EFFECTS OF SEAWATER TEMPERATURE ON SPAWNING, EGG DEVELOPMENT, HATCHING SUCCESS, AND POPULATION FLUCTUATIONS OF THE DUNGENESS CRAB, *CANCER MAGISTER*

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ABSTRACT

Dungeness crab (*Cancer magister*) fishery landings in central California declined in the early 1960's and have continued at low levels to the present. In the laboratory, female crab spawning, egg development, and hatching success were affected variously by seawater temperatures ranging from about 10 to 17°C. Crabs tended to spawn later in colder water. The time required for eggs to develop from spawning to hatching ranged from an average of 64 days at 16.7°C to 123 days at 9.4°C. Egg survival and hatching success were significantly better the cooler the water. The average number of larvæ hatched per crab egg mass ranged from 14,000 at 16.7°C to 685,000 at 10.0°C. Unusually high ocean temperature during the egg brooding period in 1957 preceded the decline in landings by three years, and landings have remained low as ocean temperatures, on the average, have remained relatively high. A similar relationship also exists between ocean temperature and fluctuations in crab landings in northern California.

RESUMEN

Las capturas del cangrejo Dungeness, *Cancer magister*, en California central disminuyeron a principios de la década de 1960 y han continuado a niveles bajos hasta el presente. En el laboratorio, el desove de las hembras, el desarrollo de los huevecillos, y el éxito de eclosión se vieron afectados por variaciones en la temperatura del agua marina, fluctuando entre 10 y 17°C. Los cangrejos tendían a desovar más tarde en agua más fría. El tiempo requerido para el desarrollo de los huevecillos, desde el desove hasta la eclosión, varió desde un promedio de 64 dias a 16.7°C, hasta 123 dias a 9.4°C. La supervivencia de los huevecillos y el éxito de la eclosión eran significativamente mejores cuanto más fría estaba el agua. El promedio de larvas eclosionadas por masa de huevecillos de cangrejos varió desde 14,000 a 16.7°C, hasta 685,000 a 10.0°C. Temperaturas oceánicas extraordinariamente altas durante la época de incubación de los huevecillos en 1957, precedieron por tres años la disminución de las capturas, y éstas han permanecido bajas mientras las temperaturas oceánicas, en un promedio, han permanecido relativamente altas. Una relación similar existe también entre las temperaturas oceánicas y fluctuaciones en la captura de cangrejos en el norte de California.

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INTRODUCTION

The Dungeness crab, *Cancer magister*, supports important commercial fisheries along the west coast of North America from central California to Kodiak, Alaska (Figure 1). Wide fluctuations in landings have been characteristic of these fisheries, but the landings in California, Oregon, and Washington have fluctuated somewhat synchronously over the years. However, in the early 1960's, landings in central California declined drastically and have continued at unprecedented low levels to the present while the landings in northern California (and northward along the coast) have continued to fluctuate widely (Figure 2).

