Recruitment of Pacific Whiting, *Merluccius productus*, and the Ocean Environment

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Introduction

Because Pacific whiting, *Merluccius productus*, is one of the most abundant fishes along the west coast of North America, its population dynamics have important consequences, not only for fishermen, but for the total ecosystem. Typically, the whiting population fluctuates markedly. For whiting and, indeed, for many other fish species, recruitment variability is the major component in stock dynamics and has a greater impact on stock production than variability in either growth or mortality (Doubleday, 1980). Whiting are long-lived and highly fecund, and their spawning produces billions of eggs each year. Since mortality during the first months of life is very high, changes in survival rates of only a few percent during egg and larval life probably generate large variations in recruitment (Gulland, 1965). It is believed that these changes in survival of early stages are the dominant cause of fluctuations in stock biomass. Like many other gadoids, recruitment of whiting does not appear to be closely coupled to the size of the spawning stock, at least over the range of stock sizes observed to date.

Pacific whiting are normally found over the continental shelf/slope within the California Current system, roughly from lat. 25° to 50° N. Most adults spend the summer months in the northern part of the range. In autumn, adults migrate southward from the Pacific Northwest waters to spawn in winter off the coasts of central, southern, and Baja California. After spawning, large fish migrate as far north as Vancouver Island, while eggs, larvae, and juveniles are found off the coast of the Californias.

The unique life history of Pacific whiting, as well as a good time series of data on planktonic, juvenile, and adult stages, has created an unusual opportunity to examine the relationship of the ocean environment to population dynamics. These data include larval surveys from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program of the Southwest Fisheries Center (since 1950) of the National Marine Fisheries Service (NMFS), midwater trawl surveys from the California Department of Fish and Game (CDFG) (since 1966), bottom trawl and midwater trawl/hydroacoustic surveys from the NMFS Northwest and Alaska Fisheries Center (NWAFC) (since 1965), and commercial fishery data collected by the NWAFC observer program (since 1973). In addition, one of the world's most extensive time series of oceanographic data, compiled by the NMFS Pacific Environmental Group, is available for the California Current region. Recruitment studies coordinated at NWAFC have combined analyses of the above data with modeling and laboratory and field studies to examine the causes and consequences of population fluctuations of whiting.

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Fluctuations of the Whiting Stock and Year-class Strength

Recruitment to the whiting population can be quite variable, as strong year classes appear infrequently and dominate the population for 5-7 years (see Figure 1 in Francis and Hollowed, 1985). Between the years 1970 and 1977, estimates of year-class strength are available from cohort analyses. The estimated number of 3-year-old recruits ranged from 0.16 to 2.37 $\times$ 10^9 individuals, a difference of about fifteenfold (Fig. 1). Prior to 1973, commercial catch data were not available and a year-class strength index (YCI) was calculated by totaling the contribution of 3-, 4-, and 5-year-old fish to research trawl surveys in successive years (Bailey, 1981). Figure 1 shows that the YCI is closely related to the estimate of the number of 3-year-old recruits calculated from cohort analysis where data for both indices exist ($R = 0.152 + 1.890$ YCI, $r^2 = 0.89$). Using this relationship, the time series for recruit abundance has been extrapolated back to 1960. Over this 18-year time series, estimates of recruitment range from about 0.03 to 2.82 billion age-3 individuals, which is a difference of about ninety-fold. In this time series, very strong year classes appeared in

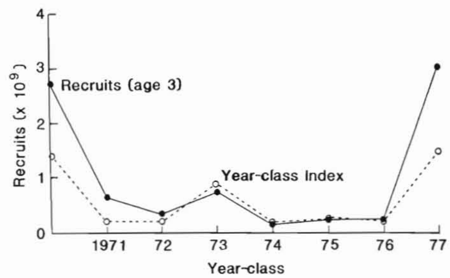

Figure 1.—The number of 3-year-old recruits estimated by cohort analysis (dots) compared with the index of year-class strength (circles), 1970-77.

