas and Warner (pers. comm.) found that much of the 1976-77 northern California landings consisted of crabs which were first recruited in the 1975-76 season. Second, and far more important, Wild found significant temperature-related effects on egg brooding period, egg mortality and hatching success among laboratory-held female Dungeness crabs. Egg brooding periods were inversely related to water temperature: at 16.7°C egg masses hatched in an average of 64 days in contrast to 123 days at 9.4°C. Egg mass volumes declined rapidly at 16.7°C, indicating egg mortality (Figure 9). Egg mass hatching success was greatest at 10°C where an average of 685,000 larvae were produced per egg mass. The overall average at ambient temperature (12.9°C and 13.9°C) was 275,000, and at 16.7°C only one egg mass out of 8 produced any significant number of larvae (100,000); at least half of these died shortly after hatching. Wild's temperature effects are also corroborated by earlier studies by Mayer (1973) who also found increasing egg mortality with increasing water temperature.

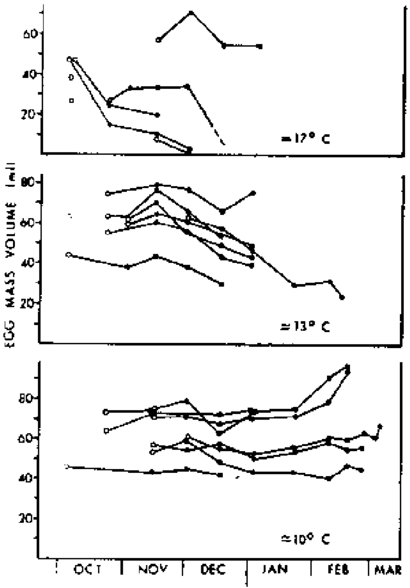

Figure 9. Trends of egg mass volume with time as a function of water temperature among laboratory-held female Dungeness crabs. Reproduced from Wild (1983) with permission.

Wild's research represents the best-documented evidence of a significant relation between an environmental factor and survival of a Dungeness crab life stage. The ocean water temperature hypothesis passes the biological test in convincing fashion; laboratory results were achieved at temperatures which are encountered by Dungeness crabs in their natural environments and demonstrated striking thermal sensitivity of eggs. The statistical relations between crab landings data and ocean water temperatures were marginally significant (see Wild et al. 1983), but were far less striking than were the laboratory results. Nevertheless, Figures 7 and 8 are certainly provocative in their suggestions of important temperature effects on landings. On balance, Wild's proposal passes the biological test in convincing fashion, but passes the statistical test in an inconvincing fashion. Of the proposed environmental hypotheses, this proposal is unquestionably the most persuasive thus far published.

4. Carcinonemertes errans, a crab egg predator. Botsford and Wickham (1978) first mentioned the possibility that C. errans might be implicated in crab landings fluctuations, but is Wickham (1979) who has been most closely associated with this possibility. Wickham (1979) found that central California female Dungeness crabs had "epidemic" infestations of C. errans and that infestations appeared to be increasinf off northern California and Washington. He speculated that worm abundance might be tied to crab abundance and that periods of extremely

high crab abundance could drive worm populations to an unusual equilibrium in which epidemic worm densities were maintained and crab stocks remained at depressed levels. Wickham concluded his 1979 paper with the following: "The increased densities seen at Eureka and Washington over the past few years may indicate that these populations are in danger of passing into the high worm equilibrium. If this occurs, the entire continental United States Dungeness crab fishery could collapse to levels comparable to those at San Francisco...". Statements of this sort have caused the egg predator worm hypothesis to receive by far the most media attention of existing hypotheses: front page headlines in at least the San Francisco Chronicle (8 May 1980) and Eureka's Times-Standard (13 March 1981), and extensive reporting in the National Fisherman (May 1981). It is without doubt the most controversial of existing hypotheses.

There seems no question that C. errans has, in some years, been a significant source of crab egg mortality in some Pacific Coast areas. However, in part because worm densities have not been recorded for long periods of time, it is difficult to evaluate the plausibility of Wickham's hypothesis. The thesis that periods of exceptionally high crab abundance could drive crab populations to new high worm equilibria appears to have been motivated in part by the "crash" of the central California fishery and the apparent "ominous" parallel behavior of the northern California fishery (Figure 10). In both of these fisheries, amplitude of landings fluctuations increased over time; the central California fishery collapse took place just after the highest landings on record. However, McKelvey et al. (1980) observed that the apparent increasing amplitude of northern California landings was more likely a reflection of generally increasing fishing effort and corresponding increased removal rates for available crabs than of real crab abundance (see Figure 12, later in this paper). More recently Methot and Botsford (1982) have generated a similar figure which makes the same suggestion (their Figure 3). Landings data since 1979 for the northern California fishery have failed to suggest that imminent collapse prophesied by Wickham (see Warner, this Symposium).

A possible biological weakness of the egg predator theory is that feeding of worms is inhibited by worm density, thus causing worm-induced egg mortality to have an apparent maximum of 50-60% (Wickham 1979). An hypothesis which involves early life stages must account for fluctuations in early life survival of about 50-fold as well as an average mortality rate of, say, 0.999990. Clearly, there must be far more significant mortality factors during early life stages than C. errans. However, if survival beyond the hatching stage were density-independent, then fluctuations in worm-induced egg mortality could indeed give rise to fluctuations in resulting survival rates which would be commensurate with those required.

The current status of this proposal is unclear. A recent report (Johnston et al. 1981), of which Wickham was co-author, stated that "studies of the crab egg predator C. errans have shown that this worm does not appear to cause the cycles in abundance. Worm abundance does not change rapidly enough with crab abundance...". It is my understanding that Hobbs et al. (this Symposium) have more recently arrived at a similar conclusion. C. errans appears an unlikely candidate for the cause of fluctuations in landings of Dungeness crabs.

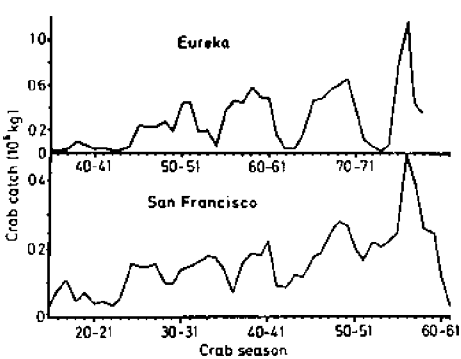

Figure 10. Apparent parallel increases in peak catches of Dungeness crabs in the northern California (Eureka) and central California (San Francisco) fisheries. Reproduced from Wickham (1979).

4. Cannibalism. Botsford and Wickham (1978) developed an age-structured continuous-time mathematical model in which juvenile survival rates depended on cannibalism by older crabs. They assumed that instantaneous juvenile mortality due to cannibalism was proportional to a weighted density of older crabs. Each crab was weighted according to its mass raised to the 0.8 power, thus giving greatest weight to large legal-sized male crabs and least weight to smaller females and younger crabs. Using accepted life history parameters for male crabs and guestimated parameters for female crabs, they showed that cannibalism of this sort could indeed give rise to cycles of abundance. Further, they showed that intensive and exclusive harvest of large male crabs could give rise to increasingly unstable cycles of increasing amplitude; this latter result was original and provocative.

McKelvey and Hankin (1981) gave a detailed explanation for their earlier (McKelvey et al. 1980) rejection of the cannibalism hypothesis. First, they argued, the Botsford-Wickham model failed to produce cycles of the length which would be required to roughly mimic landings time series; maximum model period, regardless of parameter manipulations, was about 8 years, whereas period for actual landings was between 9 and 10 years. Figure 11, which superimposes perfect sine waves of period 8 and 10 which are initially in phase, illustrates the obvious and critical importance of model period as a criterion for model plausibility. Second, the apparent trend of increasing fishing effort and exploitation rates in the northern California fishery (see Figures 2 and 5) would, according to the Botsford-Wickham model, result in a reduction of cycle period to less than 8 years; there has been no evidence for this effect (see Figure 1). Third, the apparent increasing amplitude of northern California landings fluctuations was probably not a direct reflection of increasing amplitude and instability of underlying year class strength, but rather the result of increasing fishing effort and increasing removal rates for large males. These issues are all considered, in great detail and from opposing views, in Botsford (1981) and McKelvey

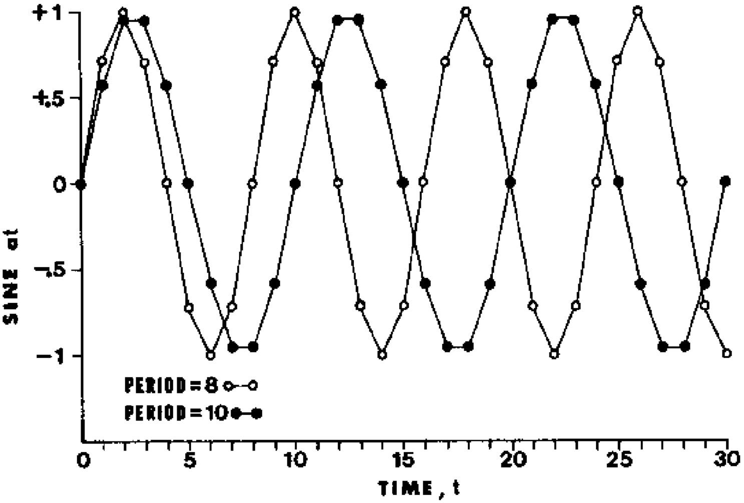

Figure 11. Superimposition of perfect sine waves of periods 8 and 10. Note that waves begin in phase, but that by t=18 (less than two full cycles of period 10) the period 8 cycle is at a minimum while the period 10 cycle is at a maximum.

and Hankin (1981) and there is little point in rehashing them here.

However, a far more serious objection to the Botsford-Wickham cannibalism model, which can be raised with equal persuasiveness regarding McKelvey et al.'s attempt to model cannibalism, is that cannibalism was incorrectly modeled as a biological phenomenon. Butler (pers. comm.) first pointed this out to the author, and this same point has more recently been made by Stevens et al. (1982) and suggested by Botsford (1984). Butler (1954) and Stevens et al. (1982) both found that cannibalism on newly-settled and early instar crabs was far more prevalent among other juvenile crabs than among adult crabs (those > 100 mm carapace width). (But see Gotshall 1977 which may conflict). Stevens et al. (1982) also pointed out that this finding was consistent with theoretical premises of optimal foraging strategy which suggest that prey size should increase with predator size; younger, smaller crabs should be more likely to prey upon newly-settled and/or early instar crabs than should older, larger crabs.

The impact of cannibalism by crabs of different sizes must depend on (a) duration of contact between predator and prey, (b) number of prey consumed per predator per unit time, and (c) predator abundance. The above studies showed that cannibalism rates were greater for smaller crabs than for larger crabs, and it must certainly be the case that there are more of these younger smaller crabs than there are older male crabs because of intensive fisheries. Thus, for cannibalism by larger crabs to be more important than cannibalism by smaller crabs, duration of contact between large crabs and newly-settled crabs and/or early instars would have to be far longer than duration of such contact for smaller crabs. However, published studies suggest exactly the reverse. Juvenile crabs (less than two years of age and less than 100 mm carapace width) generally inhabit shallow water nursery areas, often bays (Collier 1983; Armstrong et al. 1981), and are probably in contact with large adults only during the short period of time it may take for a newly-settled crab to migrate from deeper waters (if settling indeed took place in deeper waters) to shallow water nursery areas. In Humboldt Bay (Warner, pers. comm.) and San Francisco Bay (Collier 1983) juveniles do not leave these shallow waters until about 1.5 years of age beyond settling. During this period they are in contact with other juveniles of the same year class and with newly-settled and/or early instar crabs of the succeeding year class; adult crabs are virtually nonexistent in these areas. Diamond (1983), fishing crab traps which were non-selective above 85 mm carapace width, collected very few juvenile crabs (less than 100 mm) in deeper water (10-24 fathoms) areas of high adult crab abundance. Thus, duration of contact between large adults and newly-settled and/or early instars must be small compared to such duration of contact between juvenile crabs and newly-settled and/or early instar crabs. Stevens et al. (1982) also presented evidence of significant within year class cannibalism among early instar crabs. Thus, the assumptions made by the Botsford-Wickham and McKelvey et al. models of cannibalism — that effects of cannibalism dramatically increase with crab size and are therefore principally due to adult crabs — are contradicted by available biological data.

Some possible implications of these basic biological findings concerning cannibalism, as they might apply to behavior of mathematical models which formulated cannibalism in accord with these findings, were recently suggested by Botsford (1984): "If cannibalism were by juveniles it would cause a more stable population and cycles of shorter period if there were any...". In the extreme case of intense cannibalism by yearling crabs on young-of-year crabs, alternating year class strength could result: an exceptionally strong year class could ensure, through cannibalism, that the following year class was exceptionally weak. This kind of phenomenon was long ago discussed by Ricker (1954) in reference to largemouth bass, where yearlings may prey extensively on young-of-year after adult bass leave their nests. Also, Hankin (1980) documented alternating periods of good and poor survival of newly-born guppy fry as a direct result of cannibalism by larger juveniles in refuge areas. Thus, if cannibalism were correctly modeled, generated cycle period would be far less than the maximum of 8 years thus far generated by the original Botsford-Wickham model and cycles might be eliminated or, in extreme cases, there might be dramatic oscillations in year class strength of period two. The discrepancy between model behavior and empirical fishery behavior would then convincingly rule out the cannibalism hypothesis as a plausible candidate for observed fluctuations in landings of Dungeness crabs.

6. Density-dependent Egg/Larval Survival. McKelvey et al. (1980) used variants of a general age-structured discrete-time mathematical model to investigate the plausibility of several proposed explanations for Dungeness crab fluctuations. They reproduced the behavior of the Botsford-Wickham cannibalism model, but rejected this model as implausible for previously stated reasons. Instead, they proposed that

density-dependent egg/larval survival was a more plausible hypothesis. They found that density-dependent egg/larval survival could result from fluctuations in the total egg production of the unexploited female stock and that, because females were not harvested, such fluctuations would be unaffected by fishing effort. Further, this mechanism could easily give rise to cycle periods of 9-10 years, thus mimicking apparent fluctuations in northern California landings data and in extracted estimates of year class strength.

Using regression methods, McKelvey et al. were able to produce a satisfactory statistical match between their model's behavior and empirical fishery behavior. This match was partially reflected in the correspondence between (a) actual fishery landings data and estimated initial harvestable abundance (Figure 12) and (b) their model simulation of this same figure (Figure 13). Although the correspondence between the two Figures is obviously imperfect, general qualitative features of fishery and model behavior appear similar and period of fluctuations are in agreement. It is important to note that only McKelvey et al. have dared to present such a figure which allows visual assessment of model performance. No such figure exists for the Botsford-Wickham model; it would resemble Figure 11 (this paper).

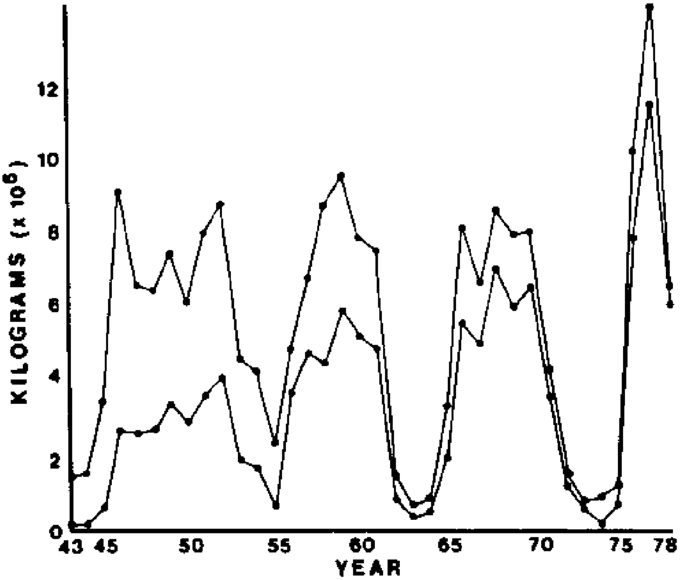

Figure 12. Estimated initial harvestable abundance (upper line) and actual crab landings (lower line) in the northern California fishery. Reproduced from McKelvey et al. (1980).

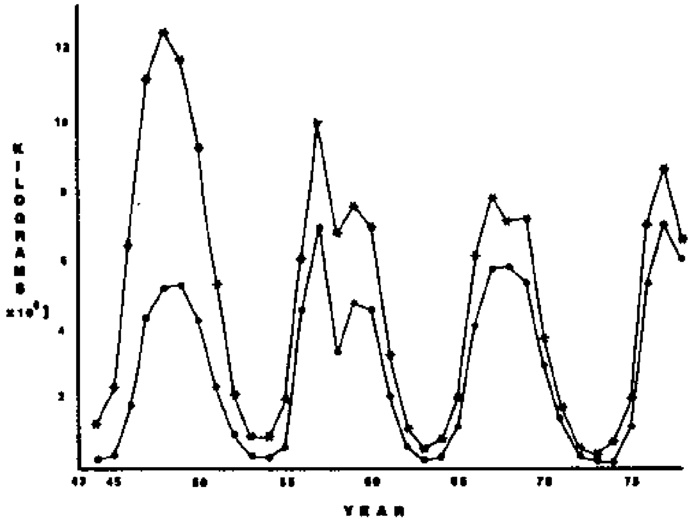

Figure 13. McKelvey et al.'s model simulation of Figure 12. Simulation assumed density-dependent egg/larval survival and was driven by estimated exploitation rates in the northern California fishery (see Figure 5). Reproduced from McKelvey et al. (1980).

Botsford (in Botsford 1981; Methot and Botsford 1982; Botsford et al. 1983; Botsford 1984) has repeatedly contested McKelvey et al.'s rejection of the cannibalism hyopthesis, but has not challenged the essential plausibility of their alternative density-dependent egg/larval survival hypothesis. Nevertheless, Botsford (1981) was correct in his comment that McKelvey et al.'s conclusions rested on an extremely tentative set of parameter assumptions regarding life history of adult female Dungeness crabs. Hankin et al. (this Symposium) reviewed the results of a project designed to establish these basic female life history parameters. Although parameter estimates derived in this study were not in direct agreement with those used by McKelvey et al., they were in agreement on those fundamental levels which would influence the behavior of the model proposed by McKelvey et al. Among other things, Hankin et al. found that (a) maximum longevity of females was probably 7 or at most 8 years; (b) annual survival rates for large adult females (those exceeding 155 mm carapace width and probably 5 years of age) were very low and averaged 10%; (c) survival rates for smaller younger females were much higher, probably about 50%; and (d) fecundity among large females that had failed to molt was significantly less than for smaller females that had recently molted and mated. These results are contrasted with the assumptions made in McKelvey et al.'s model: (a) maximum longevity was assumed to be age 6; (b) survival rates for age 6 and older were assumed to be zero (a feature of the Leslie matrix approach); (c) survival rates for age 2-5 females were either 50% or 80% (model behavior was insensitive to at least this range of survival rates). Thus, McKelvey et al.'s original assumptions regarding female crab life history were close, in substance and effect, to the findings of

Hankin et al. (this Symposium). No reproductive role was assigned to crabs beyond age 5 — an assumption not incompatible with the greatly reduced survival rates and lowered fecundity of large adult females — and assumed survival rates for younger female crabs (50%) seem close to correct. Were these new findings incorporated into a revised version of McKelvey et al.'s model, there is no reason to expect that there would be any substantial impacts on model behavior or on the merits of their arguments for density-dependent egg/larval survival.

Of the published mathematical models of density-dependence which purport to explain the fluctuations of Dungeness crabs, only the model of McKelvey et al. can meet the statistical test of significant agreement between model performance and empirical fishery data. However, because there are no biological data with which to directly assess the plausibility of density-dependent egg/larval survival, the biological plausibility of the model must rest principally on an a priori argument that egg/larval stages are most likely to exhibit density-dependent survival. Dungeness crab larvae are usually released in early January in northern California, some three to four months before the onset of upwelling (Peterson 1973) and associated increases in planktonic food. A limited food resource during larval stages could indeed give rise to density-dependent larval survival and Reilly's (1983) work on central California larval Dungeness crabs has suggested that year class strength is established during some larval stage, prior to the megalopae stage and metamorphosis. However, Lough (1976) had great difficulty establishing causes for larval mortality among Oregon Dungeness crabs.

Discussion

Of the six proposed hypotheses, only one — sunspot activity — seems utterly lacking in merit. Although the cannibalism hypothesis failed both statistical and biological tests, there is no question that cannibalism is a real and frequent phenomenon in Dungeness crab populations. Further, the cannibalism hypothesis has led to the development and examination of original mathematical population models which may see application in fisheries other than those for Dungeness crabs. The upwelling hypothesis passed the statistical test, in a possibly spurious fashion (Botsford and Wickham 1975), but failed the test of biological plausibility and conflicted with available biological data. Present data are insufficient to allow a thorough evaluation of the crab egg predator worm hypothesis, but data collected thus far do not appear to implicate C. errans as the principal cause for fluctuations. This is not to say that cannibalism, egg predation by a nemertean worm and/or upwelling do not play significant roles in the dynamics of Dungeness crabs; they probably can, and in some years do. Rather, these factors seem implausible causes for the regular, perhaps cyclic, fluctuations in landings of Dungeness crabs. As such, they can be best regarded as possible second order factors that may significantly modify some more important first order factor(s) which is principally responsible.

Wild's hypothesis that ocean water temperatures during egg brooding periods exert profound effects on egg survival is strongly supported by laboratory rsearch, but plots of crab landings in central and northern California and ocean water temperatures (with appropriate lags) are only qualitatively suggestive of a direct link between crab landings and water temperatures; statistical correlations between crab landings and ocean water temperatures are significant, but weak. The density-dependent egg/larval hypothesis of McKelvey et al. passes the statistical test; model behavior and fishery data are in significant statistical and qualitative agreement. However, there are no existing data which one could use to refute or support the suggestion that egg/larval survival is indeed density-dependent. Collection of data on either larval densities (Reilly 1983, and this Symposium) or total stock egg production (Hankin et al., this Symposium) both pose serious sampling problems and it is unlikely that direct evidence of density-dependent egg/larval survival will be forthcoming in the near future. On the other hand, density-dependent egg/larval survival is a priori plausible as it argues that year class strength must be determined during sensitive early life stages.

Thus, of the existing proposed explanations for fluctuations of Dungeness crabs, no single hyopthesis clearly passes both minimal tests in a convincing fashion. Hypotheses of Wild and McKelvey et al. are in agreement that year class strength must be determined during egg/larval stages and these hypotheses are not opposing but are rather complementary to one another. McKelvey and Hankin (1981) stated that, according to their hypothesis, a decrease in survival during early life stages (from density-independent causes) could have the result of damping fluctuations in abundance and reducing population size; this situation is not unlike that which took place in the central California fishery after the collapse and succeeding relatively warm years. Wild's research suggests that the recent record northern California landings (1975-76, 1976-77) may have been associated with a significant cold water enhancement of egg survival which resulted in an exceptionally strong year class; the model of McKelvey et al. failed to predict these peak landings. The coexistence and mutual interaction of these hypotheses seems well worth further exploration. It seems unlikely that environmental factors do not exert profound effects on early life survival of Dungeness crabs; it seems equally unlikely that Dungeness crabs are exclusively at the mercy of such factors and have no internal, density-dependent controls which would convey stability properties to populations.

Finally, it is probably wise to stress that existing explanations for fluctuations in Dungeness crab abundance are by no means satisfactory. The rough synchrony of landings fluctuations off northern California, Oregon and Washington is indeed suggestive of a large scale environmental effect (PMFC 1964). Fluctuations in ocean water temperatures could indeed produce such large scale effects. For example, the recent El Nino event may have coast-wide impacts on Dungeness crab stocks. Alternatively, dynamics of Dungeness crab stocks may be linked in some fashion, perhaps through larval drift and larval exchange between adjacent stocks.