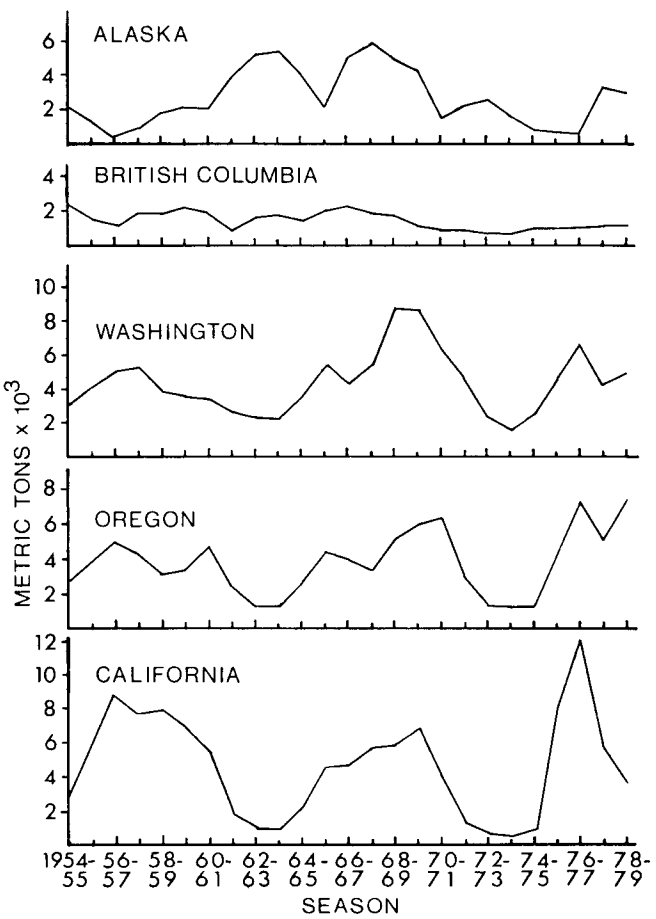

Figure 1. Dungeness crab commercial fishery landings by season, 1954-55 through 1978-79, except Alaska and British Columbia seasons are in calendar years, i.e. 1954-55=1955.

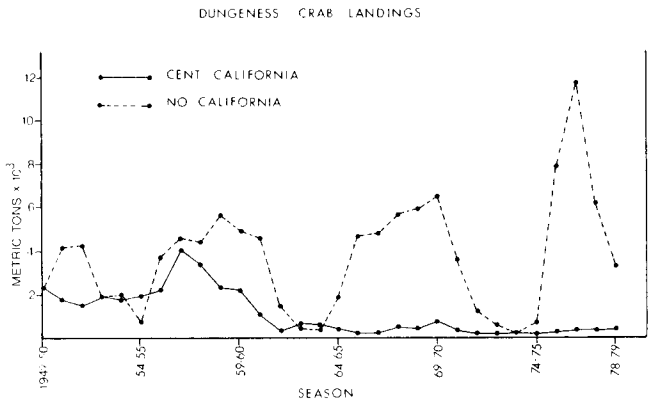

Figure 2. Northern and central California Dungeness crab commercial fishery landings by season, 1949-50 through 1978-79.

The long-term decline of the central California crab fishery has been of much concern to fishermen, dealers, consumers, and fishery biologists. In 1974 the State Legislature, by Senate Bill 1606, directed the California Department of Fish and Game (CDFG) to conduct an investigation into causes of the decline and to make recommendations to protect and increase the crab resource.

In response to the Legislature, the Department established an intensive Dungeness Crab Research Program which has been studying crab life history, pollution, and oceanographic factors for possible relationships to the decline (Orcutt et al. 1975, 1976; Orcutt 1977, 1978; Farley 1979). These studies have shown no significant relationships to environmental pollutants (pesticides, oil, chlorine-treated domestic and industrial wastes, etc.) that can explain the decline or that would prevent recovery of the crab resource. These studies do indicate that long-term oceanographic conditions may be at least partly responsible.

The present report presents information from laboratory studies on seawater temperature and Dungeness crab reproductive biology and comparisons of crab landings and ocean temperatures which suggest a possible explanation for the central California decline and for some of the fluctuations in Dungeness crab landings on up the coast.

DUNGENESS CRAB REPRODUCTIVE BIOLOGY

In California, most Dungeness crab mating occurs in the spring from about March through June. Mating occurs between a hard-shelled male and a newly molted soft-shelled female (Snow and Neilson 1966). Sperm are stored internally in the female's paired spermathecæ until spawning, which usually occurs in the fall from late September to November in California. The eggs are fertilized as they pass through the spermathecæ at the time of spawning and are extruded from the reproductive tract through paired ovipores on the crab's sternum. The eggs form in a spongelike mass (Figure 3) as they adhere individually to the pleopodal hairs on the crab's abdomen where they are brooded until they hatch. A crab must be at least partially buried in sand for the egg mass to form. An egg mass may contain as many as one to two million eggs. Egg masses are usually bright orange in color when spawned and gradually change to dark brown as the developing embryos deplete the yolk, and pigmentation and eye spots appear before hatching. Most egg brooding (ovigerous) crabs are generally found in central California from about October through December and in northern California from about October through January. Hatching in central California usually occurs from late December to early February and in northern California from about January to early March. Ovigerous females are found even later in the year on up the coast, where temperatures are cooler and the egg brooding period is longer. The newly hatched larvæ are planktonic and metamorphose through six larval stages before the benthic crab stage is reached three or four months later.

METHODS AND MATERIALS

Adult female Dungeness crabs were collected from San Francisco and Eureka areas (central and northern California respectively) during late May, June, or July of 1977, 1978, and 1979 and were transported to the Department's Marine Culture Laboratory near Carmel, California. Crabs that had obviously molted recently and thus presumably had mated were selected at the laboratory for the experiments. Twenty crabs were used in 1977, 24 in 1978, and 24 in 1979. These crabs ranged in size from 130 to 156 mm in carapace width (excluding the 10th antero-lateral spines).

