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JUVENILE SOCKEYE SALMON (ONCORHYNCHUS NERKA) PREDATION ON BERING SEA RED KING CRAB (PARALITHODES CAMTSCHATICUS) LARVAE AS A CAUSE OF RECRUITMENT VARIATION.

by

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ABSTRACT

Eastern Bering Sea red king crab underwent a dramatic decline in abundance in the early 1980s, and has remained at low levels of abundance. The so called "red king crab crash" was largely predicted by researchers as being due to the passing of a strong year-class. However, other factors such as increased predation, handling mortality, and disease may have accelerated the decline. The catch history and survey results show two peaks in red king crab abundance, one in the 1960s and another in the 1970s. Both of these are coincident with minimum levels of sockeye salmon abundance. Sockeye salmon exhibited a regular 4 year cycle in abundance until the late 1970s when they greatly increased in abundance and have remained at high levels with reduced interannual variation in abundance. The 1980s increase in sockeye salmon abundance correlates with the observed low recruitment of red king crab. These correlations lead us to hypothesize that predation by juvenile sockeye salmon migrating from natal rivers along the eastern Bering Sea coast to the North Pacific Ocean as a potential factor influencing eastern Bering Sea red king crab larval survival. The sockeye migration route transects the main concentration of red king crab zoea in the southeastern Bering Sea. Little direct observation of predation by juvenile sockeye salmon on red king crab larvae are available for the eastern Bering Sea. Sockeye predation on king crab larvae was simulated using observed predation rates from other areas and a temperature modified trophodynamic model to investigate the relationship between juvenile sockeye predation and red king crab abundance. The results of the model show that sockeye salmon predation can significantly reduce zoea abundance when salmon abundance is high and zoea abundance is low.

Introduction

Red king crab (Paralithodes camtschaticus) and sockeye salmon (Oncorhychus nerka) are two commercially important species in the fisheries of Alaska. In 1992, crab accounted for 21%, and salmon 33 % of the total ex-vessel value of Alaska fisheries ($1.6 million) (Kinoshita et al. 1993). Eastern Bering Sea king crab were abundant until the early 1980s when they declined sharply(Figure 1). A decline had been predicted (Reeves and Marasco 1980), but its precipitous nature was due in part to an unanticipated high mortality among recruiting crabs. The decline in prerecruit crabs (<age 8) was greater than anticipated, and several causes of mortality have been postulated, but data are insufficient to determine causes of excess mortality.

Coincident with the decline in king crab were increases in the abundance of flatfish, primarily yellowfin sole (Pleuronectes asper) and Pacific cod (Gadus macrocephalus)(Figure 1). Both species have been found to consume king crab. Haflinger and McRoy(1983) and Livingston et al. (1993) reported yellowfin sole predation on larval and juvenile king crab. Shimada and June (1982) and Livingston (1989) found Pacific cod consuming king crab in the Bering Sea, but most were prerecruits or adults, and predation was greatest on molting individuals. Fukahara (1985) reviewed the data on predation along with abundance data and concluded that while yellowfin sole predation could have some effect on the king crab population, there did not appear to be a very strong relationship between king crab and yellowfin sole abundance. However, a significant correlation was recently found between yellowfin sole biomass and red king crab recruitment for the 1970 to 1993 period (Livingston 1994). Also, Fukuhara (1985) found a relationship between the increase in Pacific cod abundance and the declines in king crab abundance, especially females.

Questions associated with the abundance of king crab have been focused on the population decline of the early 1980s, however, an alternative question is the origin of the high level of crab abundance that existed prior to the crash (Figure 1). King crab abundance increased sharply in the mid to late 1970s. Prior to this, trawl surveys indicate increases in the late 1950s and 1960s. The question is if the increses in king crab abundance were due relaxation of predation pressure, and the observed lack of large year-classes since the 1970s is a result of increased predation mortality.

Both Pacific cod and yellowfin sole appear to have been less abundant when king crab abundance was high. Yellowfin sole estimates are available since the late 1950s from catch-age models, but only available for cod since the mid- 1970s, although indications are that abundance was not high prior to the 1980s (Bakkala 1993). While these species could exert some predatory control, we believe that juvenile sockeye salmon may have a stronger influence on red king crab abundance.

Bristol Bay sockeye salmon was at an extreme low level of abundance at the time the strong year-classes of king crab originated. Runs of returning sockeye salmon fluctuate widely from year to year, ranging from a low of 2 million in 1974 to 58 million in 1994 (Don Rogers, FRI, Univ. Wash., Pers. Comm)(Figure 2). Since 1949 the average return of sockeye salmon to Bristol Bay has been about 25 million fish. Prior to the 1980s Bristol Bay sockeye exhibited a distinct abundance cycle and average run size was 16 million fish; in the early 1980s run size increased rapidly to an average of about 39 million and cycles diminished.

It is difficult to accurately correlate red king crab year-class strength with sockeye salmon smolt production because of a lack of consistency in measuring abundance. Abundance trends for legal male red king crab extend back to 1957 with a break in the series from 1961 to 1965 (Hayes 1983). Year-class strength of recruits (age 8) has been measured in surveys since 1971. For sockeye salmon, adult returns are a reflection of juvenile survival (Crawford et al. 1992). However, comparison of sockeye salmon abundance trends with red king crab trends (with the appropriate lags, 4 years for salmon, and 8 years for king crab) indicate a possible inverse relationship (Figure 3). Particularly noteworthy is the low king crab recruitment in conjunction with continued high levels of sockeye salmon abundance.