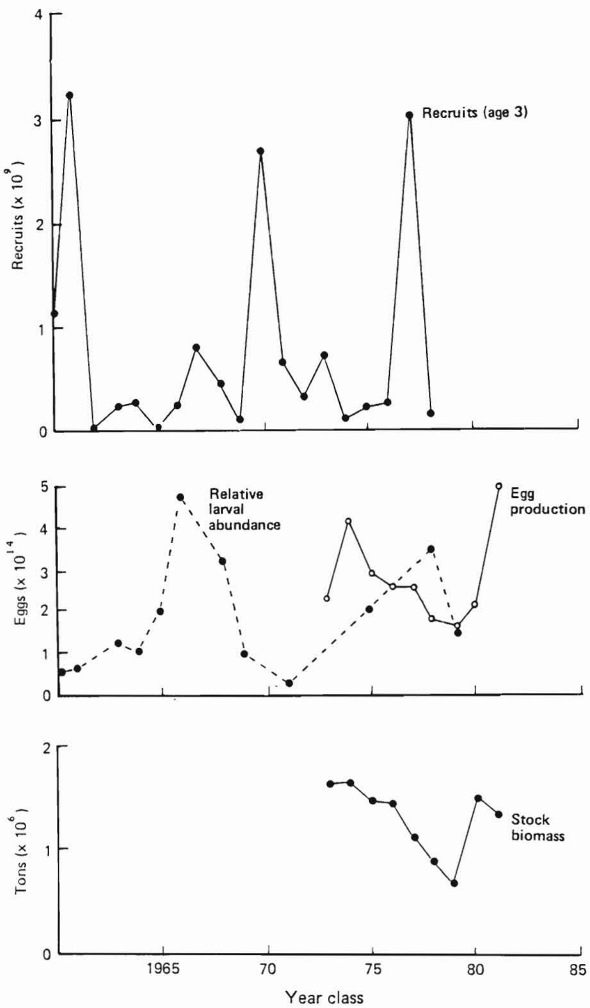

Figure 2.—The number of 3-year-old recruits (top), theoretical number of eggs produced by the spawning stock compared with larval abundance (middle), and estimated adult stock biomass (bottom) by year, 1960-81.

1961, 1970, and 1977. The years 1960, 1967, and 1973 were moderately strong year classes (Fig. 2). Preliminary data indicate that the 1980 year class is also very strong.

Estimates of stock biomass (age 3 and older fish) are also available from 1973 to 1981 (Fig. 2). Over this period, stock biomass declined to its low point in 1979 due to poor recruitment of the 1971-72 and 1974-76 year classes. In 1979 the stock was only 43 percent of its biomass in 1973. The stock was maintained by a moderately strong year class in 1973, and by the persistence of older fish from the 1970 year class. These two year classes totally dominated catches from 1974 to 1979. Whereas declines in stock biomass appear to be gradual (due to the longevity of whiting and the continued persistence of strong year classes), increases in stock biomass can be dramatic. For example, between 1979 and 1980 the estimated adult stock biomass approximately doubled due to the strong recruitment of the 1977 year class.

Rough estimates of spawning stock biomass can be reconstructed back to 1960 from historical ichthyoplankton surveys. This method assumes that the population of larvae is dominated by yolk-sac stages, that the number of larvae reflects the number of eggs spawned, and that the number of eggs spawned is directly related to the adult stock biomass. Since the surveys did not always occur in the same months each year, the numbers have been adjusted to account for time of survey. The analysis shows that peaks in larval abundance occurred in 1964-66 and in 1973-78 corresponding to the maturation and spawning of the strong year classes of 1961, 1970, and 1973. It is also possible to calculate the theoretical number of eggs produced by the population from the results of the cohort analysis (Fig. 2). These calculations tend to agree with the results of the larval surveys. However, reports of larval abundance from 1981 to 1983 indicate their numbers have declined despite the maturation of the strong 1977 year class. Since these recent surveys were conducted in March, their results may not be comparable to the earlier estimates from January and April surveys. Furthermore, 1981-83 were anomalously warm years, and spawning could have been earlier or farther north than the area covered by the March surveys. Alternatively, larval survival may have been extremely poor in these years, and larval abundance did not reflect actual spawning. Preliminary data do indicate that the 1981-1983 year classes will be weak.

Fluctuations in recruitment are apparently not a function of spawning stock biomass, as there has been no consistent trend in the relationship of these two variables. For example, the strong year classes of 1961 and 1970 were spawned by low biomass stocks, and the strong year classes of 1977 and 1980 were spawned by high biomass stocks. Furthermore, weak year classes were produced both in years of high (1966, 1968, 1975, 1976) and low (1963, 1964, 1971, 1979) spawning stock biomass.

The relative strength of a year class appears to be determined within the first months of a cohort's life. From

