THE LIFE HISTORY AND FISHERY OF PACIFIC WHITING, MERLUCCIUS PRODUCTUS

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ABSTRACT
The Pacific whiting is one of the most abundant and important fishes of the California Current region. This report synthesizes available data, published and unpublished, on the life history and population dynamics of whiting. Aspects of the life history described are distribution, spawning, early life history, feeding, and growth. Information on the population dynamics of the stock is summarized with attention to stock abundance, recruitment variability, and mortality. A synthesis of the fishery, its development and management, is presented.

RESUMEN
Merluccius productus es una de las especies más abundantes e importantes en la región de la Corriente de California. En este trabajo se recopilan los datos publicados e inéditos sobre el ciclo de vida y dinámica de poblaciones de M. productus. Los aspectos del ciclo de vida que se discuten incluyen; distribución, puesta, fases larvales y juveniles, alimentación y crecimiento. La información sobre la dinámica de la población se resume en relación con la abundancia de las existencias, variaciones en el reclutamiento y la mortalidad. Se presenta además una síntesis de las pesquerías, su desarrollo y administración.

INTRODUCTION
Commercially and ecologically the Pacific whiting (also called Pacific hake), Merluccius productus, is one of the most important fish species on the west coast of North America. It supports a large commercial fishery that has been dominated by foreign nations. In recent years, however, a U.S. fishery has developed through ventures with foreign nations. Besides being an important resource to man, whiting is an important trophic link in the California Current ecosystem. As a large predator, whiting interacts with other fish and shellfish populations, notably the commercially important stocks of Pacific herring, Clupea harengus pallasi; northern anchovy, Engraulis mordax; and shrimp. Whiting is also important as prey in the diets of marine mammals and large fishes.

The objective of this synopsis is to synthesize available information on the biology and fishery of the coastal stock of Pacific whiting. Since the publication of a similar synopsis in 1970 (U.S. Fish and Wildlife Service 1970), a great deal of new information has become available. Most of this material is unpublished and thus is generally unavailable to scientists, managers, and fishermen. Further goals of this synopsis are to present new information, particularly concerning the migration of whiting, and to suggest areas of needed research.

THE CALIFORNIA CURRENT SYSTEM—THE HABITAT OF PACIFIC WHITING
Pacific whiting ranges from the Gulf of Alaska to the Gulf of California (Hart 1973); however, it is most abundant within the region of the California Current system. The California Current system is the eastern boundary current system of the North Pacific Ocean. It extends from the coastal divergence of the westwind drift at 45°N in winter (and 50° in summer) southward to about 23°N, where California Current water mixes with equatorial water and bends westward to form the North Equatorial Current. The California Current system is composed of (1) an equatorward surface flow—the California Current; (2) a seasonally occurring poleward surface current identified as the Davidson Current north of Pt. Conception, and as the California Countercurrent in southern California; and (3) a poleward subsurface flow—the California Undercurrent. Numerous gyres, including the Southern California Eddy, are semipermanent features of the California Current system. The individual currents are briefly discussed below; a more detailed review can be found in Hickey (1979).

The flow of the California Current is driven by winds and is slow, broad, and shallow. Water of the California Current is subarctic in physical and chemical properties at high latitudes, characterized by low salinity and temperature. As the water flows southward, it becomes more intermediate in nature through mixing with the high-salinity and high-temperature water of the North Pacific Current and the Central Pacific water mass. Eventually, California Current water becomes semitropical off southern Mexico after mixing with equatorial water.

The Davidson Current is the surface poleward flow north of Pt. Conception that develops in winter. The Davidson Current appears in October off Vancouver.
Island and develops later farther south. It exists off the Oregon-Washington coast from October until February and off the California coast from November until January.

The California Undercurrent is a northward flow of high-salinity, high-temperature water occurring seaward of the continental shelf and below the main pycnocline. Wooster and Jones (1970) reported that the undercurrent was found 75 km offshore of Cabo Colnett, Baja California, and was centered at 200-500-m depth off the Oregon-Washington coast. A poleward undercurrent develops over the continental shelf in late summer and early fall (Hickey 1979).

LIFE HISTORY

Stocks and Distribution

Stocks. At least four distinct stocks of Pacific whiting may exist. These include (1) a coastal stock ranging from Canada to Baja California, (2) a Puget Sound stock, (3) a Strait of Georgia stock, and (4) a dwarf stock found off Baja California. Two of the stocks, Puget Sound and the coastal stock, have been identified as genetically distinct spawning stocks (Utter and Hodgins 1971).

The separate identities of the dwarf and coastal stocks are at present controversial. Ahlstrom and Counts (1955) examined larvae found off Baja California and were not able to distinguish two separate stocks, thus supporting a concept of one spawning stock. However, MacGregor (1971) and Vrooman and Paloma (1977) discussed several differences in adult dwarf whiting found off Baja California compared with the adult coastal whiting found farther north. Dwarf whiting grow slower from age one onwards, mature earlier, and have several different morphometric and meristic characteristics compared with the coastal whiting. Vrooman and Paloma (1977) believed that these differences indicate separate stocks. However, the differences may not be genetic, and are not inconsistent with changes caused by environmental effects in the different habitats.

The remainder of this report deals with the coastal stock, which is the most abundant and commercially important.

Distribution. As indicated previously, Pacific whiting are found within the coastal region of the California Current system. Normally whiting are not caught seaward of the continental slope, although there are occasional reports of whiting eggs and larvae (as well as of juveniles and adults) far seaward of the slope (Frey 1971). The latitudinal distribution of whiting varies seasonally. In autumn adult whiting make an annual migration from the summertime feeding grounds off the Pacific Northwest coast to spawn in winter off the coasts of southern California and Baja California. In spring and summer, large fish migrate northwards as far as central Vancouver Island, and juveniles remain off the Californias. The migration of whiting is outlined in Figure 1 and is described in detail below.