The objective of this paperwas neither to promote particular hypotheses nor to strike down alternative hypotheses. Rather, the objective was to subject each hypothesis to the same two minimal tests so as to allow an assessment of the relative merits of existing hypotheses. This exercise strongly suggested that year class strength of Dungeness crabs is indeed established during early life stages, egg and/or larval. If this suggestion is true, then future research on dynamics of Dungeness crabs should focus on egg and larval stages. Until and unless data are gathered which refute this suggestion, it seems foolish to invests funds and research efforts into avenues which cannot pass even minimal statistical and biological tests and which are highly implausible candidates for causes of the fluctuations in abundance of Dungeness crabs.

Acknowledgements

I thank Ron Warner for openly sharing data from his studies of northern California Dungeness crabs; these data proved valuable in assessing the relative merits of existing hypotheses for crab fluctuations. I also thank Paul Wild for helpful discussions of his research on female Dungeness crabs; I hope that I have done justice to his studies.

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Initiation of a Dungeness crab, *Cancer magister,* habitat study in North Puget Sound

Paul A. Dinnel, David A. Armstrong and Christopher Dungan
University of Washington
Seattle, Washington

Introduction

The Dungeness crab, Cancer magister, has been the object of commercial and sports fisheries on the west coasts of the United States and Canada since as early as 1848 (Dahlstrom and Wild 1983). Of the scientific studies specifically designed to understand Dungeness crab ecology, none have addressed the locally important crab resources of the inland waters of Puget Sound, Hood Canal, the Straits of Juan de Fuca, or the U.S. portion of the Straits of Georgia.

Puget Sound Dungeness crab stocks support a commercial and sports fishery of 1.3 to 2 million pounds annually (PMFC 1982) yet very little is known about the nearshore distribution, habitat preferences or recruitment dynamics of these stocks. Recent studies in coastal estuaries have supplied evidence that habitat type is critical during the early life history stages and that shallow embayments may be important nursery areas (Stevens and Armstrong 1984).

Recently, the state of Washington has given more emphasis to the protection of sensitive ecological habitats when considering shoreline development permits. Presently, the Washington Department of Fisheries (WDF) has been asked to consider the possible impact of a number of shoreline projects that might affect crab. As a result, the University of Washington School of Fisheries in conjunction with WDF, NOAA/Sea Grant and the Lummi Indian Tribe have initiated a major study in north Puget Sound and the Straits of Juan de Fuca to document the habitat requirements of local crab stocks. The purposes of this paper are to describe the rationale, objectives and methods associated with this new study and to discuss some early observations based on the first four months of field work.

Rationale

The dramatic and sustained depression of crab resources in the San Francisco Bay area from the early 1960's to the present day serves as a reminder that fishery stocks can be fragile and slow to recover (see review by Armstrong, 1983). Although the decline in San Francisco crab stocks may be partially attributable to changing oceanographic conditions such as water temperature (Wild et al. 1983), other substantial impacts related to loss of nursery habitats and pollution have been identified (Wild and Tasto 1983).

Studies in coastal estuaries such as San Francisco Bay (Tasto 1983), Humboldt Bay (Gotshall 1978) and Grays Harbor (Stevens and Armstrong 1984; Armstrong and Gunderson, these proceedings) have shown that protected embayments may serve as nurseries estimated to contribute as much as 83% of the adult crabs in an offshore fishery (Tasto 1983) following migration of the young recruits out of the estuaries. Similar studies also suggest that habitat type is critical during early life history stages of Dungeness crab, particularly following metamorphosis and settlement of the first instar juveniles through the next five to six months (Stevens and Armstrong 1984; Armstrong and Gunderson, these proceedings). Indeed, Cleaver (1949) concluded that "The facts of the (Dungeness crab) fishery point to a large dependence upon the survival of young from the hatch of each brood year." Predation on juvenile crabs is probably heavy during the first few months of their existence, the survivors being highly dependent on substrates that afford shelter from predators as well as adequate food supply (e.g. eelgrass, shellhash, algae, stick debris, etc.).

In Puget Sound, there is a limited amount of such nearshore intertidal habitat and the extent of its utilization by both young-of-the-year (YOY) crabs and later life history stages is not at all documented. Reasons to study crab biology and ecology in regard to substrate and habitat are based partially on proposed development in the form of dredging and landfill, as well as our concern for the possible impact of industrial pollution on invertebrates in nearshore systems. The limited amount of intertidal and subtidal habitat that might offer appropriate refuge for Dungeness crab in Puget Sound is increasingly threatened by numerous projects. Among pending proposals to construct marinas and port facilities are those at Lummi Bay, Birch Bay, Cherry Point, Tulalip Bay, Harbor Point, Everett and Anacortes. Virtually all of these projects would include dredging and/or fill of intertidal habitat. Hence, there is a critical need for well defined studies to document the importance of the nearshore habitats to Dungeness crab success.

Objectives

The present efforts on the newly initiated Puget Sound crab study dove-tail the interests and needs of two different sponsors. The primary efforts are directed towards an overall view of nearshore habitat utilization by crabs. The specific objectives of this portion of study include:

1. Identification of sampling gear and strategies for sampling intertidal and subtidal habitats for all age classes of Dungeness crab.

2. Initiation of a sampling program in several selected areas of north Puget Sound and the Straits of Juan de Fuca.

3. Estimation from first year sampling efforts of:

    a) recruitment timing, distribution, strength and habitat preferences of the 1984 year class;

    b) timing and extent of inshore-offshore migrations by juveniles and adults and;

    c) timing and location of adult molting, mating and egg production.

4. Refinement of sampling strategies for use during the following two years of study.

A secondary, site-specific portion of the program pertains to Lummi Bay which has been proposed for the site of a new boat marina. Vessel access to the marina will be provided by dredging a four meter deep channel across approximately 1500 meters of intertidal flats and area of shallow channels. Specific objectives of this portion of the study include:

1. Establishment of a "baseline" of Dungeness crab resources in Lummi Bay.

2. Rank the importance of various habitat and substrate types to Dungeness crabs.

3. Determine crab abundance as a function of depth and distance from shore.

4. Define localized migratory patterns of both adults and juveniles.

5. Determine periods of recruitment to nearshore habitats for use in determination of least detrimental times for channel dredging.

6. Development of information for assessing the usefulness of possible future management/mitigation proposals relative to Dungeness crab habitat loss.

Sampling Sites and Methods

Present sample sites include Birch Bay, Cherry Point, Lummi Bay, Hale Pass, Bellingham Bay, Samish Bay and Padilla Bay in north Puget Sound and Dungeness Bay on the Straits of Juan de Fuca (Figure 1). A portion of the embayments named above are sampled intertidally at low tide using established transects and subtidally (down to 12 m depth) by beam trawl and pots. All of the above areas (except Dungeness Bay) are additionally sampled in deep subtidal (15 to 150 m deep) offshore areas with the same beam trawl used for the shallow stations.

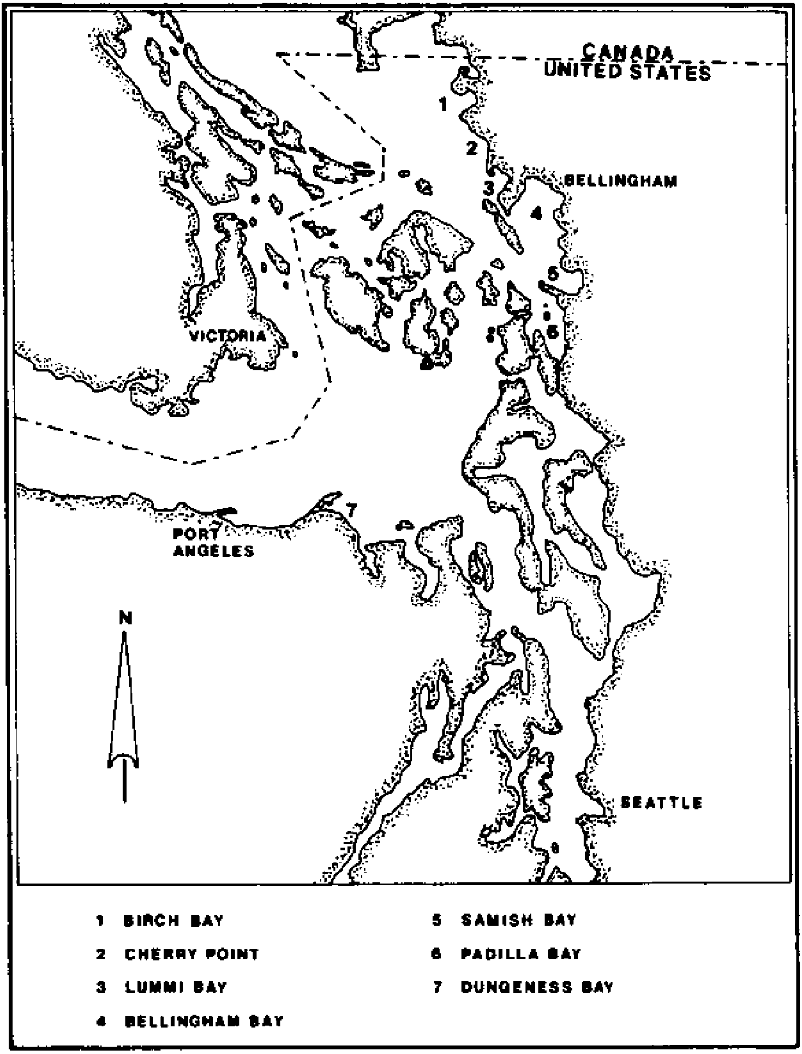

Figure 1. Map of northwest Washington showing the primary sampling areas for Dungeness crabs in north Puget Sound and the Straits of Juan de Fuca.

Subtidal sampling.

The primary gear for sampling both shallow and deep subtidal crab habitats is a 3-meter plumb staff beam trawl (see Gunderson et al. this proceedings) with a small mesh cod end liner to retain all post-larval instar stages. The trawl is towed at approximately 2 knots for two to five minutes and the catches sorted for all species of *Cancer* crabs and associated floral and faunal groups. A second subtidal sampling tool consists of baited commercial crab pots (12 to 24 hour soak times) lined with fine-mesh vexar screen to retain crabs greater than approximately 20 mm carapace width. The shallow subtidal sampling is conducted approximately once a month while the deep trawl stations are sampled 3 to 4 times per year.

Intertidal sampling.

Intertidal habitats are being assessed for crab density by sampling along representative transects running from the high tide level down to lower low water (approximately -1 m contour). Samples are collected randomly along each transect during low tide periods from within the various habitat types. Each sample consists of an area $0.25m^2$ in size with the upper 4-5 mm excavated and screened to remove Dungeness crab and related species. Intertidal samples are presently collected at monthly intervals.

Other sample methods.

Additional sampling methods under consideration for future use include: 1) ring nets fished for short durations (i.e. less than an hour; 2) hydraulic or suction sampling devices to help quantify the beam trawl efficiency for YOY crabs on various substrates; 3) underwater diver transects and; 4) underwater video systems.

Results and Discussion

Field data collected during the first four months of this study are being prepared for computer-assisted analyses and are not available for presentation at this time. However, for the purposes of this report, a two-week (27 July to 8 August, 1984) set of data has been selectively analyzed to illustrate some of the 1984 summer field observations. This data set is based on the following samples: 1) 206 intertidal samples collected from Birch, Lummi and Samish Bays; 2) 23 shallow-water (0 to 12 m depth) beam trawls in Birch, Lummi and Samish Bays and; 3) 24 deep-water (15 to 150 m depth) beam trawls offshore of Birch, Lummi, Bellingham, Samish, and Padilla Bays.

Cancer magister distribution.

The basic catch summary for each type of sample effort (Table 1) shows that there was a distinct stratification of *C. magister* age classes by depth during this period. All of the 280 Dungeness crabs recovered during the low tide intertidal transects were YOY (0+ year class) measuring less than 35 mm carapace width while almost all (157 of 164) of the deep-water trawl catch was composed of adults (≥ 2+ year classes) measuring more than 100 mm width. The shallow-water trawl

Table 1. Comparison of catch/sample and catch/100m^2 of *Cancer magister* from intertidal samples collected at low tide, shallow (0-12 m depth) trawls and deep (15-100 m depth) trawls.

Age Class		Intertidal Samples[1]		Shallow Trawl Samples[2]		Deep Trawl Samples[3]	
		Average Catch/sample	(%)	Average Catch/sample	(%)	Average Catch/sample	(%)
Adults (≥2+)		0	(0)	3.2	(28)	6.5	(96)
Juveniles	(1+)	0	(0)	1.3	(11)	0	(0)
	(0+)	1.4	(100)	6.9	(61)	0.3	(4)
All Crabs	(±SD)	1.4 ± 2.6		11.4 ± 12.6		6.8 ± 7.2	
		Average Catch/100m^2		Average Catch/100m^2		Average Catch/100m^2	
Adults (≥2+)		0.0		0.65		0.82	
Juveniles	(1+)	0.0		0.27		0.00	
	(0+)	560.0		1.41		0.04	
All Crabs		560.0		2.33		0.86	

[1] n = 206 samples of 0.25m^2

[2] n = 23 beam trawl tows; 9 at 2.5 min. and 14 at 5 min.; average area swept = 489.2m^2

[3] n = 24 beam trawl tows; 1 at 2.5 min. and 23 at 5 min.; average area swept = 799.4m^2

stations showed an intermediate catch distribution by size with each year class being represented (Table 1), although YOY were 5x more abundant than adults.

The complete lack of crabs older than 0+ in the intertidal samples may be a reflection of two circumstances: 1) limited sample area - 206 0.25 m^2 samples comprised a total sample area of only 51.5 m^2 while a single shallow beam trawl tow covered an average of 489.2 m^2 and; 2) intertidal (0 m depth) beam trawls during high tide periods did catch older crabs (12 1+ and 2 ≥ 2+ year class crabs in nine intertidal tows). It is probable that a portion of the larger *C. magister* move off the flats into deeper water during low tide periods (Gotshall 1978; Stevens and Armstrong 1984) although subsequent intertidal samples have shown that adult crabs do bury in the exposed substrates during low tides.

The virtual absence of 0+ *C. magister* at deep stations (7 of 164 crabs) suggests three possiblities: 1) settlement is insignificant at depths greater than about 15 m; 2) settlement occurs but mortality of YOY is almost 100% or; 3) settlement occurs but surviving YOY move into shallow water.

The size-depth stratification of Dungeness crab is further illustrated by size-frequency histograms for each sample type (Figure 2). This set of histograms again reflects the nearshore concentration of 0+ crabs and the transition away from YOY habitat with increasing depth.

A non-random distribution by sex for adult *C. magister* (> 100 mm carapace width) is also apparent from the beam trawl samples. Females outnumbered males by greater than a 2:1 ratio (69.2% females) in the deeper trawls while males outnumbered females (56.3% males) in the shallow trawls even though the sports/commercial crab fishery was removing legal (i.e. ≥ 152 mm) males from shallow water during this time. None of the adult females were gravid during this summer sample period.

Crab densities.

The distribution data summarized in Table 1 is also presented as calculated crab densities (crabs/100m^2) since the average areas sampled were substantially different for each catagory. For adult crabs (≥2+ year classes) the densities were very similar for the shallow and deep tows while the 1+ year class (absent from the deep trawls) was approximately half as dense as the adult crabs in the shallow water tows. The average YOY intertidal density of 560 0+ crabs/100m^2 is based on sampling methodology which is essentially 100% efficient for young crabs. However, two factors must temper this density estimate: 1) YOY settlement (and early instar mortality) is only partially complete as of the first week in August (we observed settlement of megalopae as late as October 1 of this year) and; 2) this density estimate is based on a variety of samples from different substrate compositions as well as degree and type of substrate cover and tide height. Densities of 0+ crabs in the intertidal samples

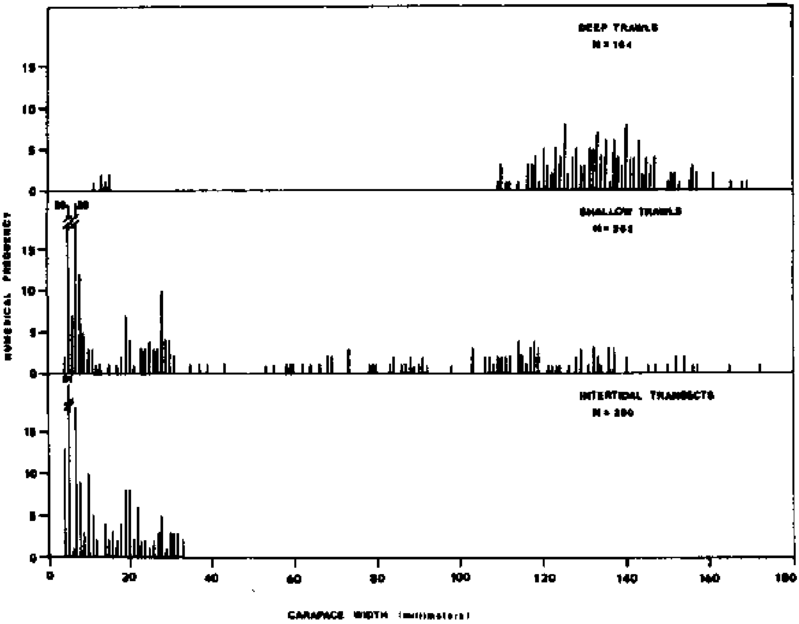

Figure 2. Size-frequency histogram for all Dungeness crabs caught in deep (15-100 m depth) and shallow (0-12 m depth) trawls and in the intertidal samples collected at low tides.

ranged from 0/m^2 in clean sand without cover to as high as 60/m^2 in samples with optimum substrate and cover (e.g. eelgrass and small cobble covered with detrital algae). The apparent densities of 0+ crabs in the shallow and deep subtidal areas sampled by beam trawl are approximately 500 and 19,000 times less (respectively) than intertidal stations collected by hand. However, this comparison assumes a trawl efficiency of 100%, an assumption not supported by the comparisons below.

Trawl efficiency.

Gotshall (1978) used SCUBA diver transects in conjunction with 4.9 m try-net trawls to estimate the efficiency of the try-net for capturing *C. magister* in Humboldt Bay, California. Gotshall estimated an overall efficiency of 45% for two year classes (0+ and 1+) of *C. magister*.

A similar (first approximation) estimate of trawl efficiency can be generated for this study for the 0+ crabs by comparing relative densities of YOY between the intertidal stations collected by hand at low tide and by beam trawl at high tide. Nine intertidal tows (three each from Birch, Lummi, and Samish Bays) produced 42 YOY crabs which is a density of $1.5/100m^2$ as compared to the low tide estimate of $560.0/100m^2$ (Table 1). These figures suggest a trawl efficiency on the sand substrate of those bays of only 0.27% for juvenile crabs ≤ 35 mm in carapace width. The possible reasons why this estimate differs so greatly from Gotshalls' estimate of 45% are at least threefold: 1) our estimate is based only on the 0+ year class instead of both 0+ and 1+ crabs; 2) divers in the previous study may have failed to observe a substantial proportion of YOY crabs often buried in the substrate to avoid predation and; 3) our estimates were generated from intertidal areas with substantial (often very thick) eelgrass (*Zostera marina*) or algal cover whereas Gotshalls' estimates came from subtidal channels free of significant plant cover.

Restraint must be used in the interpretation and application of the estimate of beam trawl efficiency for YOY crab generated above. This estimate was developed from a samling effort that was not specifically designed to assess trawl efficiency and is best used to formulate working hypotheses and specific sampling schemes to quantify the trawl efficiency over various types of substrate and vegetation cover (a goal of our 1985 proposed work). Trawl efficiency may prove to be very dependent on substrate type and cover. Most of the intertidal substrates sampled during this study were compact sands and silty sands, often with medium to thick eelgrass or algae cover. Compact substrates (especially with plant cover) may cause the trawl to "skim" over the substrate surface without "biting in" as has been observed for the more silty, less consolidated substrates typically found in Grays Harbor. In that estuary, high densities of YOY juveniles taken by beam trawl are invariably associated with epibenthic cover such as terrestrial debris, shell, and detrital eeglgrass and macroalgae which are readily caught along with silt/mud sediments as the net excavates (Armstrong and Gunderson, these proceedings). Nevertheless, it is clear that uncritical application of Gotshall's estimate of try-net efficiency (45%) may be in error by one or two orders of magnitude for YOY crab in certain substrates, especially sand with thick eelgrass cover.

Conclusions

The results presented in this paper are based on incomplete analyses of a two week period of sampling during an initial four month study in 1984. Other Dungeness crab studies have detailed major population changes between seasons and between years. These same changes will, no doubt, be observed for Puget Sound crab stocks over the course of this program.

The brief results presented here point to the distinct importance of shallow nearshore areas for post-larval recruitment success and for foraging areas for the age classes 1+ and older. An important aspect of this study will be the determination of habitat preferences for each life stage of Dungeness crab. Observations to date suggest that YOY are most often associated with habitats that offer some type of cover (e.g. eelgrass, algae, shells, cobble, wood debris, etc.; see also Armstrong and Gunderson, these proceedings; Stevens and Armstrong 1984), probably as a means for avoiding omnipresent predators. Similar data is also being collected for related species of *Cancer* crabs (*C. productus*, *C. gracilis*, *C. oregonensis* and *C. antennarius*) and should provide interesting inter-species comparisons of distribution and abundance as a function of substrate.

Acknowledgements

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Session V

Contributed Papers

Biases in crab tag recovery data

Nancy Diamond and David G. Hankin
Humboldt State University
Arcata, California

Introduction

During the years 1981-1983, we tagged and released 12,037 adult female Dungeness crabs in northern California as part of project activities designed to determine basic life history parameters and movements of female crabs. Realizing these objectives required that we place substantial reliance on tag recovery data from the northern California commercial fishery. Although these and other data allowed us to develop a remarkable description of the life history of adult female Dungeness crabs (Hankin et al., this Symposium), analyses of tag recovery data were seriously confounded by sampling biases. In particular: 1) movement analyses were biased by temporal and spatial departures of fishing effort from random or uniform distributions; and 2) estimation of annual molting probabilities was biased by a) commercial crab trap size selection, and b) loss of tags through molts.

The observation that analysis of tag recovery data for movements of crabs or other fishes is biased by the distribution of fishing effort is not new. Edwards (1979), Bennett and Brown (1983), and McKoy (1983), among others, have all presented qualitative considerations of the possible impacts of non-random fishing effort on attempted analyses of tag recovery data for movement patterns. It is obvious that animals can be recovered only at (a) locations where animals are present, and (b) locations where fishermen are present. Tag recovery data therefore give no information on movements of animals at (a) locations where animals are present, but (b) fishermen are not. Previous attempts at discerning movements of Dungeness crabs based on tag recovery data have not ignored this problem (Gotshall 1978), but analyses have been intuitive and subjective rather than quantitative and objective. That is, inferences concerning apparent movements have been drawn largely from visual inspection of tag recovery data rather than through use of statistical methods. In this paper we show that circular statistics may be used to test for the significance of directed movements of adult female Dungeness crabs and we briefly contrast our results with Gotshall's earlier work.

To our knowledge, there have been no previous attempts to adjust for biases that result from size selection of commercial trap gear in estimation of annual molting probabilities. Hancock and Edwards (1967), in their analysis of annual molting probabilities of C. pagurus, made no adjustments for size selection biases because they felt that commercial recovery gear was nonselective over the range of sizes with which they were concerned. However, they mentioned the possible importance of size selection in their paper and this problem cannot be ignored in analyses of tag recovery data for Dungeness crabs. Size selection of commercial Dungeness crab traps (in northern California) results from the large mesh size (70-100 mm on diagonal) of traps, the usual requirement for two (109 mm diameter) escape ports (to minimize capture and handling of sub-legal male and female crabs), and provision of one or two large width (about 50 mm) triggers on entrance tunnels to traps. These features of crab trap design cause retention rates for small crabs to be far less than for large crabs. In the context of estimation of annual molting probabilities, this means that tagged crabs that molt to larger sizes will have higher probabilities of being recovered in commercial gear than will crabs of the same size at tagging that fail to molt. Thus, size selection by crab traps results in a positive bias in estimates of annual molting probabilities; molted crabs are more likely to be recovered than are nonmolted crabs. In contrast, tag loss through molting results in a negative bias in molting probability estimates. Crabs that lose tags through molts cannot be recovered, and it is likely that tag loss among crabs that molt is greater than tag loss among those crabs that fail to molt. Use of crab tag recovery data for estimation of annual molting probabilities thus requires that one account for both of these kinds of biases.