The apparent inverse correlation between king crab and sockeye salmon abundance we hypothesize to be a result of predation on king crab zoea by juvenile salmon migrating through king crab larval aggragations. To develop the hypothesis we examine juvenile salmon bioenergetics and availability of king crab zoea as prey.

Sockeye salmon smolt migration

Five species of Alaskan salmon occur in the Bristol Bay region (sockeye, pink, chum, coho, and chinook), with sockeye comprising an average of 89 percent of the total catch. About 90 percent of the average total run is associated with five river systems (Wood, Kvichak-Naknek, Egegik, Ugashik, and Togiak) which empty into inner Bristol Bay (Rogers, 1977)(Figure 4).

The escapement of juvenile sockeye salmon into Bristol Bay is estimated to average 276 million smolt (Bax 1985). Production varies by river system with the following production from the major rivers:

	River System					
Run Size	Kvichak	Naknek**	Ugashik	Wood	Egegik	Total
Average	130.0	9.0	12.0	65.0	60.0	276.0
Minimum	0.1	1.0	1.0	21.0	17.0	40.1
Maximum	415.0	25.0	215.0	114.0	125.0	894.0

** No estimates since 1986.

The timing of outmigration of the smolts varies between rivers, between age classes, and between years. Egegik and Ugashik smolts enter Bristol Bay first, followed by those from the Naknek-Kvichak, and then those from the Wood River. Smolts migrate over a shorter time period from the Ugashik or Kvichak rivers than from the Naknek or Wood river systems because there are fewer sockeye rearing lakes in the former systems. Sockeye smolt begin their seaward outmigration from the spawning lakes about the middle of May, with dates varying according to temperature, ice, and climatic conditions (Straty, 1974; Straty and Jaenicke, 1980).

Smolts reach Bristol Bay several days after leaving the lake outlets, and are present across the width of the inner Bay in the early and late summer. They are most abundant on the southeast side of the inner and outer Bay with abundance declining with distance from this shore; no juveniles were found further than 56 km offshore in the outer Bay and most were within 40 km perhaps as far as Unimak Island (Figure 4) (Bax 1985).

Juvenile sockeye salmon school as they passed through Bristol Bay and are found most abundant in the top 3 m of the water column at daytime with perhaps a few as deep as 6 m where they feed on zooplankton and smaller fishes (Bax 1985).

The migratory route of outgoing smolt is apparently determined by salinity gradient and water temperature (Straty and Jaenicke, 1980). at least during the early stages. It is thought that juveniles remain close to shore on their outmigration principally in response to warmer water temperatures inshore (Bax 1985).

The smolt's activity level, and thus the speed of migration, appears to be directly related to water temperature (Straty and Jaenicke, 1980). Higher temperatures result in increased activity levels, more rapid migration, and faster growth. Increased growth rates are thought to be related both to elevated feeding activity resulting from higher temperatures and to earlier arrival into the zooplankton-rich waters offshore of the Alaska Peninsula (Straty and Jaenicke, 1980).

The absolute migration rate in centimeters per sec increases with size of fish and the average relative migration rate in body lengths per second is 0.9 (S.E. 0.4). Applying a migration rate of 0.9 Lengths/sec to the fish emigrating from the lake outlets (data from Rogers 1977), suggests that 50% of the smolts from the Ugashik, Naknek, Kvichak, and Nushigak rivers would be past Port Heiden (i.e., out of the inner Bay) by July 1, 19, 27, and August 13, respectively.

The relationship between the absolute migration rate and body length indicates that the rivers producing larger smolts would have juveniles with an overall higher absolute migration rate. Similarly, the larger age 2 smolts would migrate faster than the smaller age 1 smolts. Straty suggests that in a cold year migration rate could be decreased. There is a significant positive relationship between the 60 min sustained swimming speed for smolts between 1 and 55 grams (Brett and Glass 1973). Bax(1985) estimated that migration rates of the same size fish could have been 10% slower in 1971 than 1969 due to the colder water temperatures (6.4 vs.9.3) in Bristol Bay.

King Crab larval biology and distribution

King crab in the southeastern Bering Sea hatch from early April to June with the peak in mid-May (Weber, 1967; Haynes 1974; Armstrong, 1983). King crab metamorphose through four zoea stages and one megalops stage. The first molting (Zoea I to Zoea II) occurs 21 days after hatching and the interval between molts for the second through last zoeal stages and from Zoea IV to megalops was 14-16 days.

Subsequent experiments and observations have shown that the molting schedule is dependent upon certain environmental variables (Fukuhara 1985). Within this range of optimum temperature, 5-10 C, larval growth rate increased with higher temperature. Kurata(1961) calculated that about 465 degree-days (days X C^0) were required to develop from hatching through megalops stage, 291 degree-days of which were required to complete the four zoeal stages.

Information on the timing of development is presented by Armstrong et al. (1983). Stage I zoea occur from before April 18 into the first three weeks of June. Stage II larvae begin to occur in April, maximize in abundance in May-June and disappear after early July. Stage III zoea were encountered from about May 11 through August 10. Last stage zoea larvae occurred in samples collected from the June 1-21 period through August 10. Similarly, megalops larvae were first taken in the first three weeks of June and their abundance increased through the August 1-10 sampling period.