Spawning

Spawning schools of Pacific whiting have been difficult to locate. Nelson and Larkins (1970), Tillman (1968), Bureau of Commercial Fisheries 19641, Erich et al. (1980), and Stepanenko report spawning schools off southern California in midwater at depths of 130-500 m and over bottom depths corresponding to those of the continental slope. (Spawmed at these depths, eggs float upwards to the base of the mixed layer.) Ermakov (1974) also reports spawning over the continental slope. However, Erich et al. (1980) report a spawning school some 400 km seaward in the southern part of the Southern California Eddy, and Stepanenko reports a spawning school about 300 km offshore in central California.

The distribution of eggs and small larvae (2-3 mm) indicates that whiting spawn from Cape Mendocino to southern Baja California. Almost all eggs and larvae are located over water depths corresponding to depths of the continental slope, except in the Southern California Eddy, where eggs and larvae are often found over very deep water and far out to sea (400 km). Bailey (1981a) postulated that whiting spawn in the California Undercurrent, which usually occurs over the continental slope at depths of 200-400 m, but spreads seaward some 200-400 km in the Southern California Eddy and some other locations where eddies occur. Large concentrations of eggs and larvae are found overlying areas of northward geostrophic flow at 200-m depth (Figure 2).

Variation may exist in the latitudinal distribution of spawning. The location of the apparent northern front of spawning is correlated to the sea surface temperature (Table 1). Assuming that temperatures at the sea surface are correlated to those at the depth of spawning, this indicates that in warm years when subtropical water is farther north, spawning occurs at higher latitudes. Alternatively, larvae may be transported by a northward flow.


By July/August moving to outer continental shelf.

WINTER
Migrating offshore over slope in California current (south)

AUGUST
Adults

JULY
Juveniles

MAY
Larvae up to 300 miles offshore

SPawning
Feeding
Main Schooling Area

Figure 1. Migratory patterns of Pacific whiting.
Figure 2. Large catches of Pacific whiting eggs and larvae (all size classes) in January surveys, 1950-79, plotted on a chart showing geostrophic flow at 200-m depth (from Wyllie 1967).
Larvae of all size classes occur in significant numbers in the water from December to May (Stauffer and Smith 1977), but some 80% of eggs and small larvae are found in two months, January and February (Figure 3), which indicates a sharp peak in spawning. Most Soviet reports also indicate that January and February are the primary spawning months, but sometimes heavy spawning is reported in March. Spawning is generally completed by late March; in several consecutive years Ermakov (1974) observed schools of whiting off northern California by early March.

Pacific whiting females mature and spawn at 3 to 4 years of age and at lengths of 34-40 cm (Best 1963; MacGregor 1966, 1971; Ermakov 1974). MacGregor (1971) found some males maturing at 28 cm. Spawning whiting do not appear to migrate vertically, and bilayered schools have been observed on sonar traces. (R. McNeely, Northwest and Alaska Fisheries Center, Seattle, WA 98112, pers. comm.; J. Mason, Pacific Biological Station, Nanaimo, B.C., pers. comm.).

Several modes of eggs appear in whiting ovaries (MacGregor 1966; Ermakov et al.4). MacGregor suggests that only one mode develops, because of the poor condition of the females, but he did not examine the ovaries histologically. Foucher and Beamish (1977) reported that only one mode of eggs develops in the Strait of Georgia whiting stock. Ovaries average about 8% of the body weight of spawning females. Ripe ovaries contain 80-600 advanced-mode eggs per gram of ovary wet weight (MacGregor 1966). An equation relating total fecundity to length of the female is \( E = 0.00142 \times L^3 \) (MacGregor 1966).

In a laboratory setting, predators capable of eating whiting eggs are numerous and include, among others, medusae, ctenophores, and amphipods (Bailey and Yen, in press). Whiting eggs may be somewhat resistant to tactile and small invertebrate predators because they are motionless and have a very hard cuticle. Fish predation may also be heavy: Ermakov and Kharchenko3 report finding the stomachs of threadfin bass, Anthias gordensis, full of whiting eggs off Baja California. Northern anchovy could also be feeding on whiting eggs, for they consume considerable numbers of their own eggs (Hunter and Kimbrell 1980) and are believed to feed at depths where whiting eggs occur (Holliday and Larsen 1979).

**Early Life History**

**Egg stage.** Ahlstrom and Counts (1955) described the eggs of Pacific whiting. They are smooth spheres, have a single oil droplet, and are 1.14-1.26 mm in diameter (after accounting for 7% shrinkage caused by preservation in Formalin). Egg hatching is temperature dependent (Bailey, in press; Zweifel and Lasker 1976). Whiting eggs may be expected to hatch in 100-120 hr at temperatures found at their habitat depth on the spawning grounds, where temperatures range from 11°C to 14°C.

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**Larval stage.** Ahlstrom and Counts (1955) described the larvae of Pacific whiting. They are distinguished by a pigment band around the tail, pigment
spots on the dorsal crown of the head, sturdy bodies, and 51-54 myomeres (Figure 4). Preserved yolk-sac larvae are 2.5-3.0 mm standard length. Shrinkage of larvae due to handling is highly variable, from 10-40% depending on the preservative and on the time from death to preservation (Bailey, in press; Theilacker 1981).

Time to absorption of the yolk is temperature dependent (Bailey, in press). At ambient temperatures, absorption of the yolk may take 120-200 hours. A mouth develops before the yolk is fully depleted, and yolk-sac larvae are observed to feed (Sumida and Moser 1980). Larvae take 150-250 hours to starve after yolk depletion (Bailey, in press).

Daily growth of whiting larvae has been described by counting growth increments on their otoliths (Bailey, in press). Growth in length appears to be slow and constant for the first 20 days, after which it rapidly accelerates (Figure 5).