The intention of this paper is to illustrate the nature and potential impacts of those biases which confounded our analyses of crab tag recovery data and, where possible, to point out some steps which could or should be taken to adjust for or minimize those biases. Because more formal peer-reviewed manuscripts are in preparation or review on both the subjects of annual molting probabilities of female Dungeness crabs and on their movements, presentation of the nature of biases and of possible responses to those biases has been limited in scope and detail. However, future publications will provide full details of presented analyses and existing and/or contemplated publications have been referenced as appropriate.

Materials and Methods

Adult female Dungeness crabs were captured, tagged, measured and released from a contracted commercial crab fishing vessel out of Trinidad Bay (41°03'N), California, during January through March of 1981, 1982 and 1983. In all years, tagging was completed prior to the start of the annual molting/mating season which takes place from early April through May in northern California. Most tagging took place between the mouth of the Mad River (40°55'N) and Freshwater Lagoon (41°51'N) at depths of 18-22 m (10-12 fathoms) in 1981 and 1982, and 22 and 44 m (12 and 24 fathoms) in 1983. Carapace widths were measured to 0.1 mm across the carapace excluding the tenth anterolateral spines. Numbered FLOY anchor tags (Model # FD68B) were inserted at the posterior epimeral suture to ensure high retention rates through molts (see Poole 1967; Edwards 1965; and Butler 1957 for previous suture tagging studies with Cancer crabs).

Commercial fishermen were asked to return tagged crabs with the date, depth and location (either LORAN-C readings or specific coastal landmark) of recovery. As incentive for return of tagged crabs, an annual $500 drawing was held in which one tag was drawn from all those tags returned during a fishing season; the fisherman who had returned the winning tag received the award.

Movement vectors (straight line distances from release to recovery) were determined for crabs that were recovered at distances exceeding 2 km from the release site for two seasonal periods: a) the winter of tagging (December through February), and b) the spring following tagging (March through July). These two seasons were adopted so as to allow comparison with earlier movement analyses by Gotshall (1978), and also because they allowed separation of crab movements into those before and during the annual spring molting/mating season. Individual movement vectors within each of four designated release areas (which differed in habitat characteristics) were summed using vector algebra, and then circular statistics (Rayleigh and Moore's tests; see Batschelet 1981) were used to determine the possibility of significant directional movement (Diamond and Hankin, in review). (Movements less than 2 km were judged to be within the measurement error surrounding release and recovery locations and were assigned (0,0) rectangular coordinates with no polar equivalents). Because analysis of recovery data for movements was performed by period of recovery, and because we found no statistical dependence of distance travelled on numbers of days at large, number of days at large before recovery were not incorporated in analyses.

Size selection curves for commercial crab traps were determined by parallel fishing of nonselective experimental traps and selective commercial traps as recommended by Beverton and Holt (1957) and Pope (1975). Experimental nonselective traps were custom-built, designed on the basis of laboratory and field investigations, and had mesh size of 55 mm on diagonal, six 25 mm wide triggers per entrance tunnel, and closed escape ports. Retention in these experimental traps was 100% for crabs exceeding 85 mm carapace width. Based on the number of crabs retained at size in nonselective and selective commercial traps, parameters of a commercial gear selection curve were estimated following procedures presented in Pope (1975; see also Diamond 1983, Appendix A). Traps were usually fished for two days, but soak time ranged from two to seven days. Comparison of numbers and sizes retained in nonselective and selective traps showed that soak time did not influence size selection and retention rates when traps were fished for two days or longer before being pulled.

However, during the early part of the fishing season in northern California, fishermen frequently fish traps for periods of one day or less with the result that crabs are still activiely feeding on bait and/or have not had the time or developed the "desire" to attempt escape from traps. This short soak time prevented commercial traps from exhibiting their true selective properties (which appear to require soaks of two days or longer). Actual tag recovery rates for "small" crabs (135-145 mm) as compared to "large" crabs (≥ 155 mm) were much higher than would have been predicted on the basis of the commercial trap selection curve for soaks of two days or longer. Therefore, we developed an alternative method by which to quantify the relative recovery rates for crabs of differing sizes. For this method we used recovery data from crabs that were recovered during the early part of the season following tagging (prior to March 1). Because these crabs did not have an opportunity to molt, size at recovery was the same as size at tagging. We computed size-specific recovery rates essentially as the actual numbers recovered for a certain size interval divided by the numbers released. Relative size-specific recovery rates were then obtained by dividing the (a) (expected) recovery rate for crabs that molted to a particular (expected) size by (b) recovery rate for crabs of the same initial size that had failed to molt. The expected recovery rates for molted crabs were thus based on recovery rates for nonmolted crabs of the same size as those crabs that had molted. More satisfying descriptions of the logic behind procedures and more detailed descriptions of actual calculations are presented in Diamond (1983).

Tag loss during molting was estimated from laboratory experiments in which premating embrace females were tagged prior to molting in the laboratory. To test the possibility that tags might be lost due to the mating process itself, rather than due to molting per se, we compared tag loss between groups of females that (a) molted in the absence of males and (b) molted in the presence of males and mated at that time. Time from tagging until molting in the laboratory ranged from 1 to 37 days.

Results

Movements and migrations

The seasonal pattern of commercial fishing effort in northern California is governed by a combination of weather conditions and Dungeness crab life history. Gotshall (1978) stated that effort is distributed fairly evenly at depths of 18-75 m at the start of the season (1 December) continuing through about March. As large ocean swells and surf subside, fishing effort moves inshore during the spring months, culminating in what our local fishermen call the "beach run" (usually during April or May) when fishing effort is concentrated in shallow waters (< 18 m) along beach areas. This "beach run" coincides with the spring mating season at which time often dense aggregations of legal-sized male Dungeness crabs congregate inshore in shallow sandy areas to mate with newly molted females. Thus, the early distribution of fishing effort approximates a random distribution within the areas bounded by 18-75 m, whereas the distribution of fishing effort during the spring is highly concentrated in shallow beach areas.

Figure 1 shows the four release areas which were considered in movement analyses: Area I - an exposed sandy beach; Area II - a protected rocky coast; Area III - an exposed rocky coast; and Area IV - an exposed sandy beach. Visual examination of winter movement vectors for one of these areas (Area I) suggested a possible northward movement during the winter period (Figure 2). However, statistical tests of the summed resultant vectors within this and other areas, as well as for all areas combined, failed to support an hypothesis of significant

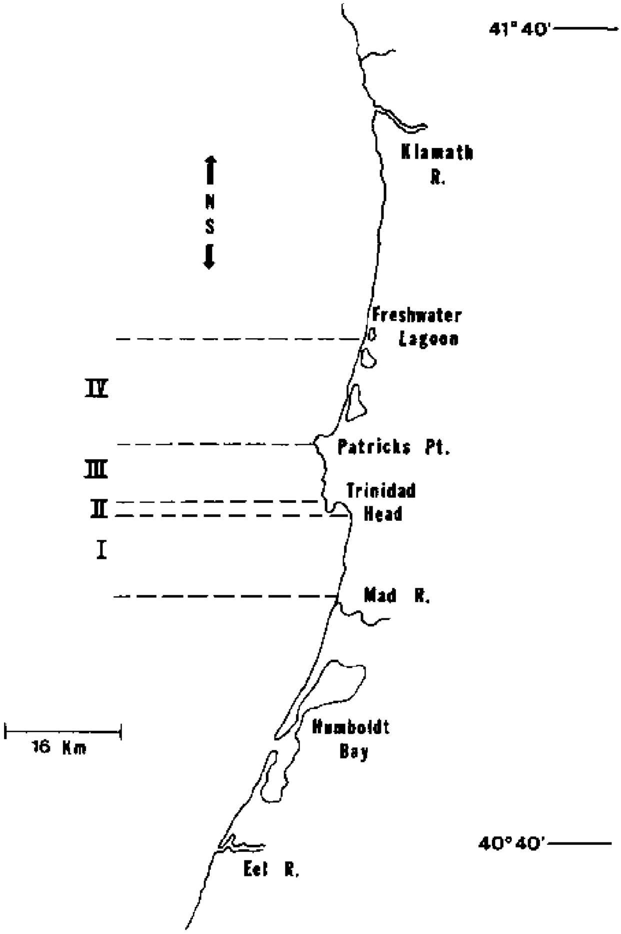

Figure 1. Map of release locations in northern California. Physical characteristics of the four distinct release locations (I-IV) are briefly described in text.

directed movement during winter (Figure 3); all tests were non-significant ($p>.05$). In contrast, individual movement vectors during the spring suggested highly directed inshore movements, particularly in Area II (Figure 4); summed resultant vectors for Areas II and III, and for all areas combined (Figure 5), were indeed significantly directed inshore ($p<.05$). However, because tag recovery data were clearly biased toward recovery of crabs that had moved inshore during the

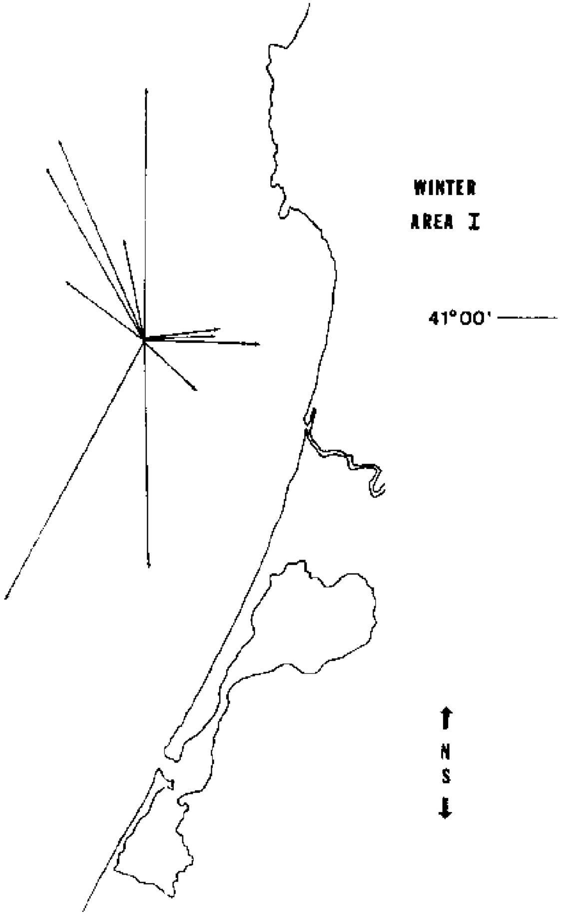

Figure 2. Winter movement vectors for female Dungeness crab tagged and released from Area I (see Figure 1). Note that, although the majority of movement vectors appear to suggest a general northward trend, circular statistics used to test for such a trend failed to support an hypothesis of directed winter movement. Vectors are drawn to scale of coastline.

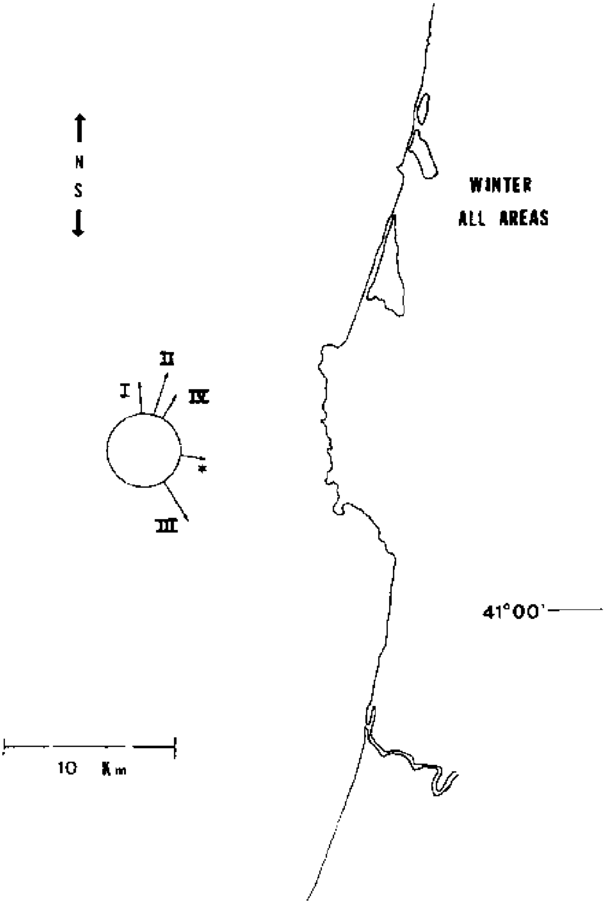

Figure 3. Summed resultant vectors for female Dungeness crabs tagged and released in Areas I-IV, and for all Areas combined, that were recovered during winter months. Note that, although three of the summed resultant vectors are in a northern direction, there were no statistically significant directional movements in any of the four areas or for all areas combined. Movement vectors are on same scale as coastline and asterisk denotes combined data.

spring, these statistical tests were of dubious validity; the test assumptions of randomly distributed fishing effort were clearly violated by the concentration of fishing effort in shallow sandy areas during this season.

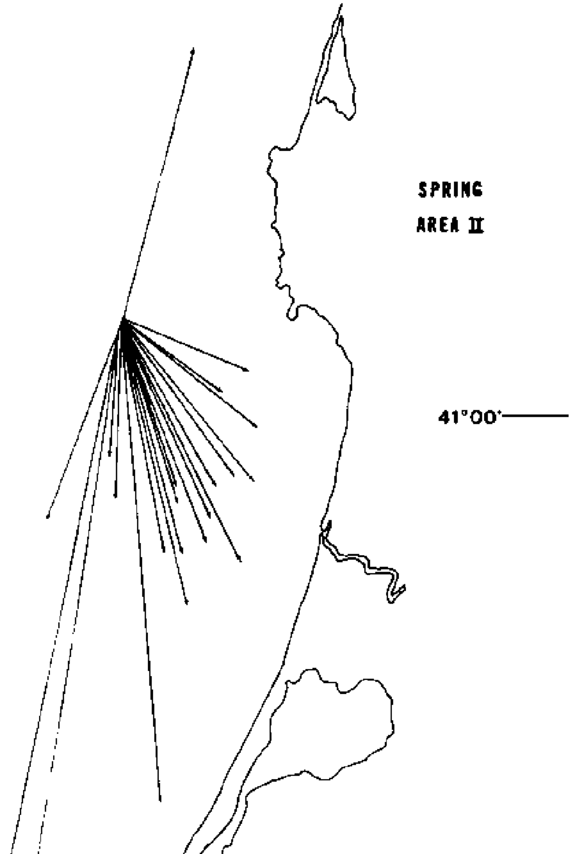

Figure 4. Individual spring movement vectors for adult female Dungeness crabs tagged and released in Area II (see Figure 1). Note that all but one of the vectors have an either south or inshore direction. However, recovery locations for these tagged crab also corresponded with locations of most concentrated fishing effort during the spring months. Vectors are drawn to scale of coastline.

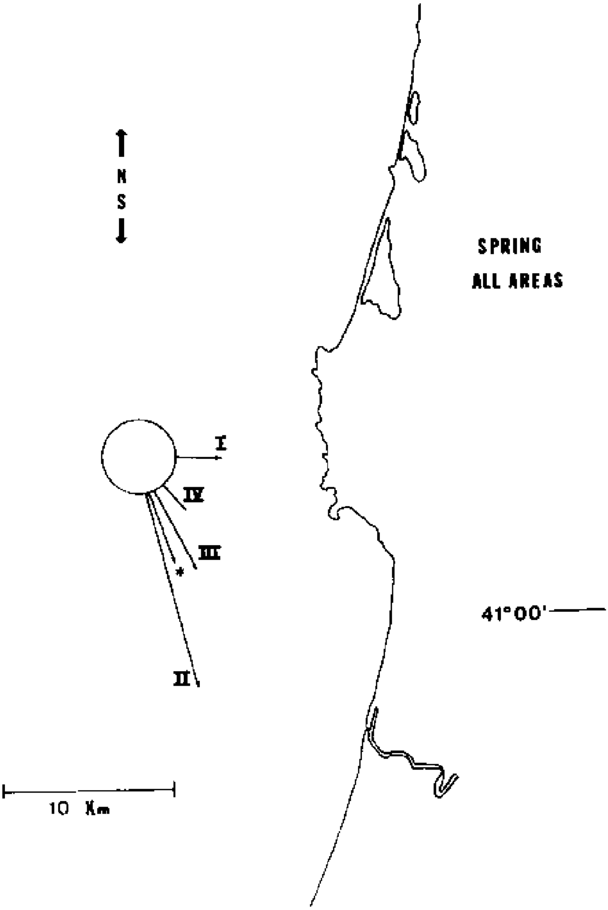

Figure 5. Summed resultant vectors for movements of crabs in areas I-IV and for all areas combined (asterisk) during spring months. Note that, three out of the four summed vectors for distinct release locations suggest movement south and inshore, and that the summed vector for all areas combined is also in a south and inshore direction. Movement vectors in areas II and III were significant, as was the movement vector for all areas combined. However, recovery locations for crabs generally corresponded to areas of concentrated fishing effort, thus invalidating an implicit assumption that fishing effort is randomly distributed. Vectors are drawn to scale of coastline.

Annual molting probabilities

Commercial gear selection. A comparsion between numbers of adult females retained at size in commercial traps and in nonselective traps dramatically illustrated the potential significance of gear selection bias in tag recovery data. This comparison is best reflected in the generated commercial gear selection curve (Figure 6). For the open port commercial trap gear, 50% retention was achieved at 153 mm, and 100% retention began at 155 mm; this is essentially a "knife-edge" selection curve. Below 134 mm carapace width, retention was effectively zero. As an illustration of the potential magnitude of commercial trap size selection bias which could result, consider recovery of two crabs each tagged at 140 mm, one of which molted to 153 mm before recovery. The molted crab would have a commercial gear retention rate of 50%, whereas the nonmolted crab would have a rentention rate of about 0.3%; the ratio of these retention rates is about 150:1. However, as previously mentioned, the above calculation assumes that all traps were fished for two days or longer before being pulled. The alternative method which we used to calculate rélative recovery rates (based on empirical recovery data, not the generated selection curve) showed that the crab that molted to 153 mm would have been about 6 times more likely to be recovered than the crab that had remained at 140 mm.

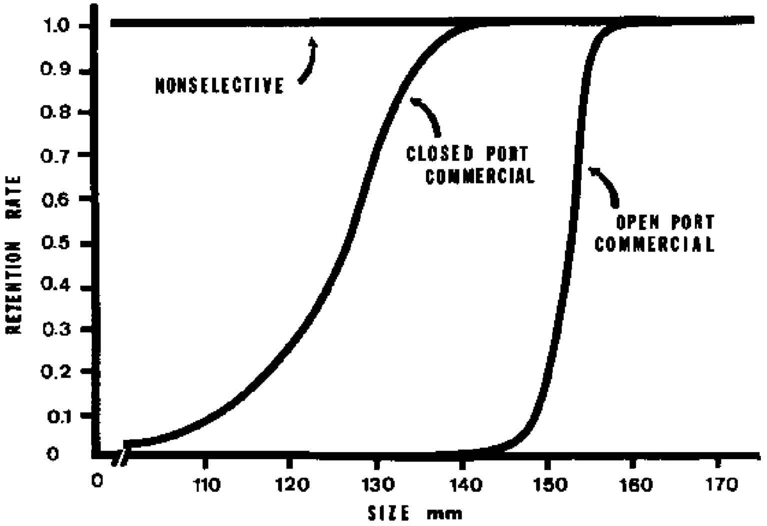

Figure 6. Selection curves for female Dungeness crabs captured by open port commercial crab traps, closed port commercial crab traps, and nonselective experimental traps (modified as described in text. Size is carapace width, excluding tenth anterolateral spines. Note that selection curves for males would not be the same as for females because of different width/depth relation.

Tag retention. The text table below presents tag loss data for female crabs that molted in the absence and in the presence of adult male crabs. Tag loss through molting was not significantly different between the two groups. Laboratory tag retention rates averaged about 0.90 for both groups combined and 95% confidence limits for tag retention rates were from 0.84 to 0.96. However, because the period from tagging to molting was so brief in the laboratory, these figures should probably be regarded as upper limits for tag retention rates.

	# Tagged	# Retained Tag	Retention Rate
Male Present	42	37	0.881
Male Absent	48	44	0.917
Pooled	90	81	0.900

An estimator for annual molting probabilities. An estimator that attempts to account and adjust for the biases of gear selection and tag loss was developed in Diamond (1983) and is presented below:

$$\hat{P}(x) = \frac{1}{1 + \dfrac{N(x) \cdot F(x+\delta) \cdot \hat{T}}{M(x) \cdot F(x)}} \qquad (1)$$

where:

P(x) = annual probability of molting from size x;

N(x) = number of crabs recovered after one molting season at large that were tagged at size x and had not molted ;

M(x) = number of crabs recovered after one molting season at large that were tagged at size x and had molted ;

$\delta=\delta(x)$ = (expected) molt increment for a crab tagged at size x;

F(x) = recovery rate for crabs of size x;

$F(x+\delta)$ = recovery rate for crabs at size $x+\delta$ (i.e. for crabs that molted to size $x+\delta$ from size x);

$\hat{T}$ = (estimated) tag retention rate through one molt.

The form of this estimator is such that, in practice, it is not necessary to separately estimate the recovery rates F(x) and $F(x+\delta)$; what is required is an estimate of the ratio of the two recovery rates [i.e. $F(x+\delta)/F(x)$].

In the numerical examples which follow, we attempt to illustrate the manner in which this estimator accounts for biases of crab trap size selection and tag loss, and to show the substantial impact that failure to account for such biases could have on estimates of annual molting probabilities. All examples are based on the following hypothetical set of data:

$$x = 140 \text{ mm}; \quad N(x) = 8; \quad M(x) = 18; \quad x+\delta = 153 \text{ mm}.$$

Thus, 26 crabs [N(x) + M(x)] were recovered that had been tagged at an initial size of 140 mm (x); of these 26 crabs, 18 [M(x)] had molted to a size of 153 mm (x+δ).

Example 1. No commercial gear selection.

In the absence of commercial gear selection, all molted and nonmolted crabs would be recovered at the same rates, regardless of size, so that $F(x) = F(x+\delta)$ and $F(x+\delta)/F(x) = 1$. If there is no tag loss (i.e. $T = 1$), then equation (1) reduces to the simple and intuitive estimator of annual molting probability: the ratio of the recovered crabs that molted to the total number of crabs that were recovered. (This is the "naive" estimator discussed in Hankin et al., this Symposium). That is,

$$\hat{P}(x) = \frac{1}{1 + \dfrac{N(x)}{M(x)}} = \frac{M(x)}{M(x) + N(x)}$$

$$= \frac{18}{18 + 8} = 0.69 \ .$$

The effect of correcting for negative bias due to tag loss is to slightly increase the resulting estimate of annual molting probability. For example, if $T = 0.7$, then

$$\hat{P}(x) = \frac{1}{1 + \dfrac{N(x) \cdot \hat{T}}{M(x)}} = \frac{M(x)}{M(x) + N(x) \cdot \hat{T}}$$

$$= \frac{18}{18 + 8 \cdot (0.7)} = 0.76 \ .$$

Example 2. Size selective commercial recovery gear.

For x = 140 mm and x+δ = 153 mm, our empirical estimates of recovery rates gave:

$$F(x+\delta)/F(x) = 6.05 \ .$$

Using the same recovery data as above and assuming that there is no tag loss ($T=1$), the molting probability estimator gives:

$$P(x) = \frac{1}{1 + \dfrac{N(x) \cdot F(x+\delta)}{M(x) \cdot F(x)}} = \frac{1}{1 + \frac{8}{18} \cdot (6.05)} = 0.27 \ .$$

Thus, adjustment for size selection bias results in a substantial reduction in the estimate of annual molting probability from 0.69 (Example 1) to 0.27 . Correcting for tag loss would again slightly increase the estimate of annual molting probability. For this same example, if T = 0.7, then the molting probability estimate would be 0.35 (which should be compared with the biased estimate of 0.76 in example 1).

