

## THE LIFE HISTORY AND FISHERY OF PACIFIC WHITING, *MERLUCCIIUS PRODUCTUS*

KEVIN M. BAILEY,<sup>1</sup> ROBERT C. FRANCIS  
Northwest and Alaska Fisheries Center  
National Marine Fisheries Service  
Seattle, Washington 98112

PAYSON R. STEVENS  
Scripps Institution of Oceanography  
University of California, San Diego  
La Jolla, California 92093

### 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 This report synthesizes available data, published and unpublished, on the life history and population dynamics of whiting.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 pallasii*; 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

<sup>1</sup>Current address: College of Fisheries, University of Washington, Seattle, WA 98195  
[Manuscript received January 11, 1982.]

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 1964<sup>1</sup>, Erich et al. (1980), and Stepanenko<sup>2</sup> 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<sup>3</sup> 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.

<sup>1</sup>Bureau of Commercial Fisheries. 1964. Cruise report: exploratory cruise No. 64. Unpubl. manusc. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

<sup>2</sup>Stepanenko, M.A. 1978. The patterns of the abundance of the California anchovy and Pacific hake, and estimation of their biomass, 1976-1977. Unpubl. manusc. Pacific Scientific Research Institute of Marine Fisheries and Oceanography (TINRO), Vladivostok, USSR.

<sup>3</sup>Stepanenko, M.A. 1980. Reproductive condition and assessment of the spawning stocks of Pacific hake, California anchovy, horse mackerel, and some other fish species in the California Current zone in 1979. Unpubl. manusc. Pacific Scientific Research Institute of Marine Fisheries and Oceanography (TINRO), Vladivostok, USSR.

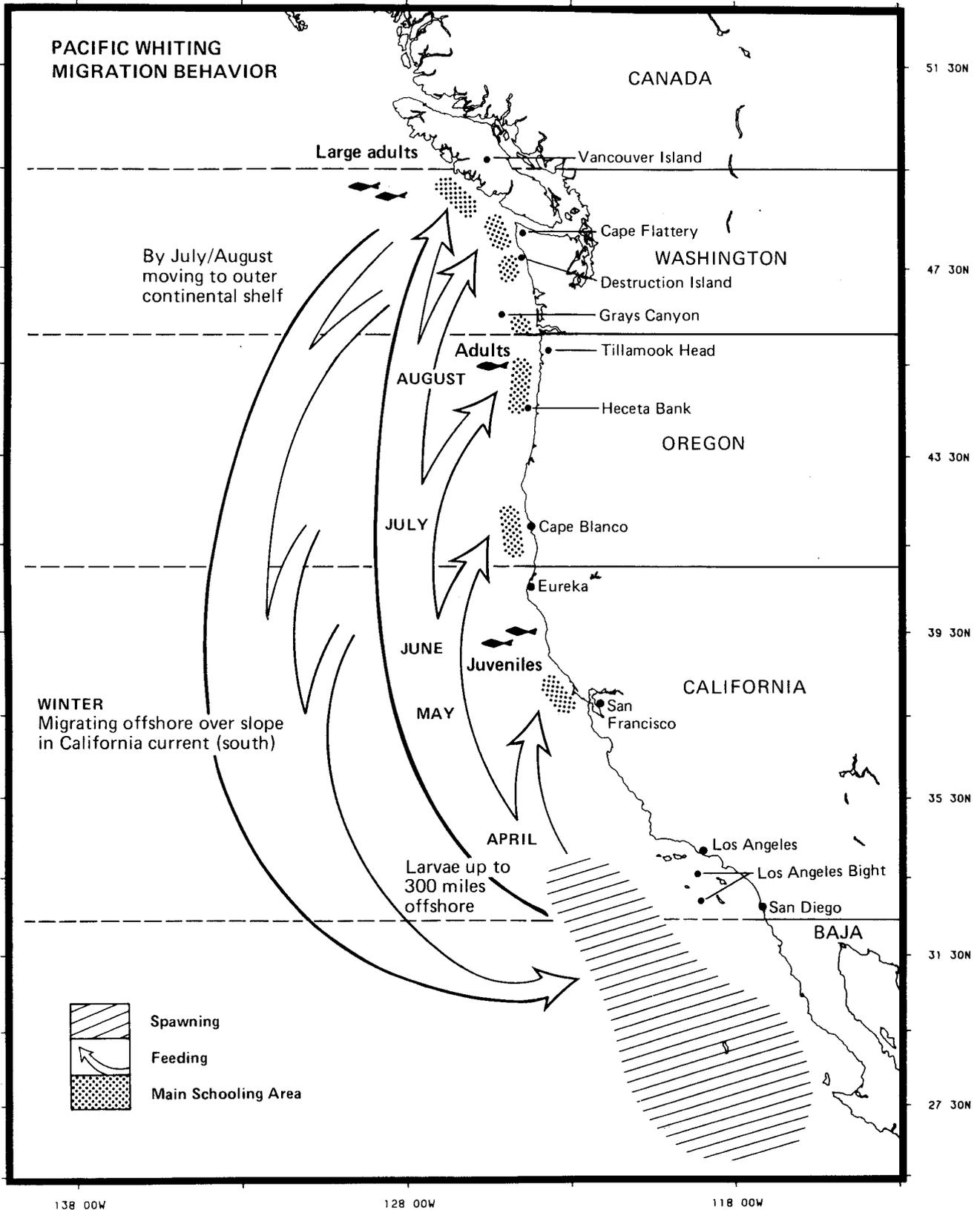


Figure 1. Migratory patterns of Pacific whiting.

