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A POSSIBLE LINK BETWEEN COHO (SILVER) SALMON ENHANCEMENT AND A DECLINE IN CENTRAL CALIFORNIA DUNGENESS CRAB ABUNDANCE

Dungeness crab, *Cancer magister*, are taken commercially along the west coast of the contiguous United States from Avila, CA, to Destruction Island, WA (Fig. 1). During the early years of the California Dungeness crab fishery, effort was concentrated on the central California population which produced most of the state's landings (Fig. 2). The northern population subsequently became the major contributor to California's landings after an expansion of the fishery there during the 1940's.

Northern California landings (Fig. 2) generally have followed a fluctuating pattern similar to one expressed in Oregon and Washington; however, landings from the relatively isolated central California population failed to recover from a coastwide low during the early 1960's. The lower landings reflect a long-term reduction in abundance which has been variously attributed to egg predation by a nemertean worm *Carcinonemertes errans* (Wickham 1979) and to the effects of a long-term change in oceanic conditions (Wild et al. 1983).

The failure of the central California population to recover from the coastwide period of low abundance also occurred about the time coho salmon, *Oncorhynchus kisutch*, reared in Oregon and Washington hatcheries began to make a significant contribution to the west coast salmon fishery (Oregon Department of Fish and Wildlife 1982). The effect of salmonid predation on commercially important marine crustaceans has received little attention, although it is suspected that predation by salmonids introduced into a number of both small and large

freshwater lakes (Nilsson 1972; Morgan et al. 1978) has substantially altered the abundance and species composition of their planktonic crustacean communities. Since numerous salmonid food habit studies (Heg and Hyning 1951; Petrovich 1970; Reilly 1983a) show that planktonic Dungeness crab megalops are a major component of the coho salmon diet, it is conceivable that an increase in the coho predation rate associated with an influx of hatchery coho into the central California region is at least partially responsible for the prolonged decline in Dungeness crab landings.

In this paper I first present evidence showing that a large portion of the coho salmon ultimately caught each summer off the west coast are in California waters during spring, the period Dungeness crab megalops are most abundant. I then compare and contrast survival indices to determine if the temporal variation in survival of both species is consistent with the predator-prey hypothesis.

Oregon Production Index Area Coho

Each spring and summer, a single coho salmon brood (year class) is recruited to the commercial salmon fishery off California, Oregon, and southern Washington, an area collectively referred to as the Oregon Production Index area or O.P.I. area (Oregon Department of Fish and Wildlife 1982). These fish entered the ocean to feed in May and June of the previous year, after having spent about 18 months in freshwater. Coho caught in the O.P.I. area before 1961 (Fig. 3) were predominately wild stocks. These stocks had declined to extremely low levels by 1960; however, the successful introduction of Oregon and Washington hatchery-reared coho resulted in a return to historical landing levels during the 1960's and 1970's. Much of the hatchery fish responsible for the increased landings are derived from early return Tbutle River coho, which tend to enter fisheries south of their stream of origin (Hopley 1978).

Coho salmon made up only 10% or less of California's ocean salmon catch prior to the development of Oregon and Washington enhancement programs (Fry 1973). Most of these wild coho originated in the streams and rivers of Oregon and Washington (Allen 1965) and were landed primarily in the northern California ports of Crescent City and Eureka. The recruitment of hatchery fish increased the average annual coho contribution to 25% of the total ocean salmon catch, with the central California ports of San Francisco and Fort Bragg accounting for a considerably larger portion of the total coho catch.