Discussion

Gotshall (1978), based on visual inspection of plotted tag recovery data, proposed that adult male Dungeness crabs moved northward in northern California during winter months, and then southward and inshore during the spring. Our analyses of movement data from female Dungeness crabs in northern California suggest that the apparent trend observed by Gotshall was probably not statistically significant; winter movements of females had no statistically significant directional tendency. Regardless of the statistical conclusion regarding winter movements, however, analyses of these movements were not seriously biased by the distribution of fishing effort. With the exception of crabs that may have moved into very deep waters (> 75 m), the distribution of fishing effort during the winter was such that movements of tagged crabs in all directions should have been equally likely to have been recorded. In such a case, the use of circular statistics to evaluate the significance of possible tendencies of crabs to move in particular directions seems a substantial improvement over qualitative and subjective visual methods (as used by Gotshall).

There is no question in our minds that many adult female Dungeness crabs move inshore to molt and then mate with adult males in shallow sandy areas during the spring in northern California. However, the fraction of the female population that engages in such movements remains unknown. Because fishing effort was concentrated in shallow waters during the spring months, movements of females that had moved to deeper waters or remained offshore would not have been recorded in proportion to their frequency had they taken place. However, if substantial numbers of female crabs remained offshore during the spring, or actually moved further offshore, we are reasonably confident that they would have to be females that were not destined to molt and mate during the spring molting/mating season. Because it is not necessary for adult females to molt and mate each year in order to produce and extrude viable egg masses in the fall (Diamond 1983; Hankin et al., this Symposium), it is indeed possible that some females may remain offshore during the spring. If these females were destined to molt, one would expect aggregations of legal-sized males in offshore locations and associated concentrations of fishing effort; these are not observed in the northern California fishery. Given these considerations, we feel confident that there is indeed an inshore spring mating migration among female crabs that are destined to molt and mate. Definitive proof that such a migration of females takes place for all females, regardless of molting state, would require an expensive large-scale sampling program in which vessels were chartered to fish at all depths during the spring months so as to ensure that fishing effort (for tag recoveries) would be uniformly distributed. Although this kind of approach has been successfully applied in small-scale localized crab tag recovery projects (see Hyland et al. 1984), we are hesitant to advocate such an approach for studies of movements of Dungeness crabs in most West Coast areas.

In contrast to a relative inability to adjust for possible biases due to the distribution of fishing effort, it seems possible (theoretically at least) to attempt adjustment for biases resulting from commercial crab trap size selection and tag loss through molts. Above all else, it seems most important to fish nonselective crab traps alongside commercial crab traps so as to allow assessment of the degree of size selection bias. Several advantages result from comparisons of size frequencies of crabs captured in the two gear types. First, the minimum size of full vulnerability to the commercial crab traps can be readily established. For crabs exceeding this size of first full vulnerability to commercial gear, it is unnecessary to make any adjustments for commercial gear size selection in analysis of tag recovery data for molting probabilities (or survival rates; see Hankin et al., this Symposium). Second, use of nonselective traps ensures that significant numbers of small crabs will be captured and allows for the tagging of these small crabs. Finally, length frequency analysis of data collected from nonselective traps can lead to a meaningful assessment of stock size composition; this is virtually impossible based on size frequencies collected from commercial crab traps or from commercial crab traps with closed escape ports. Size selection curves in fixed commercial trap gear (Figure 6) have such a steep slope that collected length frequency data have little practical value for animals smaller than the legal size for male Dungeness crabs.

Although the estimator that we developed can in theory account for biases due to size selection and tag loss, there were serious practical problems involved in actual application of the estimator to collected data. First, as pointed out previously, the selective properties of fixed crab trap gear appear to sensitively depend on trap soak time. Traps exhibited their full selective properties only after having been fished for two full days or more without rebaiting. Because early season soak times in northern California were often less than two days, Use of the formal fitted gear selection curve generated estimates of molting probabilities (not presented) which were probably biased at least as severely as were "naive" calculations which omitted consideration of possible size selection altogether. Our reliance instead upon empirically-derived relative recovery rates was certainly a preferable alternative to ignoring size selection bias altogether, but it too had practical problems in application. First, we implicitly assumed that recovery rates depended only on size and not on molting history or condition. It is possible that this assumption is false; freshly molted crabs may more aggressively search out food and may enter traps at higher rates than nonmolted crabs. Second, the use of early season data to estimate relative recovery rates was, in part, invalidated by the general trend of increasing soak time for traps as the commercial fishing season progressed and catch rates for legal males dropped. However, during the beach run most traps are once again fished for less than two day soaks. Because most recoveries took place during the early season and during the spring beach run, the overall effect of changing soak time is unclear.

Finally, it is likely that the tag retention rates reported in this paper are overestimates of real tag retention rates. Tagging conditions in the laboratory are obviously more favorable than on board a vessel during a winter storm at sea, and results of laboratory tagging may therefore not give an accurate reflection of tag retention in the field. For example, we observed that tags had migrated away from the suture line on some recovered crabs that had molted; many of these crabs would probably have lost their tags if they molted a second time. In addition, the length of time from tagging to molting was far shorter for laboratory-tagged crabs than for field-tagged crabs. Tag retention may depend on the degree of development of the newly-forming exoskeleton at the time of tagging. Presumably, this new exoskeleton will be more completely formed by the time molting is imminent (when laboratory tagging took place) as opposed to several months in advance of molting (when field tagging took place). Improved field-derived estimates of tag retention rates could probably be derived from analyses of data collected from a double tagging study. If crabs were tagged with anchor tags at both the right and left sides of the posterior epimeral suture, then the relative numbers of molted and nonmolted recoveries which retained one and two tags could be used to estimate tag loss through molting and to distinguish such loss from tag loss not associated with molting. We hope to carry out such a double tagging study on adult female Dungeness crabs in the future.

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Feeding in relation to morphometrics within the genus *Cancer*: Evolutionary and ecological considerations

Peter Lawton and Robert W. Elner
Department of Fisheries and Oceans
St. Andrews, New Brunswick

Abstract

The feeding behavior of crabs of the genus Cancer is reviewed, particularly with respect to morphological and evolutionary patterns associated with the population dynamics and ecology of commercial Cancer spp. Ten northern temperate species are considered: seven Pacific species (C. antennarius, C. anthonyi, C. branneri, C. gracilis, C. magister, C. oregonensis and C. productus) and three Atlantic species (C. borealis, C. irroratus and C. pagurus). The genus Cancer has previously been classified, based on carapacial features, into four subgenera. From an examination of the mechanics and functional morphology of the chelae and other body characteristics, together with available information on feeding behavior, a reclassification, based on ecological principles, is presented. Two groups of large (adult) Cancer crabs are recognized: the first comprises species (C. antennarius, C. anthonyi, C. borealis, C. pagurus and C. productus) which have relatively massive and powerful chelipeds. These species, which also have low relative (to carapace width) leg lengths, typically occupy rocky habitats as juveniles and prey primarily upon sedentary and slow moving hard-shelled prey forms. In contrast, the second group (C. gracilis, C. irroratus and C. magister) has proportionately smaller, less powerful, but faster closing chelipeds. These features, and the comparatively higher leg lengths of crabs in this latter group, appear associated with a capacity to feed upon mobile epifaunal prey and the occupation of sand/mud substrates. Two small species (C. branneri and C. oregonensis are considered to form a third group, ecologically distinct from the larger crabs. The occurrence, form and significance of cannibalism in representatives from the two large Cancer groups (C. pagurus and C. magister) is related to population dynamics. Implications for fisheries management of Cancer crabs deriving from our ecological grouping are suggested.

Introduction

Crabs of the genus *Cancer* form a widespread and successful group supporting important commercial fisheries on the N.E. Pacific, N.W. and N.E. Atlantic coasts. On the basis of carapace featues, particularly of the frontal region, Nations (1975) recognized four subgenera of *Cancer*:

Subgenus	Type species
Romaleon	*C. gibbosulus*
Cancer	*C. pagurus*
Metacarcinus	*C. magister*
Glebocarcinus	*C. oregonensis*

Romaleon is interpreted as the most primitive of the subgenera because of its early fossil record, relatively small size, and possession of many characters from which those of other species of *Cancer* could have been derived. The typically large size and unornamented chelipeds, smooth anterolateral margins and pronounced lateral expansion of the carapace of *Cancer*, *sensu stricto*, are in strong contrast to the features of species in *Romaleon* and are considered to be more recent (Nations 1975). The largest member of the genus is the European edible crab, *C. pagurus*, adults of which may reach a carapace width (CW) of 270 mm and live in excess of 25 years (Bennett 1974). *Metacarcinus* appears intermediate in development between *Romaleon* and *Cancer* subgenera. Nations (1975) speculated that the highly ornate and typically small *Glebocarcinus* species represent an evolutionary development away from the *Romaleon* - *Metacarcinus* - *Cancer* trend of increasing size.

The current geographic distributions and phylogenetic affinities of all recent *Cancer* species are summarized in Table 1. The present-day absence of cancrid crabs from the coasts of S.E. South America, the S., E. and W. coasts of Australia and the S.W. coast of Africa appears to be related to temperature (MacKay 1943) and other migrational barriers (Nations 1975).

There have been several autecological studies of present-day *Cancer* species (Bigford 1979; Lawton 1983; Shelton *et al.* 1979; Stevens *et al.* 1982) but, hitherto, there has been no attempt to classify the genus in terms of functional ecology and thus complement Nations' (1975) taxonomic approach. Crabs of the genus *Cancer* are typically open-coast marine species and may be distributed over a substantial depth range (Table 2); however, life-history stages of some species do occur in areas of lowered salinity (Jeffries 1966; Sugarman *et al.* 1983; Wolff and Sandee 1971). Juveniles are normally found in shallow, nearshore waters throughout the year, while adults of some species have been reported to undergo seasonal inshore-offshore migrations. The timing of these migrations appears to be related to temperature and reproductive condition (*C. irroratus*: Bigford 1979; Haefner 1976; *C. pagurus*: Brown and Bennett 1980; Bennett and Brown 1983). Jonah crabs, *C. borealis*, exclude rock crabs, *C. irroratus*, from preferred rocky habitats in the N.E. Atlantic (Jeffries 1966; Fogarty 1976; Wang 1982). Thus, there may be spatial segregation of species and age-classes within this broad distributional framework.

Table 1. Geographic distributions and phylogenetic affinities of recent species of the genus Cancer (adapted from Nations 1975).

Species	Subgenus	Distribution
	Pacific Ocean	
Cancer amphioetus Rathbun 1898	Glebocarcinus	Western North America & E. Asia
Cancer oregonensis Rathbun 1898	Glebocarcinus	Western North America & E.Asia
Cancer antennarius Stimpson 1856	Romaleon	Western North America
Cancer branneri Rathbun 1926	Romaleon	Western North America
Cancer jordani Rathbun 1900	Romaleon	Western North America
Cancer anthonyi Rathbun 1897	Metacarcinus	Western North America
Cancer gracilis Dana 1852	Metacarcinus	Western North America
Cancer magister Dana 1852	Metacarcinus	Western North America
Cancer productus Randall 1839	Cancer	Western North America
Cancer polyodon Poeppig 1836	Romaleon	Western South America
Cancer edwardsii Bell 1835	Metacarcinus	Western South America
Cancer plebejus Poepigg 1836	Metacarcinus	Western South America
Cancer porteri Rathbun 1930	Cancer	Western South America, Gulf of California
Cancer sakaii Takeda and Miyake 1972	Glebocarcinus	Eastern Asia
Cancer tumifrons Yokoya 1933	Glebocarcinus	Eastern Asia
Cancer gibbosulus (DeHaan 1835)	Romaleon	Eastern Asia
Cancer nadaensis Sakai 1969	Romaleon	Eastern Asia
Cancer japonicus Ortmann 1893	Cancer	Eastern Asia
Cancer novaezealandiae (Jacquinot 1853)	Metacarcinus	New Zealand, Tasmania and Australia
	Atlantic Ocean	
Cancer bellianus Johnson 1861	Metacarcinus	Iceland to N.W. Africa
Cancer borealis Stimpson 1859	Metacarcinus	Eastern North America
Cancer irroratus Say 1817	Cancer	Eastern North America
Cancer pagurus Linnaeus 1758	Cancer	Western & Southern Europe

Table 2. Life-history characteristics reported for selected *Cancer* crabs.

Species	Distributional limits	Habitat		Maximum CW (mm)		Recorded depth range	Information sources (additional to Rathbun 1930)
		Juvenile	Adult	Male	Female		
	North East Pacific Coast						
C. antennarius	Coos Bay, Oregon to Todos Santos Island, Mexico	Low shore, under rocks	Mud, sand, gravel substrates	$\geq$130	$\geq$130	Intertidal to 100 m	Nations 1975; Present study
C. anthonyi	Humbold Bay, California to Magdalena Bay, Mexico	Not given separately	Mud, sand, stones. Sheltered waters in north	$\geq$140	$\geq$140	Intertidal to 115 m	Present study; Wicksten 1984
C. branneri	Port Althorp, Alaska to Santa Catalina Island, California	Not given separately	Mud, coarse sand, gravel, shell substrates	58	52	Intertidal to 179 m	Hart 1982
C. gracilis	Prince William Sound, Alaska to Sebastian Vizcaino Bay, Mexico	Not given separately	Mud, sand, broken shell substrates	115	87	Intertidal to 143 m	Hart 1982
C. magister	Tanaga Island, Alaska to Point Conception, California	Near shore, sand and eelgrass beds $\leq$37 m	Mud, sand substrates; offshore in winter	230	170	Intertidal to 179 m	Dahlstrom and Wild 1983; Hart 1982; Gotshall 1978; Nations 1975; Tasto 1983
C. oregonensis	Bering Sea to Santa Barbara, California	Intertidal rocky areas; kelp holdfasts	Mud, sand, gravel, broken shell substrates	50	42	Intertidal to 436 m; British Columbia common to 125 m	Hart 1982

Table 2 (continued) Life-history characteristics reported for selected *Cancer* crabs.

Species	Distributional limits	Habitat		Maximum CW (mm)		Recorded depth range	Information sources (additional to Rathbun 1930)
		Juvenile	Adult	Male	Female		
	North East Pacific Coast						
C. productus	Kodiak, Alaska to Laguna Beach, California	Intertidal rocky areas	Mud, sand, gravel, stone substrates	180	158	Intertidal to 79 m	Hart 1982
	North West Atlantic Coast						
C. borealis	Nova Scotia to Florida; Bermuda	Shallow sublittoral rocky areas	Near shore rocky areas; mud and sand subtrates: offshore in winter	180	130	Intertidal to 870 m; maximum abundance at intermediate depths	Briggs and Mushacke 1982; Nations 1975; Present study
C. irroratus	Labrador to South Carolina	Mud, sand, eelgrass beds; intertidal to 68 m	Near shore mud and sand substrates	141	106	Intertidal to 751 m; generally at shallow depths in north	Bigford 1979; Briggs and Mushacke 1982; Nations 1975
	North East Atlantic Coast						
C. pagurus	Norway, south to Portugal; Mediterranean Sea	Intertidal rocky areas; kelp holdfasts; mussel beds; shallow sublittoral	Mud, sand, and rocky (preferred) substrates: offshore in winter.	267	242	Intertidal to 100 m	Bennett 1974; Christiansen 1969; Ingle 1980; Lawton 1983

This study reviews and compares recent and ongoing studies into the feeding behaviour and ecology of northern temperate *Cancer* species: five Pacific coast species (*C. antennarius*, *C. anthonyi*, *C. gracilis*, *C. magister* and *C. productus*) and three Atlantic species (*C. borealis*, *C. irroratus* and *C. pagurus*) that are currently exploited commercially. Two other Pacific *Cancer* species, *C. branneri* and *C. oregonensis*, included in a number of analyses to widen the scope of our intrageneric comparisons. We examine the mechanics and functional morphology of the chelae and other body characteristics, together with available information on feeding and cannibalism, and attempt a reclassification of the genus based on ecological principles. We propose that an understanding of such intrageneric patterning may be important in elucidating the population dynamics of *Cancer*.

Mechanics and Functional Morphology

The hypothesis that the chela acts as the template upon which feeding habits and prey preferences are determined (Elner 1978) has been verified in a number of autecological studies (Boulding 1984; Elner 1980; Elner and Campbell 1981; Lawton 1983). Attempts to define more general (e.g. biogeographic) relationships between claw form and predatory behavior (Vermeij 1977) have yielded equivocal results. This is partly due to methodological problems (Abele *et al.* 1981) but also due to the chela having additional functions, such as reproductive display, which may confound simple correlations with feeding habits (Elner and Campbell 1981; Stein 1976).

Cancer crabs are atypical among molluscivorous crabs in possessing monomorphic chelae, both of which may be used in active crushing roles during feeding (Lawton 1983; Vermeij 1977). Chela forms illustrated in Figure 1 appear similar, although there are differences in gross morphology, mechanical advantage and occlusive geometry which can be correlated with feeding habits.

Intrageneric comparisons

As part of an ongoing study into *Cancer* crab biometrics, we have examined the morphometrics of male and female specimens of 10 species from the N.E. Pacific, N.W. and N.E. Atlantic Oceans (Table 3). A restricted "preferred" size range was identified (100-130 mm CW) at or above the size of sexual maturity in order to reduce potential artefacts due to allometric growth and sexual dimorphism (Bigford 1979; Campbell and Eagles 1983). For species of smaller adult size (*C. oregonensis* and *C. branneri*), the largest available specimens were examined.

Ratios were calculated from measurements of selected body dimensions (Figure 2) and compared between sexes (*t*-test) and species (analysis of variance followed by Duncan's multiple range test to identify homogenous subsets among species):

- CPCSHAPE = Relative carapace shape (carapace length/CW)

- RELLEG = Relative leg length (pereiopod 3 length/CW)

- CHSIZE = Relative claw size (propodus height/CW)

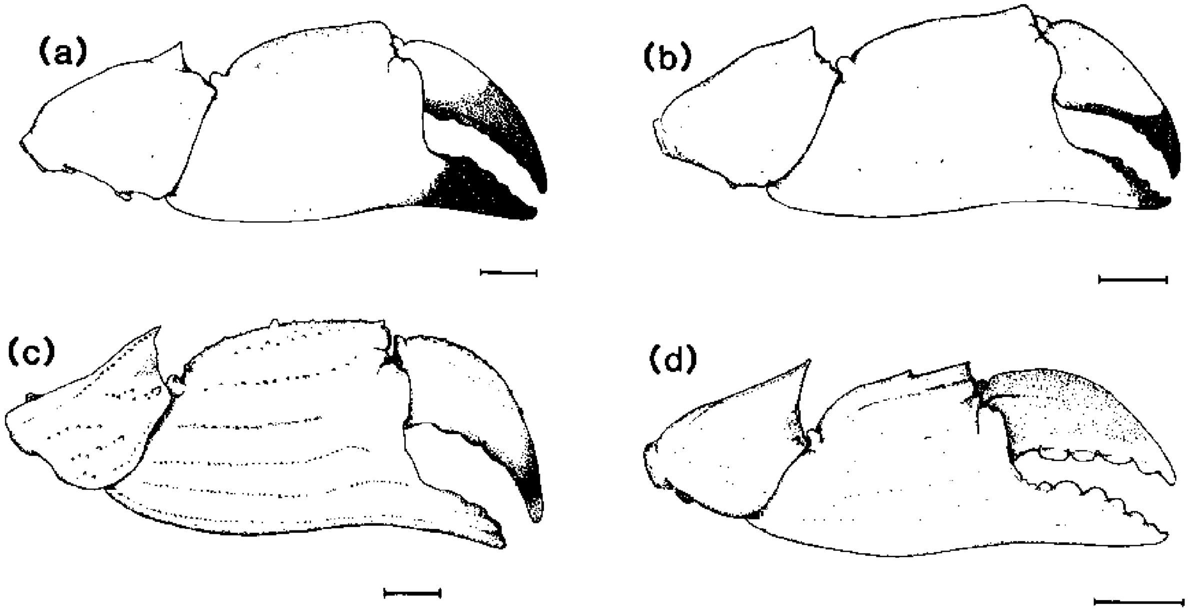

Figure 1. Chelipeds of *Cancer* species. (a) *C. antennarius* (121 mm CW male); (b) *C. anthonyi* (130 mm CW female); (c) *C. borealis* (126 mm CW male); (d) *C. gracilis* (86 mm CW male). Scale bars = 10 mm.

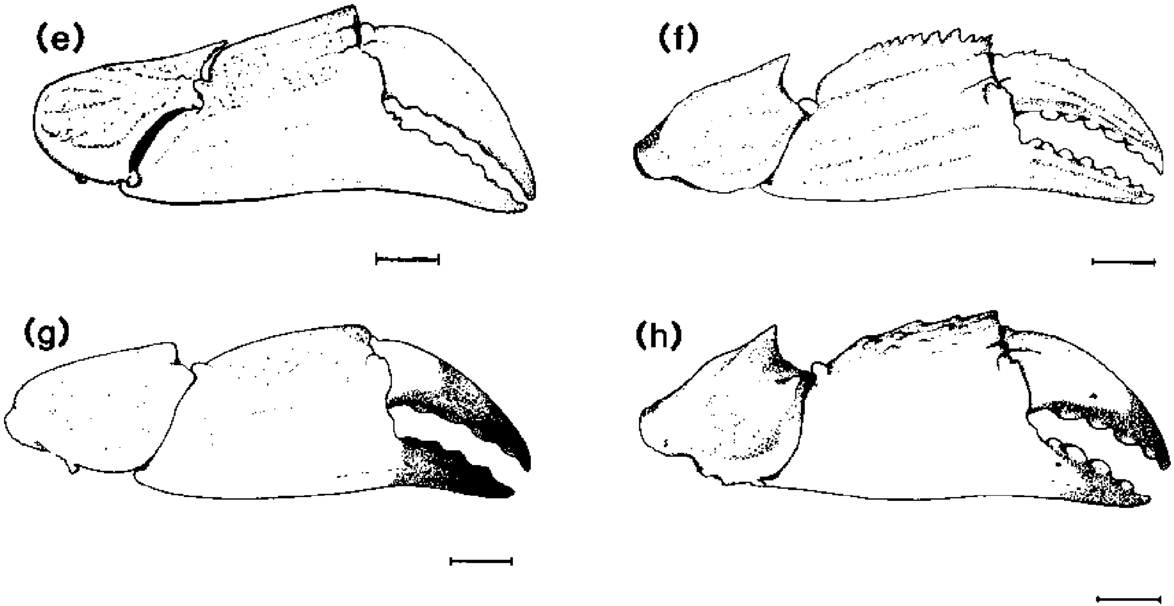

Figure 1 (continued). Chelipeds of *Cancer* species. (e) *C. irroratus* (131 mm CW male); (f) *C. magister* (154 mm CW female); (g) *C. pagurus* (124 mm CW male); (h) *C. productus* (131 mm CW male). Scale bars = 10 mm.

- MECHADV = Mechanical advantage (lever L_1/lever L_2)
- CHLENGTH = Relative dactylus length (dactylus length/propodus length)
- CHHEIGHT = Relative propodus height (propodus height/propodus width)

All claw ratios were based on measurements of the right claw (Figure 2).

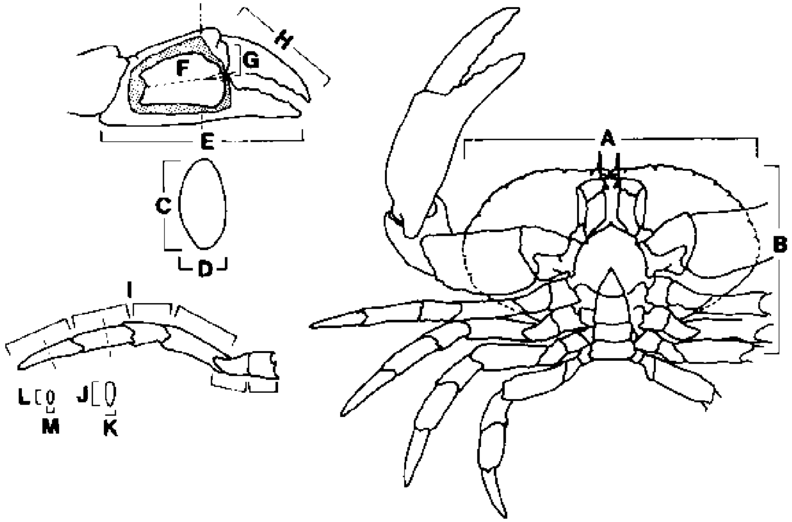

Figure 2. Carapace and appendage measurements made during morphometric analysis of Cancer crabs.