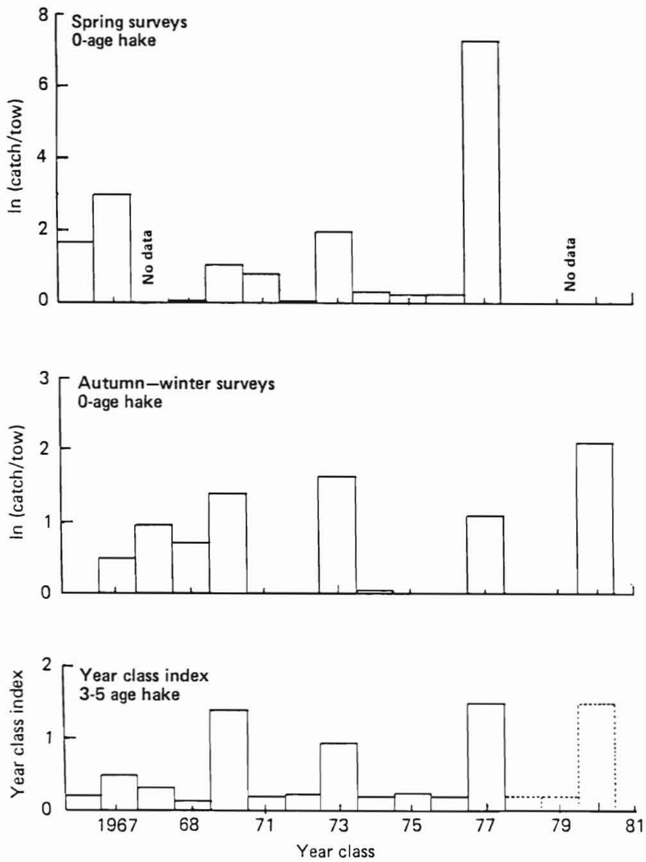

Figure 3.—Relative abundance of 0-age whiting caught in California Fish and Game midwater trawl surveys in spring (top) and autumn-winter (middle) compared with the index of year-class strength (bottom), 1966-80. Source: Bailey, K., K. Mais, and R. Francis. 1984. Incidental catches of 0-age Pacific whiting in midwater trawl surveys and forecasting year class strength. Unpubl. manuscr. Northwest Alaska Fish. Cent., NMFS, NOAA, Seattle, Wash.

analysis of midwater trawl data taken in CDFG spring and fall surveys, there is an evident relationship between postlarval abundance in the first 3-6 months (spring) of life and subsequent recruitment 3-5 years later (Fig. 3); postlarval young of the year appeared especially abundant in the spring months of 1967, 1970, 1973, and 1977. No survey data were available for spring 1980. By the autumn-winter in the first year of life, the 1970, 1973, 1977, and 1980 year classes appeared strong compared with all other year classes, and are indicative of their strength after recruitment to the fishery.

The data from these trawl surveys were collected from lat. 30° to 35°N, and are reported as catch/haul, uncorrected for duration of tow or net opening. The CDFG surveys were not systematically sampling for juvenile whiting, but recruitment strength is indicated by survey catches due to the extreme dynamics exhibited by the whiting population; i.e., there is either very good or very poor survival of larvae. More systematic surveys could be extremely useful for more precise management of the fishery, if and when that need arises.

Factors Affecting Year-Class Strength

Since recruitment appears to be established in larval life, a brief review of the larval environment is appropriate; a more complete description is available in Hickey (1979). The California Current system is characterized by four main currents. South of Point Conception, the surface California Current flows toward the Equator all year. North of Point Conception, this southward flow is replaced in winter by the poleward-flowing Davidson Current. In southern California a nearshore poleward-flowing countercurrent combines with the California Current to form the Southern California Eddy. Finally, there is a subsurface poleward flow known as the California Undercurrent.

The California Current system is driven by winds, which tend to blow poleward in winter and equatorward in summer. Upwelling events may occur during prolonged periods of strong equatorward winds (Bakun, 1973, 1975). These winds also cause advection, or horizontal movement, of cold, low-salinity water (subarctic water mass) equatorward and offshore. During relaxation of these winds or when winds blow poleward, warm saline water (the subtropical or Central Pacific water masses) flows poleward and spreads inshore. Since each water mass has its own characteristic planktonic community (Brinton, 1981), advective events have a strong effect on the composition and abundance of the zooplankton. Zooplankton biomass is normally highest in the northern portion (Point Conception to Point Reyes) of the region inhabited by whiting larvae, and abundance decreases in offshore and equatorward directions (Chelton, 1982). Large-scale variability in zooplankton abundance does not appear to be closely coupled to upwelling simply as an influx of nutrient-rich water, but rather to large-scale advective and flow patterns (Chelton, 1981; Bernal, 1981).

Spawning of whiting within the California Current system, as determined by the distribution of eggs and small larvae, appears to take place from Janauary to March in a region of transitional nature between central and Baja California. However, in