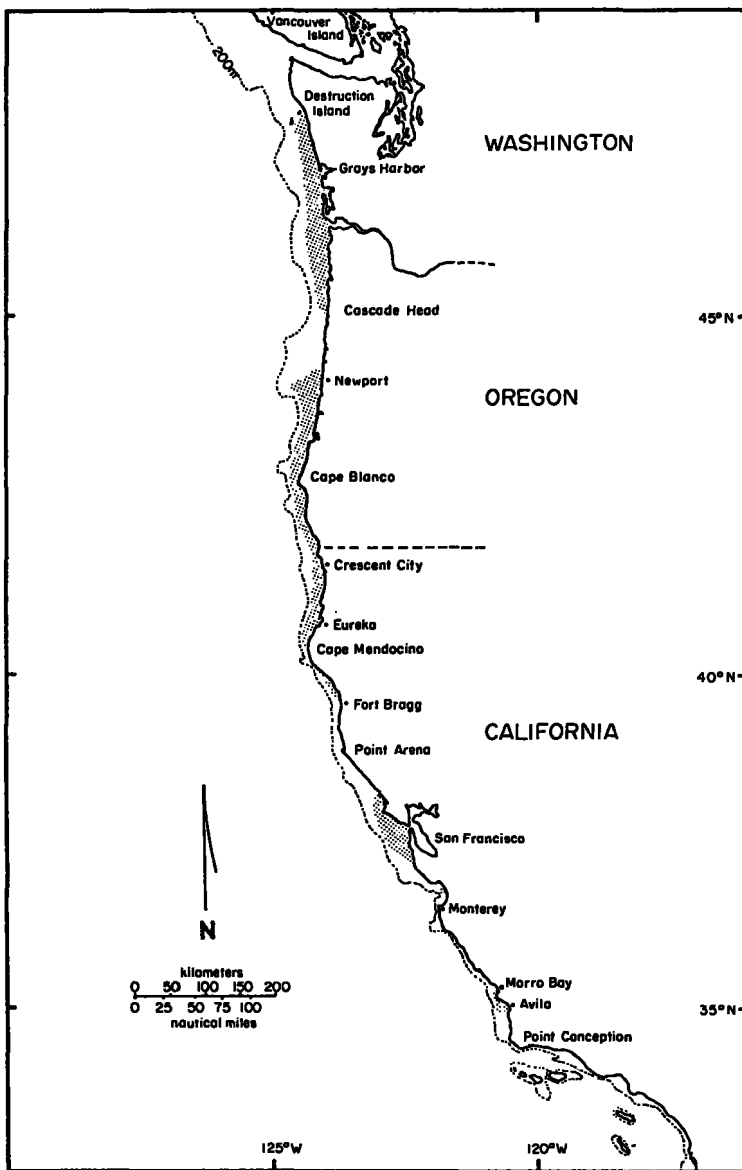


FIGURE 1.—Commercial fishing areas for Dungeness crab off Washington, Oregon, and California. (Pacific Fishery Management Council (1979).)

Before 1973, the California salmon season (coho and chinook) opened on 15 April, although few coho were landed before June because of a minimum size restriction. As Oregon and Washington hatchery coho became available, a substantial increase in the hook and release of sublegal (“shaker”) fish developed during the latter half of April to the middle of June. In an attempt to reduce the shaker problem, the season opening for coho was delayed until 15 May and the minimum size was reduced in 1973 (O’Brien and Lesh 1975).

California coho catches generally peak in July, then

drop sharply in August, 2 mo before the salmon season closure. The midsummer decline is attributed to the northward exodus of fish returning to their natal stream to spawn (Fry 1973). It is however unclear when and by what route these fish entered California waters.

A general migration model (Loeffel and Forster 1970; Godfrey et al. 1975; Hartt 1980) proposes that newly emigrated west coast coho move immediately northward into the Gulf of Alaska, then during winter, undertake a southeasterly migration which brings them back into California, Oregon, and Wash-