A = maximum width of carapace (including anterolateral teeth); B = maximum length of carapace; C = propodus height (excluding spines on upper margin); D = propodus width; E = propodus length; F = closer muscle apodeme plate (area in mm^2 of plate dissected from propodus of right cheliped); G = distance from point of articulation of dactylus with propodus to point of insertion of closer muscle apodeme plate (lever L_1); H = dactylus length (lever L_2: mechanical advantage of the cheliped system is given by L_1/L_2); I = total length of pereiopod 3 (measured as the sum of individual segment lengths between points of articulation); J = propodus height, K = propodus width, L = dactylus height and M = dactylus width of pereiopod 3; measurements I-M taken similarly for pereiopod 5. All measurements (except F) taken to nearest 0.1 mm with vernier calipers.

Table 3. *Cancer* material examined for comparison of mechanics and functional morphology.

Species	Locality	No. of specimens		Source of material
		Male	Female	
C. branneri	Vancouver Island, British Columbia, Canada	4	3	British Columbia Provincial Museum
C. gracilis		7	3	
C. oregonensis		5	6	
C. magister		4	5	SCUBA diving
C. antennarius	S. California, U.S.A.	3	3	Purchased from live markets
C. anthonyi		3	3	
C. productus		3	3	
C. borealis	Bay of Fundy, S.W. Nova Scotia, Canada	5	5	SCUBA diving
C. irroratus		6	4	
C. pagurus	North Wales, U.K.	3	3	SCUBA diving

Sexual dimorphism was apparent in certain ratios for a number of species but showed no consistent intrageneric pattern. Accordingly, the following comparisons (Table 4) were based on data obtained for males only.

Trends in CPCSHAPE conformed, in general, with Nations' (1975) observations on carapacial features of crabs in the various *Cancer* subgenera. All *Metacarcinus* and Cancer species had signficantly lower ratios than *C. branneri* and *C.oregonensis* members of *Romaleon* and *Glebocarcinus*, respectively. *Cancer antennarius*, also a member of *Romaleon*, had a significantly lower ratio than *C. branneri*, comparable to the *Metacarcinus* and *Cancer* crabs. Nations (1975) remarked that *C. antennarius* was atypical among *Romaleon*, being convergent in form to *C. anthonyi* (*Metacarcinus*). *Cancer antennarius* is the largest member of the *Romaleon* group (Table 2), suggesting that anterolateral expansion of the carapace may be related to acquisition of a large body size rather than phylogenetic origin *per se*.

The relative length of the pereiopods has previously been linked to activity level and habitat usage in two co-occurring *Cancer* species, *C. borealis* and *C. irroratus* (Fogarty 1976; Jeffries 1966). Our analysis both confirms and extends these observations. RELLEG was lowest among those species typically associated with rocky substrates (*C. pagurus*, *C. productus*, *C. borealis* and *C. antennarius*; Table 2). Species which are found more often on open sand or mud substrates had higher RELLEG ratios (Table 4) which may reflect adaptation either to feeding on faster moving epifaunal prey forms or avoiding predation in exposed habitats (Jeffries 1966). *Cancer gracilis*, *C. oregonensis* and *C. branneri* had the highest RELLEG ratios. These species attain smaller adult sizes than the other species considered in this analysis (Table 2), again suggesting a relationship with absolute body size.

The observed trends in CHSIZE reinforce the above separation of *Cancer* into two main groups; CHSIZE being lower in those species characteristic of soft-bottom substrates. Whilst differences in MECHADV were less distinct than those in CHSIZE (indicated by overlapping subsets in Table 4), it is pertinent that the lowest ratio (0.268), indicating a capacity for fast but weak closure, was found for the claw of *C. magister*. Brown *et al.* (1979) reported MECHADV values for the crusher and cutter chelae of the portunid, *Callinectes sapidus* of 0.293 and 0.232, respectively. The chela of *C. borealis* was found to have the highest MECHADV in this study at 0.394. The crusher chelae of male nephropid lobsters, *Homarus americanus*, examined by Elner and Campbell (1981) had a mean MECHADV of 0.33. Examination of the subsets generated for the CHLENGTH and CHHEIGHT ratios (2 and 6, respectively) indicates that the high MECHADV of the claws of species such as *C. antennarius*, *C. anthonyi* and *C. borealis* has been achieved primarily through increasing lever length L_1 (indirectly measured by CHHEIGHT) than by changes in lever length L_2 (approximated by CHLENGTH).

Table 4. Comparison of body, leg and cheliped ratios of male *Cancer* crabs.

Dimension or ratio measured		Low			Species codes and parameter values						High
Carapace width (mm)	Spp.	OREG	BRAN	GRAC	CPAG	CBOR	CANT	CIRR	ANTH	PROD	CMAG
	Mean	33.0	49.3	75.8	107.7	120.2	123.6	124.2	131.0	141.0	154.3
	± S.E.	4.16	3.80	5.97	13.66	5.44	3.34	1.79	3.94	1.36	17.76
	$\bar{n}$	5	4	7	3	5	3	6	3	3	4
CPCSHAPE		PROD	CANT	CBOR	CMAG	CPAG	CIRR	GRAC	ANTH	BRAN	OREG
		.595	.620	.620	.622	.624	.631	.633	.634	.678	.750
RELLEG		CPAG	PROD	CBOR	CANT	ANTH	CIRR	CMAG	GRAC	OREG	BRAN
		.982	.951	.974	1.06	1.118	1.125	1.165	1.247	1.250	1.285
CHSIZE		CMAG	CIRR	GRAC	CPAG	BRAN	PROD	CBOR	ANTH	CANT	OREG
		.203	.216	.228	.232	.238	.248	.282	.286	.332	.390
MECHADV		CMAG	BRAN	GRAC	CIRR	CPAG	OREG	PROD	CANT	ANTH	CBOR
		.268	.306	.322	.330	.364	.365	.368	.378	.387	.394
CHLENGTH		ANTH	CMAG	GRAC	CIRR	CBOR	PROD	CANT	BRAN	CPAG	OREG
		.486	.492	.494	.495	.503	.508	.514	.519	.525	.587
CHHEIGHT		CMAG	GRAC	BRAN	CIRR	CPAG	PROD	ANTH	CBOR	CANT	OREG
		.415	.442	.444	.451	.474	.477	.499	.539	.548	.638

Species codes: ANTH = *C. anthonyi*; BRAN = *C. branneri*; CANT = *C. antennarius*; CBOR = *C. borealis*; CIRR = *C. irroratus*; CMAG = *C. magister*; CPAG = *C. pagurus*; OREG = *C. oregonensis*; PROD = *C. productus*. Lines link homogenous subsets indicated by Duncan's multiple range test ($P \geq 0.05$).

Brown *et al.* (1979) categorized the patterns of occlusion of the teeth of the cheliped systems of five diverse species of decapod crustaceans from the families Grapsidae, Ocypodidae, Xanthidae, Portunidae and Astacidae. They found that each cheliped possessed a linear array of 2-4 distinctive regions, each differing in functional capability. Furthermore, they concluded that single descriptors of claw form (such as MECHADV) seriously underestimate the potential capabilities of the claws to which they are applied. We are currently analyzing the occlusive geometry of *Cancer* claws to gauge the range of variation in these features at an intrageneric level. Preliminary observations reveal differences both in teeth number (4 in *C. productus*; 7 in *C. magister*) and form (simple dentition in *C. magister*; complex, multi-cusped, dentition in *C. antennarius*) between species (see also Figure 1), which perhaps relate to feeding activity.

Cancer oregonensis has the largest CHSIZE of the species considered in this study, and apparently of the genus as a whole (Vermeij 1977). From a standard predation viewpoint, a low CHLENGTH ratio would be expected for this chela, resulting in a high MECHADV. However, the species also has the highest CHLENGTH ratio thus resulting in a mechanically weak chela (Table 4). Hence this chela form may have resulted from selective pressures other than predation. *Cancer oregonensis* has a similar body form (including relatively large claws) and habitat preferences (intertidal rocky areas among kelp) to the N.E. Atlantic xanthid crab, *Pilumnus hirtellus* (L.), in which the chelae are important in agonistic and reproductive displays (Lobb 1972).

Ontogenetic considerations

Propodus height of male crabs from four species (*C. borealis*, *C. irroratus*, *C. pagurus* and *C. productus*) for which data from a wider size range of animals were available was regressed against CW (ln-ln transformed data) and compared between species (analysis of covariance).

There were no significant differences between the slopes ($P > 0.05$), but there were significant differences in elevations ($P < 0.05$) of the propodus height: CW relationships, over similar CW ranges, between *C. borealis* and the other three species (Table 5). The adjusted mean values for propodus height were 12.54 mm (*C. irroratus*); 12.97 mm (*C. productus*); 12.97 mm (*C. pagurus*) and 13.86 mm (*C. borealis*). The trends in propodus height between these four species are comparable to those obtained using CHSIZE and CHHEIGHT ratios based on a narrow size range of adult crabs and suggest that the relationships we have identified apply equally to juveniles.

Although some studies of decapod claw mechanics have indicated that claw features, such as mechanical advantage, do not change appreciably through ontogeny (Elner and Campbell 1981; Warner and Jones 1976), Costello and Lang (1979) found that the MECHADV of both chelae of the lobster, *Homarus americanus*, was the same during early development and that MECHADV of the crusher chela alone increased to the asymptotic adult value. Interregional variation in chela morphology and size may also occur (Elner and Campbell 1981). In view of these factors and in consideration of the small sample sizes used in the present analysis, our conclusions should be regarded as tentative, attendant upon examination of more comprehensive collections of claw material.

Table 5. Regression constants for the propodus height (Y in mm) and CW (X in mm) relationship ($\ln Y = \ln a + b \cdot \ln X$) for male crabs of four *Cancer* species. r = correlation coefficient.

Species	Regression constants a	b	r	n	CW (mm) Min.	Max.
C. irroratus[1]	-1.665	1.022	0.929	30	30	119
C. pagurus[2]	-1.954	1.101	0.998	31	24	118
C. productus[3]	-2.150	1.149	0.995	24	23	115
C. borealis[1]	-1.922	1.109	0.994	29	26	120

Data sources: [1] A. Campbell and P. Lawton (unpublished data).
[2] P. Lawton (unpublished data).
[3] E. G. Boulding (unpublished data).

Natural Diet

Previous studies into *Cancer* crab natural diet have adopted various taxonomic approaches to categorize prey type. Thus, Gotshall (1977) extracted eight major taxa from 40 different identifiable food items in his study of *C. magister* stomach contents, while Stevens *et al.* (1982) compared utilization of 'bivalves', 'crustaceans' and 'fish' in eight studies of *C. magister* diet. As in our preceding analyses, we have interpreted natural diet at a more functional level. Prey were categorized on the basis of their general distributional and morphological attributes into one of 10 groups (Table 6). Successful predation on each group requires particular foraging strategies and morphological adaptations,on the part of the predator, which may preclude or compromise success on other prey groups.

Table 6. Distributional and morphological attributes of prey organisms utilized by *Cancer* crabs.

Distributional attributes	Morphological attributes Hard-shelled	Soft-bodied
Epifaunal		
Essentially sedentary	mussels, gastropods	errant polychaetes
Fast-moving	crabs, shrimp	fish
Infaunal		
Superficial	cockles, scallops	
Shallow	clams	sedentary polychaetes
Deep	razor shells	

Studies on *C. irroratus* natural diet in the Northumberland Strait, Prince Edward Island (Scarratt and Lowe 1972) and off McNutts Island, Nova Scotia (S. Lanteigne and R. W. Elner, unpublished data), indicate that this crab preys primarily on essentially sedentary epifaunal prey, represented by hard-shelled forms, such as chitons and mytilids, and soft-bodied forms such as polynoids. Faster moving prey such as decapod crustaceans were found only at low frequencies of occurrence. Infauna, with the exception of shallow burrowing, soft-bodied types, such as *Nereis*, were not important prey types in either study. Data collected by S. Lanteigne and R. W. Elner (unpublished data), concerning the natural diet of *C. borealis* at McNutts Island, indicate a broad overlap in resource utilization with sympatric *C. irroratus* in that essentially sedentary hard-shelled epifaunal prey are important to both crab species. Partitioning was apparent for only one major prey taxon, namely ophiuroids, which was utilized exclusively by *C. borealis*. Feeding on infauna by *C. borealis* was inferred from the high frequency of occurrence of sediment in the stomachs of larger *C. borealis*.

Shelton *et al.* (1979) examined stomach contents of adult *C. pagurus* from the Inner Sound of Loch Torridon on the N.W. coast of Scotland. Most of the dietary intake was derived from infaunal prey, both shallow burrowers such as *Nucula* and *Thracia* spp. and deep burrowers such as *Ensis* spp. Scuba divers observed *C. pagurus* at the bottom of pits, up to 0.2 m deep, feeding upon *Ensis* spp. Similar observations were reported by Warner (1977).

Published information (Bernard 1979) on the natural diets of *C. productus* and *C. gracilis* comprises observations from 27 and 48 specimens, respectively. Based on concurrent studies on stomach contents of 202 *C. magister* from the same area, Bernard (1979) concluded that whilst *C. gracilis* was a competitor with *C. magister*, *C. productus* fed largely upon epibenthos not utilized by *C. magister*. Although complicated by sample sizes, a re-appraisal of these data indicate that *C. magister* has a much broader diet than either *C. productus* or *C. gracilis*. Partitioning appears more pronounced between *C. gracilis* and *C. productus* than between *C. magister* and *C. productus*. Soft-bodied epifaunal forms (errant polychaetes) were relatively uncommon in *C. productus* (3 spp.) and were utilized more by *C. gracilis* (10 spp.) and *C. magister* (15 spp.). Whereas, all three crabs fed on hard-shelled, essentially sedentary epifauna, *C. productus* showed some degree of specialization on gastropods and heavier-shelled bivalves, such as *Mytilus edulis*, whilst the other two crabs preyed principally upon lighter-shelled forms. Mobile epifaunal prey were consumed by *C. productus*, however, fast-moving forms such as shrimp were less common than slower moving anomuran and brachyuran crabs. The shrimp, *Crangon alaskensis*, was frequent in both *C. gracilis* and *C. magister* diets. Infaunal hard-shelled and soft-bodied forms were present in the diets of all three crab species.

Studies on *C. magister* diet have been reviewed by Stevens *et al.* (1982). For our analysis, we note that most studies have indicated that *C. magister*, particulary during juvenile stages (60-100 mm CW), has a strong dependence on fast-moving prey types such as shrimp and fish. Adult *C. magister* (100-160 mm CW) have been shown to prey on infauna, including deep burrowers such as basket cockles, *Clinocardium* *nuttalli*, in offshore areas (Gotshall 1977). In inshore sandy bay areas, these large crabs may also feed upon juvenile teleost fish (Stevens *et al.* 1982).

Cannibalism

Cannibalism, or intra-specific predation is part of the biology of many species, and may influence population structure, life-history, competition for resources, and behaviour (Fox 1975; Polis 1981). Crustaceans, including *Cancer* crabs, are known to be cannibalistic in laboratory culture systems (Bigford 1979; Ebert *et al.* 1983; Klein Breteler 1975). Conspecific exoskeletal fragments have also been found in stomach contents of wild-caught *Cancer* crabs (*C. irroratus* (Scarratt and Lowe 1972; S. Lanteigne and R. W. Elner, unpublished data); *C. magister* (Stevens *et al.* 1982). Estimates of the occurrence of cannibalism (based on frequency of occurrence data) range from 0 for *C. borealis* (S. Lanteigne and R. W. Elner, unpublished data) to 24.9% for small (15-60 mm CW) *C. magister* (Stevens *et al.* 1982). Inference of active cannibalism from these data is difficult, however, due to the possible ingestion of cast exoskeletal material.

Intrageneric comparisons

Botsford (1984; this Proceedings) and McKelvey (this Proceedings) summarize research on the cause(s) of the observed cycles in northern California *C. magister* landing records. One potential mechanism, inter-age density-dependent recruitment, and more specifically cannibalism, has been debated since originally advanced by Botsford and Wickham (1978). In the debate, it has been assumed that cannibalism can be adequately modelled on a simple encounter rate (Botsford and Wickham 1978) or metabolic rate (Botsford 1984) basis.

Research into cannibalism in *C. pagurus* (Lawton 1983) indicates that both of these assumptions should be reappraised. In the laboratory, recently captured edible crabs exhibited a rejection behaviour (in the form of an anterolateral extension of the cheliped and release of the prey) when initial attempts to capture conspecific prey led to the release of prey body fluids. Such rejection behaviour was not as pronounced in crabs which had been maintained in the laboratory on molluscan prey only. When the prior dietary experience of predatory crabs was controlled (Table 7), crabs held on a restricted diet (molluscs only) attacked conspecifics more readily (Mann-Whitney *U* test, $P < .05$) and exhibited cannibalism at a lower hunger level (Mann-Whitney *U* test, $P < 0.05$) than crabs which had been maintained on diets including other decapod species. A similar rejection behaviour has been noted for *C. irroratus* (P. Lawton, pers. obs.) and experiments are underway to examine factors influencing the occurrence of cannibalism in this species.

These studies indicate that dietary factors additional to energetic value influence cannibalism. Clearly, cannibalism is a complex phenomenon which cannot be adequately modelled by the simple functions used previously.

Table 7. Effect of previous dietary experience (1-month conditioning period) on the exhibition of cannibalism by *Cancer pagurus* (71-91 mm CW) (after Lawton 1983).

Dietary experience	Molluscs and decapods				Molluscs only			
Predatory behaviour	Time after presentation (h) when predatory behaviour first noted							
First presentation								
Attack	24	24	24	24	18	0	0	20
Cannibalize	144	48	not in 144	93	18	24	19	20
Second presentation								
Attack	NP	0	NP	NP	0	0	0	0
Cannibalize		not in 288			193	48	67	20

NP = A second presentation not carried out due to the long time required for the first exhibition of cannibalism.

0 = On presentation of prey to predatory crab.

Ontogenetic considerations

A further assumption in early papers on density-dependent recruitment mechanisms in *C. magister* was that cannibalism was primarily due to adults preying on newly settled crabs. Stevens *et al.* (1982) documented a high incidence of cannibalism amongst juvenile crabs in a study of *C. magister* feeding habits in Grays Harbour, Washington. If intra-year-class and juvenile inter-year-class cannibalism is more important than adult cannibalism then, as Botsford (1984) states, "... it would cause a more stable population or cycles of shorter period if there were any."

Prompted by observations of the low predation success rate of adult crabs on small mobile decapod prey, Lawton (1983) examined ontogenetic aspects of cannibalism in *C. pagurus*. Recently captured crabs were assigned to year-classes (based on information from concurrent studies of growth rates) and presented with a small number of prey of incoming (1980) or previous (1979) year-classes, collected from a low intertidal habitat. Predatory behaviour and prey mortality was monitored until either all prey had died due to injury (or cannibalism) or 312 h had elapsed with no cannibalism. In the latter event, feeding "condition" of the predator was established by presentation of similarly sized decapod prey of another species.

Cannibalism was more pronounced in the juvenile predator treatments (Table 8). The uniformly low prey survival rate in the experiment was ascribed to the confined conditions in which prey and predator were maintained and to absence of prey refuges. Recent detailed laboratory studies on the ontogeny of behaviour in *C. magister*, in particular of agonistic behaviour (Jacoby 1983), add further support to the conclusion that cannibalism is more frequent amongst juvenile crabs than between adults and juveniles.

Table 8. Intra-and inter-year-class cannibalism by *Cancer pagurus*. (after Lawton 1983).

Predatory year class	1980		1979		1979		1978	
Age (yr)	1		early 2		late 2		3	
CW (mm)	29	30	44	52	66	72	88	91
Predatory behaviour	Time after presentation (h) when behaviour first noted							
First attack	45	96	1	21	48	21	96	24
First mortality	45	168	1	45	120	21	312	69
First cannibalism	45	168	5	-	-	-	-	120
Termination of trial	71	264	70	117	312	45	312	165
Prey mortality	n of prey							
Presented	3	3	3	3	4	4	4	4
Consumed by predator	2	3	3	-	-	-	-	2
Dead due to injury	1	-	-	3	3	4	1	2
Survival	0	0	0	0	0	0	3	0

Factors such as habitat usage, refuge availability and molting frequency, may also be important in determining the extent and source of cannibalism and its significance in the life histories of different *Cancer* crabs. Juveniles have similar habitat requirements to smaller conspecifics and would thus be expected to have a high encounter rate with these vulnerable stages. Juvenile *C. pagurus* occupy rocky substrates and tend towards cryptic habitats (under rocks) when in the vulnerable, immediate post-molt stage, thereby reducing predation risk (Lawton 1983). Cannibalism in *C. magister* has been reported from populations occupying sandy substrates (Jacoby 1983; Stevens *et al.* 1982). Newly-molted individuals, although buried into the substrate, may be vulnerable to conspecific predators: Butler (1954) describes a foraging process in *C. magister* in which partly opened chelae probe sand subtrates, closing quickly over any encountered prey. Published growth information indicates a faster growth rate (and therefore number of molts) for *C. magister* (Botsford 1984) than for *C. pagurus* (Bennett 1974; see also Table 8), particularly in the first year following settlement. *Cancer magister* may, thus, be vulnerable to cannibalism for a greater proportion of time than *C. pagurus* for this period.

Discussion

We have reviewed the general evolutionary and ecological factors which characterize crabs of the genus *Cancer*. From a series of intrageneric comparisons of functional morphology, we identify two major feeding or life-history specializations in larger *Cancer*. Crabs which, in juvenile phases, occupy rocky habitats tend to have larger, more powerful chelae (on the basis of mechanical advantage) and lower relative leg lengths (e.g. *C. productus*, *C. borealis*). Crabs which are associated with sandy, open habitats (e.g. *C. gracilis*, *C. magister*) have proportionately smaller and less powerful claws, but higher relative leg lengths. *Cancer* spp. which attain small adult sizes (e.g. *C. branneri* and *C. oregonensis*) form a third group, but have not been considered in detail in this study.

Our review of the natural diets of *Cancer* crabs indicates a number of correlations with these morphological analyses. Crabs with powerful chelae, such as *C. productus*, *C. borealis* and *C. pagurus*, utilize hard-shelled epifaunal and infaunal prey, which are essentially sedentary yet require considerable effort to access prey flesh (a long "pursuit" time *sensu* Hughes 1980). Crabs, such as *C. gracilis* and *C. magister*, with less powerful but faster closing chelae and characteristic of soft, sandy areas, prey on thinner-shelled or soft-bodied prey (decapods, fish, polychaetes) which may require short pursuit times, but longer "search" times (*sensu* Hughes 1980).

Although we have stressed differences between *Cancer* species in our analyses, these crabs are nonetheless remarkably similar considering the wide range of claw morphology found in brachyuran crabs (Brown *et al.* 1979; Schäfer 1954; Warner 1977). The similarity amongst *Cancer* is possibly due to evolutionary constraints on modes of development, or may reflect the retention of a functionally efficient appendage form. A number of *Cancer* crabs are capable of exploiting infauna as adults (Boulding and Hay 1984; Gotshall 1977; Peterson 1983; Shelton *et al.* 1979). In the absence of commercial fishing, this is the longest life-history phase. The monomorphic chelae, characteristic of the genus may well represent an adaptation to burrowing in the adult stage. Portunid crabs preying on infauna, have dimorphic chela systems and tend to burrow only superficially (Blundon and Kennedy 1982). Some *Cancer* crabs, however, are capable of capturing deep burrowing members of the infauna (Gotshall 1977; Shelton *et al.* 1979; Warner 1977), thus gaining access to prey resources largely unavailable to other decapod competitors.

Cannibalism has been implicated in the population dynamics of *Cancer* species. Our review indicates that further information will be required before the process can be adequately modelled as a possible density-dependent recruitment mechanism. Dietary factors additional to energetic considerations are implicated. Cannibalism may well vary in importance between *Cancer* species, depending upon the propensity and capability of larger conspecifics to cannibalize and the degree of vulnerability of juveniles (a possible function of habitat usage, refuge availability and growth rate).

