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PROJECTED EFFECTS OF CO₂-INDUCED CLIMATE CHANGE
ON THE PINK SHRIMP (Pandalus borealis) FISHERY
IN THE EASTERN BERING SEA AND GULF OF ALASKA

Prepared by:

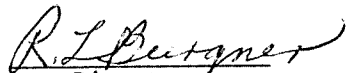
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INTRODUCTION

Pandalus borealis is a Pandalid shrimp with a circumpolar distribution. Ekman (1953) described it as a discontinuous circum-boreal species (Fig.1). Although adults have been observed north of the Bering Strait and off Franz Josef Land at 82°N (Allen 1959), large populations generally occur farther south. The species has been found at depths of 20 to 900 m although fishable concentrations typically range from depths of 54 - 400 m. In the Atlantic, fisheries occur in the Gulf of Maine, along the west coast of Greenland, in the North Sea, in the Norwegian Sea, and near Iceland (Balsiger 1981). On the west coast of the U.S., P. borealis ranges from the Bering Sea to the Columbia River (Fox 1972b). In waters off British Columbia and Washington the range of P. borealis overlaps with P. jordani (Jones 1971), which is the target species for shrimp fisheries off Washington, Oregon, and California (Balsiger 1981). In the Gulf of Alaska and in the Bering Sea, at least 85% of the catch is P. borealis (North Pacific Fisheries Management Council [NPFMC] 1976).

This report considers the populations of P. borealis in the Gulf of Alaska and Bering Sea. We provide a description of the fisheries and the life cycle of the species with an emphasis on those stages of the life cycle that may be sensitive to environmental changes. The final section presents our conclusions and speculations regarding the potential effects of climate change on shrimp populations in the Bering Sea and Gulf of Alaska.

FISHERIES

Bering Sea

In 1960 commercially valuable concentrations of P. borealis were located near the Pribilof Islands and a fishery was started with one Japanese mothership and 25 catcher boats. Total catch from 1960 through 1977 for the Bering Sea and other regions in the northeast Pacific is shown in Fig. 2. Catches increased rapidly to a maximum of 34,775 metric tons in 1963 and declined equally rapidly with only 3,230 metric tons caught in 1966 (Chitwood 1969). In 1963 the USSR also fished near the Pribilof Islands, utilizing 6 trawlers for one month. By 1964 the USSR had shifted its effort to the Gulf of Alaska (National Marine Fisheries Service [NMFS] 1976, Chitwood 1969). Since 1967 no significant fishery for P. borealis has taken place in the eastern Bering Sea. In 1976 three Japanese vessels were observed fishing for shrimp near the Pribilof Islands. When boarded by U.S. fisheries officers, the skippers reported catches of 10 metric tons per day (NMFS 1976). Since 1977 other nations have been prohibited from taking any shrimp in U.S. waters in the Bering Sea, and shrimp populations are too small for U.S. fishermen to profitably travel to the eastern Bering Sea to harvest shrimp.

There is little information about the stocks of shrimp in the western Bering Sea. Following the decline in stocks of P. borealis on the Pribilof grounds, Japanese trawlers began harvesting north of 60°N and further west (Fig. 1). On these grounds a maximum catch of just over 10,000 metric tons was obtained in the first year, 1968. Catches declined each subsequent year (Pruter 1973, Kurada 1981). In the absence of a fishery, no estimates of current levels of abundance or maximum sustainable yield are available.

Gulf of Alaska

Three species of pandalid shrimp are important to the domestic fishery in the Gulf of Alaska: Pandalus borealis (pink shrimp) accounts for about 85% of the commercial catch and Pandalus gonuirus is second in importance; the third most important species, Pandalopsis dispar, is sometimes the target of trawlers because of its large size (NMFS 1976, Balsiger 1981). Since P. borealis dominates the shrimp catch in Alaskan waters, statistics referring collectively to "shrimp" generally reflect the same trends as would those for P. borealis alone.