Very little reliable information is available regarding mortality in larval king crab. Marukawa (1933) concluded that larval mortality was extremely high from observations of larvae reared in laboratory experiments and from zoea field collections. Zoea I were found to have poorest survival (6.5%). Eighty percent of the surviving Zoea II lived to be Zoea III and 86% of these survived to the last zoea stage. Survival from the last zoea to the megalops stage was also about 86%. From these observations, about 3.58% of the eggs hatched survive to become megalopae. This is a mortality of 96.4% up to the megalops stage all but about 3% of which occurs during the first zoeal stage. On the basis of estimates of the quantity of zoea larvae, fecundity, observed larval mortality and estimated postmegalops survival rates, Marukawa estimated that only 14 crab out of 1,000,000 hatches survive to the desired commercial size of 160 mm carapace width.

Distribution and abundance data on the zoeal stages is quantitative to the extent of ascertaining areas and timing of hatching from differences in relative abundance of the larval stages Takeuchi (1962), Korolev (1964), Rodin (1970), Haynes (1974), Armstrong et al.(1983) , and Fukahara (1985). Rodin (1970) and Haynes (1974) have shown that the greatest abundance of first stage zoea also occurs from Unimak Pass to Port Moller, particularly in the latter area. Annual variation in distribution and abundance are suggested, but are difficult to quantify due to the small number of samples relative to the timespace dimensions of larval distribution Armstrong et al. (1983).

Haynes (1974) observed a progression in the abundance of king crab larvae in southeastern Bering Sea from the Black Hill-Port Moller area in May northeastwardly to the area off Ugashik Bay at the head of Bristol Bay in mid-July when no more larvae were taken (Figure 5). This eastward shift in areas of abundance was accompanied by a progression in larval stages. First stage zoea decreased in abundance and conversely, last stage zoea increased in abundance as the season progressed (Figure 6). Larvae were most abundant (more than 1000/square meter of sea surface) near Unimak Pass and Port Moller and least abundant (less than 10/square meter of sea surface) in the more central and western sampling stations,

Armstrong et al. (1983) analyzed over 1000 zooplankton samples taken in southeastern Bering Sea in 1976 through 1981. Red king crab larvae occurred from off western Unimak Island eastward to about Port Heiden, with the highest densities from western Unimak Island to Port Moller where concentrations were typically 5,000-50,000 larvae/100 m^2. Maximum densities were 67,000 larvae/100 m^2 off Otter Pt., Unimak Island in one sample in 1977, and 114,000 larvae/100 m^2 in one sample taken in 1980 off Port Moller.

Sockeye salmon bioenergetics and potential king crab consumption

It is clear that juvenile sockeye salmon and king crab zoea co-occur along the Alaska Peninsula. Also inverse abundance trends are suggestive of some interaction. There is some evidence that juvenile salmon consume king crab larvae in the Bering Sea. Straty (1974) investigated juvenile sockeye food habits in the Bering Sea in 1969-1972 and found the major prey items to be euphausiids, copepods, cladocerans, and sandlance; however, decapod larvae were also found to occur in the diet. Healey (1980) found juvenile salmon in Georgia Strait, British Columbia, Canada consuming significant numbers of crab zoea and megalops.

To examine if sockeye salmon juvenile predation could influence king crab abundance a model was developed using the bioenergetic parameters for sockeye salmon of Beauchamp et al. (1989) in the bioenergetic equations of Hewett and Johnson (1992). Total daily food intake ($gg^{-1}d^{-1}$) for sockeye salmon was obtained using the above parameters and equations along with the estimates of Bristol Bay surface temperature and sockeye juvenile size. A juvenile sockeye weight of 10 grams was used, the average size of outmigrating smolts. A crab zoea stage 2-3 average weight of 0.037 g was computed using dry weights reported by Armstrong et al. (1983) converted to wet weight by a factor of 0.8.

Estimates were made with water temperatures of 5, 8, and 10 °C which are the range of tempertures in which juveniles were found (Straty 1974). At each temperature average, minimum, and maximum levels of sockeye juveniles were input against the same estimates for crab zoea. Zoea estimates came from 1971-1992 estimates of total red king crab egg production and Marukawa's (1933) estimates of stage survival rates.

In the model zoea were estimated to comprise 1% of the diet and were available to the juvenile sockeye salmon for 30 days.

The results of the bioenergetic model indicate that smolt induced mortality can be large at high levels of juvenile abundance and low levels of zoea crab (Table 1, Figure 7). At high and average levels of sockeye and average zoea abundance the impact is not great at a 1% consumption rate. However, increasing the consumption rate a few percent at this level could reduce survival and subsequent recruitment. Temperature does not influence consumption greatly in the range examined, but may impact actual consumption by altering migration and developmental rates, and thus encounter rates.

Table 1. Fraction of king crab zoea consumed by sockeye salmon juveniles in Bristol Bay at 3 different levels of zoea abundance, salmon juvenile abundance, and surface temperature with zoea constituting 1% of the diet.

			Salmon in millions		
Temperature C	Stage 2-3 Zoea in millions		40 Minimum	276 Average	894 Maximum
5	2,142	Minimum	0.07	0.45	1.46
5	24,489	Average	0.01	0.04	0.13
5	97,518	Maximum	0.00	0.01	0.03
8	2,142		0.08	0.53	1.72
8	24,489		0.01	0.05	0.15
8	97,518		0.00	0.01	0.04
10	2,142		0.08	0.57	1.85
10	24,489		0.01	0.05	0.16
10	97,518		0.00	0.01	0.04

Consumption greater than 1 indicates complete grazing of zoea.