Our findings have implications for fisheries management of *Cancer* species. Major fisheries currently exist for two species, *C. pagurus* and *C. magister*. In N.E. Atlantic waters, *C. pagurus* has been exploited for at least 2,000 years and currently forms the basis of important commercial fisheries off the coasts of Scotland, N.E. and S.W. England, Norway and Brittany (Edwards 1978). Apart from fluctuations in landings associated with changing economic factors (Edwards 1978), the productivity of these crab populations appears remarkably stable. On the west coast of North America there are major commercial and sport fisheries for *C. magister* (Dahlstrom and Wild 1983). Over recent decades, Dungeness crab landings along this coast have exhibited either dramatic declines from historic levels (Dahlstrom and Wild 1983) or cyclic fluctuations (see papers in this Proceedings). Differences in morphometrics and feeding between these two species could contribute to the observed population responses to exploitation. In the development of fisheries for other *Cancer* species, an estimate of "expected" response to exploitation might be obtained by comparison with species exhibiting a similar functional ecology. Based on our classification, we propose the following groupings of *Cancer* crabs for such purposes:

Type species	*C. magister*	*C. pagurus*
Included species	*C. gracilis*	*C. antennarius*
	C. irroratus	*C. anthonyi*
		C. borealis
		C. productus

The two N.W. Atlantic species, *C. borealis* and *C. irroratus* are subject to low level exploitation in Atlantic Canada (Elner 1984). Exploitation of both these species in the N.E. United States remains at a similar low level (Bigford 1979; Briggs and Mushacke 1982). Small-scale commercial and sport fisheries currently exist for *C. antennarius*, *C. anthonyi*, *C. gracilis* and *C. productus* (Dahlstrom and Wild 1983; S. Kato, R. N. Tasto and C. Toole, pers. comm.).

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Oceanography of Cook Inlet and its relation to Dungeness crab distribution

A. J. Paul
University of Alaska, Fairbanks
Seward, Alaska

Abstract

This paper reviews oceanographic and biological information which may explain the distribution of Dungeness crab in Cook Inlet, Alaska. This species exhibits a restricted distribution in Cook Inlet occurring primarily in Kachemak Bay, where standing stocks of 0.04 to 0.7 gm^2 are located. Kachemak Bay is a shallow bay with depths of 30 to 40 meters common. The current pattern of Kachemak Bay includes a strong double gyre system which acts to increase the residence time of water in the Bay and prevents crab larvae from being carried away. Associated with the double gyres is an increase in water column stability which results in the early development of a large spring phytoplankton bloom that continues through August. During the phytoplankton bloom, primary production may exceed 7 gCm^{-2} d^{-1}. This compares to 2 gCm^{-2} d^{-1} typically observed in other Alaskan fjords which generally have blooms only during the March to May period. The values observed in coastal upwelled waters off Peru, one of the most productive ecosystems, is on the order of 3 to 12 gCm^{-2} d^{-1}. The bloom phytoplankton of Kachemak Bay are dominated by diatoms, especially *Thalassiosira*. In Kachemak Bay, numbers of *T. aestivalis* as high as 10^6 cells per liter have been reported. This compares with total phytoplankton cell counts of 500 to 4,000 cells per liter which are typically encountered during blooms in other Alaskan fjords. It has been demonstrated that *Thalassiosira* can serve to some extent as food for the first four larval stages of Dungeness crab. Zooplankton grazers in Kachemak Bay are not abundant and consume only 6.5% of the phytoplankton biomass on a daily basis.

Approximately 60 gCm^2 is produced during the spring and summer season and 11% is sedimented to the bottom. This compares with 17 gCm^2 of which 6% reaches the bottom in the adjacent central portion of Cook Inlet. The high carbon input from primary production, augmented with

allochthonous organic material, directly supports the crabs' prey species. Stomach contents indicate that small bivalves, barnacles, amphipods, and polychaetes are the primary benthic prey of Dungeness crab.

It is suggested that the current gyres, a phytoplankton bloom which develops early in the spring, the high rates of Thalassiosira production during the larval period, and high flux of carbon to the benthos in Kachemak Bay create an environment which is conducive to the survival of Dungeness larvae and post larvae.

Because there exists a considerable amount of information on oceanography, primary production, carbon flux, and larval crab distribution for the area, Kachemak Bay is ideally suited for recruitment studies of Alaskan Dungeness crab. Concurrently, information could be gathered on most of the other commercially important decapods which co-occur with Dungeness crab in the bay.

Introduction

The Dungeness crab, Cancer magister, supports a small but locally important fishery in Cook Inlet, Alaska. The fishery is restricted primarily to Kachemak Bay. Dungeness crab occur throughout much of Cook Inlet, which is a large body of water, and the northeast Gulf of Alaska. Currently, it is not understood why commercial quantities of this species are restricted to Kachemak Bay within the Cook Inlet system. As part of the Outer Continental Shelf Environmental Assessment Program, studies on the oceanography, primary production, and faunal distribution and abundance were conducted in the inlet. Much of this material occurs in unpublished reports or scattered papers in a variety of journals. The objective of this paper is to review the existing physical and biological oceanographic information which might explain the concentrated distribution of Dungeness crab in Kachemak Bay.

Methods

Literature on Cook Inlet currents, primary production, larval and benthic Dungeness crab distribution, and food sources of crab was collected. Additional related information on oceanography and Dungeness crab biology from other areas of the North Pacific was also reviewed.

Results and Discussion

Distribution. An extensive trawl survey of Cook Inlet was conducted during the years 1976 - 1978 (Feder and Paul, 1981). Forty-seven stations throughout the inlet were sampled at a variety of times (Fig. 1). Dungeness crab were encountered primarily in Kachemak Bay. There, Dungeness crab biomass estimates of 0.04 - 0.7 gm^2 were observed. Harvest records for Cook Inlet also support the observation that Dungeness crab occur primarily in Kachemak Bay (Table I). Likewise, the concurrent meroplankton surveys found the highest concentrations of Dungeness larvae in Kachemak Bay (English, 1979).

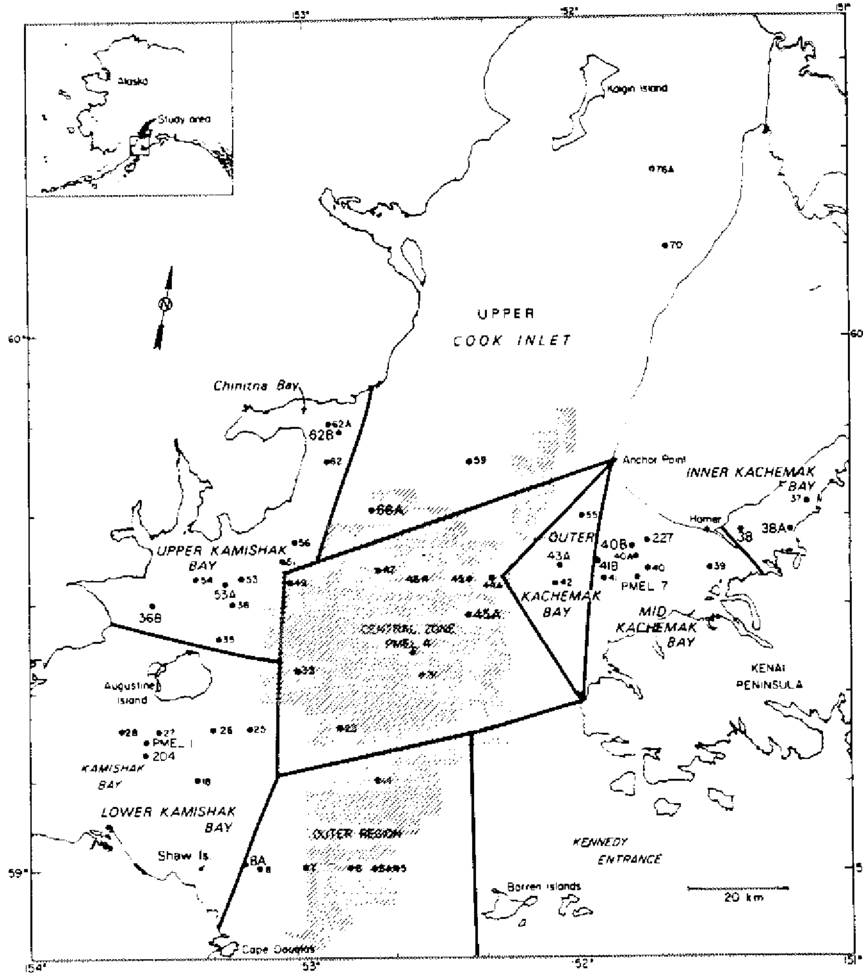

Figure 1. Trawl stations in Cook Inlet (Feder and Paul, 1981).

TABLE I. Summary of 1960-1974 Cook Inlet Region Catch Statistics, Data as a Percent of Total Catch (data from ADF&G).

PERCENT OF COOK INLET CATCH

Species	Kachemak Bay & South Dist.	Kamishak District	Barren Islands District	Outer District
Dungeness	99.7	0.0	0.0	0.0
Shrimp	99.0	0.0	0.0	1.0
King Crab	34.0	58.0	7.0	0.0
Tanner Crab	15.0	55.0	11.0	18.0

TABLE II. Densities of Zooplankton, Kachemak Bay, Alaska, April-August, 1976 in Numbers per Meters Cubed (Damker, 1977).

	April 6-13	May 5-9	May 24-30	July 8-15
COPEPODA				
Pseudocalanus spp.	55	61	113	435
Acartia longiremis	38	109	13	374
Oithona similis	27	48	54	194
CHAETOGNATHA				
Sagitta elegans	4	3	3	47
CIRRIPEDIA				
Nauplii	372	0	0	118
Cyprids	0	3	0	10
Crab Larvae	0.1	3	3	10
AMPHIPODA	0	0.1	0	0.1
EUPHAUSIACEA	2	2	4	25
Larval Fish	0	0.5	0	0

Oceanography

Physical oceanographic aspects of Cook Inlet have been treated by Gatto (1976), Burbank (1977), and Muench *et al.* (1978). During spring and summer, ocean water entering the inlet from the Gulf of Alaska via Kennedy Entrance in conjunction with the seaward flow of water from inner Kachemak Bay, creates a double gyre system in Kachemak Bay (Fig. 2). These gyres act to increase the residence time of water in outer Kachemak Bay and stabilize the water column. Since the major source of water for Kachemak Bay originates in the Gulf of Alaska, it does not contain the heavy load of suspended particles present in upper Cook Inlet water. The clarity of the water allows for an early thermal stratification of the bay and consequently, spring phytoplankton bloom initiates earlier than the rest of the Inlet.

Primary Production

The spring bloom in Kachemak Bay coincides with the hatching of Dungeness crab larvae (Larrance and Chester, 1979; Feder and Paul, 1981). During the bloom, diatoms exhibit a sequence of dominance starting with several species of *Thalassiosira* which remain predominate until June or July, when they are supplanted by *Chaetoceros* spp. During the bloom, *T. aestivalis*, 20-45 micron diameter (Cupp, 1943), reach concentrations of $2x10^5$ to $1x10^6$ cells per liter in May (Larrance and Chester, 1979). Concurrent with the large May bloom in Kachemak Bay, diatom counts, all genera included, in the rest of lower Cook Inlet ranged from 10 to 1,100 cells per liter (Larrance and Chester, 1979). Figure 3 demonstrates the relatively high primary production of Kachemak Bay compared to other areas of the lower inlet (see Fig. 4 for location of stations for Fig. 3).

Dungeness Larvae

The two major factors likely to affect the survival of Dungeness crab larvae are food availability and predation. It has been demonstrated that most decapod larvae have a "critical period" that occurs when they first begin to feed (Anger *et al.*, 1980; Paul and Paul, 1980). Generally, larvae must successfully initiate feeding within the first three days after hatching to survive. The natural food of Dungeness crab larvae is undescribed, but several authors have reared them on brine shrimp larvae (Reed, 1969; Buchanan *et al.*, 1975). Hartman and Letterman (1978) determined that unialgal cultures of *Skeletonema costatum* or *Thalassiosira pseudonana* allowed development to the third and fourth stage, respectively; while a mixture of the two diatoms supported larvae through the fifth stage. Unfortunately, the latter authors did not provide information on phytoplankton concentrations which allowed survival. Incze and Paul (1983) working with first feeding *Chionoecetes bairdi*, another Alaskan crab found in Cook Inlet, determined that zoeae could obtain about 7% of its respiratory requirement feeding on Gulf of Alaska *Thalassiosira* at concentrations of 1,700 cells per liter. In Kachemak Bay, *Thalassiosira* concentrations are 125 to 6,000 times greater than used in the feeding experiment by Incze and Paul (1983). Thus, it is highly probable that Dungeness larvae obtain considerably more than 7% of their energy from ingesting diatoms.

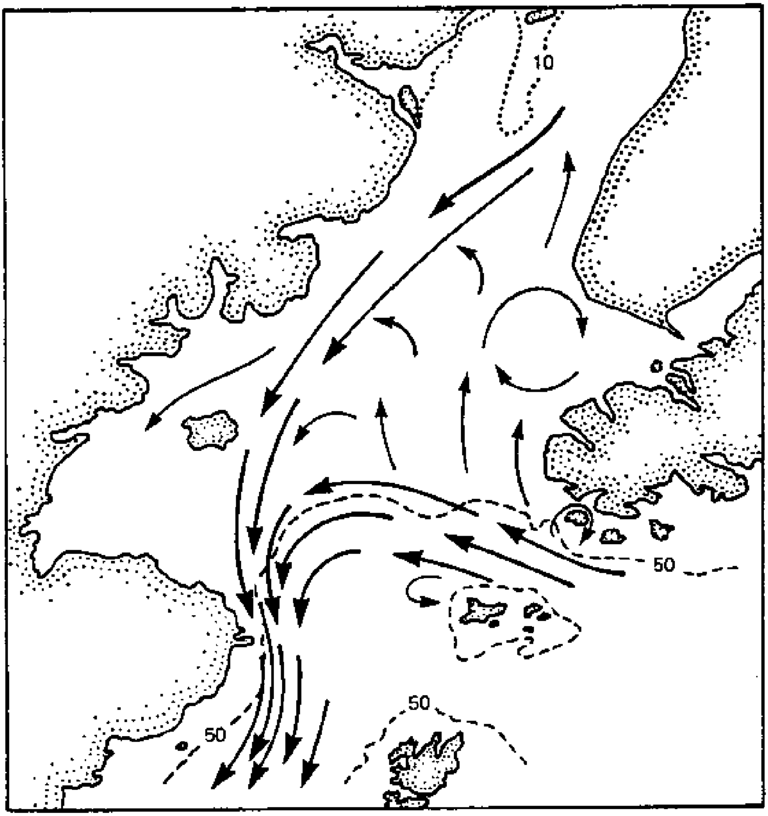

Figure 2. Spring and summer mean flow in Cook Inlet (Muench _et al._, 1978).

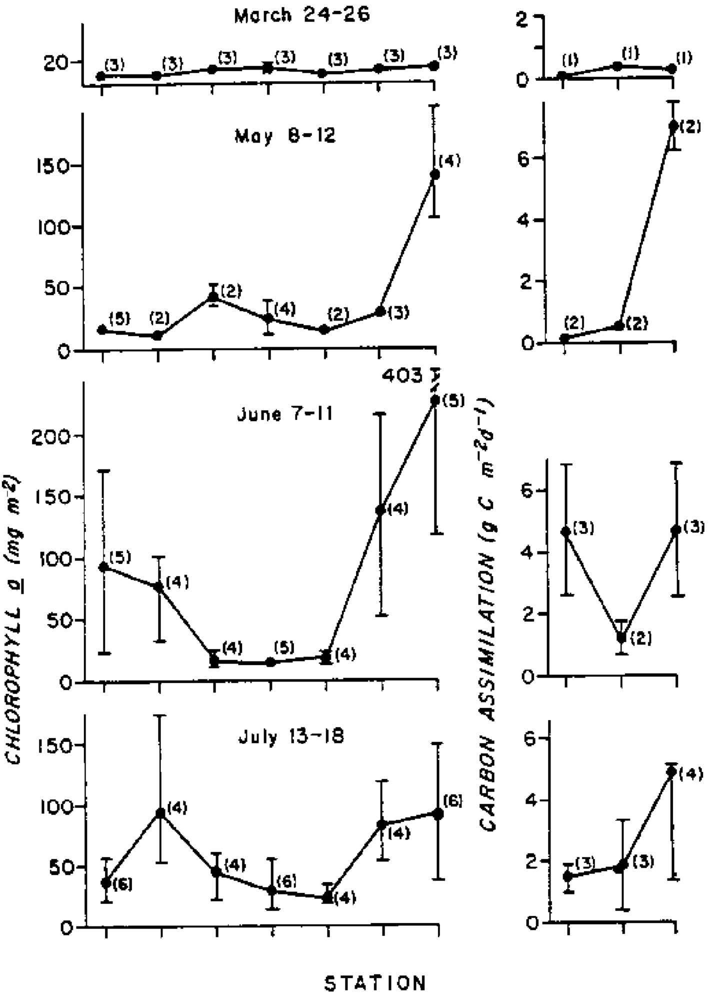

Figure 3. Chlorophyll and carbon assimilation in the euphotic zone of lower Cook Inlet, 1978. Bars = range, Points = mean. (Larrance and Chester, 1979)

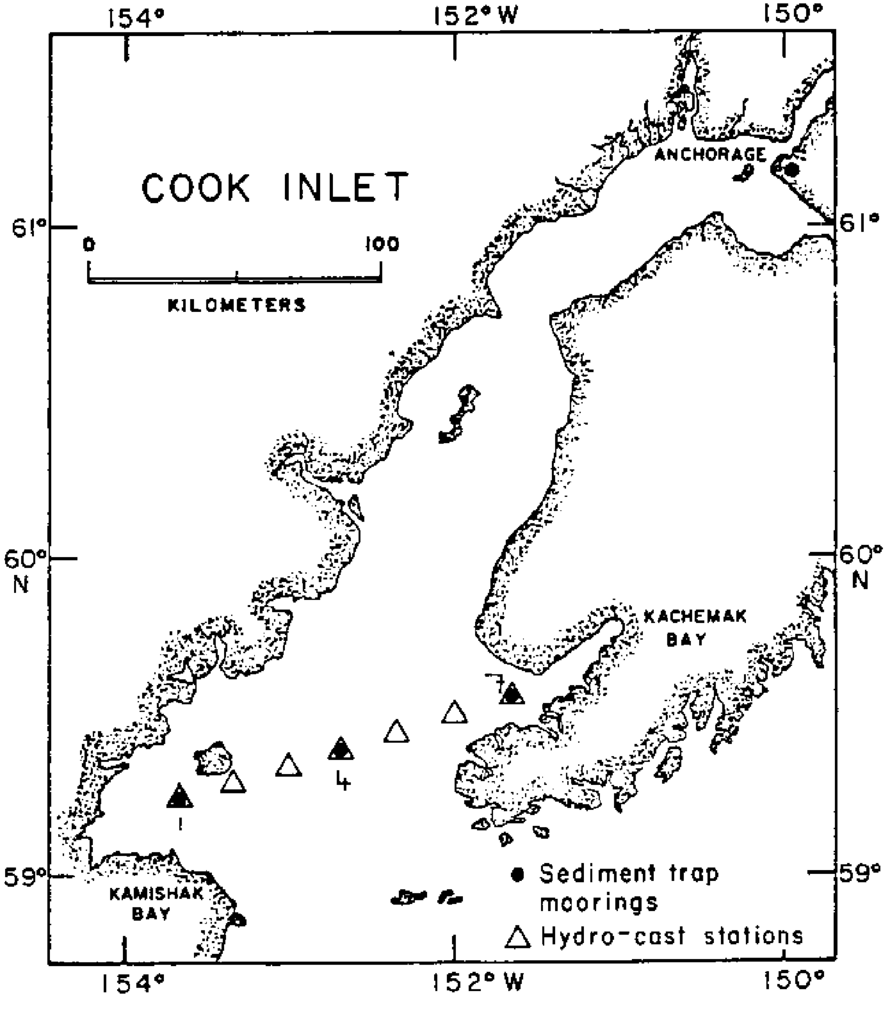

Figure 4. Sediment trap and primary production stations in Cook Inlet (Larrance and Chester, 1979).

During April in Kachemak Bay, barnacle nauplii are the most common zooplankton (0.4 per liter), while copepods (0.1 per liter) are next in abundance (Table III; Damker, 1977). Read (1969) demonstrated in the laboratory that barnacle nauplii can support C. magister larvae through the megalops. It has not been shown that Cook Inlet Dungeness crab larvae consume barnacle larvae; however, since they may be the most abundant potential prey (Table III), it is plausible that they are an important food. Barnacle larvae have been observed in the stomachs of Cook Inlet king crab larvae, which co-occur with Dungeness larvae.

One of the factors known to regulate success of a year class of barnacle larvae is the concentration of preferred diatoms during the naupliar stages (Barnes, 1956). In Kachemak Bay, the spring phytoplankton bloom generally occurs one to three weeks earlier and exhibits a higher primary production rate than the remainder of Cook Inlet (Larrance and Chester, 1979). The longer residence time of water in Kachemak Bay, due to the current gyres, results in a retention of diatoms so their populations can build to high levels (Larrance and Chester, 1979). High concentrations of diatoms early in the spring would have a beneficial effect on survival of Dungeness larvae and their grazing zooplankton prey.

Carbon Flux

Observation of carbon flux in Kachemak Bay during the May-August season of 1978, indicated that 60 gCm^{-2} was sedimented to the benthos (Chester and Larrance, 1981). This would equal approximately 11% of the estimated water column primary production during the same period. The mechanism responsible for 83% of the downward transport was traced to zooplankton grazing and subsequent fecal pellet production. Comparative observations for the central portion of the inlet and Kamishak Bay, where Dungeness crab occur in low numbers, were 17 gCm^{-2} and 40 gCm^{-2}.

Filter feeding bivalves, barnacles and detritivorous amphipods are important prey of Kachemak Bay Dungeness crab. These organisms must all benefit nutritionally from the high carbon flux to the bottom of Kachemak Bay.

It is suggested that the current gyres, the prolonged phytoplankton bloom which begins early in the spring, the high rates of Thalassiosira production during the larval period, and high flux of carbon to the benthos in Kachemak Bay create an environment which is conducive to the survival of Dungeness larvae and post larvae. This set of oceanographic conditions appears to be unique to Kachemak Bay within the Cook Inlet system and may explain the restricted distribution of Dungeness crab within the inlet.

A major problem facing scientists interested in understanding population fluctuations of Dungeness crabs, and other decapods, is the inability to predict recruitment. There are several reasons why Kachemak Bay is ideally suited as a site for a recruitment experiment for several species of Alaskan decapods: 1) The Bay is relatively small in size, about 75km x 25km. Thus establishing the position of sampling stations and returning to them repeatedly would be fairly simple. 2) Dungeness crab, red king crab, Tanner crab, and all the species of commercially harvested shrimp co-occur in the bay. 3)

There exists a considerable amount of historical information on physical oceanography, primary production, as well as larval and benthic decapod distribution. In addition, there is limited information on zooplankton and decapod larvae settlement areas. 4) Shore based laboratores occur near the proposed study area. 5) Population surveys of adult crustaceans are done yearly by Alaska Department of Fish and Game. 6) The work could be accomplished year-round with a relatively small vessel.

I propose that a large scale larval decapod recruitment study be initiated with the field work to be accomplished in Kachemak Bay. The focus for the project should be the recruitment process. The obvious problem with the proposal is finding a source of funds to support such forward looking research.

Acknowledgements

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Evidence that a single size-class of *Cancer magister* has supported the Yakutat commercial fishery since the 1981-1982 season

Timothy M. Koeneman
Alaska Department of Fish and Game
Petersburg, Alaska

Abstract

A brief analysis of carapace shoulder width, shell condition, and wet weight data indicates that in the Yakutat commercial fishery a major proportion of *Cancer magister* harvested during the 1981/82 season was comprised of a single size-class. Continued data series indicate that significant recruitment did not occur during subsequent seasons. The size-class which predominated the fishery in 1981/82 continued to increase in size, weight, and proportion of anexuviants through the 1984/85 season. One potential alteration of the existing management strategy in this fishery is discussed.