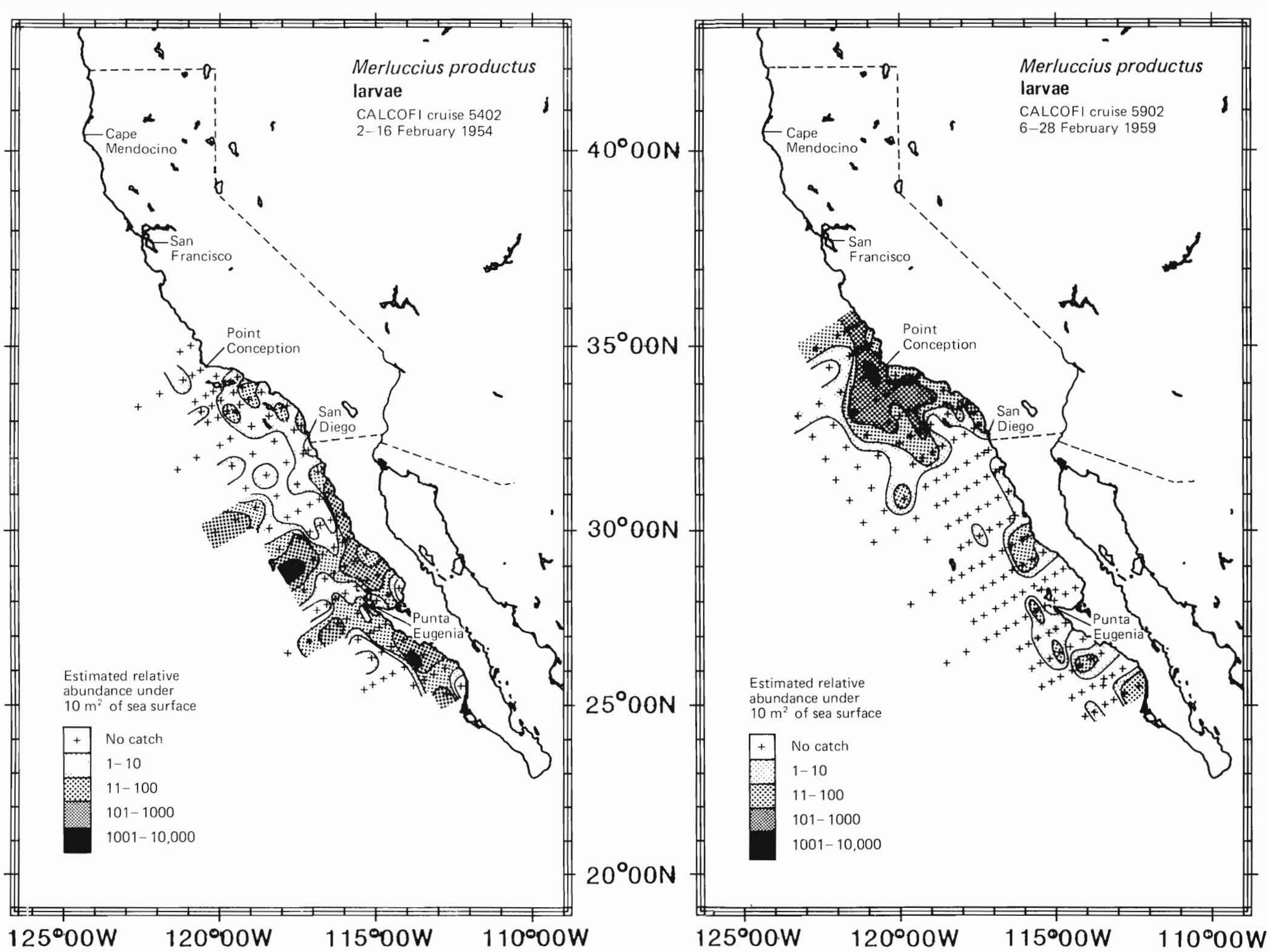

Figure 4.—Comparison of the north-south, onshore-offshore distribution of whiting larvae in a cold year (1954) and a warm year (1959). Source: Ahlstrom 1969.

periods of unusually warm or cold temperatures, spawning may occur considerably to the north or south, respectively. For example, in 1954, a cold year, larvae were distributed southward and offshore compared with larval distribution in 1959, a warm year (Fig. 4). As sampling for spawning adults has been unsuccessful, it is not known if larval distribution is a result of advection or actual spawning location.

After hatching, whiting larvae live below the upper mixed layer. As a consequence of living in cold water, the growth and developmental rates, metabolic rates, and energy requirements of whiting larvae are low (Bailey, 1982) compared with other larvae such as anchovy and mackerel living in the same geographic region but located in the warm upper mixed layer. Whiting larvae also have relatively large mouths compared with other larvae and are able to feed on a wide spectrum of food particles (Hunter, 1981; Sumida and Moser, 1980).

The determination of whiting year-class strength appears to be related to environmental conditions in the California Current ecosystem within the first few months of life. However, our present understanding of this relationship is probabilistic and not deterministic. Previous studies using linear regression analysis showed direct relationships between environmental conditions and recruitment, but these studies were limited by a short time-series (Bailey, 1981). The inverse relationship between recruitment and upwelling or temperature has not remained as strong in recent years. However, it appears that certain conditions are required for good larval survival, while other conditions apparently decrease survival. From 1960-77, cold years produced weak year classes in 7 of 7 cases (Fig. 5). On the other hand, all strong year classes

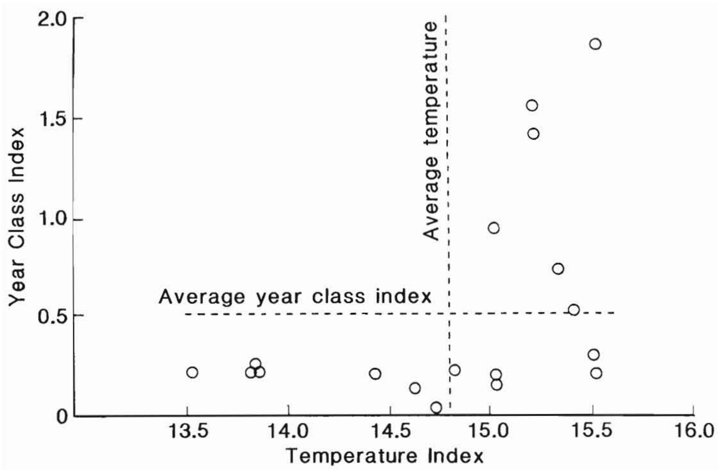

Figure 5.—The year-class index as related to the mean sea-surface temperature in the area and at the time of spawning (Marsden square 120-2, January-March). Dotted lines are the mean values for the sea-surface temperature and year-class index.