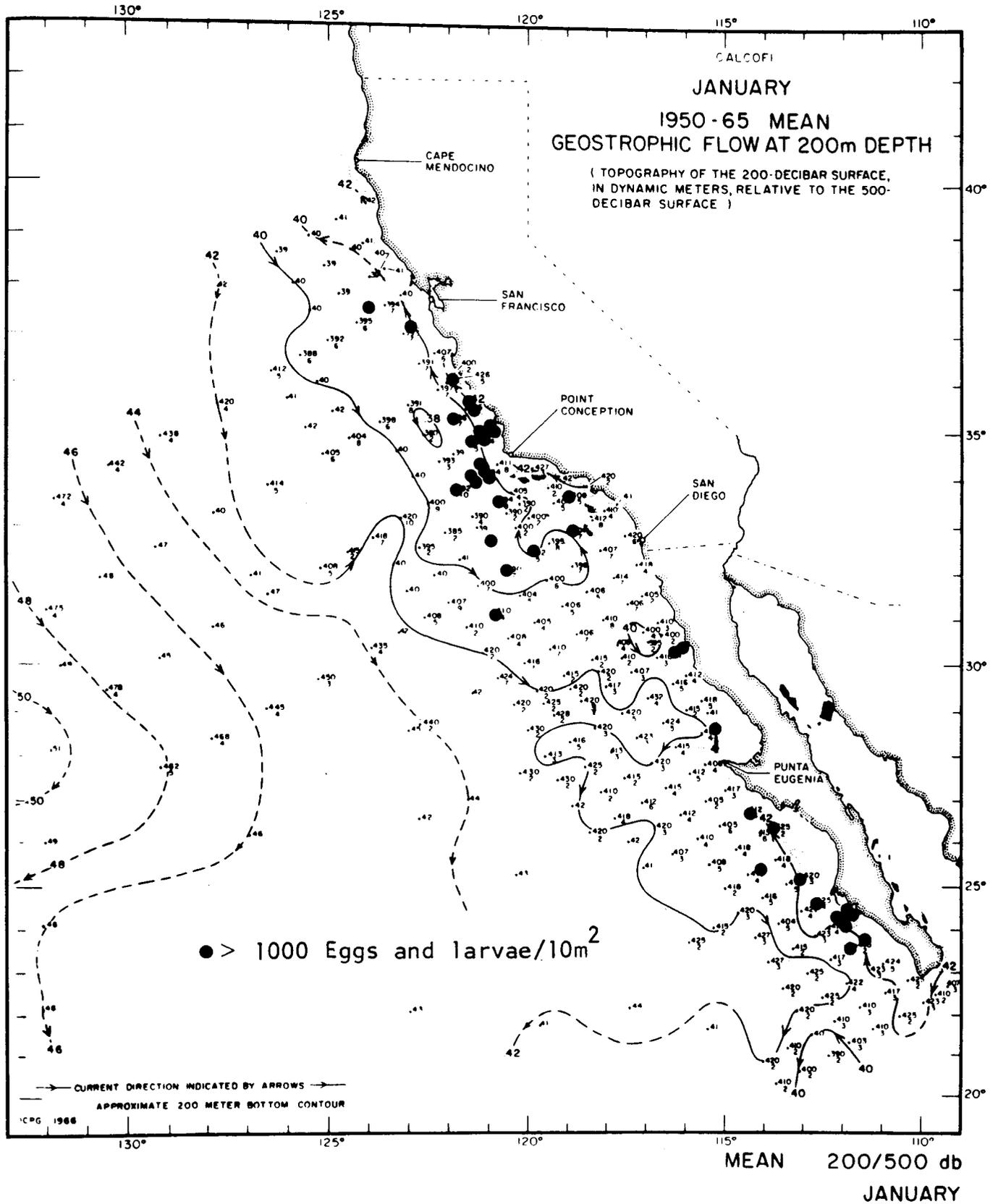


Figure 2. Large catches of Pacific whiting eggs and larvae (all size classes) in January surveys, 1950-79, plotted on a chart showing geostrophic flow at 200-m depth (from Wyllie 1967).

TABLE 1  
The Northward Extent of 2-3-mm Standard Length Whiting Larvae\* during January Surveys, Compared to the Average January 50-Meter Temperature in the Los Angeles Bight

Year	Temperature		Distance	
	°C	Rank	Line	Rank
1963	12.0	9	87	8.5
1964	13.2	4	76	4
1965	12.4	7	80	6
1966	13.5	3	70	2.5
1968	12.8	5	70	2.5
1969	13.6	2	80	6
1972	12.2	8	87	8.5
1975	12.6	6	80	6
1978	13.9	1	63	1

\*Measured by the northernmost CalCOFI line where larvae occurred in numbers greater than 100 larvae/10 m<sup>2</sup>.

Smaller line numbers are farther north. Temperature and northward extent of larvae are significantly correlated using a Spearman rank correlation statistic ( $P < .01$ ).

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 postspawning 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.<sup>4</sup>). 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  $E = 0.00142 * L^3$  (MacGregor 1966).

<sup>4</sup>Ermakov, Y., V. Snytko, L. Kodolov, I. Serobaba, L. Borets, and N. Fadeev. (Date unknown). Biological characteristics and the condition of stocks of Pacific hake, rockfish, blackcod, and pollock in 1972. Unpubl. manusc. Pacific Scientific Research Institute of Marine Fisheries and Oceanography (TINRO), Vladivostok, USSR.

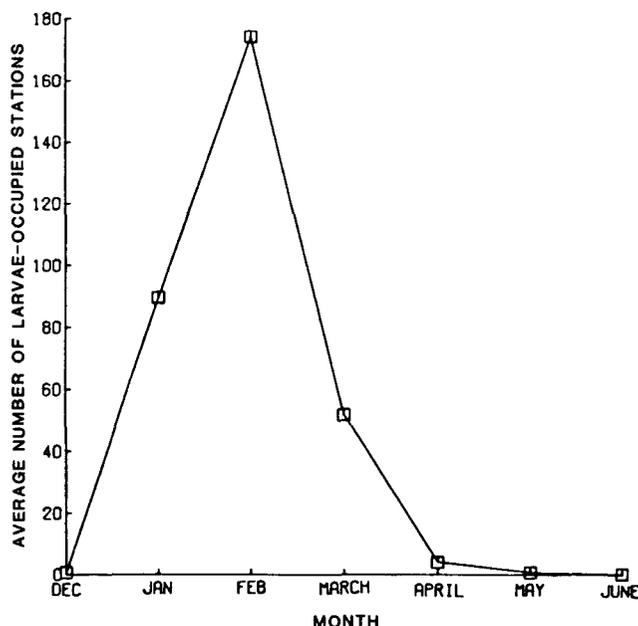


Figure 3. The average monthly number of small whiting larvae per occupied station in the California Cooperative Oceanic Fisheries Investigations survey region, lines 60-120, over the years 1963-79. Small larvae are 2-3 mm-SL.

### 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° to 14°C.

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 Kharchenko<sup>5</sup> 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).

**Larval stage.** Ahlstrom and Counts (1955) described the larvae of Pacific whiting. They are distinguished by a pigment band around the tail, pigment

<sup>5</sup>Ermakov, Y., and A.M. Kharchenko. 1976. Biological characteristics of Pacific hake and the estimation of its abundance in 1975. Unpubl. manusc. Pacific Scientific Research Institute of Marine Fisheries and Oceanography (TINRO), Vladivostok, USSR.

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  $\mu$ m 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

TABLE 2  
 Percent Biomass of Juvenile Pacific Whiting by  
 Depth Interval and by Age

Depth (fathoms)	Age (yr)			
	0	1	2	3
0-99	95.4	35.8	14.6	30.7
100-199	4.4	63.4	59.6	41.8
150-199	0.2	0.8	25.8	27.5
	100.0	100.0	100.0	100.0

From the summer 1977 Northwest and Alaska Fisheries Center bottom-trawl survey.

(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

TABLE 3  
 Average Trawl Catches (Pound per Hour) of Pacific Whiting by Month and Year

Year	Jan.	Mar.	May	July	Aug.	Sept.	Nov.	Dec.
1961	—	—	—	2,403	—	9,784	—	97
1962	—	45	71	—	11,131	—	425	—
1963	100	—	175	—	4,315	—	450	—
Mean	100	45	123	2,403	7,723	9,784	438	97

From Alton 1972.