Introduction

Generally accepted concepts utilized as a basis for management of Dungeness crab, *Cancer magister*, are size, sex, and season. A minimum legal size for male crab, a prohibition against the harvest of female crab, and a closure during the mating season, provide for essential elements in stock reproduction. In addition, a closure during the male molting season and subsequent growth period provides benefits to industry and ultimately the consumer. Inherent in such management is the concept that male Dungeness crab, above an established minimum size, are surplus to population reproduction and other requirements.

Considering such management, estimates of harvest rates utilizing various methods are quite high. Based upon tagging studies in the Washington ocean fishery, Cleaver (1949) provided estimates of annual exploitation of .79 and .87 for the years 1947 and 1948, and considered those minimal estimates based on the method utilized. Annual exploitation rates based on catch per unit of effort (CPUE) data expressed as catch per trap in the northern California fishery for the period 1966/67 through 1971/72 ranged between .63 and .87 (Gotshall 1978). Annual exploitation rates based on CPUE data expressed as catch per delivery ranged from .43 to .93 for the period 1951 through 1977 in the northern California fishery (Methot and Botsford 1982). The findings of Methot and Botsford (1982) indicate that during periods of increasing population abundances very significant escapements occurred and a large year-class can contribute to a fishery for several years.

Yakutat Fishery

The Yakutat Dungeness fishery occurs in waters between Cape Fairweather and Cape Suckling (Figure 1). Geographic similarities exist between this coastline and others producing significant quantities of Dungeness crab. Washington based boats have historically harvested Dungeness crab from the Yakutat waters and, to a degree, the most significant effort levels and resulting high commercial harvests in the Yakutat fishery have occurred during periods when crab availability in the Washington ocean fishery have been low. Beginning with the 1981/82 season through the 1983/84 season effort levels increased (Table 1). Effort levels during the 1984/85 season were quite high compared to historic levels, but below those experienced during the 1983/84 season. The commercial catch increased with effort from the 1981/82 season through the 1982/83 season and subsequently declined.

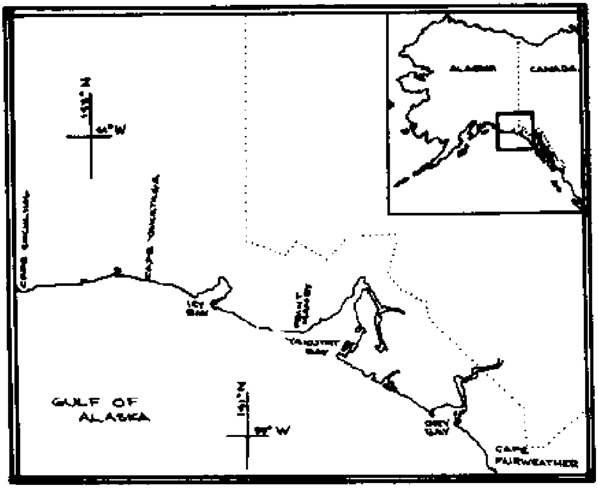

Figure 1. Location of the Gulf of Alaska Coastline Utilized in the Yakutat Commercial Dungeness Crab Fishery.

While this fishery exhibits many commonalities with other Dungeness fisheries, it is dissimilar in at least one respect. The importance of this fishery relative to other Alaskan fisheries and the remote location have detered the development of programs to adequately collect and analyze biological data. However, certain information has been collected. Data collected from commercial landings since the opening of the 1981/82 season have included carapace width frequency as measured inside the tenth antero-lateral spine (termed carapace shoulder width), shell condition, and average weights. These data are briefly examined with respect to size-class representation, and in light of findings by Methot and Botsford (1982).

Table 1. Yakutat, Alaska Dungeness Crab Harvest Statistics from the Commercial Fishery since 1960.

Year or Season	Catch in Pounds	Number of Vessels	Number of Landings
1960	543,762		
1961	1,023,545		
1962	937,051		
1963	1,383,298		
1964	637,140		
1965	910,278		
1966	528,060		
1967	2,031,460		
1968	2,096,119		
1969/70	1,207,061	11	107
1970/71	1,589,945	10	88
1971/72	1,250,118	8	91
1972/73	2,207,061	12	99
1973/74	2,532,778	22	274
1974/75	1,097,508	19	173
1975/76	628,879	16	129
1976/77	542,726	8	28
1977/78	131,052	2	11
1978/79	1,875,088	13	134
1979/80	1,474,149	19	99
1980/81	881,681	7	56
1981/82	3,300,158	16	175
1982/83	5,880,409	33	356
1983/84	3,133,531	54	493
1984/85	763,994	37	

Considering the Yakutat, Alaska fishery, initial inspection of summarized carapace shoulder width data from dockside samples (Table 2) indicates mean carapace shoulder width gradually increased from 180.6 mm to 193.9 mm from 1981/82 through 1983/84 seasons, then decreased slightly to 190.6 mm during the 1984/85 season. The slight decline in mean carapace shoulder width during the 1984/85 season is most probably due to an increase in recruit-size crab which exhibited a mode at approximately 170 mm (Figure 2).

Figure 2 represents a more detailed view of dockside samples expressed in one millimeter increments, and presents a visual perception of the single size-class passing through the fishery. A gradual increase in the number of crab larger than 200 mm in carapace shoulder width can also be identified. Table 3 represents the summarized results of whole wet weight dockside samples collected beginning with the 1981/82 season and indicates an increase in weight as the single size-class moves through the fishery during the four seasons under consideration.

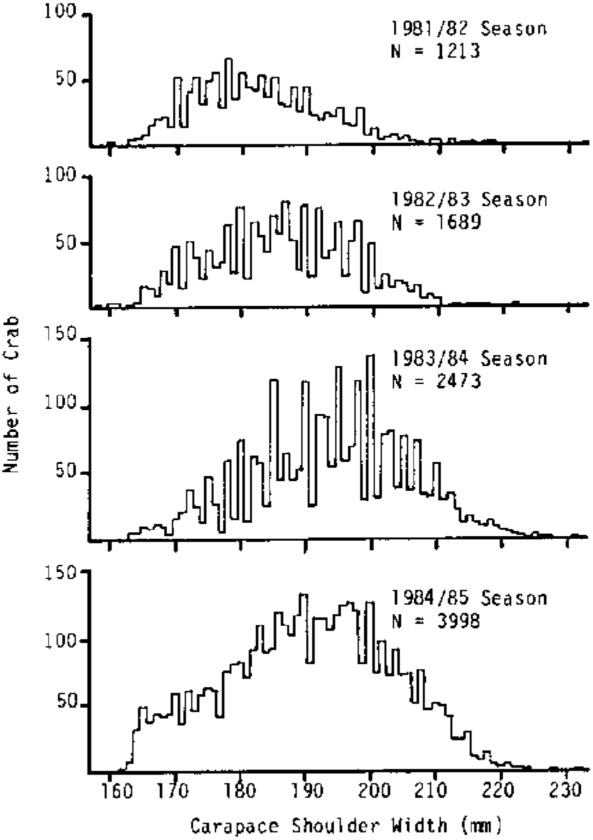

Figure 2. Width Frequency Distribution from Commercial Landings of Male Dungeness Crab, Cancer magister, from the Yakutat, Alaska Fishery.

The proportion of anexuviant crab in the dockside sample data (Table 2) generally increased over the four seasons which may indicate that crab of a single size-class are approaching, or are at, maximum size. It should be noted that shell condition data is relatively imprecise due to the subjective decisions required of individual samplers, with varying levels of experience.

Table 2. Summary of Carapace Shoulder Width Frequency Samples of Male Dungeness Crab, Cancer magister, from Commercial Landings in the Yakutat, Alaska Fishery.

Season	Number Landings Sampled	Number Crab Measured	Mean Width (mm)	Percent Anexuviant
1981/82	11	1,213	180.6	4.7
1982/83	16	1,689	186.2	0.5
1983/84	31	2,473	193.9	7.5
1984/85	39	3,998	190.6	14.3

Table 3. Summary of Whole, Wet Weight Samples of Male Dungeness Crab, Cancer magister, from Commercial Landings in the Yakutat, Alaska Fishery.

Season	Number Landings Sampled	Number Crab Sampled	Total Weight Crab Sampled (Pounds)	Mean Weight per Crab (Pounds)
1981/82	7	638	1,449	2.27
1982/83	19	1,921	4,627	2.41
1983/84	30	2,365	6,270	2.65
1984/85	34	3,463	8,969	2.59

These four small pieces of data (mean carapace shoulder width increases, carapace shoulder width distribution shift to the right, mean weight increases, and anexuviant proportion increases) provide evidence that a single size-class has provided a major portion of the Yakutat Dungeness crab harvest for the past four seasons, 1981/82 through 1984/85. Total harvest for this period exceeded 13 million pounds. These data also support statements by other authors (Methot and Botsford 1982) relative to the occurrances of significant escapements from the fishery, and that a single year-class can prevail in a fishery for a number of successive seasons.

Management Implications

Information presented is far from complete but is an addition to the knowledge concerning Alaskan Dungeness crab stocks. Periodically, a review of basic management strategies with respect to life history data is enlightening. In particular, the concept that males above an established minimum legal size have had sufficient opportunities to contribute to stock reproduction and are surplus to the population (Mackay 1942) will be briefly considered.

Based upon Butler's growth model (1961), and assuming that size at maturity and growth of Alaskan and Canadian Dungeness crab are similar, it would appear that the average crab harvested in 1981/82 was 4 to 5 years of age. Assuming that 1981/82 was the first season that this size-class entered the fishery, and considering that the size-class persisted at substantial levels for the next two seasons (1982/83 and 1983/84) and to a lesser degree for an additional season (1984/85), a significant portion of that single size-class was 7 to 8 years old. The proportion of that single size-class surviving and growing at age 7 to 8 years is considerably more than initially perceived by previous authors (Butler 1961; Cleaver 1949). Conditions predicating such survival or growth are not understood, but intuitively result from a number of natural conditions. It may be prudent to assume that some aspect of Dungeness crab life history or population dynamics benefits from periodic survival of males to an older age and growth to a larger size. Accepting such an assumption would necessitate modification of the existing management strategy to provide opportunities for increased longevity and size. One method of accomplishing such a modification would be to establish catch limits based on population trends. From 1909 until 1933 catch limits were established in the Oregon fishery (Waldron 1958) and have been suggested as necessary in the Southeast Alaska fishery (Benitz 1969). Positive or negative results from catch limits have not been adequately addressed, but might be appropriately considered in the future.

ACKNOWLEDGEMENTS

The author wishes to acknowledge the assistance of A. Brogle, A. Kimker, G. Woods, and K. Iverson who developed a keen interest in the fishery and collected much of the basic dockside data. Mr. G. Curtiss receives thanks for his assistance in summarizing the collected data.

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The controversial use of the insecticide Sevin in Pacific Northwest estuaries: Its effects on Dungeness crab, Pacific oyster, and other species

David V. Buchanan and Daniel L. Bottom
Oregon Department of Fish and Wildlife
Corvallis, Oregon
and
David A. Armstrong
University of Washington
Seattle, Washington

Abstract

The use of the insecticide Sevin (carbaryl) to treat oyster grounds has become a controversial issue in the Pacific Northwest. Oyster growers maintain that Sevin is needed to kill two types of burrowing shrimp which render Pacific oyster, *Crassostrea gigas*, beds soft and silty, preventing oyster culture. Oyster beds have been annually sprayed with Sevin in Washington's Willapa Bay and Grays Harbor since the early 1960's. In 1984, an Environmental Impact Statement was prepared by the Washington Department of Fisheries and Washington Department of Ecology to review the treatment program and allow public comment. In Oregon, the Oregon Fish and Wildlife Commission issued a Sevin spraying permit to oyster growers in August 1982. However, the Audubon Society and others protested this permit before the Oregon Court of Appeals. In April 1984, the court upheld a previous ruling by the Land Use Board of Appeals that the ODFW Commission violated a state land use regulation that protects estuaries, and that there was a lack of information on the impacts of Sevin on non-target estuarine organisms. In this paper, the known toxic effects of Sevin on Dungeness crabs, *Cancer magister*, are reviewed. Also reviewed are potential impacts of the insecticide on Dungeness crab and other non-target species not documented in the literature but that may need study to satisfy the courts and the concerned public. The authors suggest negative environmental impacts may be minimized by a February or March application but that further research is necessary to resolve the controversy.

Background and the Controversy

Oyster culture became widespread in the Pacific Northwest when the Pacific oyster, *Crassostrea gigas*, was imported from Japan in the 1930's (Oregon Department of Fish and Wildlife, ODFW, 1982). Washington's oyster industry is the richest molluscan fishery in the Pacific Northwest, and Willapa Bay produces over 50% of the state's annual harvest (Nosho et al. 1980). Most of the oysters in Willapa Bay and Grays Harbor, Washington and Tillamook Bay, Oregon are cultured directly on intertidal substrate. Oyster cultch, which is oyster shell bearing spat or juvenile oysters, requires substrate that is sufficiently compact to support the weight of growing oysters. If the substrate is unstable, then heavy mortality results from sinking and suffocation of the oysters (Washington Department of Fisheries, WDF, 1970).

Two species of burrowing shrimp that adversely affect oyster culture are indigenous to and very abundant in estuaries of the Pacific Northwest. The ghost shrimp, *Callianassa californiensis*, and the mud shrimp, *Upogebia pugettensis*, are infaunal crustaceans that construct extensive burrows on intertidal mud and sand flats during feeding. These shrimp occur in the same intertidal zone occupied by oysters and can reach densities in excess of 45 or 50 per square meter. However at smaller densities, burrowing activity by the shrimp reduces the compaction of the substrate. Consequently, oysters are smothered either by mud that is deposited during excavation of the burrows or by sinking into the altered substrate (WDF 1970). It is the strong contention of the oyster industry that control and occasional eradication of ghost shrimp is necessary to sustain the oyster industry at its current level.

To control populations of burrowing shrimp, tideflats have been annually treated with the insecticide Sevin since the early 1960's under the supervision and study of the Washington Department of Fisheries (WDF and Washington Department of Ecology, WDOE, 1984). Following the 1983 El Nino along the Pacific Northwest coast, ghost shrimp populations in Washington's estuaries approached record densities and resulted in requests to treat an extensive area of the estuary in the summer of 1984. Early in 1984, WDF and WDOE determined that an Environmental Impact Statement should be prepared on ghost and mud shrimp control, primarily to review the treatment program and to allow public comment.

The draft environmental impact statement (DEIS) released for agency and public review in June 1984 became the focus of a controversy over the affects of Sevin on non-target estuarine organisms such as Dungeness crab, *Cancer magister*. Citing results of Buchanan et al. (1970), the draft stated, "it is clear that crabs are fairly resistant to sprayed Sevin. This resistance is especially evident when crabs are exposed to the actual conditions present when intertidal areas are treated" (WDF and WDOE 1984). In a very deragatory agency review of Washington's DEIS, the National Marine Fisheries Service (NMFS) cited laboratory and field studies to conclude that Sevin sprayed onto tideflats causes massive mortalities of estuarine animals. [1]

The NMFS also noted that within the DEIS "the references and data selected for inclusion were not comprehensive and their selection appears biased. Additional pertinent literature exists (including pertinent facts omitted from cited literature) which substantially expands upon or contradicts some of the DEIS' findings". For example, "The statement within the DEIS that ... it is clear that crabs are fairly resistant to sprayed Sevin is to some extent contradicted by measurement of a 96 h EC_{50} of 0.26 ppm for adult Dungeness crabs and 0.25 ppm for late juveniles (Buchanan et al. 1970)."

The controversy over the use of Sevin in estuaries is not restricted to the state of Washington. In Oregon the issue has advanced to the courts. Until recently only two experimental treatments of Sevin in Oregon's estuaries have been approved by state agencies and these occurred prior to 1970. However in August 1982, the Oregon Fish and Wildlife Commission issued a spraying permit to oyster growers in Tillamook Bay, Oregon's third largest estuary. This permit was protested by the Audubon Society, the Oregon Shores Conservation Coalition, and the Oregon Environmental Council when they petitioned the Oregon Department of Fish and Wildlife, the Oregon Fish and Wildlife Commission, and three Tillamook Bay oyster growers before the Oregon Court of Appeals. In April 1984, the Court of Appeals upheld a previous ruling by the Land Use Board of Appeals (LUBA) that the spraying permit failed to comply with State Land Use Goal 16 that protects estuaries. The Court of Appeals agreed with LUBA that "the Commission could not protect the estuary or assume minimum adverse affects from the pesticide (Sevin) without determining what organisms live in the estuary and whether the pesticide would adversely affect those organisms."

Oyster culture has become important in British Columbia and has been introduced into Southeastern Alaska. As area growers try to maximize oyster yields, they may consider use of Sevin in other estuaries inhabited by mud or ghost shrimp. Our objectives in this paper are to: 1) review the toxic effects of Sevin; 2) list potential effects on some non-target species and make recommendations to help resolve the controversy; 3) increase knowledge of Sevin toxicity and; 4) reduce potentially harmful effects to Pacific Northwest estuaries.

Review of Toxic Effects of Sevin

Laboratory Studies

Sevin is an insecticide which acts as a toxic inhibitor of cholinesterase and thereby causes paralysis and death of insects (Casida 1963) and probably has a similar action in marine arthropods. There has been substantial laboratory work conducted on the toxicity of both Sevin and its first metabolite, 1-naphthol, to fish and invertebrates in seawater bioassays (Davis 1961; Stewart et

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[1] *A seven-page comment letter from Dale Evans Division Chief of NMFS to Duane Phinney Chief of Habitat Management Division WDF.*

al. 1967; Butler et al. 1968; Buchanan et al. 1970; Armstrong and Millemann 1974b, c). The target species (mud and ghost shrimp) are highly suceptible to Sevin while Pacific oysters are less so, however, many other non-target species also show sensitivity to Sevin (Stewart et al. 1967). A comparison of three major animal groups shows that marine crustaceans are 10 to 300 times more sensitive to Sevin in seawater than mollusks or fishes (Table 1).

The effects of Sevin on Dungeness crab have been extensively studied in the laboratory because of the economic importance and abundance of crab in northwest estuaries. Of the *C. magister* stages tested, the early larvae are the most sensitive to Sevin (Stewart et al. 1967; Buchanan et al. 1970). The 96-h EC_{50} (effective concentration that produces death or irreversible paralysis on 50% of the test animals) for larval first stage zoeae, late juveniles, and adults were 0.01, 0.25, and 0.26 mg/liter, respectively. Young juvenile crabs are 5 to 9 times more sensitive to Sevin than are older juveniles. The 24-h EC_{50s} for death of second-stage and ninth-stage juveniles were 0.076 and 0.35 - 0.70 mg/liter, respectively (Buchanan et al. 1970). Sublethal effects probably occur at much lower concentrations. In a continuous 25-day exposure of *C. magister* zoeae to Sevin, larval molting was delayed at concentrations as low as 0.0001 mg/liter.

Snow and Stewart (1963) observed many paralyzed cockle clams, *Clinocardium nuttali*, on oyster grounds in Tillamook Bay, Oregon, that had been experimentally treated with Sevin. A day later they found a large number of dead Dungeness crabs in the immediate area. In laboratory experiments Buchanan et al. (1970) found that adult crabs can be killed within 6 h after eating cockle clams previously exposed to Sevin. These results suggest that crabs could be killed either by direct contact with the insecticide or by feeding on paralyzed clams.

Field Observations

There has been little research on effects of Sevin on natural estuarine communities to ascertain overall impacts of spraying tideflats. The amount of Sevin in contact with treated ground, its dispersal, and its effects on organisms in the water column are not thoroughly reported in the literature. Most field studies only describe observations immediately following treatment. Snow and Stewart (1963) studied a field treatment of Sevin in Tillamook Bay in early March 1963. They observed mortality and distress of non-target species including sand shrimp *(Crangon* spp. *)*, juvenile sole (probably *Parophrys vetulus)*, cockle clams, Dungeness crab, hermit crab *(Pagurus* spp. *)*, annelid worms, amphipods, cottids, and blennies. Armstrong and Millemann (1974a) found dead shrimp, *Crangon nigricauda*, and English sole, *P. vetulus* as far as 15 meters in the direction of tidal recession from areas treated with Sevin. They also found that numbers of juvenile gaper clams, *Tresus capax*, and the bent-nosed clam, *Macoma nasuta*, were significantly reduced in plots treated with 2.3 and 4.6 kg (5 and 10 lbs)/acre of active Sevin. Despite more than two decades of use in Pacific estuaries, rigorous studies on the long-term effects of Sevin, including changes

Table 1. Acute toxicity of Sevin in seawater bioassays to adult (Ad) juvenile (Ju), or larval (Lv) stages of several species of estuarine animals.[a]

Species-life history stage	EC_{50}[b] (mg/liter) 24 h	48 h	96 h
Crustaceans			
Mud shrimp-Lv *(Upogebia pugettensis)*	0.03-0.16	0.03-0.14	--
Ghost shrimp-Ad *(Callianassa californiensis)*	0.13	--	--
Ghost shrimp-Lv	0.17-0.47	0.03-0.08	--
Dungeness crab-Ad *(Cancer magister)*	0.49	--	0.26
Dungeness crab-9th stage-Ju	0.35-0.70	--	--
Dungeness crab-2nd stage-Ju	0.076	0.057	--
Dungeness crab-Lv	0.08	0.005	0.01
Molluscs			
Bay mussel-Lv *(Mytilus edulis)*	--	1.4 -2.9	--
Pacific oyster-Lv *(Crassostrea gigas)*	--	1.5 -2.7	--
Cockle clam-Ju *(Clinocardium nuttalli)*	7.3	--	3.75
Fishes			
English sole-Ju *(Parophrys vetulus)*	3.2-5.0	--	--
Shiner perch-Ju *(Cymatogaster aggregata)*	3.8-4.0	--	--

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[a] *This table combines data from Stewart et al. 1967; Butler et al. 1968; and Buchanan et al. 1970. All experiments used test solutions that were prepared from the stock solutions by serial dilution using filtered, sterilized sea water adjusted to 25% salinity with distilled water.*

[b] *The EC_{50} values are the effective concentration that produces death or irreversible paralysis on 50% of the test animals.*

in the structure of benthic invertebrate communites following treatment, have not been completed on the initial, *Callianassa* -dominated community and that which replaces it.

Persistance and Toxicity in the Environment

The net effect of Sevin on natural estuarine communities may depend on water temperature and a complex interplay between decreasing longevity of the pesticide vs. increasing metabolic activity of organisms at higher temperatures. In Willapa Bay and Grays Harbor, spraying of Sevin on estuarine mud flats is allowed during June through August with the understanding that relatively high summer temperatures will rapidly hydrolyse Sevin in the water column and reduce the toxicity to non-target organisms (WDF and WDOE 1984). However, Buchanan et al. (1970) found that Sevin showed higher toxicity to adult crabs at 18° than at 11°C (Figure 1). The 24 h EC_{50}'s for death or paralysis at 18° and 11°C were 0.32 and 0.49 mg/liter, and the 96 h EC_{50}'s were 0.18 and 0.26 mg/liter, respectively. Stewart et al. (1967) found comparable results for burrowing shrimp. The mean 48 hour EC_{50}'s for death on mud shrimp larvae at 20° and 16°C were 0.04 and 0.09 mg/liter, respectively and the mean 48-h EC_{50}'s for death of ghost shrimp larvae at 20° and 17°C were 0.03 and 0.08 mg/liter, respectively. It is not certain that more rapid breakdown of Sevin at warm temperatures is more important than relative toxicity when selecting a period of treatment that will minimize toxicity to non-target species.

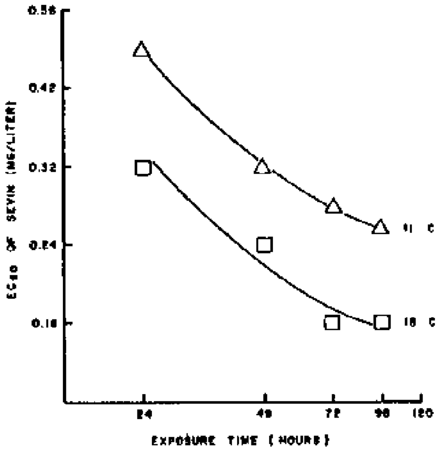

Figure 1. EC_{50}'s of Sevin for death or paralysis of adult female crabs at 11° and 18°C (from Buchanan et al. 1970).