Discussion-Conclusions

The model results suggest that juvenile sockeye salmon predation on king crab larvae can influence recruitment. However, insufficient data exist on the proportion of king crab larvae in the diet or the actual time span of spacial overlap. The dynamics are complex and further work needs to be done before conclusions are drawn. We plan to refine the analysis and increase realism using dynamic temporal and spatial modelling.

Some of the important factors to investigate are variability in zoea distribution resulting from variation in time of egg release and larval development. Both influenced by temperature and variation in drift due to wind-variability. The size and age of outmigrating smolts are variable both due to growth and proportion of age 1 and 2 smolts from a spawning. Also the amount of salmon contributed by each river system is variable. All of these factors can affect the interaction between the species.

The tendency has been to overlook juvenile salmon predation, but the large number transiting the Bering Sea each year require their consideration in Bering Sea ecosystem dynamics. We have demonstated the potential for salmon to reduce king crab abundance through predation, and should be considered as another possible source of mortality along with Pacific cod and yellowfin sole. An additional interesting aspect of salmon-king crab interaction is the bioeconomics of balancing population and yield between two high value species, if in fact juvenile salmon predation controls king crab recruitment.

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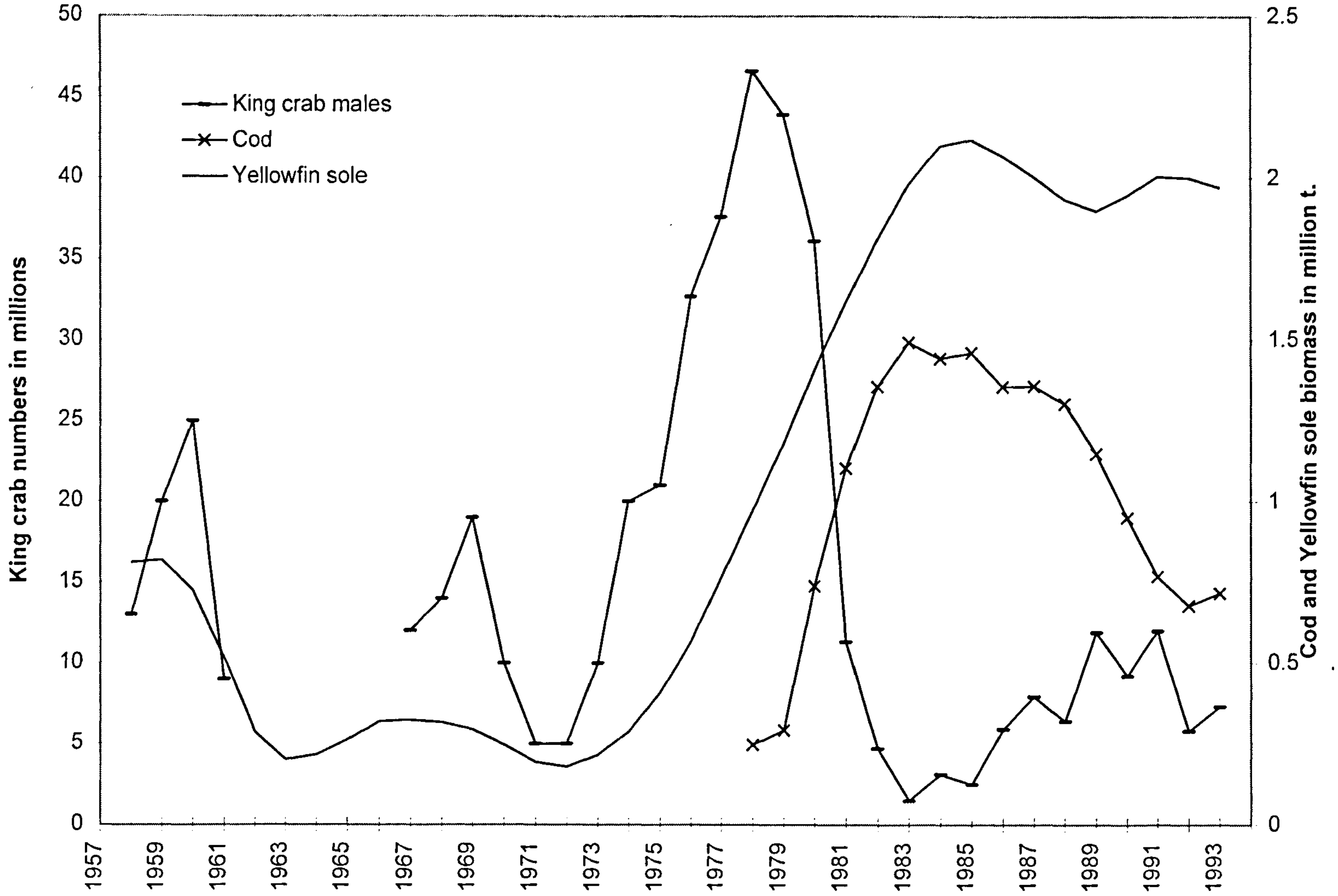

Figure 1. Abundance trends for eastern Bering Sea king crab, cod, and yellowfin sole by year.