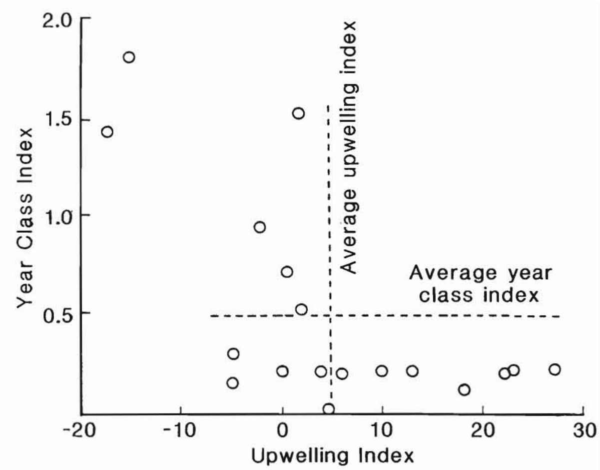

Figure 6.—The year-class index as related to the upwelling index in the area at the time of spawning (36°N, January). Dotted lines are the mean values for the upwelling index and the year-class index.

resulted from spawning in warmer than average years, although not all warm years resulted in strong year classes. Preliminary qualitative data indicate that the 1978 (warm) and 1979 (warm) year classes will be weak, and the 1980 (warm) year class will be very strong. We may hypothesize that cold years consistently produce weak year classes due to the presence of some dominant large-scale environmental conditions, and warm years may produce strong year classes, but there is much variability in warm years due to the multiplicative effects of many environmental forces acting on larval survival.

A comparison of sea-surface temperatures in warm years that produce strong year classes with cold years that produce weak year classes shows marked differences. In cold years, equatorward flow and upwelling are dominant events, pushing the 60° F isotherm south to Point Eugenia (27°N). Isotherms tend to be oriented parallel to the coast, and the nearshore water is cold in the region where whiting normally spawn. By contrast, in warm years the 60° F isotherm lies at the southern end of the Los Angeles Bight (30° N), isotherms are nearly perpendicular to the coast, and nearshore water is warm. These marked differences may 1) affect the location of spawning by adults, 2) influence the local conditions that determine larval survival (e.g., food production, predator abundance, etc.), and 3) reflect events that themselves influence survival (e.g., advection).

In cold years of strong upwelling, whiting larvae are often found offshore. Either advection of eggs and larvae or spawning by adults offshore may be detrimental to larval survival. Although a strong linear correlation does not exist between year-class strength and offshore transport, all strong year classes were spawned in years of lower-than-average upwelling (Fig. 6). Strong upwelling has always resulted in weak year classes. Unfortunately, these effects are difficult to separate from the covarying effects of temperature. Some evidence exists indicating that whiting larvae located offshore have slower growth rates and may not be surviving (Bailey, 1981). Furthermore, by the summer after spawning, virtually all surviving postlarvae are located over the continental shelf or near islands in the Los Angeles Bight. From CDFG midwater trawl surveys, it is seen that all large catches of 0-age whiting are inshore over the shelf/slope, even though eggs and larvae may have been distributed far offshore (Fig. 7). Theilacker[1] reports from histological studies that 60-70 percent of first-feeding jack mackerel, *Trachurus symmetricus*, larvae in the open ocean (200 miles offshore) are starving, whereas only 6-12 percent near islands or banks in the Los Angeles Bight are starving. Also supporting the hypothesis that larvae located offshore are starving is the Arthur (1977) study demonstrating that the abundance of zooplankton suitable as larval food decreases in an offshore direction.

Spawning by adults southward or advection of eggs and larvae in that direction may also be detrimental to survival. Zooplankton abundance decreases toward the south where the continental shelf is also narrow, limiting suitable juvenile habitat. Even though larvae may be abundant

[1]Theilacker, G. 1984. Starvation-induced mortality of young sea-caught jack mackerel *Trachurus symmetricus*, determined with histological and morphological methods. Southwest Fish. Cent., NMFS, NOAA, La Jolla, Calif. (Abstr. presented at Int. Symp. on the Early Life History of Fishes, Univ. Brit. Col., Vancouver, B.C. May 6-10, 1984.)

off Baja California in some years, large catches of juveniles there are relatively uncommon.

Growth may be poor in offshore regions; however, there is no evidence that surviving larvae or postlarvae in nearshore regions that produced strong year classes grew any faster compared with larvae producing weak year classes. Although sample sizes are small, a comparison of length vs. otolith increments from 1977 to 1979 shows wide variability with no apparent differences in growth between the strong 1977 year class and the weak 1978 and 1979 year classes (Fig. 8). In fact, there is some evidence that strong cohorts may grow slower as juveniles due to density-dependent effects (Dark, 1975). There have been no comparisons of larval growth in cold years as opposed to the above warm years. However, in cold years, due to offshore spawning or transport, a larger proportion of larvae may inhabit waters where food is less plentiful, causing a lower proportion of the population to survive. Although counting otolith increments may be a valuable tool for ageing fish larvae, measuring growth rates from otolith increments and body lengths may be inadequate for comparisons due to shrinkage of larvae during sampling (Theilacker, 1980); a more sensitive technique may be histological examination of larvae for evidence of starvation (Theilacker, 1978; O'Connell, 1980).