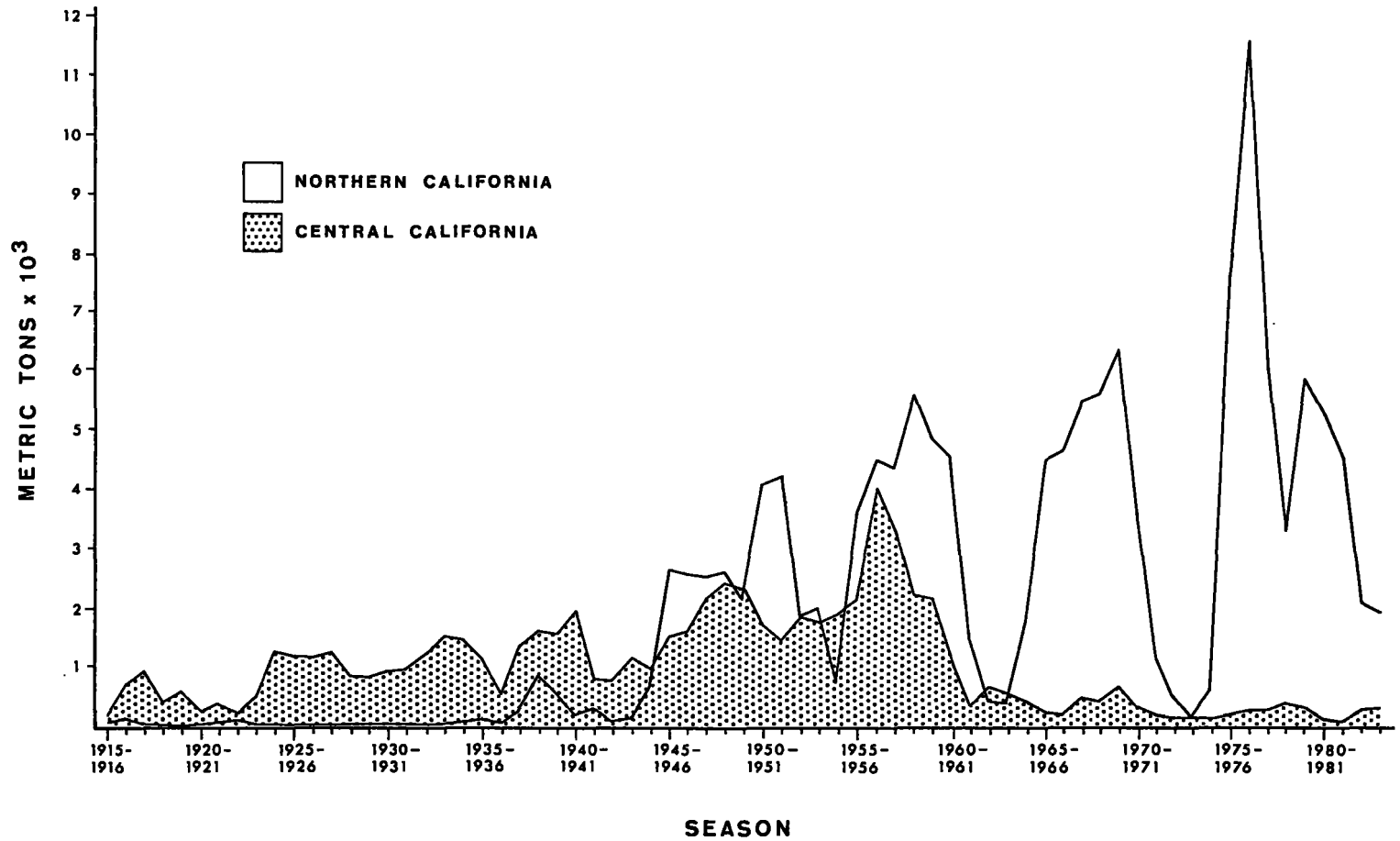


FIGURE 2.—Northern California (Crescent City, Eureka, Fort Bragg) and central California (Bodega Bay, San Francisco, and Halfmoon Bay) commercial Dungeness crab landings in thousands of metric tons, 1950-51 through 1983-84 seasons.