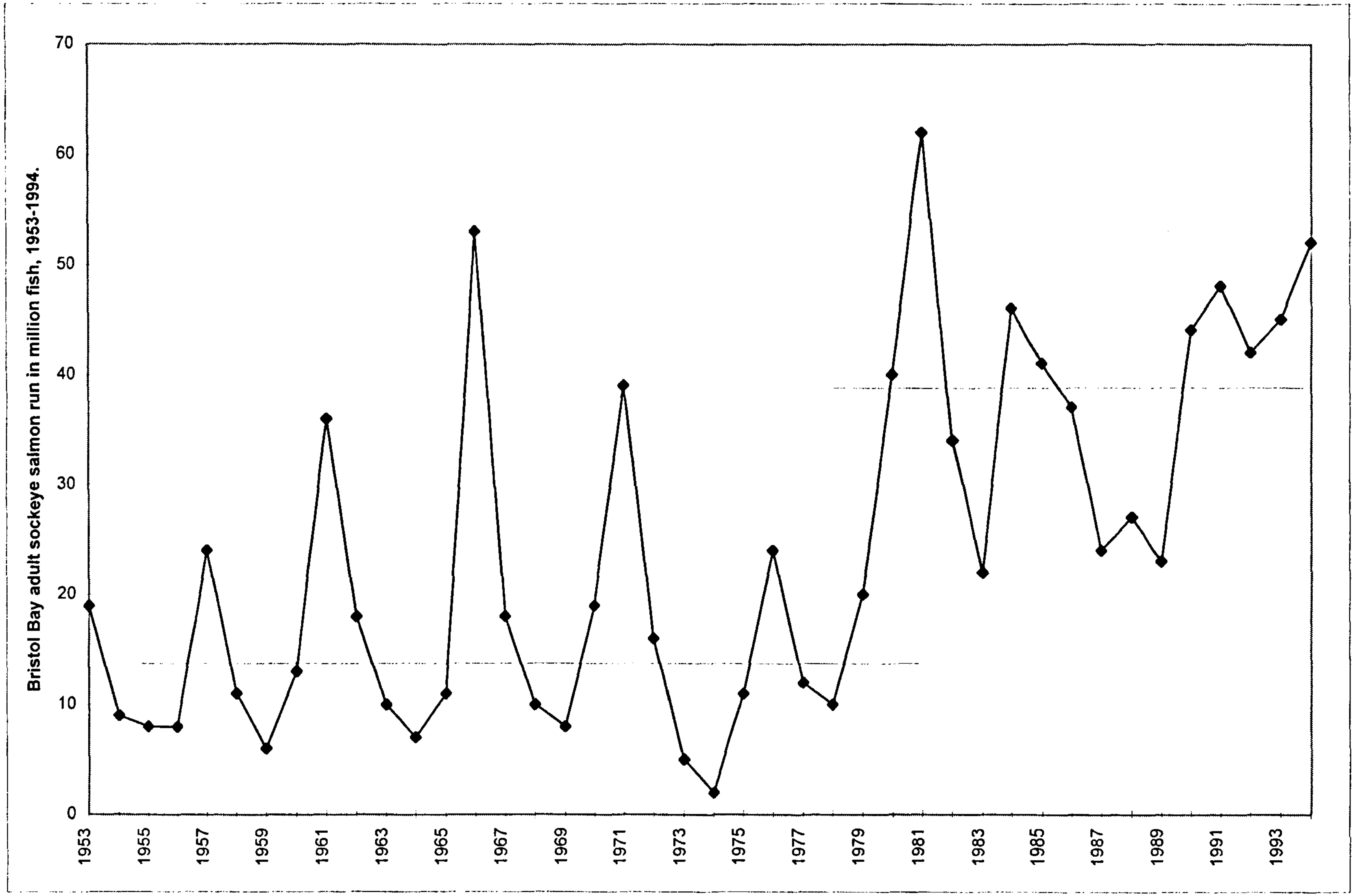

Figure 2. Run size of Bristol Bay adult sockeye salmon in million fish, 1953-1994. Horizonal lines denote means, 1953-79 and 1980-1994.