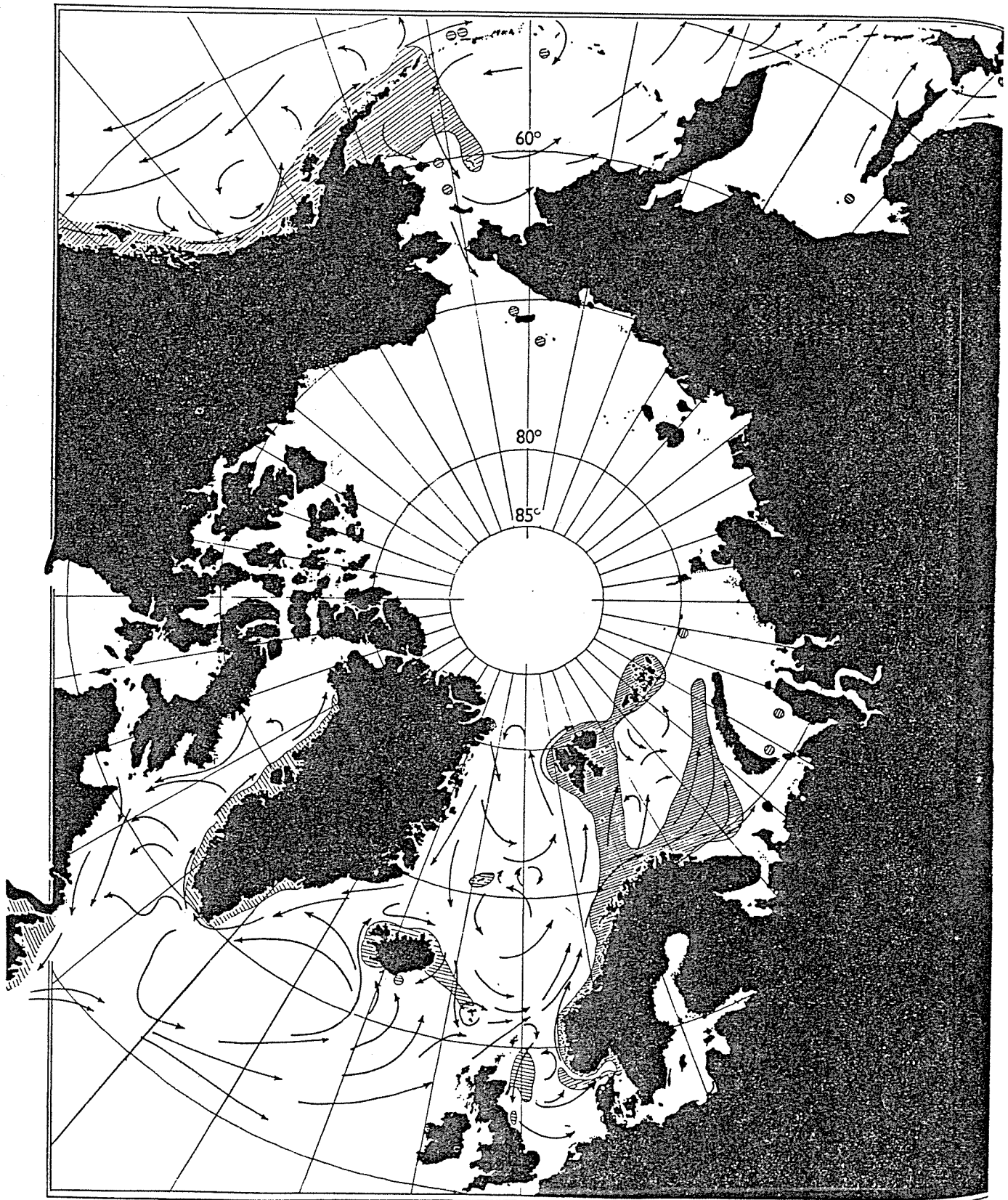


Fig. 1. Circumpolar distribution of *Pandalis borealis*. Shaded areas indicate locations of recorded populations, arrows indicate general circulation pattern of surface waters. [from Allen 1959]