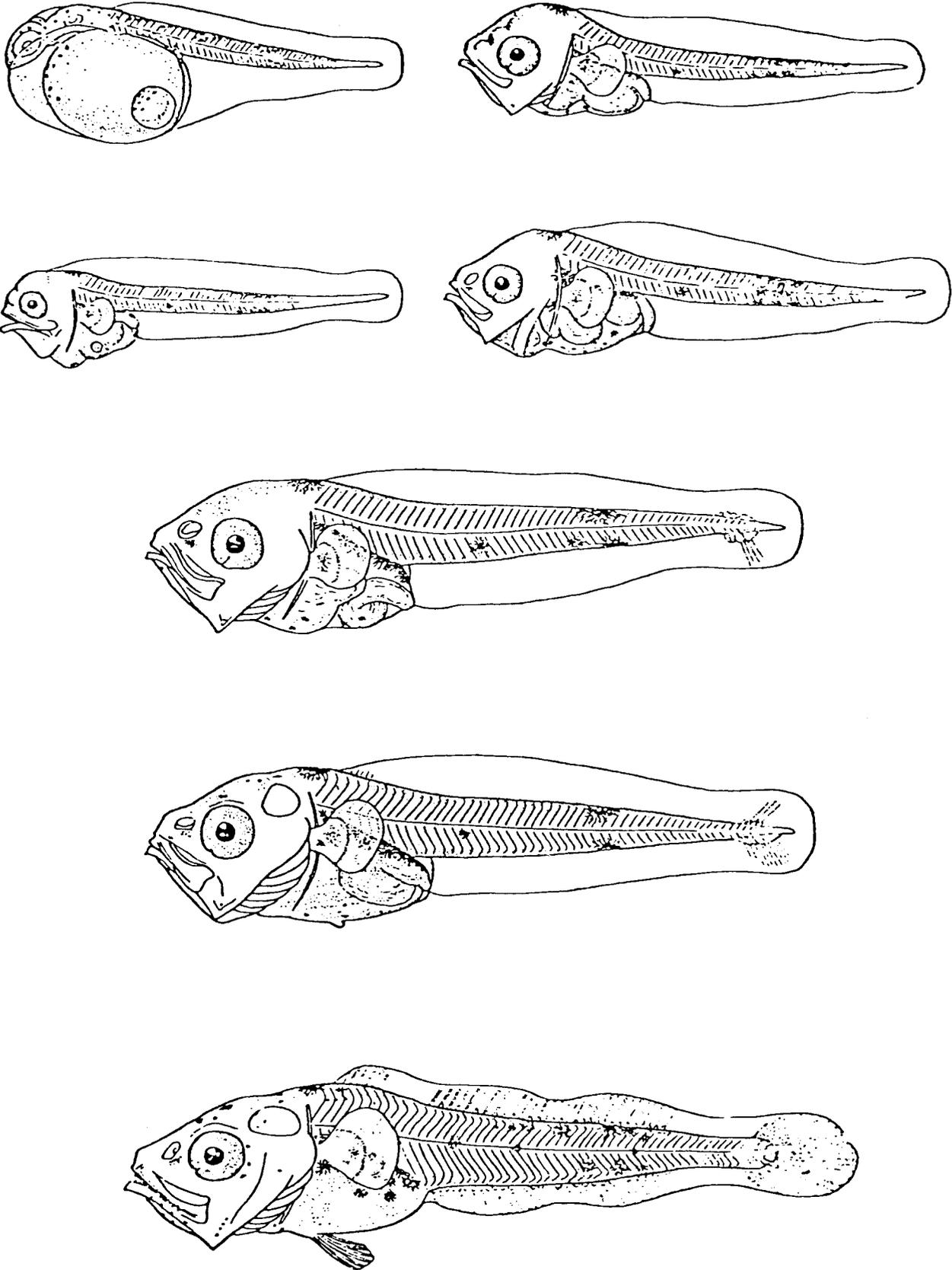


Figure 4. Stages of Pacific whiting larvae (from Ahlstrom and Counts 1955).

TABLE 4  
 The Proportion of Soviet Catches in the INPFC  
 Vancouver-Columbia Area by Month, 1973-76

Month	1973	1974	1975	1976	x
1	—	—	—	—	—
2	—	—	—	—	—
3	—	.012	—	—	.003
4	.032	.073	—	—	.026
5	.008	.085	.026	.122	.060
6	.106	.049	.163	.207	.131
7	.305	.212	.406	.202	.281
8	.296	.116	.167	.261	.210
9	.158	.453	.136	.188	.234
10	.094	—	.086	.017	.049
11	—	—	.016	—	.004
12	—	—	—	.002	—

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,

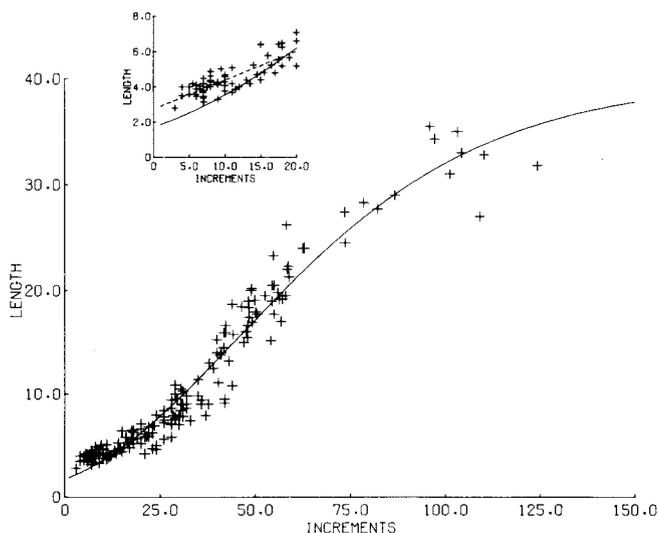


Figure 5. The growth of larvae caught off southern California determined from otolith increments. A Gompertz curve was fitted to the data,  $Y = 1.72 \cdot \exp[3.15 \cdot (1 - \exp[-0.02624 \cdot X])]$ . Insert: daily growth for the first 20 days was better fitted with a straight line ( $Y = 2.75 + 0.16X$ ) (from Bailey, in press).

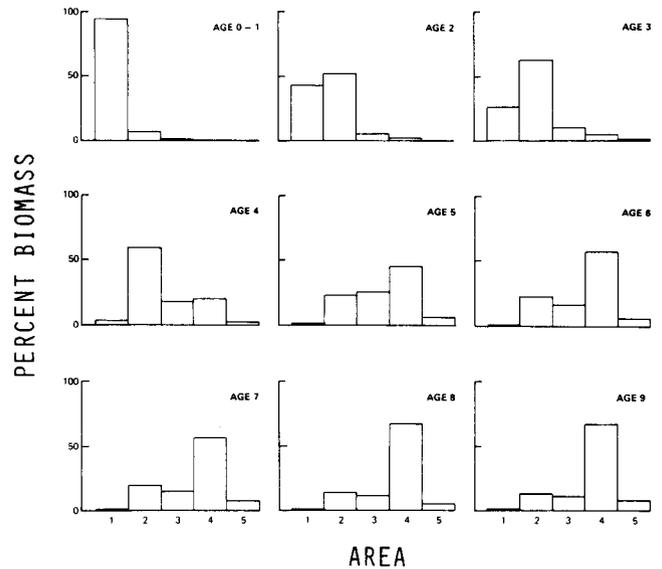


Figure 6. The distribution of biomass by International North Pacific Fisheries Commission area for each age class in the 1977 Northwest and Alaska Fisheries Center trawl survey: Area 1, Conception; Area 2, Monterey; Area 3, Eureka; Area 4, Columbia; Area 5, Vancouver (from Bailey and Ainley, in press).

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.