Little is known about predators of whiting eggs and larvae, and much less is known of their impact on the population off the California coast. Hunter (1981, 1984) reviewed the potential predators of anchovy and gadoids. Hunter and Kimbrell (1980) found that anchovy adults consumed large numbers of their own eggs;

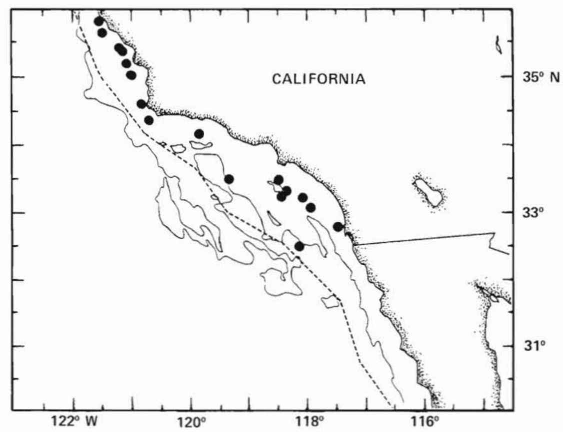

Figure 7.—The location of catches of juvenile whiting >1000 fish/haul in California Fish and Game midwater trawl surveys. The area generally covered by the surveys is surrounded by the dashed line.

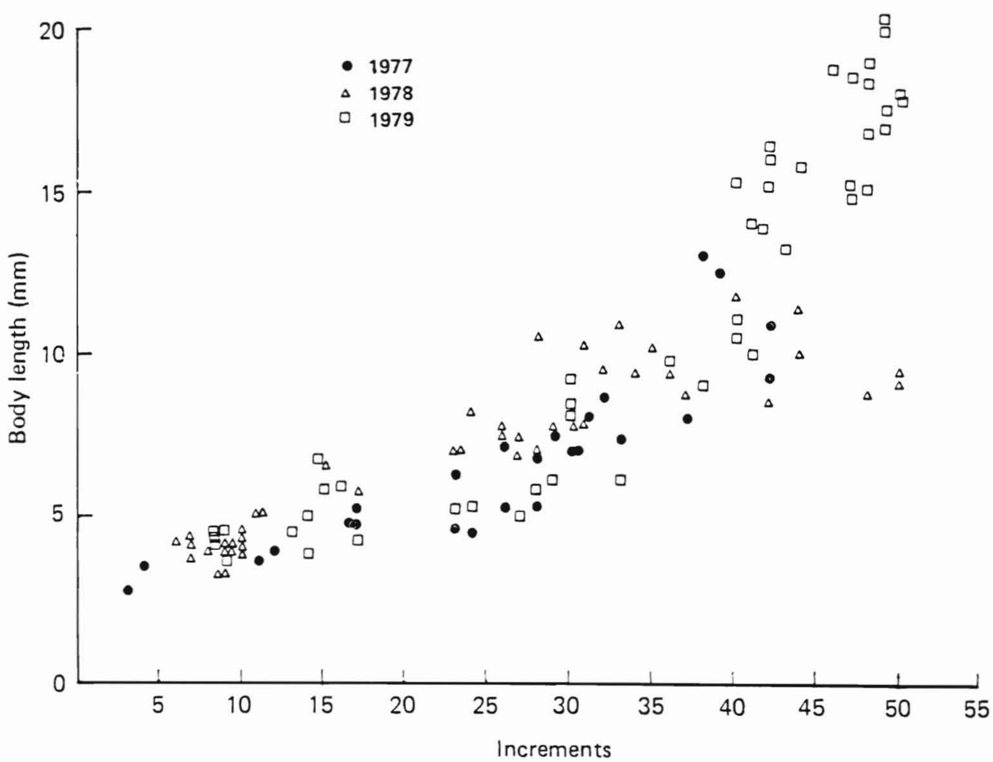

Figure 8.—The length of whiting larvae as related to otolith increments in 3 years, 1977-79.

however, Hunter[2] reports finding few if any whiting eggs. A study of predation on whiting eggs and larvae by invertebrate animals in Puget Sound attributed a significant decline in egg and larval survival to an increase in the predator population. The predatory copepod *Euchaeta elongata* was identified as a major predator on the basis of melanin pigments from fish larvae in its guts. Yolksac and starved first-feeding whiting larvae were the stages most vulnerable to *E. elongata* in simultaneous laboratory studies. Slowed growth and starvation were identified as environmentally controlled processes which could extend the duration that larvae are in these vulnerable stages (Bailey and Yen, 1983).

Predation on eggs and larvae of some species is currently considered to be a major source of larval mortality that can generate variability in recruitment. Because of their small size, gadoid larvae, in general, are extremely vulnerable to predators when compared with the larger larvae of herring and some flatfish (Bailey, 1984). Considering this importance, there is a disproportionate lack of research on predation of larvae relative to studies of larval feeding. Several new methods show great promise in studies of predation, including immunological techniques (Feller, 1982), identification of whole larvae (Purcell, 1981), fish otoliths (Yen[3]), and fish pigments (Bailey and Yen, 1983) in predator guts, and encounter rate models (Bailey and Batty, 1983). Given development of these methods, our knowledge of the importance of predation over the next few years should increase dramatically.