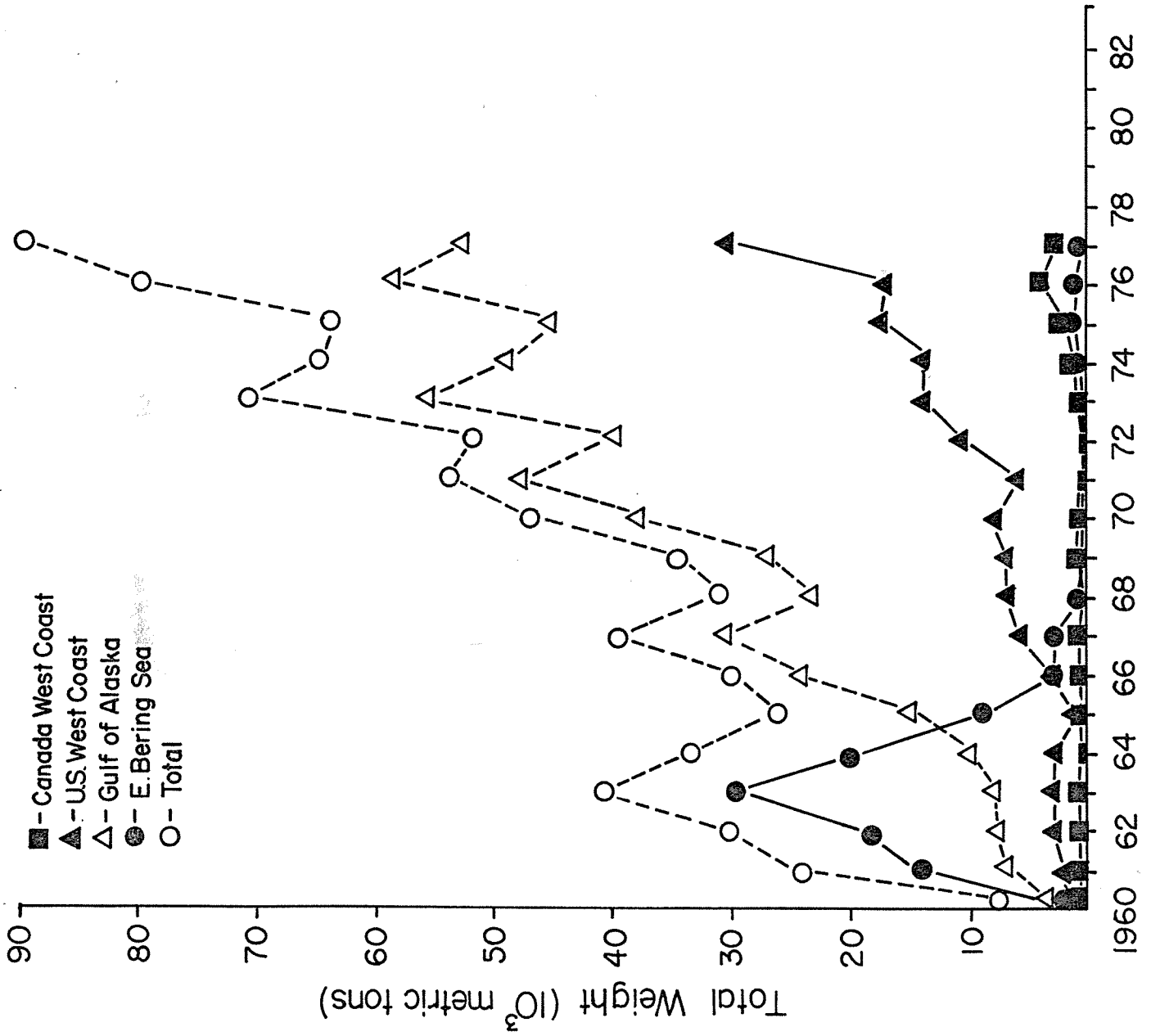


Fig. 2. Annual catch (1960-1977) of *Pandalis borealis* from different regions of the northeast Pacific. [data obtained from Miles et al. 1982]

A *P. borealis* fishery began as early as 1915 in southeast Alaska, reaching a harvest of 1500 metric ton by 1955 (NMFS 1976). In 1953 the Bureau of Commercial Fisheries made an exploratory cruise to the Yakutat area searching for concentrations of shrimp that could be exploited (Ronholt et al. 1978). In following years cruises were made farther north and west until most of the Gulf of Alaska was surveyed. The last cruise was made in 1970.

Commercially significant concentrations of pink shrimp were found near Kodiak Island and along the Alaska Peninsula. In 1958 a fishery was initiated in Kodiak, and the first mechanical peeling machines were introduced. In 1959 the total catch was 1,318 metric tons. However, the commercial catch of pink shrimp in the Gulf of Alaska increased steadily from 1960 until 1967, and despite year to year fluctuations nearly doubled between 1967 and 1976 (Fig. 2). In excess of 54,000 metric tons were caught in 1976 (Fig.2). Since 1976 catches have declined drastically (Alton 1981). The 1982-83 catch of 4,871 metric tons is the lowest since 1964 (Jackson et al. 1983).

Before the U.S. prohibited shrimp fishing by foreign vessels in 1977, both Japan and the USSR fished for pink shrimp in the Gulf of Alaska. The Japanese fished near the Shumagin Islands and offshore from Twoheaded Island from 1964-1968. Catches were small, ranging from 231 to 2000 metric tons annually (Ronholt et al. 1978). The Soviets also began fishing in 1964, initially with only two trawlers. Effort was rapidly increased until the catch reached 12,000 mt in 1966. The Russian catch declined thereafter, to 2,000 mt in 1973 and 1000 mt in 1974 (NPFMC 1976). The precipitous decline in the early 70's resulted from the enforcement of a ban on foreign vessels within 12 miles of the U.S. coast. This ban forced the Soviet fleet out of the area where most of the catch had been taken in previous years.

Both the number and the type of vessels used in the domestic fishery for *P. borealis* changed with time (Jackson et al. 1983). During the first years of the fishery single-rigged otter trawlers 50-70 feet long were used. In 1970 the first double-rigged otter trawlers appeared, and by 1973 at least half the fleet could fish two trawls simultaneously. Between 1960 and 1970 the number of vessels ranged from 6-26. However, a significant increase occurred in 1971 and between 1971 and 1981 the number of vessels ranged from 49-75. These changes in effort, coupled with complex regulations including closures of certain fishing areas, make it difficult to use the catch statistics to estimate population abundance.

The area in which the fishery operated changed with time as well. Most of the catch was taken in the Westward Region, a management area of the Alaska Department of Fish and Game (ADF&G). The Westward Region extends southwestward from Kodiak Island along the Alaska Peninsula and includes the Aleutian District (Fig.3). Before 1971 the catch from areas along the Alaska Peninsula south of the Kodiak District made up only 2-13% of the total for the Westward Region. However, in 1977 catch from the Alaska Peninsula and Aleutian Districts represented 71% of the total for the region. The contribution to the total from these areas subsequently declined to only 3.2% by 1982-83, partially as a result of closures (Jackson et al. 1983).

For management purposes, and to interpret the effect of environmental changes on shrimp populations, it is necessary to delineate unit stocks, the interbreeding population units that share a common environment and gene pool. Shrimp stock units in the Gulf of Alaska are thought to be relatively small, perhaps confined to single bays or offshore canyons (Hayes 1983). By analyzing genetic and morphological differences, Gardner (1983) concluded that shrimp from Kodiak, Yakutat, Alaska Peninsula, and the Bering Sea should be considered as separate stocks for management purposes. Stock differences were especially marked between Bering Sea shrimp and shrimp from other areas.