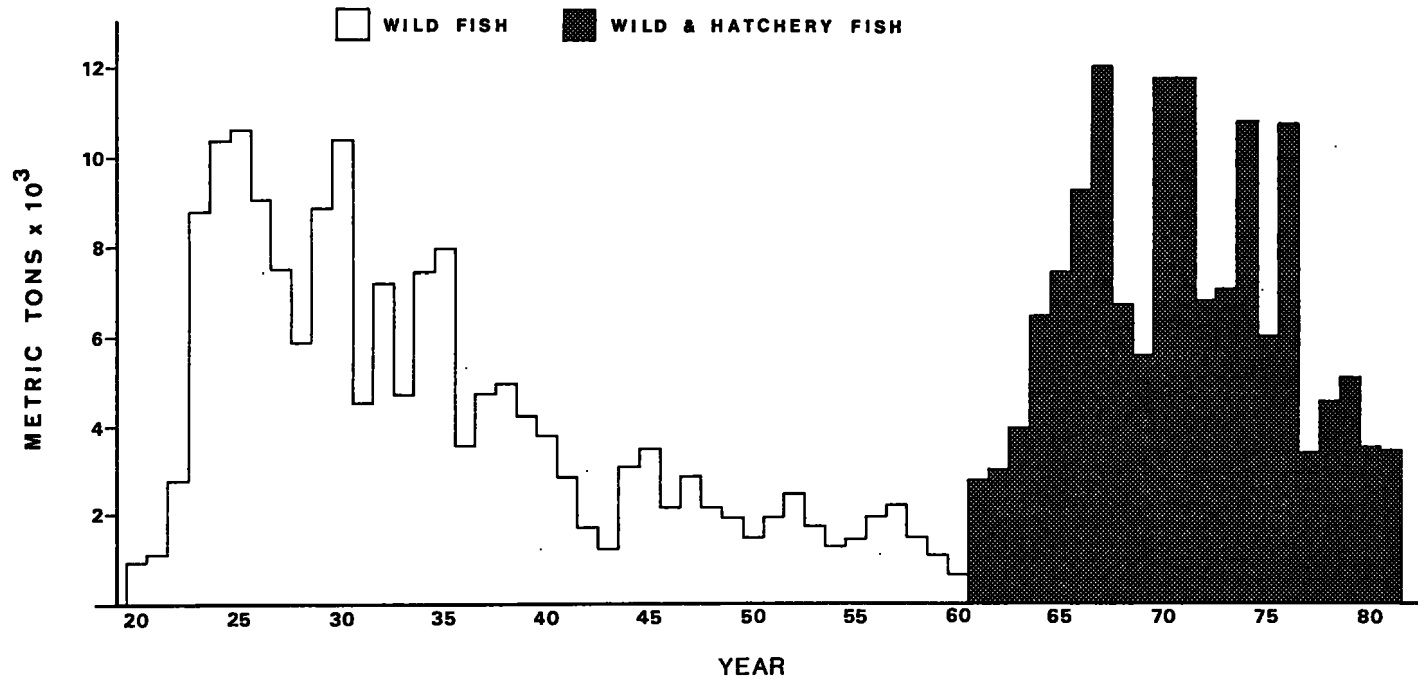


FIGURE 3.—Coho salmon landings in the Oregon Production Index area, 1920 through 1981, in thousands of metric tons. Figure adapted from Oregon Department of Fish and Wildlife (1982).

ington coastal waters each spring. Coho returning to the coast south of their natal stream would subsequently undergo the observed northward spawning migration. Each of these authors conceded however, that certain stocks or different portions of the same stocks may follow entirely different migratory routes. Scarnecchia (1981) felt that many coho produced along the west coast may either remain in adjacent coastal waters or move directly south after emigration from freshwater.

The dispersal pattern of 437 coho salmon tagged off northern California early in the 1971 and 1972 seasons clearly showed the northward movement of adult coho out of California (O'Brien 1973). Nearly all of the tagged fish recaptured in California were caught in May and June of each year while tagging was still being conducted. Oregon recoveries peaked in July and the first half of August, while most Washington recoveries occurred during the latter half of August through September.

California's share of the recaptured coho tagged off northern California (O'Brien 1973) was 9.3% in 1971 and 8.8% in 1972. These percent returns are very similar to California's 13.0% and 8.3% share of the O.P.I. area catch in 1971 and 1972 respectively. Because, for practical purposes, one can assume that all of the coho caught in California originate to the north, the similarity between California's catch and tag returns would indicate that nearly all O.P.I. area coho stocks were off California during the tagging period. This supposition is extreme, but the results do suggest that a major portion of the coho ultimately caught in the O.P.I. area each year are in California waters during spring. The northward migration of large numbers of coho is further supported by the northward progression of peak monthly catches within the O.P.I. area (Pacific Fishery Management Council 1983), and the monthly catch distribution of hatchery marked coho (Hopley 1978).