The crabs were held in separate compartments in fiberglass aquaria, four crabs (two from each area) in each aquarium. The aquaria were equipped with sand and aerated sub-sand filters and were supplied with seawater in an open (non-recirculating) system. The seawater was

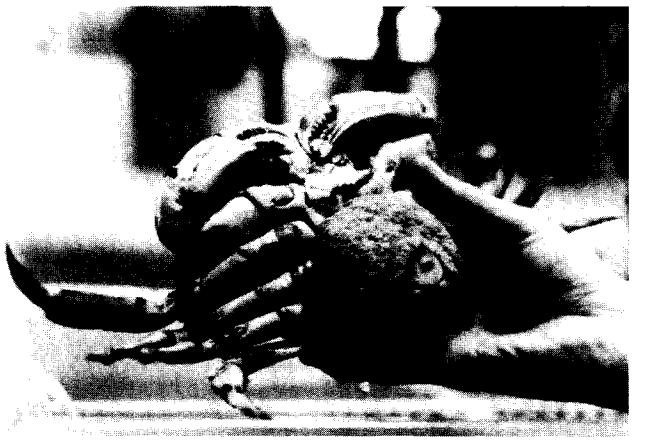

Figure 3. Dungeness crab with egg mass.

pumped from the ocean nearby and was filtered and ultraviolet-treated at the laboratory.

Three seawater temperature regimes were used each year, including one at approximately 17°C, one at approximately 10°C, and one at ambient which, fluctuating between the other two, averaged 13-14°C during the experiments. Ambient laboratory temperature approximates ocean tempreatures off San Francisco, whereas the other two are respectively higher and lower; the lower regime is closer to conditions off Eureka. The crabs were maintained at these temperatures during prespawning, spawning, egg brooding, and hatching periods.

Each experiment was begun with eight crabs in each temperature regime, except in 1977 when only four crabs were held in ambient. Also in 1977, air and seawater supplies to one warm aquarium malfunctioned, and all four crabs died before spawning, leaving only four crabs in warm seawater that year.

At least three times per week throughout each experiment, seawater temperatures were monitored, crab behavior was noted, and the crabs were fed. Food consisted of frozen market squid, *Loligo opalescens*, diced before feeding, and frozen ocean shrimp, *Pandalus jordani*.

During all three experiments, time of spawning, condition and color of the egg masses, and time of hatching were recorded. During 1978 and 1979, egg mass volumes were measured periodically and estimates of numbers of larvæ hatched were calculated by serial dilution and counting. Egg mass volumes were obtained by removing a crab from an aquarium, gently pressing seawater from the egg mass, and forming aluminum foil over it to form a cup, The cup was removed and filled with seawater, which was then measured in a graduated cylinder. The mean of about five repeated fillings was recorded as the volume. Of several methods considered, this method, although somewhat imprecise, was considered the least traumatic to the crabs and egg masses; also, it allowed for periodic measurements and gave values that were useful in comparisons of egg mass volumes within and between seawater temperatures.

RESULTS AND DISCUSSION

Spawning

All spawnings occurred between mid-September and early December, although most occurred before mid-November. A few crabs died before spawning, but all of the remaining crabs spawned during this period (Figure 4). Nonparametric Kruskal-Wallis tests (Hollander and Wolfe 1973) were used to determine the significance of differences in dates of spawning by year, by location, and by temperature.

There were no significant differences in dates of spawning by year within temperature regimes except in ambient seawater where the differences were only slightly significant ($P = 0.076$) with spawning dates tending to be later in 1978.

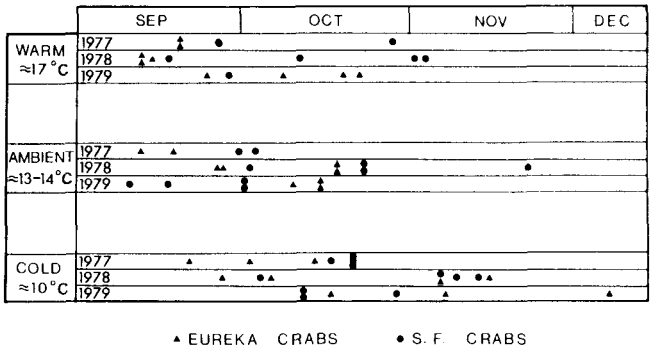

Figure 4. Spawning dates of female Dungeness crabs from Eureka and San Francisco areas in three different seawater temperature regimes in the laboratory during 1977, 1978, and 1979.