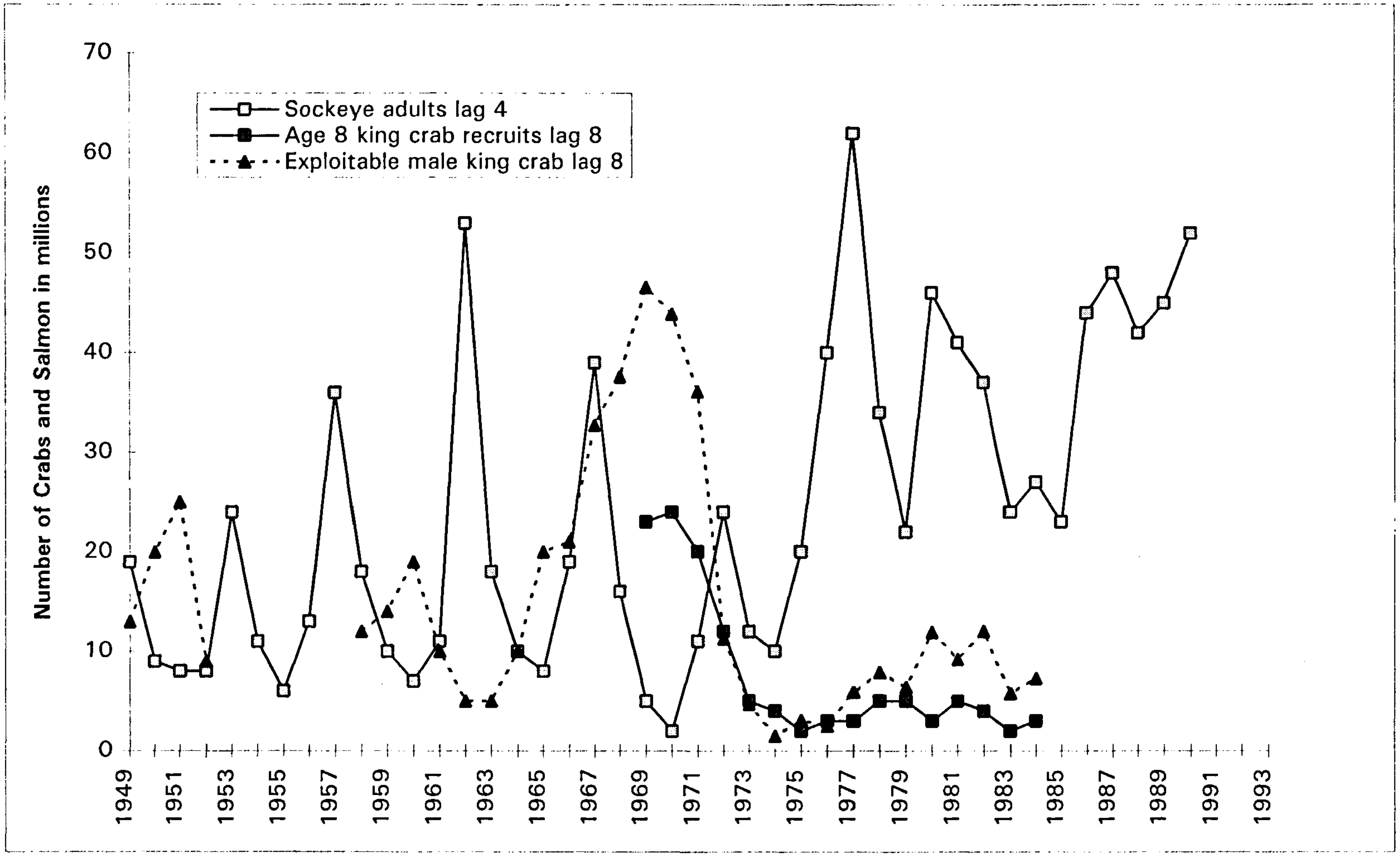

Figure 3. Comparison of adult sockeye salmon abundance lagged 4 years to exploitable male red king crab abundance and age 8 king crab abundance, both lagged 8 years.

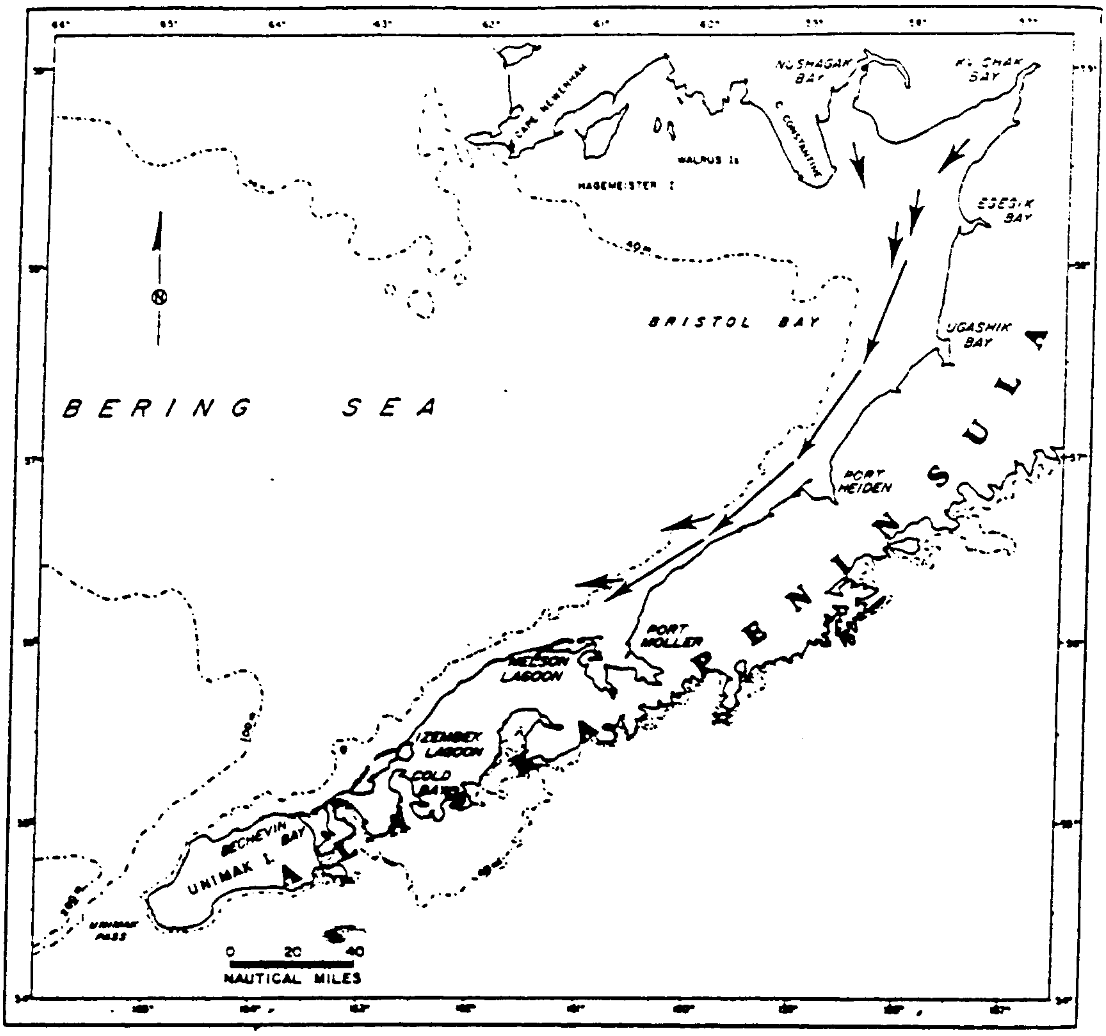

Figure 4. Juvenile sockeye salmon outmigration route through Bristol Bay from natal streams