Survival Indices Comparison and Discussion

Dungeness crab, unlike coho salmon, do not move any appreciable distance, therefore local landings are considered to be a good indicator of local abundance. In California seasonal landings are composed of at least three year classes, however northern California landings are generally dominated by 4-yr-old crab (Warner 1985), while central California landings, because of a faster growth rate, are dominated by 3-yr-old crab (Collier¹).

An alignment of Dungeness crab seasonal landings

with their dominant or "primary" year classes (Fig. 4) generates reasonably representative year class indices, if it is taken into consideration that extremely abundant year classes, such as the 1966 and 1972 year classes in northern California, probably dominate landings for more than 1 yr (Methot and Botsford 1982). The Dungeness crab year class indices (Fig. 4) suggest that a period of poor landings in both central and northern California during the early 1960's (Fig. 2) reflects poor survival of the 1958-60 year classes.

As mentioned earlier, northern California landings have been characterized by large seemingly cyclic fluctuations, the cause of which has been the subject of considerable research and debate (see Methot and Botsford 1982; Botsford 1984, for a review of this work). Of the hypotheses generated by these investigations, Wild et al. (1983) presented, in my opinion, the most tenable explanation for this particular period of low survival. They attributed the drop during this period to a reproductive failure caused by an unprecedented warming of coastal waters associated with the 1957 El Niño (the "warm water years" 1957-59, Radovich 1961).

The apparent recruitment of Dungeness crab to the northern California population of a "normal" year class in 1961 (Fig. 4), with the return of "normal" environmental conditions, ushered in several years of good survival. This recovery was not duplicated in the central California population, where a drop in the strength of the 1961 year class anteceded an extended period of poor survival. Wild et al. (1983) further proposed that a major change in the oceanic regime off central California is the primary cause of the continued poor survival there, although they do concede that ocean temperatures in certain years appear to have been favorable to Dungeness crab survival. Wickham (1979), on the other hand, suggested that the central California population has reached a new equilibrium, with worm predation now being the dominant biological control. It has yet to be proven which, if either, of these mechanisms is the primary cause of the continued poor survival in central California.

Alternatively, a direct comparison of O.P.I. catches with central California Dungeness crab year class indices (Fig. 5) illustrates a long-term inverse relationship which developed with the first recruitment of hatchery-reared coho salmon stocks in 1961. O.P.I. area landings are used to express the annual survival of coho potentially impacting central Califor-

¹P. Collier, California Department of Fish and Game, 619 Second St., Eureka, CA, 95501, pers. commun. November 1984.