In the laboratory, predators on yolk-sac larvae are more varied than those on eggs and include euphausiids, medusae, ctenophores, amphipods, and carnivorous copepods. Invertebrate predation on whiting larvae is stage- or size-specific; larger larvae are not as vulnerable to predators as yolk-sac larvae (Bailey and Yen, in press).

The diet of larval whiting is composed mostly of copepod eggs, calanoid copepod nauplii, copepodites, and copepod adults (Sumida and Moser 1980). Whiting larvae have relatively large mouths and feed on a broad size range of prey from 50-400 μm in width.

Competitors of whiting larvae in the ichthyoplankton sharing the same temporal and spatial distributions are California smoothtongue, Bathylagus stilbius, and snubnose blacksmelt, Bathylagus wesethi. Overlap in the vertical and horizontal distribution also occurs with Vinciguerria lucetia; rockfish, Sebastes spp.; and jack mackerel, Trachurus symmetricus. Numerous carnivorous invertebrates are also competitors.

The vertical distribution of whiting eggs and larvae. Eggs are released at 130-500 m in spawning, and most rise upwards to a depth of neutral buoyancy, usually at 40-60-m depth, near the base of the mixed layer (Ahlstrom 1959). If a strong pycnocline does not exist, eggs and larvae may be distributed through the mixed layer. Some evidence exists that larger larvae may be distributed deeper than small larvae (Bailey, in press).

Juvenile stage. Not much is known about juvenile whiting. Juveniles 1-3 years of age are found primarily off central and southern California (Figure 6). Most 0-1 year-olds occur inshore of the 200-fathom (fm) isobath, and older fish are distributed somewhat farther offshore than younger fish (Table 2). The food of juvenile whiting is mainly copepods and euphausiids (P. Livingston "The Feeding Biology of Pacific Whiting," in review).

Adult Life History

Migratory behavior. Tagging of Merluccidae has not proved feasible (Jones 1974); thus the migrations of Pacific whiting are inferred from survey and fisheries data.

Pacific whiting become scarce in survey catches (Table 3) and in the fishery (Table 4) from autumn until early spring (see also Jow 1973; Best 1963; Alton 1972), and whiting eggs and larvae are most abundant in winter off California. These observations have led to a hypothesis that adult whiting leave the coastal waters in autumn to migrate from the shelf and southward for spawning in winter, and then return northward in early spring (Alverson and Larkins 1969). This migratory pattern has been verified from more recent data (Ermakov 1974; Dark et al. 1980).

Speeds of migration may be estimated from the sequential appearance of fish up the coast after spawning. Postspawning accumulations of whiting normally
Figure 4. Stages of Pacific whiting larvae (from Ahlstrom and Counts 1955).
have appeared around San Francisco (38°N) in early March (Ermakov 1974; Erich et al. 1980) and have been later observed off southern Oregon (42°N) in the third week of April for five consecutive years from 1966 to 1971 (Ermakov 1974). A population traveling on this schedule would move, on the average, about 10 km/d. By May, concentrations appear off Vancouver Island. These estimated mean population speeds compare favorably to speeds obtained from direct observation of individual schools. Ermakov (1974) concluded from direct observation of a lead school that the northward migration is at speeds of 5-11 km/d.

Ermakov (1974) hypothesized that the timing of the spawning migration was linked to the seasonal appearance of the Davidson Current off the Oregon-Washington coast. Analysis of the movement of the Soviet fishing fleet in relation to Bakun's (1973, 1975) indices of wind stress tends to support this hypothesis. Adult whiting generally begin to disappear from the Pacific Northwest in autumn when the wind direction shifts and the Davidson Current appears.

Adult whiting also make seasonal inshore-offshore migrations. Ermakov (1974) reports that in spring and early summer whiting schools concentrate over the continental slope. By mid-June, a large portion of the stock moves inshore to depths less than 100 m. Later, in early August, whiting move offshore, and by mid-October they begin to migrate southward for spawning. These observations of bathymetric migrations are supported by data in Alton (1972) showing that the average depth of catches in bottom trawls decreased in early summer and increased in autumn (Figure 7). These movements are similar to the dynamics of the California Undercurrent, which is located over the continental slope in spring and spreads over the shelf in early summer (Huyer et al. 1975; Huyer and Smith 1976). Further research on the migration of whiting in relation to ocean currents is needed and would be of value to stock assessment and management efforts.

Adult whiting also migrate on a diurnal schedule. Fish are dispersed from near surface to 20-m depth at night (10 p.m. to 3 a.m.). They descend quickly at dawn and form schools. At night they rise to the surface again in 30-40 min (Nelson and Larkins 1970; Ermakov 1974). These diurnal migrations have been compared to the migrations of their primary prey, euphausiids, as a causal mechanism (Alton and Nelson 1970). As noted previously, spawning whiting do not appear to migrate vertically.

![Figure 5](image1.png)

**Figure 5.** The growth of larvae caught off southern California determined from otolith increments. A Gompertz curve was fitted to the data, \( Y = 1.72 \exp[3.15 (-0.02624 \cdot X)] \). Insert: daily growth for the first 20 days was better fitted with a straight line \( Y = 2.75 + 0.16X \) (from Bailey, in press).

![Figure 6](image2.png)

**Figure 6.** The distribution of biomass by International North Pacific Fisheries Commission area for each age class in the 1977 Northwest and Alaska Fisheries Center trawl survey: Area 1, Conception; Area 2, Monterey; Area 3, Eureka; Area 4, Columbia; Area 5, Vancouver (from Bailey and Ainley, in press).