Currently the ADF&G treats each bay or section as a separate stock for management purposes. For example, within the Westward Region, 35 separate sections

165°

160°

155°

Fig. 3. Westward Region (Alaska Department of Fish and Game) for management of pink shrimp fishery. The region is divided into 5 districts and 35 different sections. Numbers on map indicate different sections that are treated separately for management purposes. [Figure adapted from Jackson et al. 1983]

South Peninsula Legend

No.	Section
24.	Stepovak Bay
25.	Unga Strait
26.	West Nagai
27.	Beaver Bay
28.	Kennoys Islands
29.	Pavlof Bay
30.	Belkofski Bay
31.	Morzhovoi Bay

Chignik District Legend

No.	Section
15.	Kujulik Bay
16.	Chignik Bay
17.	Seal Cape
18.	Kuiukta Bay
19.	Mitrofanias Island
20.	Ivanof Bay

Aleutian District Legend

No.	Section
32.	Unalaska Bay
33.	Makushin Bay
34.	Beaver Inlet
35.	Usof Bay

NORTH PENINSULA DISTRICT

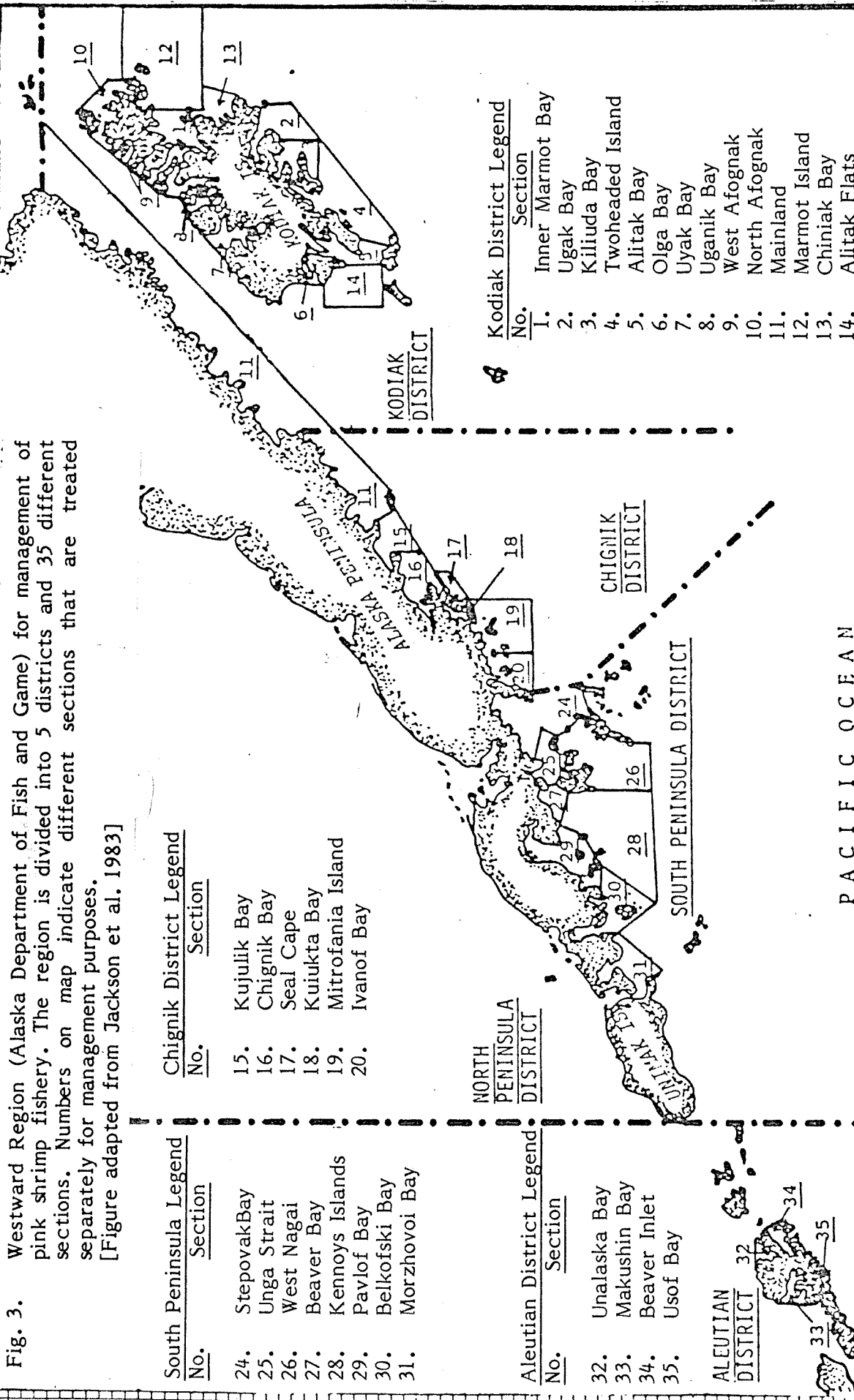
- | No. | Section |
|-----|-----------------|
| 21. | Stepovak Bay |
| 22. | Unga Strait |
| 23. | West Nagai |
| 24. | Beaver Bay |
| 25. | Kennoys Islands |
| 26. | Pavlof Bay |
| 27. | Belkofski Bay |
| 28. | Morzhovoi Bay |
| 29. | Unalaska Bay |
| 30. | Makushin Bay |
| 31. | Beaver Inlet |
| 32. | Usof Bay |

CHIGNIK DISTRICT

SOUTH PENINSULA DISTRICT

Kodiak District Legend

No.	Section
1.	Inner Marmot Bay
2.	Ugak Bay
3.	Kiliuda Bay
4.	Twoheaded Island
5.	Alitak Bay
6.	Olga Bay
7.	Uyak Bay
8.	Uganik Bay
9.	West Afognak
10.	North Afognak
11.	Mainland
12.	Marmot Island
13.	Chiniak Bay
14.	Alitak Flats



PACIFIC OCEAN

are identified. Catch data are collected and tabulated section by section. However, the previously mentioned problem of determining effort (Jackson 1980) make these data sets of doubtful use in interpreting the influence of the environment on shrimp stocks, even if the sections correspond closely to unit stocks. Annual catch reported for different districts is shown in Figure 4.