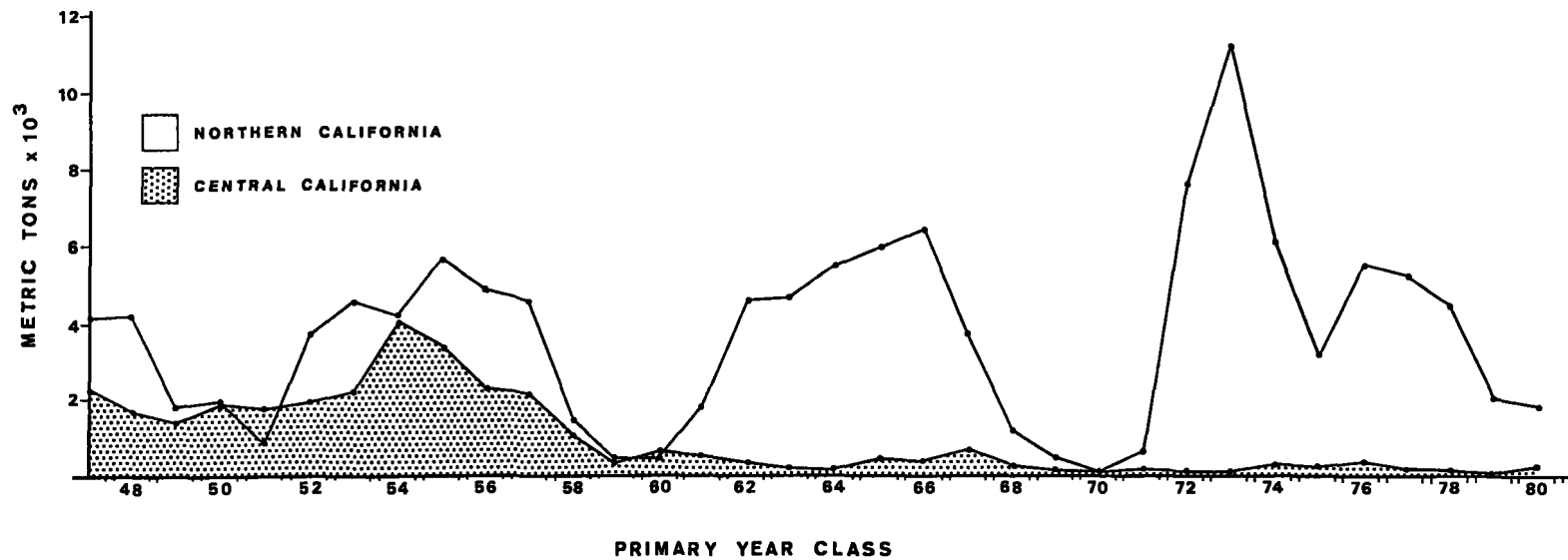


FIGURE 4.—Alignment of "primary" Dungeness crab year classes (1947-80) with the seasonal landings they dominate. Landings are lagged 3 yr in central California and 4 yr in northern California.