Predation on juvenile whiting probably is not a major source of variability in recruitment. First, from the evidence presented above, we believe that the strength of a year class is largely determined within the first few months of hatching. Second, juvenile whiting do not appear to be the major prey of large fishes in the California Current system. Third, changes in the abundance of large predators occur over a long time period compared with the interannual variability in recruitment. Fourth, some rough calculations show that one major type of predator, marine mammals, has little impact on the population. The maximum annual consumption of whiting by its three main mammal predators, California sea lions, northern sea lions, and northern fur seals, is about 100-200 million kg given a daily consumption rate of 10 percent body weight per day (Bailey and Ainley, 1982). Given a more conservative ration of 5 percent body weight per day and an average fish weight of 0.32 kg (most prey are 2- to 4-year-olds) this calculates to 150-300 million fish. Of these, perhaps 50 percent will be from a single year class (80-150 million fish). These numbers are 20-40 times smaller than the rather conservative estimates of recruitment that result from a cohort analysis. These predators may have an effect on weak year classes; however, when whiting are not abundant, mammals appear to switch to feeding on rockfish and perhaps squid (Bailey and Ainley, 1982; Antonellis and Perez, In press). When a strong year class appears, nearly 90 percent of the diet of marine mammals may be composed of whiting (Bailey and Ainley, 1982). Regardless of this high predation pressure, strong year classes survive to remain abundant up to age 10. Consequently, it appears that a strong year class can swamp the predatory capacity of the ecosystem.

Discussion

Bernal (1981) evaluated the importance of the interaction of the physical oceanographic environment with planktonic organisms in the California Current. He concluded that interannual variability in the strength of the current and related flow patterns determine the behavior of the biological component of the ecosystem. Furthermore, he hypothesized that this ecosystem might not operate under equilibrium conditions, and that classic interactive biological processes, such as competition and predation, might play a secondary role in regulating the abundance of species when compared with the role of physical conditions. Whereas Bernal's thesis related to zooplankton, the importance of environmental variability (Parrish et al., 1981) and the lack of equilibrium conditions might apply also to fish production in the California Current region. Recent developments in ecological theory (Lewin, 1983) concur with the idea that the assumption of equilibrium conditions is not valid in ecosystems where environmental perturbation may be a dominant feature.

In the California Current, the dynamics and production of fish populations are strongly influenced by environmental processes. These processes may affect the feeding of young fishes and predation upon them. This argument is supported by the dynamics of the whiting stock; recruitment is apparently tied to environmental conditions during early life, and, at our current state of understanding, predatory or competitive interactions involving older juveniles appear to be of secondary importance to recruitment. However, at low levels of stock abundance, predation may have a significant effect on recruitment. The influence of favorable environmental years is not restricted to observations of whiting, but also is seen for many other species. For example, where information on relative recruitment of different species exists, it is obvious that 1961, 1970, and 1977 were exceptionally good recruitment years for many species from southern California to the Gulf of Alaska (Hollowed et al.[4]).

[2]Hunter, J.R. 1983, Southwest Fish. Cent., NMFS, NOAA, La Jolla, Calif. Pers. commun.
[3]Yen, J. 1984. Predation on larvae of the cod (*Gadus morhua* L.) by the predatory copepod, *Euchaeta norvegica*. Unpubl. manuscr. Department of Oceanography, Univ. Hawaii, Honolulu, Hawaii 96822.

[4]Hollowed, A., K. M. Bailey, and W. S. Wooster. 1984. Coherence in year-class strengths of fishes along the west coast of North America. Unpubl. manuscr. Northwest Alaska Fish. Cent., NMFS, NOAA, Seattle Wash.

Although more is known about the dynamics of the whiting stock than about most other fishes in the eastern North Pacific, little is known about the underlying causes of recruitment fluctuations. It is apparent that cold years demonstrate little variability in recruitment and the likelihood of a strong year class is small. In warm years the variability in recruitment is much higher with greater probability of a strong year class. Compared with warm years, spawning in cold years is further south, eggs and larvae develop more slowly, predation mortality may be higher, and advection offshore or southward may be more significant. How these conditions result in the relative success or failure of a year class is not presently well understood. Considering the importance of whiting as a keystone species to the California Current ecosystem, more research is needed. This research should include work on 1) temporal and spatial variability in spawning related to environmental conditions; 2) comparative growth and starvation condition of larvae in areas hypothesized to be favorable and unfavorable nursery grounds, i.e., onshore vs. offshore and the Los Angeles Bight vs. coastal Baja California; 3) the process of egg and larval advection in relation to oceanographic conditions; 4) predation on eggs and larvae and development of techniques to quantify predation effects; 5) the biology of juvenile whiting, including studies of otoliths to determine the birthdate distribution of survivors; 6) development of midwater trawl surveys for estimation of prerecruit abundance; and 7) effects of predators on the dynamics of juvenile whiting, especially at low levels of whiting stock abundance.

Literature Cited

Ahlstrom, E. H. 1969. Distributional atlas of fish larvae in the California Current region: Jack Mackerel, *Trachurus symmetricus*, and Pacific hake, *Merluccius productus*, 1951 through 1966. Calif. Coop. Oceanic Fish. Invest. Atlas 11, 187 p.