LIFE HISTORY AND BIOLOGY

The life history of *P. borealis* has been documented in all the areas supporting fisheries including: 1) Greenland (Smidt 1969, Carlsson and Smidt 1978); 2) the North Atlantic and Norwegian Sea (Paulsen 1946, Rasmussen 1953 and 1969, Allen 1959, ICES 1977); 3) the Gulf of Maine (Appollonio and Dutton 1969, Haynes and Wigley 1969); 4) the northeast Pacific (Berkeley 1930, Butler 1964, 1971 and 1980, Barr 1970a); 5) Japan and the Ohkotsk Sea (Kurata 1981); and 6) the Bering Sea (Ivanov 1969).

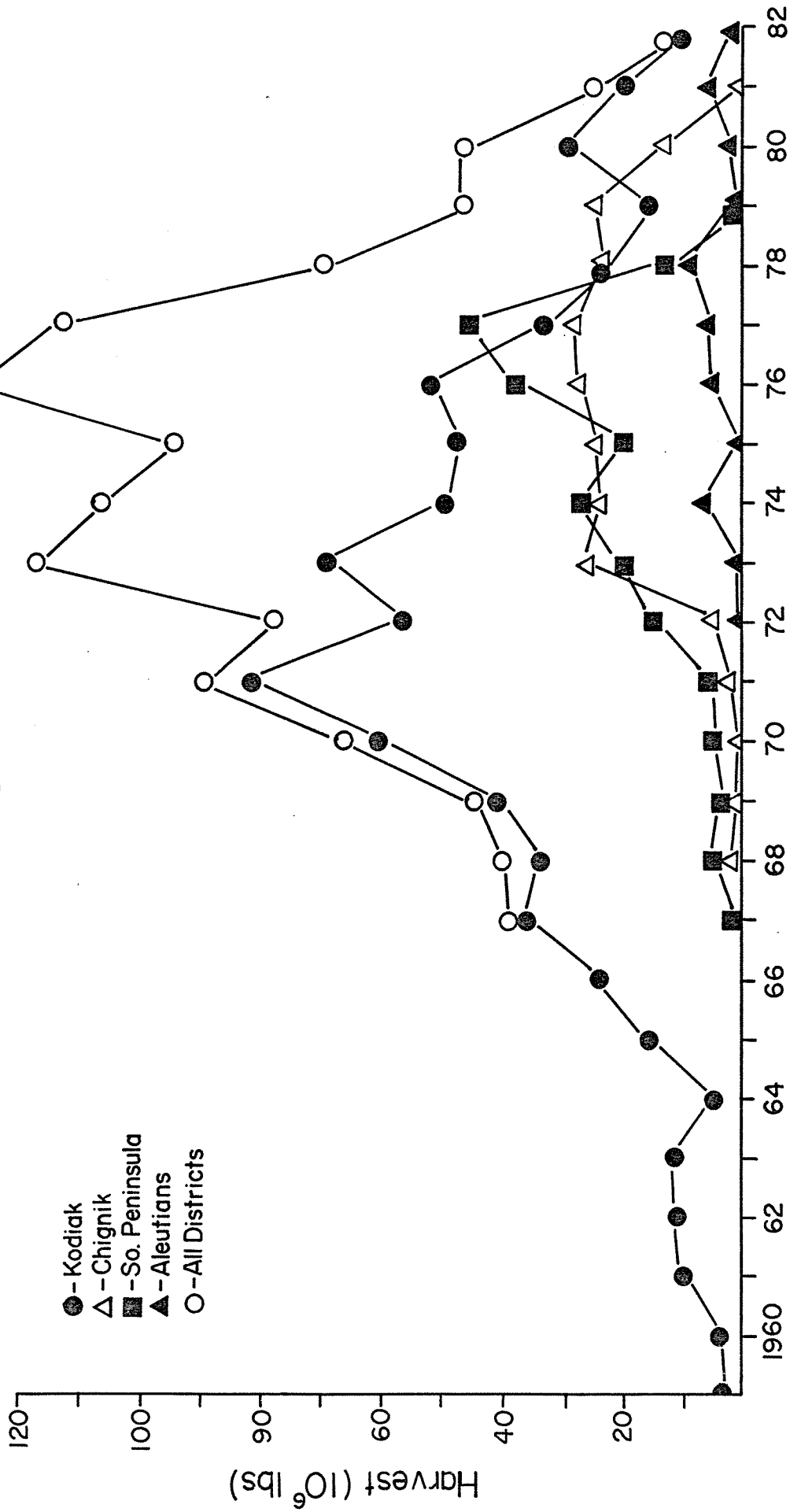
In all areas pink shrimp are protandric hermaphrodites, first maturing as males and then transforming into females (Carlisle 1959). Thus, all large shrimp are females. Spawning takes place in the fall after spermatophores containing sperm are attached to the females during copulation. Females produce 500-2,500 eggs per brood, which are fertilized as they are extruded and are carried on the abdomen of the female (Dahlstrom 1970). The number of eggs is greater for larger females. The eggs hatch in spring into planktonic larvae, which pass through six larval stages before reaching the juvenile stage. Larvae are found in large numbers just above the spawning beds, and may be geographically confined since they do not migrate into surface layers (Pearcy 1971). As development proceeds young shrimp become semi-benthic, spending part of their time on the bottom and part in the water column.