Karinen et al. (1967) found that Sevin will rapidly hydrolyse in seawater to 1-naphthol which further undergoes degradation by the action of light to carbon dioxide and several unknown products. After spraying in estuaries, however, the pesticide would probably be rapidly absorbed into bottom sediments. Once Sevin is in the bottom mud its decomposition continues at a much slower rate than in water. In a field experiment on tideflats, Karinen et al. (1967) found Sevin concentrations of 0.1 to 0.2 ppm in estuarine mud 42 days after treatment with 4.6 kg/acre of active Sevin (Table 2). Unfortunately, they did not continue their studies after 42 days.

Table 2. Sevin and 1-naphthol concentrations in estuarine mud flats treated with Sevin at 4.6 kg/acre of active Sevin (from Karinen et al. 1967).

	Concentrations of Sevin			
	Top 2.5 cm of mud		5-8 cm level of mud	
Days after treatment	Total ppm [a]	Sevin only ppm	Total ppm [a]	Sevin only ppm
0	10.7	5.4	0.34	0.32
1	3.8	3.3	0.46	0.46
2	4.1	5.2	0.35	0.27
4	1.5	1.5	0.18	0.18
7	2.1	2.2	0.54	0.38
16	0.5	0.3	0.13	0.10
42	0.1	0.1	0.20	0.20

[a] *Includes Sevin and 1-naphthol calculated as total carbaryl.*

The persistance of Sevin in bottom sediments and its delayed toxicity to target and non-target estuarine animals has been only cursorily studied. Adverse impacts have been documented on polychaetes and bivalves (Armstrong and Millemann 1974 a, b), but effects are unknown for decapods, amphipods, and other epibenthic crustaceans.

Circumstantial evidence points toward Sevin's continued toxicity to crustaceans in mud. Sevin concentrations found in treated mud flats after 42 days(0.1 to 0.2 ppm) are certainly above the concentration (0.076 mg/liter) that will kill second-stage juvenile Dungeness crab when exposed to Sevin in seawater bioassays for 24 hours. Armstrong and Millemann (1974 a) found that Sevin continued to reduce ghost shrimp populations 11 months after application. The mean number of shrimp holes/m^2 were 161 in the control plot, and 32, and 25 in the treatment plots of 2.3 and 4.6 kg/acre of active Sevin, respectively. These reduced populations could stem from long-term toxicity of Sevin or failure of the ghost shrimp populations to re-colonize. Also, estuarine flats treated with Sevin to control burrowing shrimp only required retreatment every 3 or 4 years (ODFW 1982). It is reasonable to assume that Sevin may also have a long-term effect on recruitment of non-target invertebrates in treated tideflats.

Lamberton and Claeys (1970) found that Sevin and 1-naphthol degrade into a reddish-blue precipitate which may inhibit cholinestarase. This precipitate was two-thirds as toxic as 1-naphthol to bay mussel embryos. Lamberton and Claeys speculated that the persistence of the precipitate may explain an observed lack of recolonization for 18 months after treatment with Sevin. It may also explain why Sevin applied to freshwater mud is still toxic to insect larvae 3 months after application (Mulla 1960). Clearly, the long-term toxicity and persistence of Sevin under natural conditions needs to be more carefully studied.

Potential Effects on Some Non-Target Species

Among the controversial issues regarding the use of Sevin to enhance oyster production in estuaries is the potential for reduced production of other commercial and non-commercial species. This concern is a result of: 1) the toxicity of the insecticide to diverse animal groups; and 2) the importance of estuaries as fishing grounds, feeding grounds, and nursery areas for a variety of species (crabs, fishes, and birds). It is important to understand the role of the estuary in the life history and ecology of non-target species in order to evaluate potential affects of Sevin or establish guidelines that will minimize impacts.

Dungeness Crab

The possible role of estuaries as nurseries for *C. magister* and other crab species has been studied from California through Washington but until recently the data have been inconclusive (Cleaver 1949; Gotshall 1978; Collier 1983). Evidence presented by Stevens and Armstrong (1984) and Armstrong and Gunderson (this proceeding) for the Grays Harbor estuary strongly indicates that young-of-the-year (YOY = 0+), 1+ and 2+ crab make extensive use of the estuary from early spring to late fall. YOY enter estuaries as megalopae, settle and metamorphose in a variety of habitats. Older juveniles that apparently over-winter offshore to avoid extremely low bottom water temperatures in estuaries, also enter these systems in April-May to reside through the summer. In general, indications are that a significant portion of 0+ and older juvenile age classes use Grays Harbor estuary (and likely others as well) as a nursery area (Carrasco et al., this proceeding; Armstrong and Gunderson, this proceeding). Maximum numbers of crabs also occur in Tillamook Bay during the late spring and summer months (Forsberg et al. 1977).

Stevens and Armstrong (1984) concluded that the combined recruitment of Dungeness crab to Grays Harbor and Willapa Bay could support a substantial portion of the offshore commercial fishery. The apparent importance of the San Francisco estuarine complex to Dungeness crab was discussed by Tasto (1983) who also provides one of the few other estimates of population abundance. He concluded that from 38% to 83% of a 0+ year class might use the estuary, again underscoring the importance of such areas as nursery grounds.

Distribution and abundance of 0+ juveniles and observations of behavioral tendencies to burrow and hide, suggest that these small animals are dependent on benthic refuge to enhance survival in estuaries and offshore. Reilly (1983) reviewed literature regarding predation on Dungeness crab that shows substantial pressure is directed toward early life history stages which, in and offshore of San Francisco Bay, declines once animals exceed 30 mm carapace width.

From studies of long-term distribution and abundance of 0+ Dungeness crab it is apparent that early instars rely on epibenthic cover for maximum survival during the first summer and are not able to survive on open mud/sand substrate. In the subtidal areas of Grays Harbor, such refuge includes allochthonous sticks, leaves and grasses, but also clam and oyster shell, dislodged eelgrass and macroalgae (Stevens and Armstrong 1984; Armstrong and Gunderson, this proceeding). Whereas trawls on open sand substrate will often catch hundreds of 1+ and 2+ crab with little else in the net, large catches of 0+ juveniles are invariably associated with substantial amounts of epibenthic material. On the extensive intertidal flats of Grays Harbor, the highest long term densities of YOY are primarily in shell debris and secondarily in eelgrass (Armstrong and Gunderson, this proceedings). Areas where empty *Mya arenaria* shell accumulates provide excellent refuge for small first through sixth and seventh instar crab as evidenced by densities of 10 to over 100 per m^2. In north Grays Harbor, an abandoned oyster reef sampled through the summer of 1983, accounted for densities of juvenile crab comparable to densities in *Mya* shell habitat and higher than in eelgrass. At virtually no time in 2 years of intertidal sampling (1983, 1984) have YOY been found on open, unprotected substrate except for a few days following settlement; thereafter natural mortality is apparently 100% in such areas. These results suggest an interesting paradox regarding the potential effects of Sevin on crab populations. Spraying on open tideflats may cause immediate mortality of older juvenile crabs, particularly if treatment occurs during spring and summer. However, reduced predation or improved survival of YOY crab could result from improved cover offered by mature oyster communities.

Estuarine Fishes

The toxicity of Sevin to crustaceans also raises concern about the effects of spray programs on food chains supporting estuarine fishes. In most estuaries in the Pacific Northwest, crustaceans comprise the bulk of the diet of pelagic and demersal fishes (Bottom et al. 1984). In Tillamook Bay, Oregon, arthropod groups--decapods (including larvae of ghost or mud shrimp), copepods, barnacles, other crustaceans and insects--are among the primary food items for juvenile chinook salmon, starry flounder, English sole, surf smelt, and rockfish spp. (Forsberg et al. 1977).

Results of research on juvenile chinook salmon in estuaries provide a good illustration of potential effects of spraying on a commercially important fish species. In many estuaries juvenile chinook salmon rear for a few weeks to several months before migrating to sea (Reimers 1973; Healey 1980, 1982a). During a Tillamook Bay survey, juvenile chinook were found in the estuary between June and November with peak abundance during August and September (Forsberg et al. 1977). Scale patterns from adult salmon show that most chinook surviving to spawn in the Tillamook Bay drainage system are fish that reared in the estuary for some portion of their juvenile life history before they migrated to sea (Jay Nicholas, Oregon Department of fish and Wildlife, unpublished data). The significance of estuarine rearing on survival is probably related to the size of fish entering the ocean. Experiments with hatchery chinook (Bilton 1984) and coho (Johnson 1982) show a positive correlation between adult survival and juvenile size at release. Healey (1982b) showed evidence that small juvenile chum salmon had a higher mortality rate than large juveniles during a brief period of early sea life. These results emphasize the importance of adequate growth rates prior to seaward migration of juvenile salmon. Treatment of estuarine tideflats with Sevin could influence salmon production if spraying occurs when young salmon are dependent on estuarine crustaceans to sustain adequate growth rates for subsequent survival at sea.

Tube dwelling amphipods of the genus *Corophium* spp. are among the most important prey taxa for juvenile chinook salmon in Oregon's Sixes River (Reimers et al. 1979) Coquille River (Nicholas and Lorz 1984) and Columbia River (Bottom et al. 1984) estuaries and are frequently consumed by salmon in Tillamook Bay (Forsberg et al. 1977; Bottom and Forsberg 1978). There are two major broods of *Corophium* in Pacific Northwest estuaries (Reimers et al. 1979; Wilson 1983): one in the spring (April or May) and a second in late summer or early fall (August or September). Even if the toxic effects of Sevin are short lived, the treatment of tideflats during spring or summer could reduce amphipod production throughout most of the rearing cycle of chinook. The second brood of *Corophium* spp. is not produced or would not reach a size preferred by young salmon (>2.0 mm) until most chinook have migrated from the estuary.

Similar concerns could be raised regarding predator-prey relationships for other important fishes in the estuary. However, food chain effects are always among the most difficult to predict. Obviously, many factors will determine whether the effects of Sevin on prey or predator species are significant, such as the size of the area treated, the concentration and persistence of the insecticide, and a host of environmental factors we do not understand. However, we do know that the risk of negative effects on estuarine food chains increases during the spring and summer months, when the greatest number of species depend on the estuary. Figure 2 illustrates the pronounced seasonality in number of fish species and individuals in the Tillamook Bay estuary (Bottom and Forsberg 1978).

Conclusions and Recommendations

The controversy concerning treatment of estuaries with Sevin reflects the diversity of user groups that have an economic or recreational interests in these highly productive ecoystems. The controversy is intensified by the general lack of data documenting long term beneficial and detrimental effects in areas where spraying has been an accepted practice for more than 20 years. A poor data base leaves the oyster industry and state regulatory agencies vulnerable to

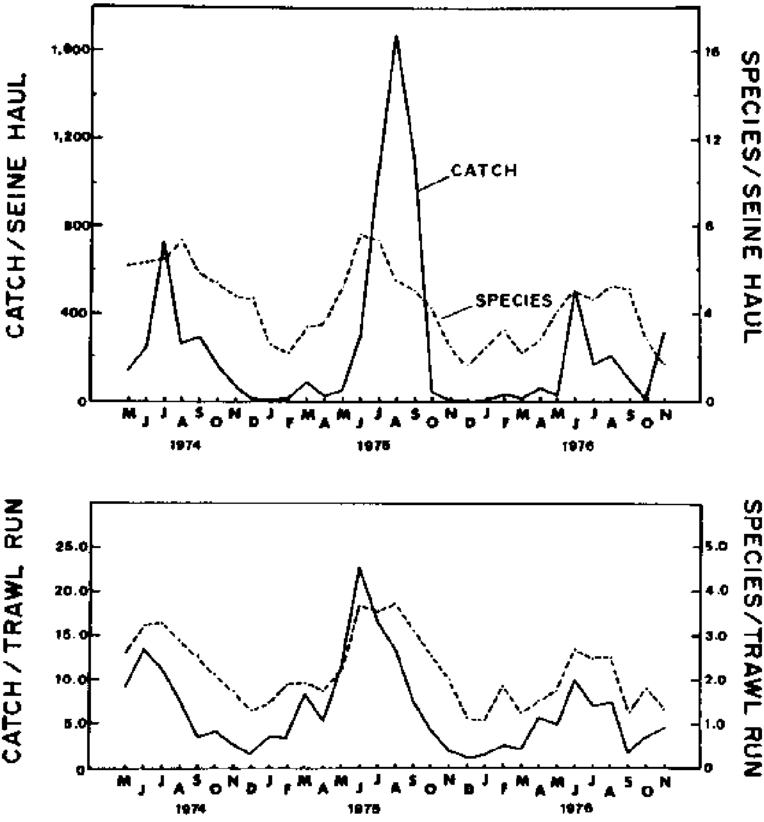

Figure 2. Number of individuals and species per seine and trawl effort for each month of a survey of Tillamook Bay (Bottom and Forsberg 1978).

complaints and lawsuits regarding unknown but potentially widespread environmental consequences. A variety of viewpoints (not all mutally exclusive) cloud the issue:

1. The oyster industry views burrowing shrimp as pests that curtail production and eliminate desirable culture grounds. Ghost shrimp can and do reach densities that deleteriously impact oyster culture (WDF 1970). Sevin kills burrowing shrimp and enables oyster culture on treated ground (WDF 1970; Snow and Stewart 1963).

2. Crab fishermen are concerned that the application of Sevin to estuaries hurts their industry by killing juvenile crab. Laboratory tests show comparable susceptibility between mud shrimp, ghost shrimp and Dungeness crab (Stewart et al. 1967; Buchanan et al. 1970) and dead Dungeness crabs have been observed near treatment sites (Snow and Stewart 1963; Armstrong and Millemann 1974a). On the other hand oyster cultch may increase Dungeness crab production by providing protective shell habitat. Crab use of and densities on *Callianassa* -dominated tideflats is low, but may be extremely high in areas of clam and oyster shell that afford refuge for small YOY instars (Stevens and Armstrong 1984; Armstrong and Gunderson, this proceeding). Short-term harm to crab populations may be offset by long-term habitat improvement.

3. In Oregon, bait fishermen are concerned that treatment of oyster grounds in Tillamook Bay will have a negative impact on other tideflats where they harvest burrowing shrimp. They cite mortalities of shrimp that were harvested in untreated areas soon after oyster grounds were sprayed as evidence for a negative impact on their industry.

4. State fisheries agencies are responsible for the management of three invertebrate fisheries seemingly at odds. They also have a general responsibility for the long-term persistence and health of estuarine communities.

5. Environmental groups claim that direct and indirect impacts of Sevin on estuaries are poorly studied but cite laboratory toxicity studies as evidence for potential harm to a variety of species. They are concerned that possible persistence of the pesticide in estuarine mud will have long-lasting effects. The data of Lamberton and Claeys (1970) and Mulla (1960) support this concern. Environmental groups are concerned about the possibility of widespread harm to estuarine food chains.

6. Oregon's courts and land use laws mandate that estuarine plans and activities shall protect such ecosystems, including its natural biological productivity, habitat, diversity, unique features, and water quality (Oregon Land Use Goal 16). The Oregon Court of Appeals and the Land Use Board of Appeals used this mandate to reject a spraying permit issued by the Oregon Fish and Wildlife Commission.

Counting mortalities immediately following spraying and laboratory toxicity studies have not provided sufficient understanding to adequately answer the questions raised by opponents of estuarine shrimp control programs. Decision makers need data that will allow them to weigh the ecological costs and benefits of converting natural tideflat communities to oyster communities. Among the types of research most needed are the following:

1. Comparisons of invertebrate community structure in untreated, recently treated, and established oyster habitats.

2. Test plots and experimental controls to follow successional stages in benthic communities following treatment with Sevin.

3. Live box studies and test plots to evaluate the persistence of Sevin in estuarine mud and its effects on recolonization.

4. Benthic invertebrate sampling programs to determine the extent of biological impacts, if any, beyond the immediate spray zone.

5. Studies to determine the effects of Sevin on production of adult crab resulting from initial mortality and long term establishment of mature oyster habitat.

6. The role of *Callianassa*, itself a dominate and productive tideflat species, in overall community ecology, materials transfer between trophic levels, and foodweb interactions.

7. Evaluation of the potential effects of Sevin on estuarine fishes and shore birds based on changes in prey communities following treatment of tideflats and subsequent development of mature oyster beds. The final anaysis of impact on fishes and shore birds will be subjective; nevertheless, additional data are needed to describe which food chains are most likely to be affected if the amount of oyster habitat is increased and natural tideflat habitat is decreased.

If spraying is to continue with or without additional research, the timing should be adjusted to minimize environmental risks. As an interim solution, we recommend a February or March application to reduce adverse impacts on non-target species. In Washington spraying is presently conducted in June through August during low tides. This coincides with the period of migration and increased estuarine populations of juvenile Dungeness crab (Forsberg et al. 1977; Stevens and Armstrong 1984; Armstrong and Gunderson, this proceedings) and peak abundance and diversity of fishes in Tillamook Bay (Bottom and Forsberg 1978). Application during June through August may have an indirect effect on juvenile chinook salmon and other estuarine fishes by reducing prey populations (Reimers et al., 1979; Bottom et al., 1984). Although the long days and daylight tides of the summer allows best control of application and monitoring, Sevin has been successfully applied in early March. Snow and Stewart (1963) treated a tideflat in early March and found 82 to 94% reduction in the shrimp population and a general firming of the substrate.

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List of Attendees

David Armstrong
University of Washington
School of Fisheries, WH-10
Seattle, WA 98195

William R. Bechtol
Alaska Dept. of Fish & Game
P.O. Box 234
Homer, AK 99603

David R. Bernard
Alaska Dept. of Fish & Game
333 Raspberry Road
Anchorage, AK 99502

Forrest Blau
Alaska Dept. of Fish & Game
P.O. Box 686
Kodiak, AK 99615

Jacky Booth
Pacific Biological Station
Nanaimo, B.C.
CANADA V9T 5K6

Louis W. Botsford
University of California
Dept. of Wildlife & Fisheries
Biology
Davis, CA 95616

Ken Carrasco
University of Washington
School of Fisheries, WH-10
Seattle, WA 98195

Jay C. Carroll
Tera Corporation
Marine Studies Group
P.O. Box 400
Avila Beach, CA 93424

John Clark
Alaska Dept. of Fish & Game
P.O. Box 3-2000
Juneau, AK 99802

Michael R. Dean
Alaska Dept. of Fish & Game
P.O. Box 3-2000
Juneau, AK 99807

Darrell Demory
Oregon Dept. of Fish & Wildlife
Marine Science Drive, Bldg. No. 3
Newport, OR 97365

Braxton Dew
National Marine Fisheries Service
P.O. Box 1638
Kodiak, AK 99615

Nancy Diamond
Humboldt State University
Arcata, CA 95521

Paul Dinnel
University of Washington
School of Fisheries
Seattle, WA 98195

Wayne Donaldson
Alaska Dept. of Fish & Game
P.O. Box 686
Kodiak, AK 99615

Dan Dunaway
Alaska Dept. of Fish & Game
P.O. Box 308
Dutch Harbor, AK 99692

Martin F. Eaton
Alaska Dept. of Fish and Game
P.O. Box 686
Kodiak, AK 99615

Doug Eggers
Alaska Dept. of Fish & Game
P.O. Box 3-2000
Juneau, AK 99802

Don H. Erickson
University of Alaska
11120 Glacier Highway
Juneau, AK 99801

Dan Foley
Icy Passage Fish
P.O. Box 57
Gustavus, AK 99826

Christine Forrest
University of Alaska
School of Fisheries & Science
Juneau, AK 99801

Lincoln Freese
National Marine Fisheries Service
P.O. Box 155
Auke Bay, AK 99821

David Hankin
Humboldt State University
Dept. of Fisheries
Arcata, CA 95521

Mike Hawkins
Alaska Dept. of Fish & Game
333 Raspberry Road
Anchorage, AK 99502

Ray Highsmith
University of Alaska
Institute of Marine Science
Seward Marine Center
Seward, AK 99664

John Hilsinger
Alaska Dept. of Fish & Game
P.O. Box 686
Kodiak, AK 99615

Thom Hooper
Washington Dept. of Fisheries
331 S.R. 12
Montesano, WA 98563

David Jackson
Alaska Dept. of Fish & Game
P.O. Box 686
Kodiak, AK 99615

Glen Jamieson
Fisheries and Oceans
Pacific Biological Station
Nanaimo, British Columbia
CANADA V9R 5K6

Merle Jefferson
Lummi Indian Fisheries
4085 Lummi Shale Road
Bellingham, WA 98225

Al Kimker
Alaska Dept. of Fish & Game
P.O. Box 669
Cordova, AK 99574

Timothy Koeneman
Alaska Dept. of Fish & Game
P.O. Box 667
Petersburg, AK 99833

Scott Kyle
Alaska Dept. of Fish & Game
P.O. Box 234
Homer, AK 99603

Peter Lawton
Dept. of Fisheries and Oceans
Biological Station
St. Andrews, New Brunswick,
CANADA EOG 2X0

Mike MacKay
Lummi Indian Fisheries
2526 Kwina Road
Bellingham, WA 98225

Bob Marshall
Alaska Dept. of Fish & Game
University of Alaska
Juneau, AK 99821

Scott L. Marshall
Alaska Dept. of Fish & Game
333 Raspberry Road
Anchorage, AK 99502

Ole Mathisen
University of Alaska
11120 Glacier Highway
Juneau, AK 99811

Charles P. Meacham
Alaska Dept. of Fish & Game
333 Raspberry Road
Anchorage, AK 99502

T. Anthony Mecklenburg
P.O. Box 307
Auke Bay, AK 99821

Peggy Merritt
Alaska Dept. of Fish and Game
P.O. Box 234
Homer, AK 99603

Theodore R. Meyers
University of Alaska
School of Fisheries & Science
11120 Glacier Highway
Juneau, AK 99801

Phil Mundy
University of Alaska
School of Fisheries & Science
11120 Glacier Highway
Juneau, AK 99801

Bill Nippes
Alaska Dept. of Fish & Game
P.O. Box 686
Kodiak, AK 99615

Charles O'Clair
National Marine Fisheries Service
Auke Bay Lab
P.O. Box 155
Auke Bay, AK 99821

Ken Parker
Alaska Dept. of Fish & Game
P.O. Box 3-2000
Juneau, AK 99801

A. J. Paul
University of Alaska
Seward Marine Center
P.O. Box 617
Seward, AK 99664

Ellen Pikitch
Oregon State University
Marine Science Center
Newport, OR 97365

Jerry Reeves
National Marine Fisheries Service
2725 Montlake Blvd., East
Seattle, WA 98112

Paul N. Reilly
California Dept. of Fish & Game
411 Burgess Drive
Menlo Park, CA 94025

Christopher Rogers
University of Washington
Rm M15, Fisheries Ctr., WH-10
Seattle, WA 98195

Dana Schmidt
Alaska Dept. of Fish & Game
2207 Spenard Road
Anchorage, AK 99503

Jonathan Shenker
Oregon State University
Marine Science Center
Newport, OR 97365

Jeffrey Shields
University of California
Dept. of Biological Science
Santa Barbara, CA 93106

Susan M. Shirley
University of Alaska
School of Fisheries & Science
11120 Glacier Highway
Juneau, AK 99801

Thomas C. Shirley
University of Alaska
School of Fisheries & Science
11120 Glacier Highway
Juneau, AK 99801

Al Spalinger
Alaska Dept. of Fish & Game
P.O. Box 686
Kodiak, AK 99615

Bradley Stevens
National Marine Fisheries Service
P.O. Box 1638
Kodiak, AK 99615

David M. Taylor
Fisheries & Oceans, Canada
P.O. Box 5667
St. John's, Newfoundland
CANADA A1C 5X1

Gregory J. Thomason
Alaska Dept. of Fish & Game
230 S. Franklin, #301
Juneau, AK 99801

Ronald W. Warner
California Dept. of Fish & Game
619 2nd St.
Eureka, CA 95501