## Table 4

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**TABLE 4**

The Proportion of Soviet Catches in the INPFC Vancouver-Columbia Area by Month, 1973-76
Schooling. Pacific whiting form schools in daytime near the bottom. Schools are sometimes shaped in bands composed of distinct clusters (T. Dark, Northwest and Alaska Fisheries Center, Seattle, WA 98112, pers. comm.) whose long axes are often parallel to isobaths (Nelson and Larkins 1970). Soviets reported that schools may be from less than 0.5 km up to 20 km in length and 0.25 to 3.2 km in width. Above the shelf, schools are, in general, within 20 meters of the bottom and are 6-12 m thick. Often the underside of a school is 2 m off bottom. Quite a bit of variability in school size, depth, and structure is observed (M. Nelson, Northwest and Alaska Fisheries Center, Seattle, WA 98112, pers. comm.), and school characteristics are more variable and less oriented over the continental slope than over the shelf (Nelson and Larkins 1970).

Ermakov (1974) concluded that schools are formed of similar-sized fish. He reports densities of 15-19 fish/1000 m³ in daytime and less than 1 fish/1000 m³ at night. Spawning schools of whiting form dense aggregations in the pelagic layer, ranging in depth from 100 to 500 m (Stepanenko6; Ermakov 1974; Nelson and Larkins 1970). Stepanenko7 reported one school of spawning whiting that was 4.2 miles long and had a biomass of 81 thousand MT.

Age and growth. Age compositions of commercial catches are determined from annual growth patterns observed from otoliths. The primary source of data on Pacific whiting age and growth comes from the analysis of commercial age compositions (Dark 1975; Francis 1982). Growth in length is rapid during the first 3 years, then it slows and approaches an asymptote in the oldest ages (10-13 yr). At about 4 years of age, females grow noticeably faster, and by age 11 may average 32 cm larger than males (Dark 1975).

Individual males may reach 66 cm, and some females may reach 80 cm in length. Growth in length was analytically described by the von Bertalanffy growth equation:

\[ l_t = l_\infty (1 - e^{-kt}) \]

where \( l_t \) = body length at age \( t \)
and \( l_\infty \), \( k \), and \( t_0 \) are parameters of the curve.

Table 5 gives values of these parameters estimated for Pacific whiting. Francis (1982) found that between ages 3 and 7 growth in length is not uniform throughout the main feeding season (April-October) and that it appears to reach a maximum during midsummer (June-August).

The length-weight relation empirically fits the following equation:

\[ W = a L^b \]

where \( W \) = weight in grams, and \( L \) = length in centimeters.

Table 6 gives estimates of \( a \) and \( b \) for Pacific whiting. By age 3, males have grown to between 50 and 60% of their total weight at age 11, and females to between 40 and 50% of their total weight at age 11. Males attain an average weight of between 900 and 1000 g by age 11 and females between 1100 and 1200 g. Francis (1982) found that growth in weight is markedly seasonal. During the winter spawning season (November-March), adults between ages 4 and 11 lose a minimum of between 5 and 10% of their total body weight, and during the feeding season (April-October) adults between ages 4 and 11 gain a minimum of between 11 and 30% of their initial body weight. Francis (1982)

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**Figure 7.** The average depth of Pacific whiting bottom-trawl catches by month, plotted from data in Alton (1972).
TABLE 7
The Percent Occurrence of Food Types in the Diet of Pacific Whiting Determined by Soviet Scientists

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<th>Food type</th>
<th>Washington-Oregon</th>
<th>California</th>
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<td>Month</td>
<td>Month</td>
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<tr>
<td>Euphausiids</td>
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<td>Shrimp</td>
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<td>Squid</td>
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<td>Fish</td>
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Washington-Oregon California
Month Month
6 9 10 3 4 5 6 11
99.6 1.2 40.2 83.3 83.1 99.8 84.0 93.5
9.9 1.2 4.0 8.3 8.3 9.9 8.4 9.3

Feeding. The feeding behavior of Pacific whiting has been studied by several investigators, but a comprehensive seasonal and geographic examination of feeding is lacking.

Adult whiting probably do not feed on the spawning grounds (Tillman 1968) but begin to feed "ravenously" during the postspawning migration north (Ermakov 1974). In summer, whiting are observed to feed at night towards the surface (Alton and Nelson 1970); however, if patches of prey are abundant near bottom, whiting may remain there at night to feed (Ermakov 1974).

There are apparent geographic, seasonal, annual, and size-specific differences in feeding behavior. The most frequently occurring prey items in the summer diet are euphausiids and Pacific sand lance, Ammodytes hexapterus, off Vancouver Island (Outram and Haegele 1972) and euphausiids and shrimps from California to Washington (Alton and Nelson 1970; Gotshall 1969a). Ermakov and Kharchenko* found that off Washington and Oregon euphausiids decrease also found that to accurately represent the seasonal dynamics of growth a separate weight-length equation was needed for each age. Figure 8 gives a comparison of the weight-age relationships arrived at by Dark (1975) for 1964-69 and Francis (1982) for 1976-80.

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Livingston ("The Feeding Biology of Pacific Whiting," in review) found that Pacific herring were an important component in the diet of whiting off Oregon-Washington in 1980, composing almost 70% of the diet (by weight) of whiting greater than 55 cm, and 50% of the diet of whiting less than 55 cm. Alton and Nelson (1970) found that in the spring and summer of 1965 and 1966, euphausiids, mostly Tysanoessa spinifera, composed 57% of the biomass of whiting stomach contents. Fish, mostly deepsea smelts or Osmeridae spp., composed another 34% of stomach contents.

Gotshall's (1969a) study demonstrated considerable seasonality in the diet of whiting off northern California. Crustaceans, which are the major food in spring

*See footnote 5 on page 85.

FIGURE 8. The annual growth in weight of Pacific whiting (from Dark 1975, solid lines) compared to seasonal estimates of growth by age class (from Francis, unpubl. manuscr., dotted lines).
and summer, decline in the diet in winter, and are replaced by fish as the dominant food (Figure 9). In spring and summer an average of 50-60% of the stomach contents of whiting was ocean shrimp; however, these results should be viewed conservatively because the sample size was small.