Stickney and Perkins (1981) have begun studies of the food of larval shrimp in the Gulf of Maine, and Paul et al. (1979) investigated feeding requirements of newly hatched larvae in the Gulf of Alaska. Both studies found that food densities necessary for survival in the laboratory were much higher than average concentrations encountered in the sea. These results imply that higher than average food concentrations (patches) are important for survival of larval pink shrimp. The larval drift of pink shrimp has not been determined for any stock. Since many stocks seem to be confined to bays, and since larvae are not abundant in surface layers, it may be that transport away from food supplies is not as important a source of variable mortality for shrimp as it is for many fish with planktonic larvae.

In the Bering Sea pink shrimp mature as males at ages 2 1/2 or 3 1/2, become females at 5 1/2, and by age 6 1/2 are sterile. Eggs are carried for 7 to 8 months. In the western Gulf of Alaska, sexual development occurs one year earlier. Females breed twice, at ages 4 1/2 and 5 1/2. Few survive to age 6 1/2. Although most juveniles mature into males, some may develop directly into females. These early maturing females are referred to as primary females. The percentage of primary females in some populations is positively correlated with the ratio of first breeding shrimp to older shrimp (Charnov et al. 1978, Charnov 1979). This means that when females (older shrimp) are less abundant, the population produces females at a greater rate by the direct development of some juveniles into females thus optimizing the sex ratio.

The unique life history of shrimp makes comparisons of growth rate for different stocks difficult. Males and females grow at different rates, and males transform to females at different ages in different areas. Therefore, the interpretation of length-frequency plots is complicated. However, the growth of pink shrimp is definitely slower in the Bering Sea than in the western Gulf of Alaska (Davis 1982, Gardner 1983). Pink shrimp attain a carapace length of about 26 mm after 6 years in the western Gulf of Alaska. In three areas of the Gulf examined by Gardner (1983) different year-classes (1975-80) grew at similar rates. However, development

Fig. 4. Annual catch (1959-1982) of shrimp reported for different districts of Westward Management Region, Alaska.
 [data obtained from Jackson et al. 1983]



and growth rate are faster at higher latitudes (Ivanov 1969, Gardner 1983). Since the Alaska Stream is warmer in the northern part of the Gulf and loses heat as it flows south along the Alaska Peninsula (Ivanov 1969), this is the expected relationship between rate of development and temperature. Ivanov (1969) suggests that in the western Gulf, pink shrimp avoid areas where warm Alaska Stream waters reach the bottom. Instead, shrimp are concentrated near fronts, areas with strong horizontal temperature gradients where water masses interact. This behavior may be a response to food supply rather than temperature.

Pink shrimp do not seem to exhibit systematic annual migrations. Neither feeding nor spawning migrations have been definitively identified (Hayes 1983). Although there is some evidence of a shoreward spawning migration in the fall (Haynes and Wigley 1969, Clark et al. 1979, Feder and Jewett 1980), migrations along the coast are not considered to be significant in the Gulf of Alaska (NPFMC 1976). In the eastern Bering Sea, however, there may be a seasonal migration of 30-40 miles southward in winter to avoid extreme cold (Ivanov 1969).

Pink shrimp are thought to require a muddy bottom with a high organic content (Bigelow and Schroeder 1939, Allen 1959, Wigley 1960, Haynes and Wigley 1969, Ivanov 1969). However, Fox (1972a) points out that neither commercial trawls nor trawls used in scientific surveys can adequately sample shrimp above rocky bottoms, so substrate requirements are not completely established.

The diet of adult shrimp in the eastern Bering Sea (Feder and Jewett 1981) and the Gulf of Alaska (Barr 1970b, Crow 1977, Feder 1980, Feder and Jewett 1980) consists of crustaceans, polychaetes, detritus, diatoms, forams, fishes, and bivalves. The percentage of each of these items in the diet differs between shrimp taken in bays and shrimp taken from areas on the outer shelf (Feder and Jewett 1980). The importance of zooplankton in the diet may be underestimated in these studies because few samples were collected at night. Pink shrimp have a diurnal vertical migration, moving off the bottom at night to feed in the water column (Barr and McBride 1967, Barr 1970b, Percy 1971, Fox 1972a). In order to evaluate the importance of the nightly feeding migrations, it is necessary to sample periodically throughout the entire 24 hour period.

Predators of pink shrimp include cod, pollock, sculpins, flathead sole, tomcod, arrowtooth flounder, dogfish, and seals (Feder 1980, Feder and Jewett 1980, 1981, Rogers et al. 1979, Simenstad 1979) and population density might be controlled by predation. In Cook Inlet and Kodiak, pink shrimp are the most common fish prey. Cod are the major predator on shrimp in several locations and shrimp are the most important food for cod. Predation pressure on shrimp appears to be so high that any change in predator abundance will ultimately affect the abundance of shrimp. Recent declines in shrimp stocks in the Westward Region have been accompanied by large increases in numbers of juvenile pollock (Gaffney 1978). Jackson et al. (1983) believe that increased predation by cod might explain the declines in stocks. Predation was invoked rather than disease or year-class failure because the decline was observed in all year-classes simultaneously, and because cod and pollock populations increased in abundance at the same time that shrimp stocks declined.

The survival of pink shrimp is known to be highly variable. In Pavlov Bay in the western Gulf, a strong year-class resulting from the hatch in 1971 was easily identified in length-frequency plots for at least seven consecutive years (Anderson 1981). Investigations of the sources of this variability in recruitment of pink shrimp have only begun; we do not know the cause(s) of strong or weak year classes.