Antonellis, G. A., and M. Perez. In press. Estimated food consumption by northern fur seals in the California current. Calif. Coop. Oceanic Fish. Invest. Rep.

Arthur, D. K. 1977. Distribution, size and abundance of microcopepods in the California Current system and their possible influence on survival of marine teleost larvae. Fish. Bull., U.S. 75:601-612.

Bailey, K. M. 1981. Larval transport and recruitment of Pacific hake, *Merluccius productus*. Mar. Ecol. Prog. Ser. 6:1-9.

________. 1982. The early life history of the Pacific hake, *Merluccius productus*. Fish. Bull., U.S. 80:589-598.

________. 1984. Comparison of laboratory rates of predation on five species of marine fish larvae by three planktonic invertebrates: effects of larval size on vulnerability. Mar. Biol. (Berl.) 79:303-309.

________, and D. Ainley. 1982. The dynamics of California sea lion predation on Pacific hake. Fish. Res. 1:163-176.

________, and R. S. Batty. 1983. A laboratory study of predation by *Aurelia aurita* on larval herring (*Clupea harengus*): Experimental observations compared with model predictions. Mar. Biol. (Berl.) 72:295-301.

________, and J. Yen. 1983. Predation by a carnivorous marine copepod, *Euchaeta elongata* (Esterly), on eggs and larvae of the Pacific hake, *Merluccius productus*. J. Plankton Res. 5:71-82.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671, 103 p.

________. 1975. Daily and weekly upwelling indices, west coast of North America, 1967-73. U.S. Dep. Commer., NOAA Tech. Rep. SSRF-693, 114 p.

Bernal, P. A. 1981. A review of the low-frequency response of the pelagic ecosystem in the California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 22:49-64.

Brinton, E. 1981. Euphausiid distributions in the California Current during the warm winter-spring of 1977-78, in the context of a 1949-66 time series. Calif. Coop. Oceanic Fish. Invest. Rep. 22:135-154.

Chelton, D.B. 1981. Interannual variability of the California Current system—physical factors. Calif. Coop. Oceanic Fish. Invest. Rep. 22:34-48.

________. 1982. Large-scale response of the California Current to forcing by the wind stress curl. Calif. Coop. Oceanic Fish. Invest. Rep. 23:130-148.

Dark, T. A. 1975. Age and growth of Pacific hake, *Merluccius productus*. Fish. Bull., U.S. 73:336-355.

Doubleday, W. G. 1980. Coping with variability in fisheries. Food Agric. Organ. U.N., Rome, FAO Fish. Rep. 236:131-139.

Feller, R. 1982. Deep guts: A shallow-water solution using immunological methods, *In* G. M. Cailliet and C. A. Simenstad (editors), Gutshop '81, fish food habits study, p. 211-223. Univ. Wash. Sea Grant WSG-WO 82-2.

Francis, R. C., and A. B. Hollowed. 1985. History and management of the coastal fishery for Pacific whiting, *Merluccius productus*. Mar. Fish. Rev. 47(2):95-99.

Gulland, J. A. 1965. Survival of the youngest stages of fish and its relation to year-class strength. Int. Comm. Northwest Atl. Fish., Spec. Publ. 6:363-371.

Hickey, B. M. 1979. The California Current system—hypotheses and facts. Prog. Oceanogr. 8:191-279.

Hunter, J. R. 1981. Feeding ecology and predation of marine fish larvae. *In* R. Lasker (editor), Marine fish larvae: Morphology, ecology, and relation to fisheries, p. 33-77. Univ. Wash. Press, Seattle.

________. 1984. Inferences regarding predation of the early life stages of cod and other fishes. *In* E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal (editors), The propagation of cod, *Gadus morhua* L., Part 2, p. 533-562. Inst. Mar. Res., Flodevigen Biol. Stn., Arendal, Nor.

________, and C. Kimbrell. 1980. Egg cannibalism in the northern anchovy, *Engraulis mordax*. Fish Bull., U.S. 78:811-816.

Lewin, R. 1983. Predators and hurricanes change ecology. Science (Wash., D.C.) 221:737-743.

O'Connell, C. P. 1980. Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods. Fish. Bull., U.S. 78:475-489.

Parrish, R. H., C. S. Nelson, and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175-203.

Purcell, J. E. 1981. Feeding ecology of *Rhizophysa eysenhardti*, a siphonophore predator of fish larvae. Limnol. Oceanogr. 26:424-432.

Sumida, B. Y., and H. G. Moser. 1980. Food and feeding of Pacific hake larvae, *Merluccius productus*, off southern California and Baja California. Calif. Coop. Oceanic Fish. Invest. Rep. 21:161-166.

Theilacker, G. 1978. Effect of starvation on the histological and morphological characteristics of jack mackerel, *Trachurus symmetricus*, larvae. Fish. Bull., U.S. 76:403-414.

________. 1980. Changes in body measurements of larval northern anchovy, *E. mordax*, and other fishes due to handling and preservation. Fish. Bull., U.S. 78:685-692.