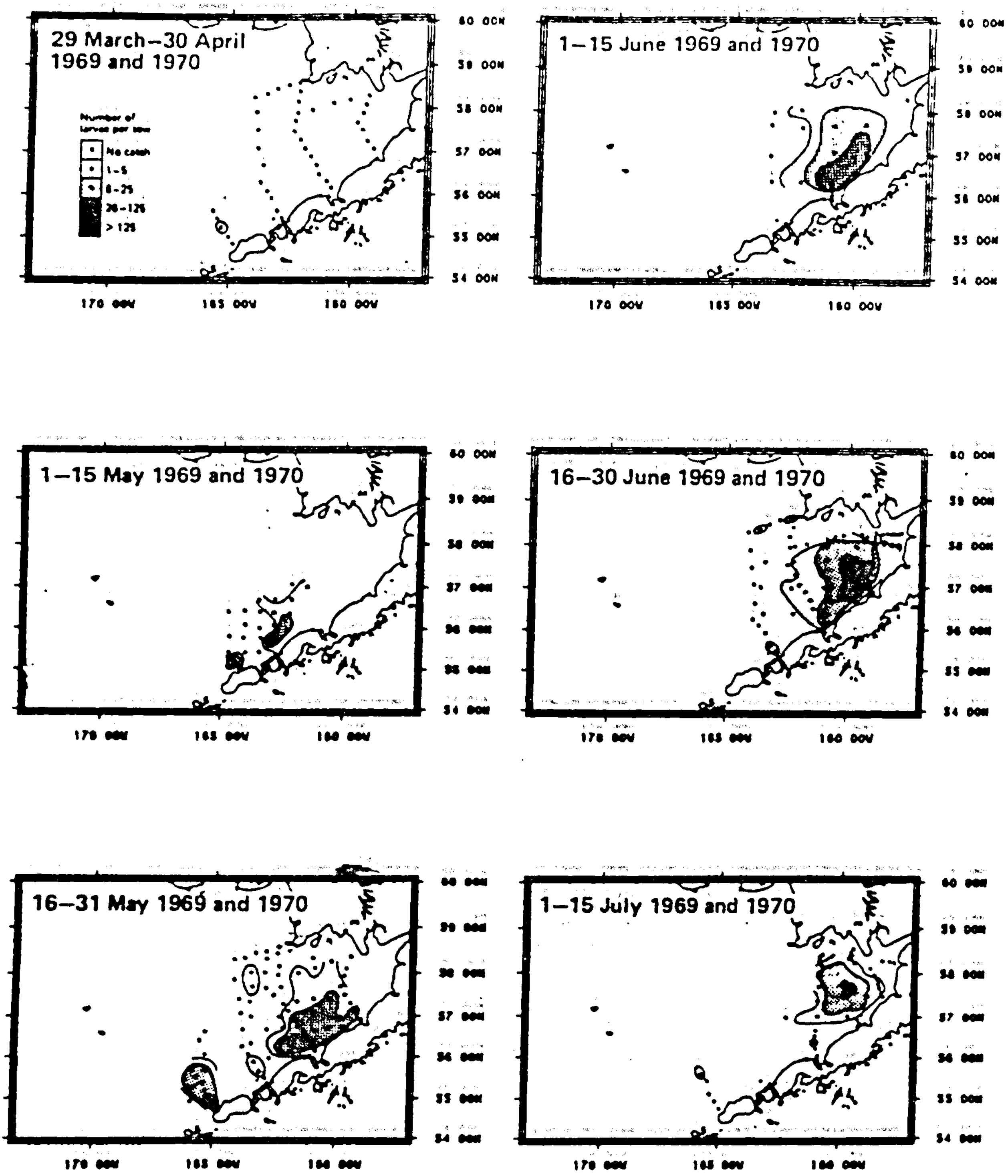

Figure 5. Distribution of red king crab zoea in the eastern Bering Sea in 1969 and 1970. (Figures from Haynes 1974 redrawn in Fukahara 1985)