Larger whiting more frequently eat fish and less frequently eat euphausiids compared to smaller whiting (Figure 10). Larger whiting also appear to consistently eat more shrimp than smaller whiting (Figure 11).

The question of whether whiting's feeding on ocean shrimp is a significant factor in shrimp abundance has provoked some controversy. Catches of shrimp off the Oregon-Washington coast have increased significantly since the late 1960s, and this increase appears correlated to the harvest of whiting (Figure 12). It has been hypothesized that removing large whiting by fishing has reduced predation pressure on the shrimp population. This same trend has occurred off the California coast. However, other factors, such as increasing fishing effort or normal changes in abundance, cannot be ruled out as responsible for the increase in shrimp catches, and the question of a whiting-shrimp interaction deserves more rigorous examination. Francis (1982) briefly addresses this issue.


Bailey and Ainley (1982) analyzed otoliths collected from California sea lion scats at the Farallon Islands for 4 yrs, 1974-78, and describe the seasonal and annual dynamics of sea lion feeding on Pacific whiting. Sea lions fed most heavily on whiting, primarily juveniles, in spring and summer and may consume about 185 thousand tons each year.

### POPULATION DYNAMICS

#### Size of Stocks

The abundance of the Pacific whiting stock has been assessed from trawl-hydroacoustic surveys. In 1980 the abundance of whiting from central California to southern Vancouver Island over the continental shelf was estimated by scientists of the Northwest and Alaska Fisheries Center to be 1.52 million metric tons (MT). Most of this biomass was composed of juveniles off the coast of central California. From similar surveys in 1975 and 1977, the stock biomass was estimated at 0.44 million and 1.20 million MT (Table 9). Based on earlier surveys by the U.S. Bureau of Commercial Fisheries, Alverson (cited in Tillman 1968) calculated about 0.68 million MT of whiting. Estimates of whiting abundance based on hydroacoustic methods (Kramer and Smith 1970; Dark et al. 1980), however, have limitations. Critical problems include (1) the difficulty in calibrating target strength, (2) the failure to identify species by acoustic signals, and (3) the detection of whiting near the bottom (Thorne 1960). Regardless of these problems,
whiting offer one of the more optimum circumstances for hydroacoustic assessment compared with many other species.

Soviet scientists have determined that the average biomass of whiting from 1967-73 was 1.36 million MT (Efimov11, Ermakov and Kharchenko12, and Vologdin13). They estimated 1.40 and 1.86 million MT of whiting in 1974 and 1975, respectively. The Soviets conducted two surveys in 1979 with resulting estimates of 1.20 and 2.88 million MT.

Estimates of spawning biomass of whiting determined from egg and larval surveys are considerably higher than those stated above. Ahlstrom (1968) calculated that the spawning biomass of whiting was 1.8 to 3.6 million MT. Stepanenko14 estimated that the spawning biomass of whiting was 2.4 million MT in 1977 and 2.65 million MT in 1979.

Estimates of spawning biomass from egg and larval surveys are extremely crude in the case of whiting because: the size composition and fecundity of the spawners is relatively unknown; the stage duration of eggs and larvae was not used for these approximations; fecundity schedules of adults are based on very little data; and it is unknown whether whiting are multiple spawners. Estimates are further confounded by the extreme patchiness of eggs and larvae. In spite of these problems, ichthyoplankton surveys are useful for assessing the relative abundance of the stock, and the California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton surveys conducted since 1950 have been useful in monitoring changes in the spawning potential of the population. The spawning stock appears to have decreased in the late 1960s and early 1970s compared with earlier years, but has recently increased to previous levels (Stauffer and Smith 1977).

Recruitment

Because of the spatial distribution of age classes, recruitment of the exploited stock occurs at 3-6 years of age depending on the location of fishing. Inter-annual variations in recruitment are great, as exemplified by the dominance of the age composition of the stock by strong year classes for several consecutive years (Figure 13).

The factors most often considered to affect reproductive success of marine fishes are cannibalism, food supply, predation, and larval transport. Although cannibalism is sometimes observed, it is probably fairly low because the majority of adult whiting spend a limited time in the spawning area (1-3 mo). However, Sumida and Moser (1980) found that some large larvae eat smaller larvae, and there are a few reports of adult predation on juveniles.

Bailey (in press) found that the food requirement of whiting larvae is low because of relatively low growth and metabolic rates. The large mouth size of larvae enables first-feeding larvae to ingest a wide spectrum of food particles, including juvenile and adult copepods (Sumida and Moser 1980). Bailey (in press) calculated that a first-feeding whiting larva can satisfy growth and metabolic requirements by ingesting 31 copepod nauplii, 6 small calanoid adult copepods, or 0.6 Calanus copepodites per day. By comparison, a first-feeding northern anchovy larva, with its small mouth, must capture at least 200 Gymnodinium cells per day to satisfy metabolic (excluding growth) requirements alone (Hunter 1977). It was concluded that starvation from first-feeding failure is probably not as variable for whiting larvae as it appears to be for northern anchovy and that whiting may not be as dependent on finding patches of prey as are northern anchovy (Lasker 1975).

Predation on eggs and larvae is a difficult problem to assess and is poorly understood. A wide variety of invertebrate organisms are capable of feeding on whiting eggs and larvae. Yolk-sac stages are most vulnerable to predation by invertebrates (Bailey and Yen, in press). Predation by invertebrates may be

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11Efimov, Y.N. 1974. The size of stocks and status of fishery of Pacific hake. Unpubl. manuscr. Pacific Scientific Research Institute of Marine Fisheries and Oceanography (TINRO), Vladivostok, USSR.