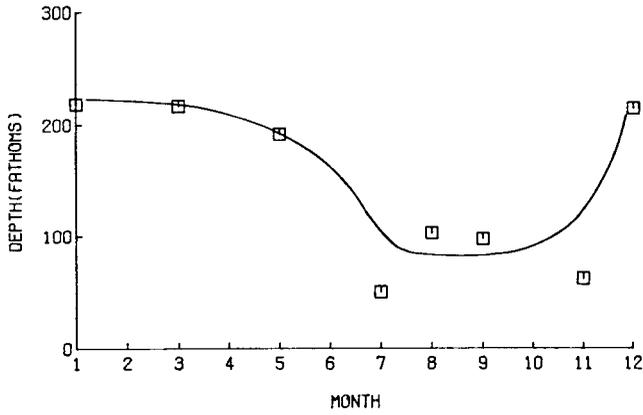


Figure 7. The average depth of Pacific whiting bottom-trawl catches by month, plotted from data in Alton (1972).

**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 m<sup>3</sup> in daytime and less than 1 fish/1000 m<sup>3</sup> at night. Spawning schools of whiting form dense aggregations in the pelagic layer, ranging in depth from 100 to 500 m (Stepanenko<sup>6</sup>; Ermakov 1974; Nelson and Larkins 1970). Stepanenko<sup>7</sup> 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).

<sup>6</sup>See footnote 2 on page 82.

<sup>7</sup>See footnote 3 on page 82.

TABLE 5  
 Parameters of the von Bertalanffy Growth Equation

Source and sex classification	$l_{\infty}$	$k$	$t_0$
Dark (1975)			
Male	56.29	0.39	0.20
Female	61.23	0.30	0.01
Male, female combined	60.85	0.30	0.03
Francis (1982)			
Male, female combined	55.40	0.26	-1.61

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:

$$l_t = l_{\infty} (1 - e^{-k(t-t_0)})$$

where

$$l_t = \text{body length at age } t$$

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

$$W = \text{weight in grams, and}$$

$$l = \text{length in centimeters.}$$

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)

TABLE 6  
 Parameters of the Weight-Length Equation  $w = a l^b$

Source and sex classification	$a$	$b$
Dark (1975)		
Male	.034682	2.55618
Female	.020444	2.69509
Francis (1982)		
Male, female combined	.001815	2.73343

TABLE 7  
 The Percent Occurrence of Food Types in the Diet of Pacific Whiting Determined by Soviet Scientists\*

Food type	Washington-Oregon Month				California Month				
	5	6	9	10	3	4	5	6	11
Euphausiids	81.6	99.6	1.2	40.2	83.3	83.1	99.8	84.0	93.5
Shrimp	4.9	0.4	17.3	1.3	—	—	—	—	15.2
Squid	—	—	—	1.3	—	—	—	—	—
Fish	14.3	—	12.4	37.7	5.6	0.9	1.4	1.4	10.9

\*Ermakov, Y., and A.M. Kharchenko. 1976. Biological characteristics of Pacific hake and the estimation of its abundance in 1975. Unpubl. manusc. Pacific Scientific Research Institute of Marine Fisheries and Oceanography (TINRO), Vladivostok, USSR.

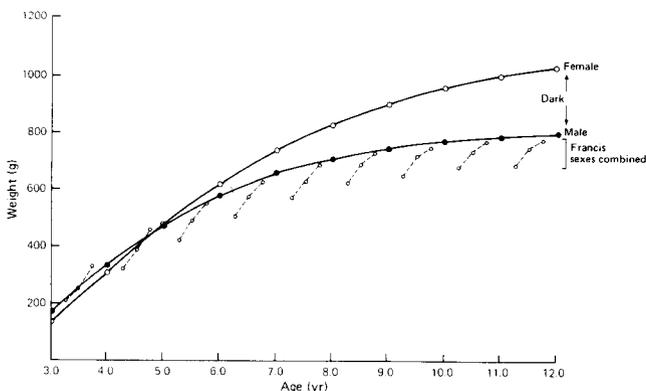


Figure 8. The annual growth in weight of Pacific whiting (from Dark 1975, solid lines) compared to seasonal estimates of growth by age class (from Francis, unpubl. manusc., dotted lines).

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.

**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<sup>8</sup> found that off Washington and Oregon euphausiids decrease

<sup>8</sup>See footnote 5 on page 85.

TABLE 8  
 The Percent by Weight of Food Types in the Diet of Pacific Whiting Determined by Polish Scientists\* in Summer 1979

Food type	Region		
	Eureka	Columbia	Vancouver
Euphausiids	94.2	94.0	85.6
Juv. rockfish	1.0	1.6	—
Pacific herring	—	—	5.9
Juv. Pacific herring	—	—	6.6
Osmerids	—	0.4	—
Pacific whiting	0.5	—	—
Sablefish	—	2.0	0.1
Flatfish	—	0.4	—
Squid	0.7	—	—
Shrimp	—	1.6	—
Other fish	3.2	—	1.7
Other	0.4	—	0.1

\*Jackowski, E. 1980. Biological characteristics of Pacific whiting from Polish surveys of the west coast of the U.S.A. and Canada in 1979. Unpubl. manusc., presented at the U.S.-Poland bilateral meetings, 1980.

in frequency of occurrence in the diet in autumn compared to summer (Table 7). Shrimp and fish sometimes occur frequently. Jackowski<sup>9</sup> found that in summer off Vancouver Island, Pacific herring were important in the diet of whiting (Table 8); and in northern California waters where adult and juvenile distributions overlap, cannibalism is often observed (T. Dark, pers. comm.).

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 *Thysanoessa 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

<sup>9</sup>Jackowski, E. 1980. Biological characteristics of Pacific whiting from Polish surveys of the west coast of the U.S.A. and Canada in 1979. Unpubl. manusc., presented at the U.S.-Poland bilateral meetings, 1980.

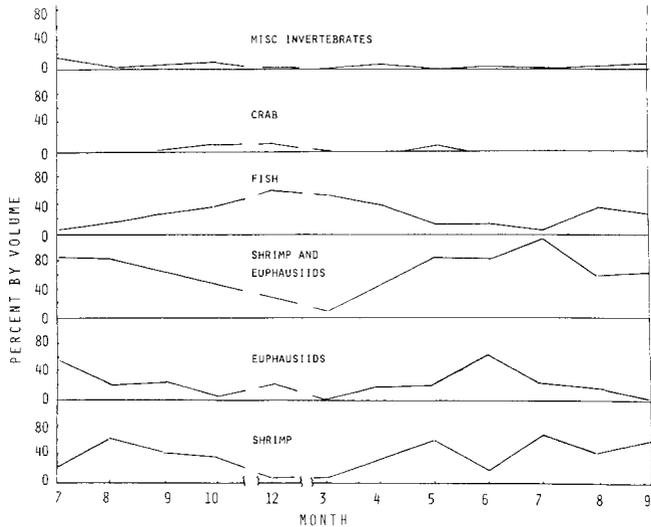


Figure 9. The percentage (by volume) of different food types in the diet of Pacific whiting by month (data from Gotshall 1969a).