EFFECT OF ENVIRONMENTAL PARAMETERS

Nearly all of the events in the life history of pink shrimp have been shown to be correlated with latitude, presumably as a result of differences in temperature. Each life stage has a longer duration in the more northerly parts of the range. For

example, eggs are carried for 9 months by pink shrimp from the Arctic, while those from near the southern limit of the range carry eggs for only 5 months (Rasmussen 1969). Other factors that vary as a function of latitude (temperature) include date of spawning, date of hatching, growth rate, age at maturation, maximum age observed, age at transition to female sex, number of broods per lifetime, and duration of larval stages.

Apparently developmental events are keyed to size rather than age. In colder environments a reduced growth rate delays development, in some locations to such an extent that the populations are barely self-reproducing. For example, in waters colder than 1.5°C. off Newfoundland, Squires (1968) found small shrimp with only 4-14% as females. In warmer waters the shrimp were larger and approximately 50% were females. Figure 5 shows a comparison of growth rates for different shrimp stocks.

It is possible that high or low temperatures could have direct lethal effects on some stages of the life history. Horsted and Smidt (1956) report mass mortality of adult P. borealis in west Greenland waters when temperatures of -1°C persisted for 2 months in the winter of 1948-49. Abercrombie and Johnson (1941) found that P. borealis adults could survive only 4 days on the average at temperatures of 11.5°C. Rasmussen (1953) assigned an upper limit of 8°C for the survival of P. borealis, but Allen (1959) found that P. borealis could survive and reproduce in waters as warm as 11.1°C. Paulsen (1946) reported that larvae survived temperatures as high as 14°C, and salinities from 25.9-35.7 o/oo. In Alaska pink shrimp can tolerate temperatures from -2°C to 11.5°C (NPFMC 1976). In the Gulf of Alaska and Bering Sea female pink shrimp carrying eggs are reported to be particularly sensitive to temperature (Ivanov 1969). In British Columbia waters, the upper limit of temperature tolerance is 11.1°C (Butler 1964).

The direct effect of temperature and salinity on the survival of P. jordani larvae was investigated by Rothlisberg (1979). The results cannot be applied directly to P. borealis larvae, but the demonstration of a relatively narrow tolerance for temperature suggests that larval P. borealis may also be more sensitive to temperature than are adults. Paul and Nunes (1983) measured oxygen consumption rates as a function of temperature and observed thermally induced respiratory stress above 9°C. They concluded that the increased metabolic demands in warmer years could reduce year-class success of pink shrimp.

Temperature has been correlated both positively and negatively with shrimp abundance. In west Greenland waters higher than average temperatures are correlated with increased catches. The increased stock densities are caused by an inflow of warm water through Davis Strait, advecting adult shrimp into water of west Greenland where they are harvested (Carlsson and Smidt 1978). Catches of some penaeid shrimp are better in years with warmer than average winters. This relationship was strong enough for Williams (1968) to propose winter temperature as a useful predictor of catch. In the Gulf of Maine, Dow (1964, 1966, 1979) correlated warmer than average years with a poor catch four years later. Since no causal mechanism was established, this relationship cannot be extrapolated to the Gulf of Alaska or Bering Sea. No correlation between temperature and catch has been established for the stocks being considered in this report. However, Ivanov (1969) reports that the strength of year classes in the Bering Sea is related to the extent of ice cover during their first winter; severe winters produce poor year classes.

Some of the limitations in the data sets available for constructing correlations between indices of abundance and temperature have been already mentioned. The problems of such an approach are discussed fully by Austin and Ingham (1978). Even if problems with the data sets can be overcome, the lack of an established causal mechanism to explain observed correlations make prediction of changes in abundance or catch uncertain. Therefore, the indirect effects of the environment on abundance

and distribution should be examined individually in an attempt to elucidate cause and effect relationships.

PROJECTED EFFECTS OF CLIMATE CHANGES

Cold bottom temperatures limit the northern distribution of pink shrimp in the Bering Sea (Pruter 1973), the northeastern Atlantic (Allen 1959) and Greenland (Horsted and Smidt 1956). An increase in temperature could directly affect the distribution of P. borealis by extending its range farther north as water temperatures increase. The bottom topography of the Bering Sea north of the present distribution of pink shrimp should not prevent the hypothesized extension of range, since it is similar to that in areas where shrimp occur at present. A gradual warming of the environment may have the greatest direct effect on P. borealis distribution near the southern limit of its range. In British Columbia waters and possibly even in southeast Alaska waters, a gradual warming could result in the replacement of P. borealis by the more southern species P. jordani, which has a higher temperature optimum. Such a replacement should have little effect on the fishery since both P. borealis and P. jordani are commercial species. Since shrimp in the Gulf of Alaska are located near thermal fronts, the distribution of shrimp may change if the location of the fronts changes.

An increase in temperature might affect the distribution and abundance of pink shrimp in the Bering Sea and/or Gulf of Alaska by changing the abundance of prey and predators of P. borealis. However, the effect of temperature on the abundance of pink shrimp prey is unknown. Furthermore, the present state of knowledge is inadequate even to predict that an increase in shrimp abundance would follow an increase in the abundance of their prey, although it seems likely. Interactions between shrimp and their prey species may be altered if increased temperatures affect vertical migration of shrimp. The effect of increased temperature on vertical migration is unknown, but migrations might be reduced in vertical extent if surface waters become too warm. Presumably this would decrease the amount of food available for the shrimp.