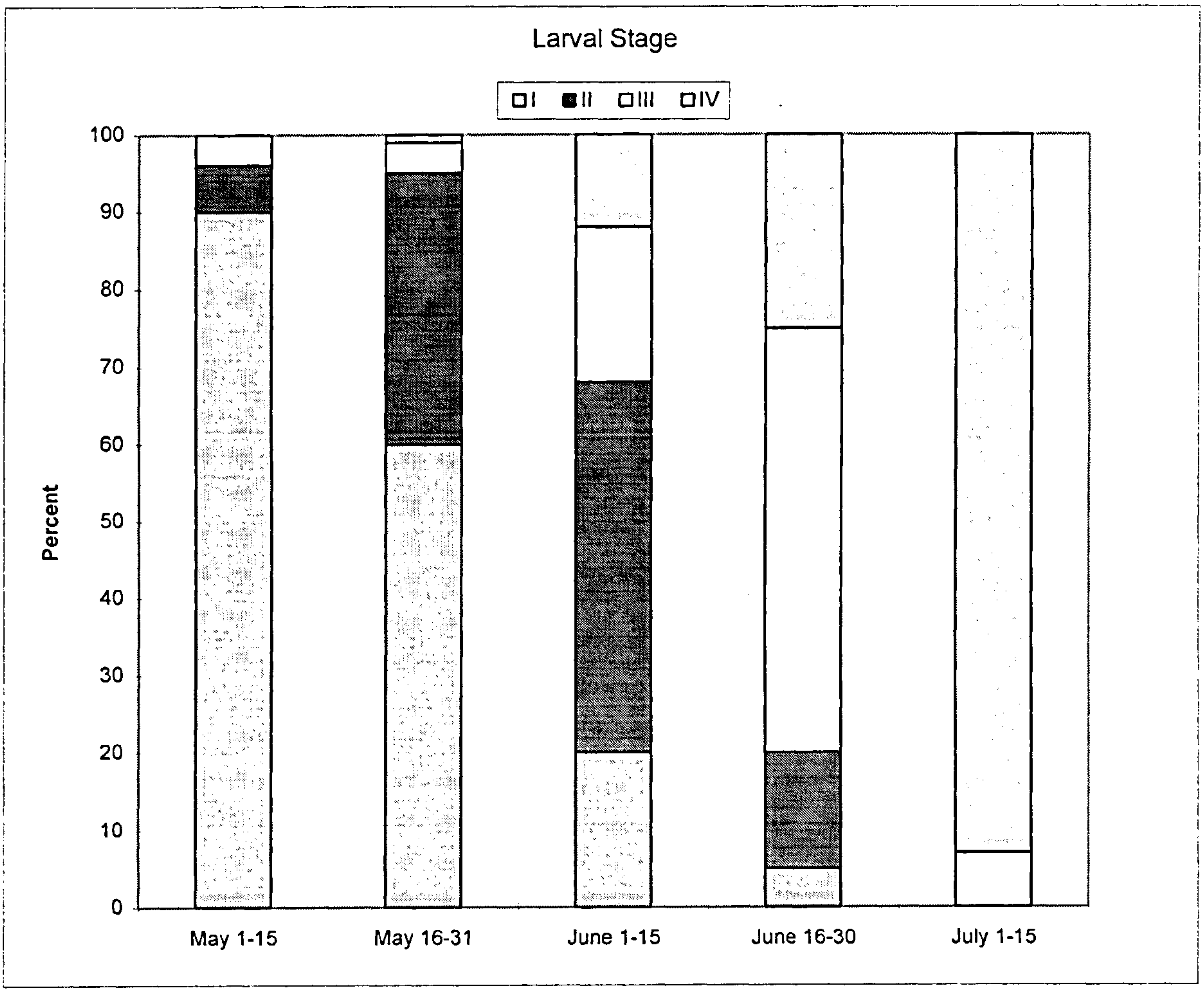

Figure 6. Percentages of king crab zoeal stages in the eastern Bering Sea, May-July 1969-70.

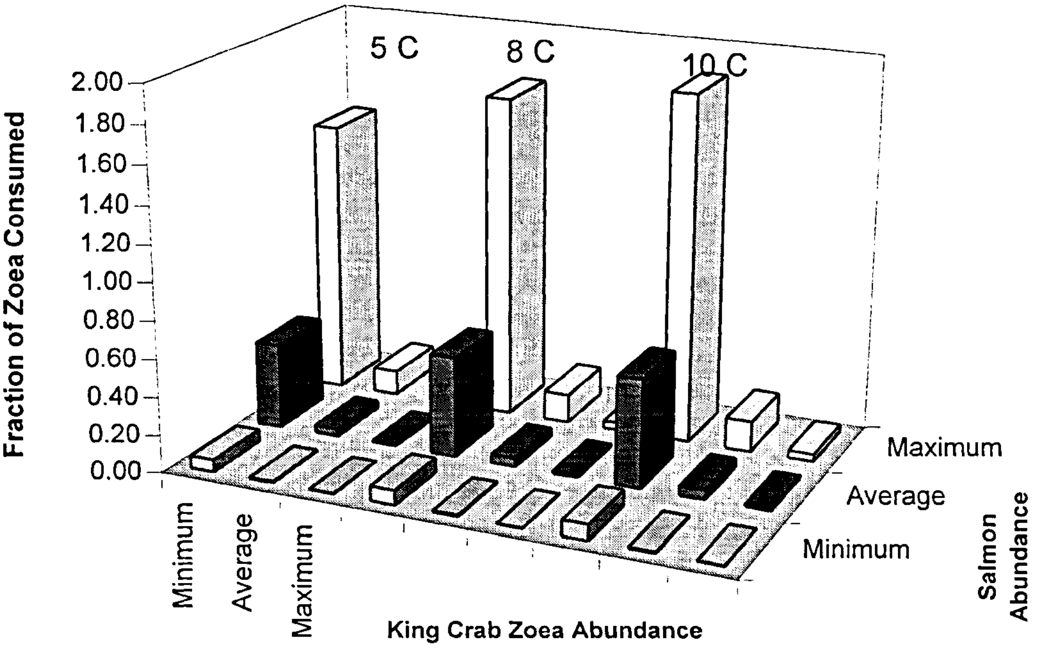

Figure 7. Estimated relative predation of king crab zoea by sockeye salmon smolts at 3 different levels of zoea and sockeye abundance and 3 temperture levels.