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

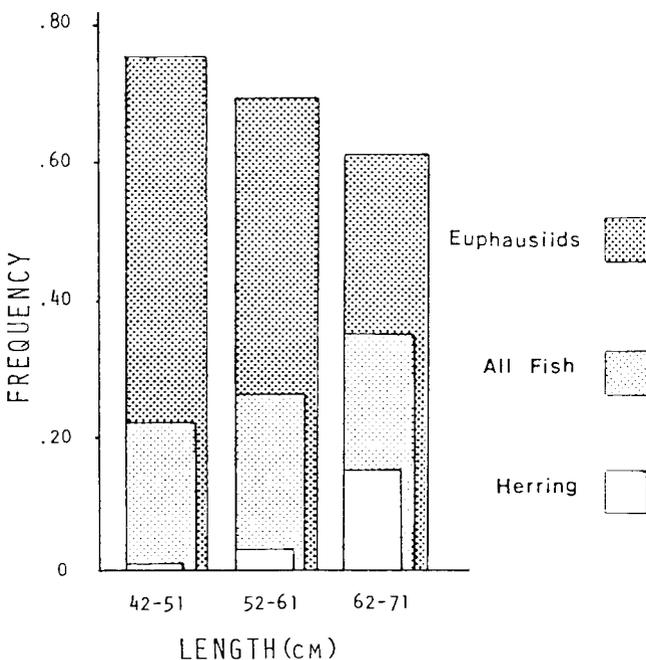


Figure 10. Frequency of occurrence of prey types in different Pacific whiting size classes off Vancouver Island (data from Outram and Haegele 1972).

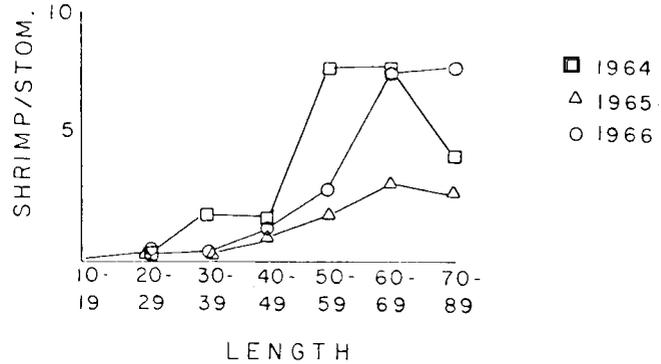


Figure 11. The number of ocean shrimp per stomach of Pacific whiting off Vancouver Island (data from Gotshall 1969b).

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.

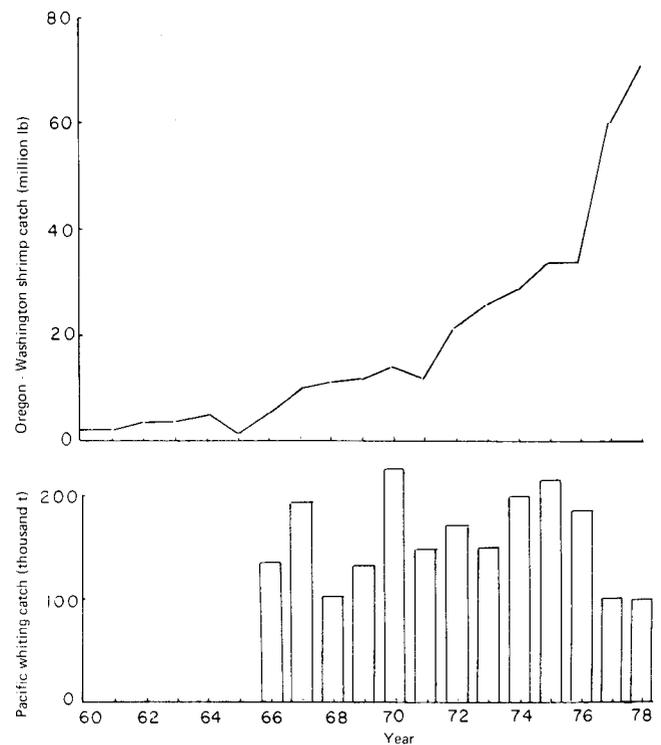


Figure 12. Shrimp catches off the Oregon-Washington coast and catches of Pacific whiting.

TABLE 9  
 Distribution of Pacific Whiting Biomass by INPFC Area from Three Northwest and Alaska Fisheries Center Surveys

Year	Source	Vancouver	Columbia	Metric tons		Total	
				Eureka	Monterey and Conception		
1975*	Midwater	3,791	165,941	25,596	42,020	237,348	
	Percentage	2	70	11	18		
	Bottom	667	189,630	7,222	10,107		207,626
	Percentage	—	91	3	5		
	Total	4,458	355,571	32,818	52,127		444,974
Percentage	1	80	7	12			
1977	Midwater	343,821	316,440	360,944	108,087	1,129,292	
	Percentage	30	28	32	10		
	Bottom	6,560	32,917	9,501	20,662		69,640
	Percentage	9	47	14	26		
	Total	350,381	349,357	370,445	128,749		1,198,932
Percentage	29	29	31	11			
1980	Midwater	322,335	260,476	182,783	578,841	1,344,435	
	Percentage	24	19	14	43		
	Bottom	16,678	16,938	13,579	127,647		174,832
	Percentage	10	10	8	73		
	Total	339,013	277,404	196,362	706,488		1,519,267
Percentage	22	18	13	47			

\*1975 areas do not correspond to 1977 and 1980 survey areas.

**Competitors.** Competitors with Pacific whiting for food resources are numerous. Among competitive fishes are other Gadidae; flatfish, Pleuronectidae; soles, Bothidae; smelts, Osmeridae; Cottidae; Pacific herring; albacore, *Thunnus alalunga*; Hexagrammidae; lingcod, *Ophiodon elongatus*; Myctophidae; rockfish, Scorpaenidae; sablefish, *Anoplopoma fimbria*; and Salmonidae. Numerous marine mammals may also be competitors, including the rough-toothed dolphin, *Steno bredanensis*; gray whale, *Eschrichtius robustus*; minke whale, *Balaenoptera acutorostrata*; Bryde's whale, *B. edeni*; sei whale, *B. borealis*; fin whale, *B. physalus*; blue whale, *B. musculus*; humpback whale, *Megaptera novaeangliae*; and right whale, *Balaena glacialis* (Fiscus 1979).

**Predators.** Predators of Pacific whiting reported in the literature include the great white shark, *Carcharodon carcharias*; soupfin shark, *Galeorhinus zyopterus*; Pacific electric ray, *Tetranarce californica*; bonito, *Sarda chiliensis*; albacore; bluefin tuna, *Thunnus thynnus*; rockfish; sablefish; lingcod; dogfish, *Squalus acanthias*; and arrowtooth flounder, *Atheresthes stomias* (Best 1963; Nelson and Larkins 1970; Pinkas et al. 1971). Marine mammals that feed on whiting include the California sea lion, *Zalophus californianus*; northern elephant seal, *Mirounga angustirostris*; Pacific whiteside dolphin, *Lagenorhynchus obliquidens*; killer whale, *Orcinus orca*; Dall porpoise, *Phocoenoides dalli*; sperm whale, *Physeter macrocephalus*; northern sea lion, *Eumetopias jubatus*; and northern fur seal, *Callorhinus ursinus* (Fiscus 1979).

Bailey and Ainley (1982) analyzed otoliths col-

lected 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<sup>10</sup>). Regardless of these problems,

<sup>10</sup>Thorne, R.E. Assessment of population abundance by echo integration. SCOR, Working Group No. 52. Symposium on assessment of micronekton, April 27-30, 1980.