As mentioned above, changes in the abundance of predators seem certain to affect shrimp populations. Projected effects of climate change on populations of pollock (Strickland and Sibley 1984) and yellowfin sole (Horrocks et al. 1984) suggest that these fish species should increase in abundance with an increase in temperature. We would expect, therefore, to see an associated decline in the shrimp population.

The survival and growth of larval shrimp could be affected by changes in temperature, directly or indirectly. Increased mortality could result if the rate of development of eggs and larvae were accelerated more than those of the prey organisms on which larvae feed. This would produce an inadequate food supply at the time of hatching. Alternatively, food supplies may develop in excess of the increased metabolic demands of the shrimp. Since the food requirements of larval shrimp are not known, we cannot fully evaluate the potential interactions. However, the increased metabolic demands (Paul and Nunes 1983) coupled with the apparent shortage, or patchiness, of food in nature (Paul et al. 1979) suggest that increased larval mortality may be a significant consequence of higher temperatures. Another effect on larvae may be transport to areas without adequate food supply, if the new temperature regime changes circulation patterns. However, shrimp are less likely to be affected by changes in circulation patterns than are species with planktonic larvae in surface waters.

Another potential effect of a temperature increase is an increased incidence of disease. Egg parasitism of P. borealis in the Gulf of Maine was higher in years with above average temperatures (Clark et al. 1979). Parasites similar to those infecting shrimp in the Gulf of Maine (Stickney 1981) have been observed on P. borealis caught off Kodiak Island (Fox 1972a). Unusually high egg mortalities have been observed

occasionally in Kodiak waters with no apparent explanation (Fox 1972a). However, so little is known about the diseases and parasites of P. borealis in the Gulf of Alaska and Bering Sea that the effect of environmental changes cannot be evaluated.

Some of the hypothesized changes caused by increased temperature would increase shrimp abundance and some would decrease shrimp abundance. Furthermore, all these effects must be evaluated simultaneously to make realistic predictions of the overall impact. The best available predictive tool is numerical simulation, which models the cause and effect relations between environmental changes and changes in shrimp abundance. Since predation is particularly important for shrimp, a useful simulation must be a multi-species or ecosystem model. According to Laevastu (1983), "the only known dynamic marine ecosystem model that includes environmental processes in it and that permits simulation of the steady state as well as the dynamics of the standing stocks of species in space and time as affected by interspecific interactions (e.g., predation), environmental factors (e.g., temperature, currents), and the activities of man (e.g., fishing)" is the Dynamic Numerical Ecosystem model (DYNUMES III) formulated at the Northwest and Alaska Fisheries Center (Laevastu and Larkin 1981). This model could be used to predict shrimp abundance in the Bering Sea and could be adapted to the Gulf of Alaska as well. Of course, the reliability of the model predictions will be limited by the lack of physical oceanographic and fisheries data noted earlier. In addition, since recruitment is made proportional to biomass in the model, many of the potential causes of year-class variability cannot be investigated. However, the model does allow several important factors affecting biomass to be quantified and ranked. The model has not yet been applied to shrimp in the Bering Sea, nor to any species in the Gulf of Alaska, but such an exercise would undoubtedly be worthwhile.

CONCLUSIONS

1) A drastic decline in the Bering Sea stock of Pandalus borealis was caused by overfishing. Since there is currently no fishery in the Bering Sea, and since surveys of crabs and demersal fish do not adequately sample pink shrimp, the effect of increased temperature (or any other environmental variable) will be difficult to document.

2) In the Gulf of Alaska there is a relatively short time series of survey data and interpreting the catch and effort data from the fishery is difficult. Therefore, we cannot explain the recent dramatic declines in most of the shrimp stocks in the Gulf of Alaska. Nevertheless, for Pandalus borealis stocks in the Gulf of Alaska changes in the environment may produce biological effects that can be documented.

3) Factors controlling year-class strength in shrimp stocks are unknown; until they are determined any conclusions regarding the effects of environmental changes must be tentative.

4) A gradual increase in bottom temperature of a few degrees will probably cause the distribution of P. borealis to move northward, allowing it to expand its range to include more of the Bering Sea Shelf. Any loss to fisheries in the southern portion of the range is liable to be offset by an increase in abundance of P. jordani.

5) An increase in temperature will result in faster growth rates, earlier maturation, and, provided enough food is available, a higher production rate.

6) A gradual increase in temperature of a few degrees will not have a direct lethal effect on any stage of development.

7) The abundance of P. borealis is sensitive to changes in the abundance of cod, pollock, and other fish. Therefore, effects of environmental change on fish abundance will also affect shrimp abundance.

8) Because larval shrimp may not drift far after hatching, potential changes in circulation patterns are probably not too important in determining year-class strength. In particular, changes in circulation should not cause increased transport of larvae away from favorable feeding grounds.

9) Any advancement in timing of the larval shrimp hatch is likely to be matched by an advance in the timing of the spring phytoplankton bloom and food supply of larvae. Although a gradual increase in temperature is unlikely to cause a mismatch between larvae and food supply, any decrease in the overall primary production of the system will probably result in lowered production of pink shrimp. Furthermore, unless the food supply for larval shrimp increases, the metabolic demands at higher temperatures are likely to produce higher larval mortality.

10) Stocks of P. borealis are excellent candidates for monitoring programs designed to evaluate and document the effects of environmental warming trends. The application of the ecosystem model DYNUMES to stocks of shrimp in the eastern Bering Sea and Gulf of Alaska should yield useful hypotheses about the effect of increasing temperature.

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