When all temperature regimes are considered together, there was a tendency for Eureka area crabs to spawn earlier than San Francisco crabs in both 1977 ($P = 0.008$) and 1978 ($P = 0.045$) whereas in 1979 there was a tendency for San Francisco crabs to spawn earlier ($P = 0.041$).

There appears to be a trend towards crabs spawning later the colder the water. However, Dunn's multiple comparisons (Hollander and Wolfe 1973) show that spawning dates were not significantly different between ambient and warm regimes but they were significantly different between cold and ambient and cold and warm regimes with an experimental error rate 0.05. Therefore crabs in the coldest temperature tended to spawn later than those in either ambient or warm regimes.

One additional observation of interest is that spawning dates of San Francisco crabs in ambient seawater were not significantly different from Eureka area crabs in cold seawater ($P = 0.19$). In both cases, these crabs were in temperatures approximating their natural environments. This may suggest that crabs in San Francisco and Eureka areas tend to spawn at similar times.

The reversal in spawning trends by areas in the 1979 experiment may be due to differences in maturation rates of ovaries in crabs in these areas. Ovaries in Eureka area crabs in June 1979 were considerably delayed in development compared to ovaries in both San Francisco and Eureka area crabs in 1976-1978. San Francisco crab ovaries were not examined in 1979, but the laboratory results indicate that they matured earlier than Eureka crabs that year.

Egg Brooding Period

Differences in average egg brooding temperatures from year to year produced differing egg brooding periods even within regimes. The warmest regime averaged 16.7°C for

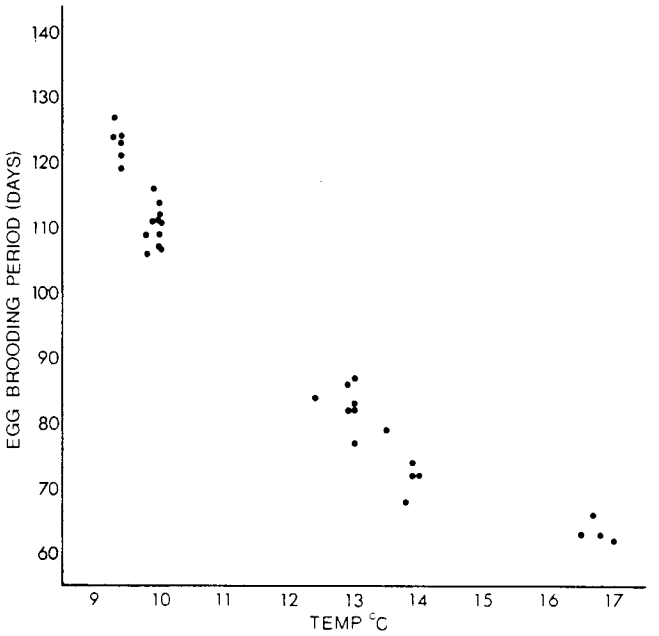

Figure 5. Dungeness crab egg brooding periods at various seawater temperatures in the laboratory.

all three years and varied the least in egg brooding periods. Average ambient egg brooding temperatures ranged from 12.9°C in 1978 to 13.9°C in 1979. Cold egg brooding temperatures averaged 9.4°C in 1977, and 10.0°C in 1978 and 1979. The egg brooding periods varied inversely with these seawater temperatures (Figure 5). Prolonged egg brooding periods in the colder water in the laboratory are consistent with prolonged occurrences of ovigerous crabs and cooler ocean temperatures progressively northward along the coast.

Hatching Success

Although the eggs developed faster at the warmer seawater temperatures, hatching success (the number of larvæ hatched from an egg mass) was lower the warmer the water. Lower hatching success at the warmer temperatures was the result of egg mortalities and deterioration of egg masses during the egg brooding period, which also resulted in declining egg mass volumes in warm and ambient regimes (Figure 6). These egg mass volumes declined even though the surviving eggs increased in size from about 0.4 mm in diameter at spawning to about 0.5 mm by the time they hatched. The increase in egg size resulted in increasingly larger egg mass volumes in the coldest temperature (Figure 6) where egg mortalities were the lowest and hatching success was the highest.