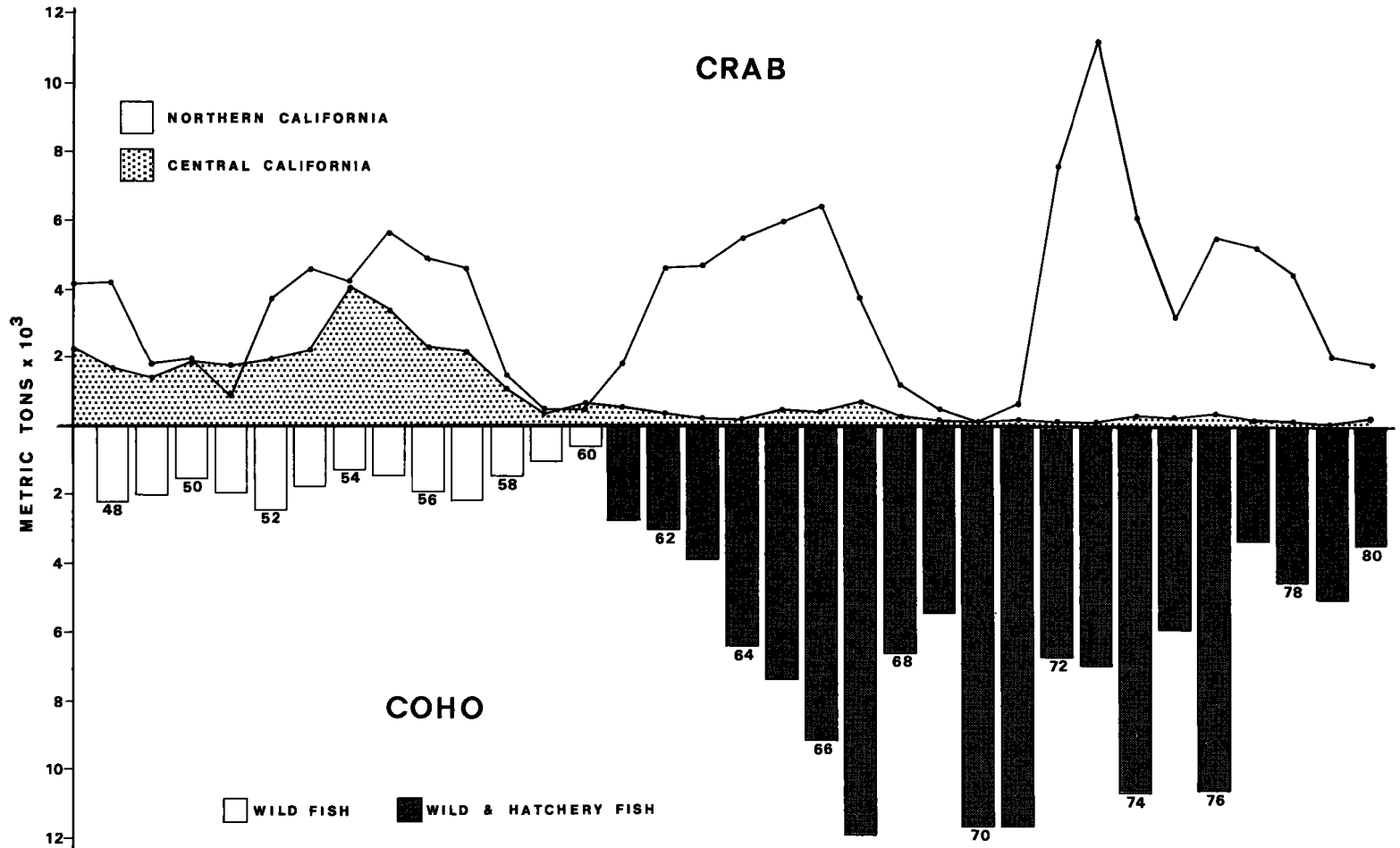


FIGURE 5.—Northern and central California Dungeness crab year class indices (primary year classes) 1947-77, aligned with Oregon Production Index area coho salmon landings, 1948-80.

nia Dungeness crab because of the evidence that California catch statistics underestimate the number of fish actually in the state during spring. These landings provide a straightforward measure of brood survival that is independent of distribution and local catchability.

Even though the relatively low O.P.I. area landings in 1961, 1962, 1963, 1977, and 1980 are comparable with the predecline era, the general pattern of correspondence in Figure 5 is consistent with an increase in the coho salmon predation rate on Dungeness crab megalops. Within the framework of the predator-prey hypothesis, the association of low O.P.I. area coho catches during the early years of the hatchery era with reduced Dungeness crab survival would indicate that a relatively small number of hatchery coho can effectively suppress megalops survival. This is particularly apparent when it is considered that hatchery production was at a minimum during the 1961-63 period and wild fish still dominated the catch (Oregon Department of Fish and Wildlife 1982).

The proposed impact of hatchery coho salmon on the Dungeness crab resource is best explained by the differences in the "functional response"² of wild and hatchery coho salmon. In controlled behavioral experiments, Glova (1978) found that hatchery fry (43-88 mm) were largely nonterritorial, exhibiting a stronger tendency to aggregate than the wild fry. This behavioral pattern is believed to be the direct result of the unnaturally high densities found in hatchery operations. If adult hatchery coho retain this behavior, the tendency for Dungeness crab megalops to aggregate or "swarm" in coastal surface waters (Lough 1976) would theoretically make them more susceptible to predation (Eggers 1976). Also a reduction in the number of "search images" available to hatchery fish is believed to result in a more homogenous diet (Sosiak et al. 1979). Under these circumstances Dungeness crab megalops may become a more important component of the hatchery coho salmon diet.

The apparent good survival of the 1961-66 year classes in northern California (Fig. 5) suggests that the majority of the hatchery coho salmon produced during those years concentrated to the south of that population during the period when Dungeness crab megalops are most abundant. This supposition, together with recently acquired evidence that the central California Dungeness crab population is at

least partially dependent on the recruitment of southward drifting megalops (Hatfield 1983; Reilly 1983b), further suggest that the theoretical predation zone critical to the central California population lies somewhere in the region of strong upwelling and high productivity between the two populations (Fig. 1). Not surprisingly, commercial fishermen have found coho salmon concentrated either before or early in the season in this region. The coho salmon stocks initially released during the early 1960's may possess an innate affinity for these waters.