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 (Efimov<sup>11</sup>, Ermakov and Kharchenko<sup>12</sup>, Vologdin<sup>13</sup>). 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. Stepanenko<sup>14</sup> 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

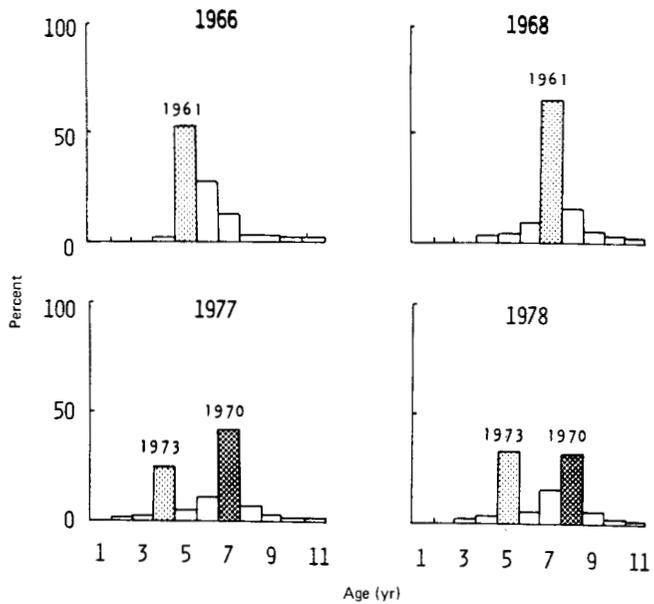


Figure 13. Age compositions of Pacific whiting caught off Oregon and Washington from research surveys (1966 and 1968) and from U.S. observer fishery data (1977 and 1978) (from Bailey 1981a,b).

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

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

<sup>12</sup>See footnote 5 on page 85.

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

<sup>14</sup>See footnotes 2 and 3 on page 82.

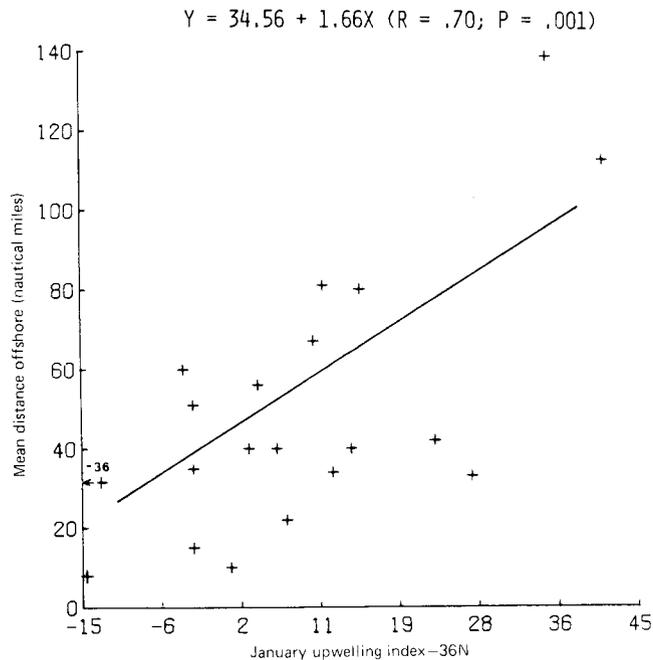


Figure 14. The distribution of larvae offshore in January-February surveys versus the January upwelling index, 1950-79 (linear correlation coefficient,  $R = 0.70$ ,  $P = 0.001$ ) (from Bailey 1981 a,b).

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

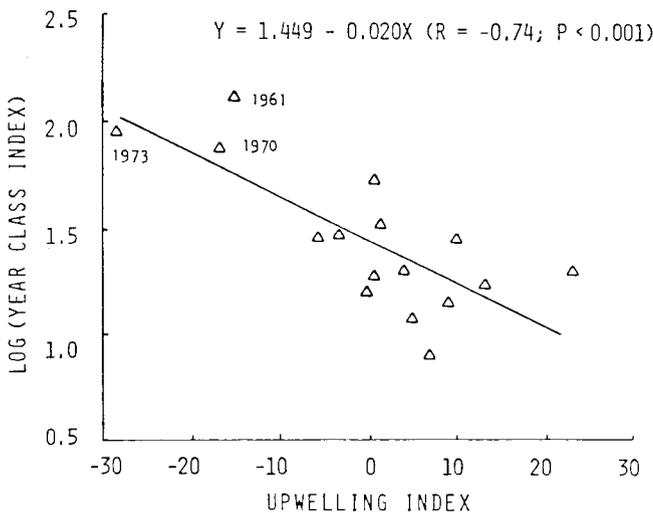


Figure 15. Log of the year-class index against the January upwelling index (from Bailey 1981a,b).

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.

TABLE 10  
 Estimates of Annual Instantaneous Mortality Rates  
 of Pacific Whiting

Investigators	Males	Females	Both Sexes
<i>M: natural mortality</i>			
Tillman (1968)	0.72	0.62	$x=0.67$
Nelson and Larkins (1970)			0.56
Efimov (1974) <sup>1</sup>			0.35
PFMC <sup>2</sup>			0.30-0.60
Jackowski (1980) <sup>3</sup>			0.30
Ehrich, et al. (1980)			0.56
Low (1978) <sup>4</sup>			0.50
Francis (in prep.)			0.19-0.86 (variable age- specific natural mortality)
<i>F: fishing mortality</i>			
Efimov (1974) <sup>1</sup>			0.30
Ehrich, et al. (1980)			0.67
<i>Z: total mortality</i>			
Efimov (1974) <sup>1</sup>			0.65
Ehrich et al. (1980)			1.23

<sup>1</sup>Efimov Y.N. 1974. The size of stocks and status of fishery of Pacific hake. Unpubl. manusc. Pacific Scientific Research Institute of Marine Fisheries and Oceanography (TINRO), Vladivostok, USSR.

<sup>2</sup>Pacific Fishery Management Council. 1980. Pacific coast groundfish plan. Draft report. Pacific Fishery Management Council, 526 S.W. Mill St., Portland, OR 97201.

<sup>3</sup>Jackowski, E. 1980. Biological characteristics of Pacific whiting from Polish surveys of the west coast of the U.S.A. and Canada in 1979. Unpubl. manusc., presented at the U.S.-Poland bilateral meetings, 1980.

<sup>4</sup>Low, L.L. 1978. Hake natural mortality and yield potential. Unpubl. manusc. Northwest and Alaska Fish. Cent. Natl. Mar. Fish. Serv. NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

**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 underreported from 1968 to 1976.

TABLE 11  
 Annual All-Nation Catches of Pacific Whiting ( $\times 10^3$  MT) in U.S. and Canadian\* Waters.