The average number of larvæ hatched per egg mass in 10.0°C seawater in 1978-79 was 685,000. Problems with a new seawater intake pump in late December 1979 after most hatching was completed in ambient and warm regimes resulted in high egg mortalities and low hatching success in the egg masses in cold water. This precluded an evaluation of hatching success due to cold water in the 1979-80 experiment. In ambient seawater at 12.9°C in 1978, an average of 257,000 larvæ per egg mass hatched and in 1979 at 13.9°C, the average was 292,000. The overall average for ambient was 275,000. In the warmest regime at 16.7°C in both 1978 and 1979, the only egg mass that produced any significant amount of larvæ hatched approximately 110,000, at least half of which died shortly after hatching. Overall, the average hatch per egg mass in warm seawater was 14,000, but virtually no larvæ hatched from most of these egg masses. These data suggest that a temperature of about 16.0 to 17.0°C may represent an upper lethal temperature limit for developing Dungeness crab eggs.

In a study near Puget Sound, Washington, Mayer (1973) observed effects of seawater temperature on Dungeness crab eggs removed from females' pleopods and cultured at 5, 10, 15, and 20°C for about 15 days. Egg mortalities during this relatively short period were minimal at 5°C, reached about 20% at 10°C, showed "a significant increase in the slope of the mortality curve at

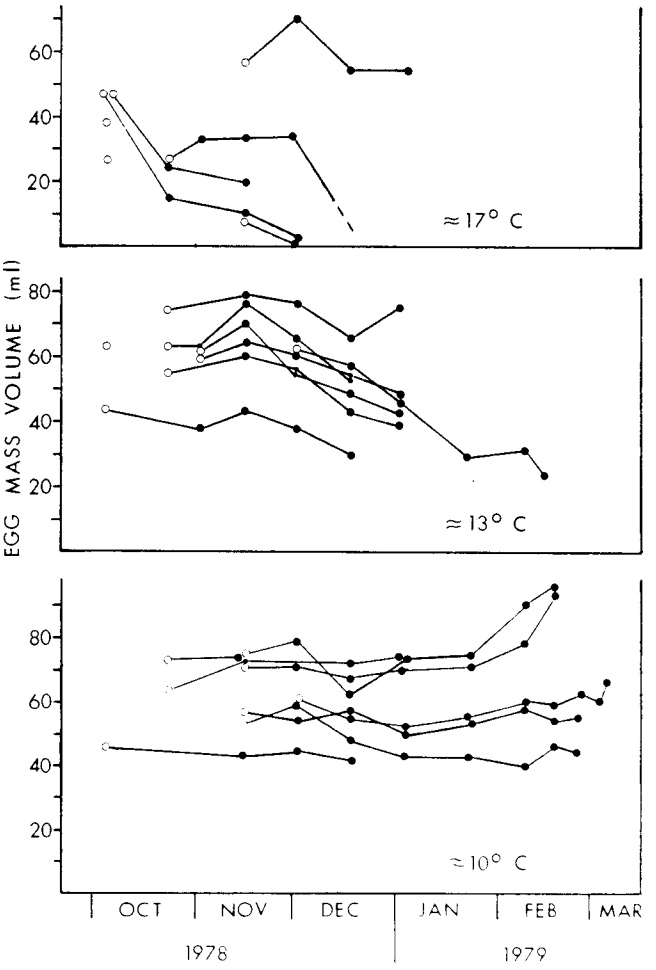

Figure 6. Progressive volumes of individual Dungeness crab egg masses in three different seawater temperature regimes in the laboratory in 1978-79.

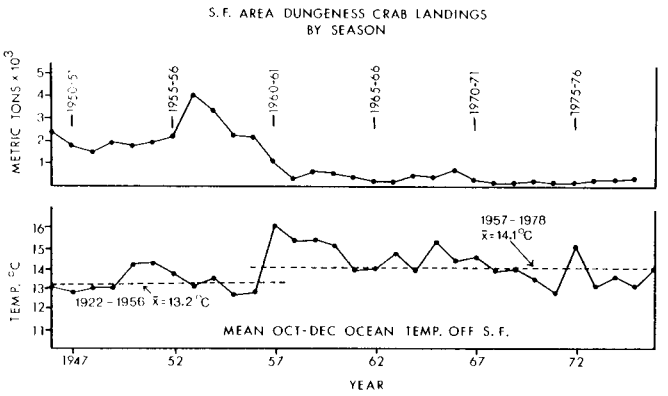

Figure 7. Commercial fishery landings of Dungeness crabs from the San Francisco area by season, 1949-50 through 1978-79; landings are shown lagged three years relative to mean October-December ocean temperatures.