12See footnote 5 on page 85.

13Vologdin, V. 1980. Results of the hydroacoustic surveys with trawlings off the Pacific coast of North America in 1979. Unpubl. manuscr. Pacific Scientific Research Institute of Marine Fisheries and Oceanography (TINRO), Vladivostok, USSR.

14See footnotes 2 and 3 on page 82.
important in cold years when development is slow through the stages most vulnerable to predation.

Oceanographic conditions appear to play a major role in the recruitment of Pacific whiting (Bailey 1981 a,b). The offshore distance of larvae is apparently positively correlated to indices of wind-driven Ekman transport (Figure 14). Although there is a good deal of variability in this relationship, it is statistically significant and indicates that larvae may be transported offshore in years of high upwelling. Since the juvenile nursery is inshore over the continental shelf, advection of larvae offshore is expected to be detrimental to survival. In fact, Ekman transport during the spawning months is negatively correlated to year-class strength (Figure 15). Further work must be done on the survival of larvae swept offshore to test this hypothesis.

Temperature may also influence recruitment, possibly by the predation-temperature interactions noted above and the previously described influence of temperature on the location of spawning. The average winter temperature and Ekman transport in a multiple regression model account for 68% of the observed variation in an index of year-class strength (Bailey 1981 a,b). There is no apparent relationship between spawning biomass of the population and recruitment.

**Mortality**

Estimates of annual instantaneous natural mortality rates range widely. These estimates, as well as several estimates for fishing and total mortality rates are presented in Table 10. A cohort analysis performed by Francis (1982) on the 1973-80 catch-by-age data gives estimates of age-specific fishery mortality (catchability) as well as recruitment of the exploited stock at age 3.

![Figure 14. The distribution of larvae offshore in January-February surveys versus the January upwelling index, 1950-79 (linear correlation coefficient, \( R = 0.70; P = 0.001 \)) from Bailey 1981 a,b.](image)

![Figure 15. Log of the year-class index against the January upwelling index (from Bailey 1981a,b).](image)

**TABLE 10**

<table>
<thead>
<tr>
<th>Investigators</th>
<th>Males</th>
<th>Females</th>
<th>Both Sexes</th>
</tr>
</thead>
<tbody>
<tr>
<td>M: natural mortality</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tillman (1968)</td>
<td>0.72</td>
<td>0.62</td>
<td>x=0.67</td>
</tr>
<tr>
<td>Nelson and Larkins (1970)</td>
<td>0.56</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Efimov (1974)</td>
<td>0.35</td>
<td></td>
<td></td>
</tr>
<tr>
<td>PFM C2</td>
<td>0.30-0.60</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jackowski (1980)</td>
<td>0.30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ehrich, et al. (1980)</td>
<td>0.56</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low (1978)</td>
<td>0.30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Francis (in prep.)</td>
<td>0.19-0.86</td>
<td></td>
<td>(variable age-specific natural mortality)</td>
</tr>
</tbody>
</table>

| F: fishing mortality   |       |         |            |
| Efimov (1974)          | 0.30  |         |            |
| Ehrich, et al. (1980)  | 0.67  |         |            |
| Z: total mortality     |       |         |            |
| Efimov (1974)          | 0.65  |         |            |
| Ehrich et al. (1980)   | 1.23  |         |            |

1Efimov Y.N. 1974. The size of stocks and status of fishery of Pacific hake. Unpubl. manuscr. Pacific Scientific Research Institute of Marine Fisheries and Oceanography (TINRO), Vladivostok, USSR.
Dynamics of the Population

Over the past 200 years the Pacific whiting population has experienced some major changes in abundance (Soutar and Isaacs 1974). Based on an analysis of fish scales deposited in sediments, at the turn of the last century the population was almost an order of magnitude larger than recent abundance levels. These changes in abundance have been correlated to changes in abundance of the northern anchovy (Soutar and Isaacs 1974) and are inversely correlated to offshore Ekman transport (Bailey 1981a,b).

Several mathematical models have been constructed that simulate changes in the whiting population. These include models by Francis (1982), Francis et al. (1982), Bernard (Oregon State University, Newport, OR), Stevens and Goodman ( Scripps Institution of Oceanography, La Jolla, CA), Tillman (1968), and Riffenburgh (1969).

THE PACIFIC WHITING FISHERY

Historical Catches and Effort

Pacific whiting has been the target of a large foreign fishery off the west coast of the United States and Canada (Table 11). A Soviet fishery for whiting began in 1966 with a catch of 137 thousand MT. From 1973-76 Poland, West Germany, East Germany, and Bulgaria joined fishing operations for Pacific whiting. Reported catches peaked in 1976 at 237 thousand MT. The average annual all-nation reported catch from 1966 to 1980 was 162 thousand MT. (These catches were compiled from data at the Northwest and Alaska Fisheries Center.)

A small domestic fishery for whiting, used in the manufacture of pet food, has existed since at least 1879 (Jow 1973). This fishery has been rather insignificant, with catches in the range of 200-500 MT/yr. However, in recent years the domestic fishery has become important: U.S.-foreign joint-venture fishing caught 9 thousand MT and 28 thousand MT in 1979 and 1980, respectively.

Historical effort statistics for the fishery, excluding Canadian waters, were calculated from weekly aerial surveillance data from the NMFS Enforcement Division (supplied by Bill Dickenson, NMFS, Northwest Regional Office, Seattle, WA). Effort for two classes of vessels—large Soviet BMRT stern trawlers and smaller Soviet SRT side trawlers (see “Technical Aspects” below)—were calculated in vessel-days on the fishing grounds. Effort by the SRT trawlers was greatest in 1966 and declined steadily (Table 12). Effort by the BMRT trawlers was greatest in 1975 and 1976.