Northern California landings of the Dungeness crab declined again during the 1970-71 season (Fig. 2). This period of low landings is apparently due to poor survival of the 1967-71 year classes (Fig. 5), which cannot be readily explained by an extended period of warmer than normal water. The various hypotheses to explain the northern California fluctuations notwithstanding, it is possible that hatchery-reared coho salmon began to limit Dungeness crab survival in northern as well as central California, concomitant with increased hatchery production³ and/or environmental caused changes in distribution. There is some evidence from coho tagging that supports this supposition.

O'Brien (1973) reported that 17.3% of his returned tags were found in Oregon and Washington hatcheries during the 1971 season, whereas in 1972 only 3% were found in the hatcheries. An exceedingly strong 1972 Dungeness crab year class in northern California (Warner 1984) is in direct contrast with the very weak 1971 year class (Fig. 5) and is inversely related to the small number of tags found in hatcheries during the 1972 season. The small percentage of hatchery returns in 1972 suggest that there were fewer hatchery coho available for tagging in the northern California area during the 1972 season, and this could indicate relatively poor survival of hatchery fish throughout the O.P.I. area. It should be remembered that hatchery-reared coho theoretically have a much larger effect on Dungeness crab survival than wild fish.

Between 1972 and 1977 (Fig. 5), O.P.I. area coho survival and northern California Dungeness crab survival became more erratic. The association of relatively good Dungeness crab survival with good coho landings in 1974 and 1976 may, however, only indicate that coho were farther south than usual. McLain and Thomas (1983) showed that both 1973

²In predator-prey theory "functional response" is defined as the relationship between the rate at which individual predators consume prey and the density of that prey (Holling 1959).

³The number of hatchery-reared coho salmon released in the O.P.I. area increased from 7.5 million fish in 1960 to 60.8 million fish in 1981 (Oregon Department of Fish and Wildlife 1982).

and 1975 were years with an unusually weak California Countercurrent, or conversely, stronger than normal southward flow and cooler than normal coastal waters. If yearling coho do move directly into California waters after emigration from freshwater, then these anomalous conditions may have caused these fish to move farther south than usual, with the result that adult coho would have been south of the predation zone critical to the northern California Dungeness crab population in the spring of 1974 and 1976.

Since 1976 O.P.I. area coho landings have undergone an inexplicable decline in spite of increasing hatchery production. Theoretically, an increase in Dungeness crab survival should have accompanied this drop in coho survival. The drop in Dungeness crab survival, evident in Figure 5, is obviously inconsistent with the general theory but can be explained in two ways. First, it should be considered that the earlier O.P.I. area coho landings contained far fewer hatchery fish than those during the later years. It has been estimated that hatchery fish comprised 75% of the west coast coho catch by 1977 (Scarnecchia and Wagner 1980). Secondly, a coastal warming trend that began in 1976 (McLain 1983) may have resulted in a northward shift in coho distribution with a concomitant reduction in Dungeness crab megalops survival.

If coho have become the major limiter of Dungeness crab megalops survival within California, then the observed survival patterns suggest that a group of coho, possibly representing the original hatchery stocks, still experience consistently good survival and continue to move into the predation zone critical to the central California population. On the other hand, the more irregular Dungeness crab survival observed in northern California suggest that megalops survival there is more dependent on the vagaries of hatchery-reared coho distribution associated with environmental nuances.

Admittedly, most of the evidence used to support the predator-prey hypothesis is circumstantial. Nevertheless, three of the considerations presented—1) the fact that coho feed heavily on Dungeness crab megalops, 2) the evidence showing that many, if not most, Oregon and Washington hatchery coho are in California during the period megalops are most abundant, and 3) the coincidence of the extended central California Dungeness crab decline with a large increase in the number of hatchery coho within the O.P.I. area—suggest a possible relationship that deserves attention.

The capricious nature of predation on the early life stages of commercially important invertebrates undoubtedly contributes to the difficulties encountered

when attempting to manage these relatively short-lived species on a sustained yield basis. If the hypothesized relationship between coho salmon and Dungeness crab eventually proves to be correct, then the salmonid enhancement process itself can be considered an experiment, offering insight into the role predators play in controlling the commercial abundance of many marine species.

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