15°C due to the effect of elevated temperatures between 10 and 15°C," and at 20°C, 100% mortality occurred in about 6 days.

Thus, laboratory studies indicate that seawater temperatures that are known to occur in central California could adversely affect the reproductive potential of crabs living there and thus could also affect Dungeness crab fishery landings.

Ocean Temperature and Dungeness Crab Fishery Landings

To determine if the central California crab decline could possibly be related to effects of ocean temperature on crab reproductive potential, historical ocean temperatures during the egg brooding period (October-December) off San Francisco were compared with commercial Dungeness crab fishery landings.[1] Only male crabs may be taken legally in the fishery, and male crabs in central California take about three years to reach legal size (159.0-mm carapace width). Thus, the onset of the crab fishery decline in 1960-61 coincides with a significant rise in mean October-December temperatures in 1957, and crab landings have remained low as ocean temperatures, on the average, have remained higher than for at least 35 previous years (Figure 7). This change in the ocean climate in the California current was well documented in a symposium on "The Changing Pacific Ocean in 1957 and 1958" (Sette and Isaacs 1960). Shifts in geographical ranges of many marine organisms were observed during this period (Radovich 1961). Huang (1972) analyzed sea-level fluctuations and contributing factors and concluded that changes observed in the ocean climate in 1957 persisted for at least a decade. Huang showed that the thermohaline effect, particularly during winter months, was the major factor contributing to the variations in sea level.

Although recent ocean temperatures occasionally appear to have been more suitable for good crab production (Figure 7), sea levels (high sea levels are usually associated with higher ocean temperatures) at San Francisco at the same time did not return to pre-1957 values. Furthermore, the crab population in central California has been depressed for so many years that recovery of crab landings could require a few consecutive years of suitable temperatures. In northern populations and in pre-decline years in central California, a holdover of large stocks of females during a few years of low landings probably provided for rapid recovery when environmental conditions improved.

Comparisons of ocean temperatures during the egg brooding period in northern California (November-January) with crab landings four years later (crabs take about four years to reach legal size in northern California) show a relationship to fluctuations in crab landings there (Figure 8); landings in Oregon and Washington also have fluctuated similarly. The highest California crab landings in history were taken in northern California in the 1975-76 and 1976-77 seasons and were associated with the lowest November-January (1971) ocean temperatures since the 1940's (Figure 8.)

Therefore, information from laboratory experiments and comparisons of crab landings with ocean temperatures during the egg brooding periods suggest that the decline in central California Dungeness crab landings as well as fluctuations in landings northward up the coast may be related to effects of ocean temperature on survival of Dungeness crab eggs.

ACKNOWLEDGMENTS

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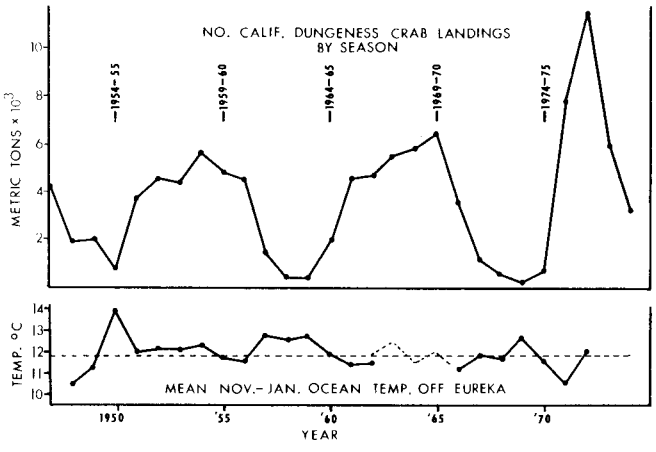

Figure 8. Northern California Dungeness crab commercial fishery landings by season; landings are shown lagged three years relative to mean November-January ocean temperatures. Dashed-line temperatures are Crescent City Harbor temperatures substituted for missing data in the offshore series.

[1]Sea-surface temperatures in a one-degree square (Marsden sub-square) were used for these analyses. Considerable vertical mixing occurs during this period (Davidson Current period), and surface temperature at this time is a good index of bottom temperature at depths where the crabs occur.

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