To obtain a rough estimate of overall catch per unit of effort (CPUE) for the foreign fishery in U.S. waters, SRT effort was converted to effective BMRT effort by assuming a relative fishing power of \( P_{srt} = 0.31 \) from the ratio of average horsepower of SRT vessels to BMRT vessels (1150 HP).

Catch/standard BMRT day indicates that the highest rates occurred in 1967 and from 1977 to 1980. Since the latter period coincides conspicuously with passage of the Magnuson Fishery Conservation Management Act of 1976 (MFCMA) and the onset of intense observer coverage, these statistics indicate that actual catches were possibly underestimated from 1968 to 1976.

TABLE 11

<table>
<thead>
<tr>
<th>Year</th>
<th>U.S.S.R.</th>
<th>Domestic/</th>
<th>Other</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>joint venture</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1966</td>
<td>137.0</td>
<td>—</td>
<td>—</td>
<td>137.0</td>
</tr>
<tr>
<td>1967</td>
<td>206.1</td>
<td>—</td>
<td>—</td>
<td>206.1</td>
</tr>
<tr>
<td>1968</td>
<td>103.8</td>
<td>—</td>
<td>0.12</td>
<td>103.9</td>
</tr>
<tr>
<td>1969</td>
<td>161.8</td>
<td>—</td>
<td>1.2</td>
<td>161.9</td>
</tr>
<tr>
<td>1970</td>
<td>226.2</td>
<td>—</td>
<td>2.3</td>
<td>228.5</td>
</tr>
<tr>
<td>1971</td>
<td>151.8</td>
<td>—</td>
<td>1.4</td>
<td>153.2</td>
</tr>
<tr>
<td>1972</td>
<td>150.8</td>
<td>—</td>
<td>0.4</td>
<td>151.2</td>
</tr>
<tr>
<td>1973</td>
<td>143.8</td>
<td>2.0</td>
<td>5.1</td>
<td>150.8</td>
</tr>
<tr>
<td>1974</td>
<td>173.7</td>
<td>44.3</td>
<td>8.4</td>
<td>226.5</td>
</tr>
<tr>
<td>1975</td>
<td>155.4</td>
<td>57.2</td>
<td>5.1</td>
<td>217.7</td>
</tr>
<tr>
<td>1976</td>
<td>138.0</td>
<td>25.7</td>
<td>5.3</td>
<td>238.6</td>
</tr>
<tr>
<td>1977</td>
<td>111.0</td>
<td>19.5</td>
<td>1.9</td>
<td>132.4</td>
</tr>
<tr>
<td>1978</td>
<td>70.9</td>
<td>27.3</td>
<td>2.7</td>
<td>104.2</td>
</tr>
<tr>
<td>1979</td>
<td>96.8</td>
<td>22.3</td>
<td>13.1</td>
<td>135.9</td>
</tr>
<tr>
<td>1980</td>
<td>0.1</td>
<td>49.0</td>
<td>40.8</td>
<td>90.7</td>
</tr>
</tbody>
</table>

*Zyblut, E. 1981. Dept. of Fisheries and Oceans, Govt. of Canada, Vancouver, B.C. Personal communication.

TABLE 12

<table>
<thead>
<tr>
<th>Year</th>
<th>BMRT vessel days</th>
<th>RST vessel days</th>
<th>Standard BMRT days</th>
<th>Catch (1000 MT)</th>
<th>CPUE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1966</td>
<td>2,670</td>
<td>14,490</td>
<td>7.128</td>
<td>137.0</td>
<td>19.2</td>
</tr>
<tr>
<td>1967</td>
<td>2,730</td>
<td>10,350</td>
<td>5.915</td>
<td>195.1</td>
<td>33.0</td>
</tr>
<tr>
<td>1968</td>
<td>5,677</td>
<td>2,079</td>
<td>6,317</td>
<td>68.0</td>
<td>10.8</td>
</tr>
<tr>
<td>1969</td>
<td>5,607</td>
<td>1,589</td>
<td>6,096</td>
<td>109.0</td>
<td>17.9</td>
</tr>
<tr>
<td>1970</td>
<td>7,847</td>
<td>658</td>
<td>8,549</td>
<td>200.8</td>
<td>24.9</td>
</tr>
<tr>
<td>1971</td>
<td>7,345</td>
<td>651</td>
<td>7,445</td>
<td>146.7</td>
<td>19.7</td>
</tr>
<tr>
<td>1972</td>
<td>5,131</td>
<td>518</td>
<td>5,291</td>
<td>111.3</td>
<td>21.0</td>
</tr>
<tr>
<td>1973</td>
<td>5,904</td>
<td>—</td>
<td>5,904</td>
<td>141.1</td>
<td>23.9</td>
</tr>
<tr>
<td>1974</td>
<td>7,717</td>
<td>—</td>
<td>7,717</td>
<td>201.1</td>
<td>26.1</td>
</tr>
<tr>
<td>1975</td>
<td>10,401</td>
<td>—</td>
<td>10,401</td>
<td>196.9</td>
<td>18.9</td>
</tr>
<tr>
<td>1976</td>
<td>6,917</td>
<td>—</td>
<td>6,917</td>
<td>177.8</td>
<td>25.7</td>
</tr>
<tr>
<td>1977</td>
<td>4,076</td>
<td>—</td>
<td>4,076</td>
<td>127.2</td>
<td>31.2</td>
</tr>
<tr>
<td>1978</td>
<td>2,779</td>
<td>—</td>
<td>2,779</td>
<td>96.9</td>
<td>34.9</td>
</tr>
<tr>
<td>1979</td>
<td>4,452</td>
<td>—</td>
<td>4,452</td>
<td>114.9</td>
<td>25.8</td>
</tr>
<tr>
<td>1980</td>
<td>1,553</td>
<td>—</td>
<td>1,553</td>
<td>44.0</td>
<td>28.3</td>
</tr>
</tbody>
</table>

Assumptions — \( P_{srt} = 0.31 \)
\( P_{BMRT}(Poland)=1.00 \)
CPUE = catch per unit effort
**Technical Aspects**

As the major country fishing for whiting, the Soviet Union has improved its whiting fleet considerably. In 1966 the fleet was mainly medium-sized side trawlers (SRTs) of about 500 gross tons. The proportion of large stern trawlers with freezing capacity (BMRTs) has gradually increased to replace the side trawlers. The typical BMRT is 3170 gross tons, has a crew of 22-26, and uses a midwater trawl with a headrope length of 97 m. The daily production capacity is 30-50 MT of frozen fish and 20-35 MT of meal and oil. Support vessels in the fishery include factory ships, refrigerated transports, oil tankers, personnel carriers, tugs, and patrols.

The Soviet fishery is a well-coordinated expedition, and acoustics are used to guide the net over fish concentrations. Prior to 1976, about 100 BMRTs would typically participate in the fishery (Pruter 1976), but lately the fleet has been reduced to about 39 large stern trawlers. In early years of the fishery most whiting were filleted, and small fish were reduced to meal. Recently the average size of hake has become considerably smaller, and an increasing proportion of the catch is frozen whole.

The foreign fishery is closely tied to the migratory movements of the whiting population. Historically, the fishery began in waters off Oregon in April and moved northward as schools made their way up the coast in summer. This was documented from aerial sightings of the Soviet fishery (Figure 16). In autumn, as fishing activity halted, whiting began to migrate offshore and southward for spawning. More recently, fishing has been restricted by treaty to the Heceta Banks, Yaquina Head, Cape Flattery, Cape Blanco, and Destruction Island. Most fish are caught in depths of 100-199 m (Table 13).

**Management**

Prior to implementation of the MFCMA in 1977, the foreign fishery was managed by bilateral agreement. Since 1977 management has been directed by a Preliminary Management Plan (PMP) for groundfish prepared by the Department of Commerce. Subsequently, the Pacific Fishery Management Council has prepared a fisheries management plan (FMP) for groundfish, including whiting, which is currently under review. A conservative estimate of maximum sustained yield in the plan is 175.5 thousand MT. The FMP specifies geographic and seasonal restrictions, mesh size, incidental catch levels, and an optimal yield (in the form of quotas). Under the MFCMA only the Soviets and Poles have been granted licenses as the major foreign interests that may fish for Pacific whiting. Recently, U.S. fishermen have become involved in the whiting fishery through joint ventures in which U.S. trawlers harvest whiting for delivery to foreign processing vessels.

Francis et al. (1982) present a management analysis of the Pacific whiting fishery in which a policy algorithm is developed that aims to use strong year classes in a practical and efficient manner while protecting the stock when it is in poor condition and environmental conditions do not appear conducive to immediate improvement.

**Effects of the Fishery on the Population**

Commercial fisheries may affect the abundance and recruitment of marine fish populations in several ways. Besides reducing the total spawning biomass of the population, removing a stock’s largest and oldest fish also (1) lowers the quality of the spawning product if offspring from smaller fish are less fit (Hempel 1979); (2) reduces the number of age classes that contribute to spawning; thus the maintenance of healthy levels of spawning stock depends on successful re-

---

**Table 13**

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>0-99</th>
<th>100-199</th>
<th>200-299</th>
<th>300-399</th>
<th>400-499</th>
<th>&gt;500</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percentage</td>
<td>15.7</td>
<td>47.7</td>
<td>26.2</td>
<td>6.9</td>
<td>2.3</td>
<td>1.2</td>
</tr>
</tbody>
</table>


---

recruitment from fewer age classes (Smith 1978); and (3) changes the distribution of spawning if the population stratifies by size or age on the spawning ground.

The spawning potential of the whiting population has had no discernible effect on recruitment from 1960-75 (Bailey 1981a,b), partly because of the overwhelming effects of environmental factors. For example, the strong 1961 year class arose from an extremely low spawning stock, but under favorable environmental conditions it became a very strong year class. Similar situations gave rise to the strong 1970 and 1973 year classes.

The long life of Merluccius spp., as well as of other gadids, is probably an adaptation to stabilize the stock from the effects of extreme recruitment variability, and reduction in the number of spawning age classes by heavy fishing must be a destabilizing influence. In a population with fewer age classes, the probability of a stock collapse would increase if recruitment failure occurred in a succession of years. This type of interaction appears to have influenced the recruitment of other stocks. In an analysis of the population dynamics of the Pacific sardine, Sardinops sagax, Murphy (1968) concluded that after the number of spawning age classes was reduced by fishing, several years of recruitment failure caused catastrophic population declines.

Since the mid-1960s, a change in the spawning grounds of Pacific whiting has occurred. Larvae have become much less abundant off Baja California and more abundant off central California compared with earlier years (Bailey 1980). In addition, the deposition of scales from young whiting markedly declined off Baja California from 1965-69 compared with earlier prefishing periods (Soutar and Isaacs 1974). Smith (1975) first suggested that this change was related to the beginning of an intensive fishery for adults in 1966. He suggested that large adults spawn farther south and that harvesting this component of the population has caused the spawning decrease in the southern end of the range. Further analysis supports an interaction between the spawning distribution and the fishery (Bailey 1980, 1981a,b). Although the spawning location of whiting is related to temperature, the recent change in the distribution of larvae is independent of temperature changes. An analysis of covariance indicated significantly different slopes and intercepts for pre- and post-spawning periods (Figure 17).

Figure 17. Regressions of the percentage of Pacific Whiting larvae off southern California compared to Baja California against the mean January-March sea surface temperature off Baja California for the pre- and postfishing periods, 1951-66 and 1967-75.

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CalCOFI Rep., Vol. XXIII, 1982