Year	Domestic/ joint venture				Total
	U.S.S.R.	Poland	Other	Other	
1966	137.0	—	—	—	137.0
1967	206.1	—	—	—	206.1
1968	103.8	—	—	—	103.8
1969	161.8	—	—	0.12	161.9
1970	226.2	—	—	2.3	228.5
1971	151.8	—	—	1.4	153.2
1972	150.8	—	—	0.4	151.2
1973	143.8	2.0	—	5.1	150.8
1974	173.7	44.3	—	8.4	226.5
1975	155.4	57.2	—	5.1	217.7
1976	158.0	25.7	—	53.0	236.8
1977	111.0	19.5	—	1.9	132.4
1978	70.9	27.3	2.7	3.4	104.2
1979	96.8	22.3	13.1	3.6	135.9
1980	0.1	49.0	40.8	0.8	90.7

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

TABLE 12  
 Historical Effort Statistics for the U.S.S.R.-Poland Foreign Pacific Whiting Fishery (Solely) in U.S. Waters

Year	BMRT vessel days	RST vessel days	Standard BMRT days $P_{ST}=0.31$	Catch (1000 MT)	CPUE (MT/BMRT day)
1966	2,670	14,490	7,128	137.0	19.2
1967	2,730	10,350	5,915	195.1	33.0
1968	5,677	2,079	6,317	68.0	10.8
1969	5,607	1,589	6,096	109.0	17.9
1970	7,847	658	8,049	200.8	24.9
1971	7,245	651	7,445	146.7	19.7
1972	5,131	518	5,290	111.3	21.0
1973	5,904	—	5,904	141.1	23.9
1974	7,717	—	7,717	201.1	26.1
1975	10,401	—	10,401	196.9	18.9
1976	6,917	—	6,917	177.8	25.7
1977	4,076	—	4,076	127.2	31.2
1978	2,779	—	2,779	96.9	34.9
1979	4,452	—	4,452	114.9	25.8
1980	1,553	—	1,553	44.0	28.3

Assumptions —  $P_{ST}=0.31$   
 $P_{BMRT}(\text{Poland})=1.00$   
 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 period from June until October. Based on aerial surveillance records and Ermakov's (1974) analysis of the fishery, rich fishing grounds appear to be associated with prominent geographical sites such as banks, sharp "curves" in the continental slope, and canyons. Especially productive grounds are found near 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)<sup>15</sup> 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

<sup>15</sup>Pacific Fishery Management Council. 1980. Pacific coast groundfish plan. Draft report. Pacific Fishery Management Council, 526 S.W. Mill St., Portland, OR 97201.

TABLE 13  
Catch (Percentage) by Depth Strata of Pacific Whiting Taken by Foreign Trawlers in 1979

Depth (m)	0-99	100-199	200-299	300-399	400-499	>500
Percentage	15.7	47.7	26.2	6.9	2.3	1.2

From: French, R., R. Nelson Jr., and J. Wall. 1980. Observations of foreign and joint venture fishing fleets off the coast of Washington, Oregon, and California, 1979. Unpubl. rep. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

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-

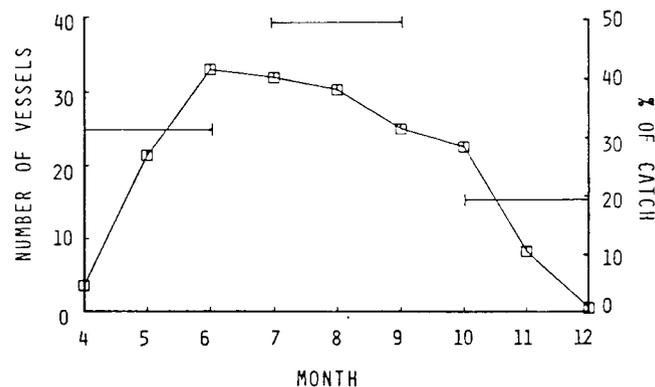


Figure 16. The average monthly number of foreign vessels fishing Pacific whiting sighted in aerial surveys, 1967-72 (squares) and the average percentage of the catch in 3-mo periods for the same years.

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 pre-fishing 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).

#### ACKNOWLEDGMENTS

Numerous scientists at the Northwest and Alaska and Southwest Fisheries Centers freely made data available. T. Laevastu, R. Schwartzlose, T. Dark, and

$$\triangle 1951-66 Y = 0.23X - 4.80 \quad (R = .63; P < .01)$$

$$\bullet 1967-75 Y = 0.10X - 1.42 \quad (R = .84; P < .01)$$

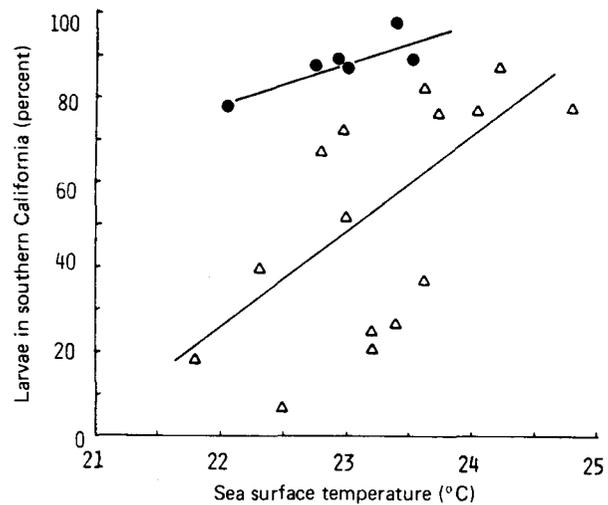


Figure 17. Regressions of the percentage of Pacific Whiting larvae off southern California compared to Baja California against the mean January-March sea surface temperature off Baja California for the pre- and postfishing periods, 1951-66 and 1967-75.

R. Lasker reviewed earlier versions of the manuscript and made helpful comments. We also appreciate the encouragement of W. Wooster and R. Marasco.

#### LITERATURE CITED

- Ahlstrom, E.H. 1959. The vertical distribution of fish eggs and larvae off California and Baja California, *Fish. Bull.*, U.S. 60:107-146.
- . 1968. An evaluation of the fishery resources available to California fishermen. In D. Gilbert (ed.), *The future of the fishing industry of the United States*. Univ. Wash. Press, Seattle, p. 65-80.
- Ahlstrom, E.H., and R.C. Counts. 1955. Eggs and larvae of the Pacific hake, *Merluccius productus*. *Fish. Bull.*, U.S. 56:295-329.
- Alton, M.S. 1972. Characteristics of the demersal fish faunas inhabiting the outer continental shelf and slope off the northern Oregon coast. In A.T. Pruter and D.L. Alverson (eds.), *The Columbia River estuary and adjacent ocean waters*. Univ. Wash. Press, Seattle, p. 583-636.
- Alton, M.S., and M.O. Nelson. 1970. Food of the Pacific hake, *Merluccius productus*, in Washington and northern Oregon coastal waters. *U.S. Fish Wildl. Serv., Circ.* 332:35-42.
- Alverson, D.L., and H.A. Larkins. 1969. Status of the knowledge of the Pacific hake resource. *Calif. Coop. Oceanic Fish. Invest. Rep.* 13:24-31.
- Bailey, K.M. 1980. Recent changes in the distribution of hake larvae: causes and consequences. *Calif. Coop. Oceanic Fish. Invest. Rep.* 21:167-171.
- . 1981a. An analysis of the spawning, early life history and recruitment of the Pacific hake, *Merluccius productus*. Ph.D. dissertation, Univ. Wash., Seattle.
- . 1981b. Larval transport and the recruitment of Pacific hake, *Merluccius productus*. *Mar. Ecol.* 6:1-9.
- . (in press). The early life history of Pacific hake, *Merluccius productus*. *Fish. Bull.*, U.S.
- Bailey, K.M., and P. Ainley. 1982. The dynamics of California sea lion predation on Pacific hake. *Fisheries Research* 1:163-176.
- Bailey, K.M., and J. Yen (in press). Predation by a carnivorous marine copepod, *Euchaeta elongata* Esterly, on eggs and larvae of the Pacific hake, *Merluccius productus*. *J. Plankton Res.*

- Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671.
- . 1975. Daily and weekly upwelling indices, west coast of North America, 1967-73. U.S. Dep. Commer., NOAA Tech. Rept. SSRF-693.
- Best, E.A. 1963. Contribution to the biology of the Pacific hake, *Merluccius productus*. Calif. Coop. Oceanic Fish. Invest. Rep. 9:51-56.
- Dark, T.A. 1975. Age and growth of Pacific hake, *Merluccius productus*. Fish. Bull., U.S. 73:336-355.
- Dark, T.A., M.O. Nelson, J. Traynor, and E. Nunnallee. 1980. The distribution, abundance, and biological characteristics of Pacific whiting, *Merluccius productus*, in the California-British Columbia region during July-September 1977. Mar. Fish. Rev. 42(3-4):17-33.
- Erich, S., F. Mombeck, and G. Speiser. 1980. Investigations on the Pacific hake stock (*Merluccius productus*) in the Northeast Pacific. Arch. Fishereiwiss 30:17-38.
- Ermakov, Y.K. 1974. The biology and fishery of Pacific hake, *Merluccius productus*. Ph.D. dissertation, Pac. Sci. Inst. Mar. Fish. Oceanogr. (TINRO), Vladivostok, USSR (in Russian).
- Fiscus, C. 1979. Interactions of marine mammals and Pacific hake. Mar. Fish. Rev. 41(10):1-9.
- Foucher, R.P., and R.J. Beamish. 1977. A review of oocyte development in fishes with special reference to Pacific hake (*Merluccius productus*). Can. Fish. Mar. Serv. Tech. Rep. No. 755.
- Francis, R.C. 1982. On the population and trophic dynamics of Pacific whiting. U.S. Dep. Commer., Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Ser., Northwest and Alaska Fish. Cent., Seattle, Wash., Processed Rep. 82-07, 68 p.
- Francis, R.C., G.L. Swartzman, W.M. Getz, R. Haar, and K. Rose. 1982. A management analysis of the Pacific whiting fishery. U.S. Dep. Commer., Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Ser., Northwest and Alaska Fish. Cent., Seattle, Wash., Processed Rep. 82-06, 48 p.
- Frey, H.W. 1971. Pacific hake. In H.W. Frey (ed.), California's living marine resources and their utilization, p. 71-74. Calif. State Dep. Fish Game. 148 p.
- Gotshall, D.W. 1969a. Stomach contents of Pacific hake and arrowtooth flounder from northern California. Calif. Fish. Game 55:75-82.
- . 1969b. The use of predator food habits in estimating relative abundance of the ocean shrimp, *Pandalus jordani*. Food Agric. Organ. U.N., Fish. Rep. 57:667-685.
- Hart, J.L. 1973. Pacific fishes of Canada. Fish. Res. Bd. Can., Bull. 180, 740 p.
- Hempel, G. 1979. Early life history of marine fish: the egg stage. Univ. Wash. Press, Seattle.
- Hickey, B.M. 1979. The California Current system—hypotheses and facts. Prog. in Oceanogr. 8:191-279.
- Holliday, D.V., and H.L. Larsen. 1979. Thickness and depth distribution of some epipelagic fish schools off southern California. Fish. Bull., U.S. 77:489-494.
- Hunter, J. 1977. Behavior and survival of northern anchovy, *Engraulis mordax* larvae. Calif. Coop. Oceanic Fish. Invest. Rep. 19:138-146.
- Hunter, J., and C. Kimbrell. 1980. Egg cannibalism in the northern anchovy, *Engraulis mordax*. Fish Bull., U.S. 78:811-816.
- Huyer, A., R.D. Pillsbury, and R.L. Smith. 1975. Seasonal variation of the alongshore velocity field over the continental shelf off Oregon. Limnol. Oceanogr. 20:90-95.
- Huyer, A., and R.L. Smith. 1976. Observations of a poleward undercurrent over the continental slope off Oregon, May-June 1975. EOS 57:263.
- Jones, B.W. 1974. World resources of hakes of the genus *Merluccius*. In F.R. Harden Jones (ed.), Sea fisheries research. John Wiley & Sons, New York, p. 139-166.
- Jow, T. 1973. Pacific hake length frequencies at California ports, 1963-1970. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. No. 2.
- Kramer, D., and P. Smith. 1970. Seasonal and geographic characteristics of fishery resources. California Current region—III. Pacific hake. Commer. Fish. Rev. 32(7):41-44.
- Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453-462.
- MacGregor, J.S. 1966. Fecundity of the Pacific hake, *Merluccius productus*. Calif. Fish Game. 52:111-116.
- . 1971. Additional data on the spawning of the hake. Fish. Bull., U.S. 69:581-585.
- Murphy, G.I. 1968. Pattern in life history and the environment. Am. Nat. 102:391-403.
- Nelson, M.O., and H.A. Larkins. 1970. Distribution and biology of Pacific hake: a synopsis. U.S. Fish Wildl. Serv., Circ. 332:43-52.
- Outram, D.N., and C. Haegeler. 1972. Food of Pacific hake (*Merluccius productus*) on an offshore bank southwest of Vancouver Island, British Columbia. J. Fish. Res. Bd. Can. 29:1792-1795.
- Pinkas, L., M. Oliphant, and I. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Fish and Game. Fish. Bull. 152.
- Pruter, A.T. 1976. Soviet fisheries for bottomfish and herring off the Pacific and Bering Sea coasts of the United States. Mar. Fish. Rev. 38(12):1-14.
- Riffenburgh, R.H. 1969. A stochastic model of interpopulation dynamics in marine ecology. J. Fish. Res. Bd. Can. 26:2843-2880.
- Smith, P. 1975. Pacific hake larval distribution and abundance, 1951-1975. Southwest Fish. Cent. Admin. Rep. LJ-75-83. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, CA 92038.
- . 1978. Biological effects of ocean variability: time and space scales of biological response. Rapp. P-v. Réun. Cons. Int. Explor. Mer 173:117-127.
- Soutar, A., and J.D. Isaacs. 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediments off California. Fish. Bull., U.S. 72:257-274.
- Stauffer, G.D., and P.E. Smith. 1977. Indices of Pacific hake from 1951-1976. Southwest Fish. Cent. Admin. Rep. LJ-77, Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, CA 92038.
- 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.H. 1981. Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation. Fish Bull., U.S. 78:685-692.
- Tillman, M.F. 1968. Tentative recommendations for management of the coastal fishery for Pacific hake, *Merluccius productus*, based on a simulation study of the effects of fishing upon a virgin population. M.S. thesis, Univ. Wash. Seattle.
- U.S. Fish and Wildlife Service. 1970. Pacific hake. U.S. Fish. Wildl. Serv., Circ. 332, 152 p.
- Utter, F.M., and H.O. Hodgins. 1971. Biochemical polymorphisms in the Pacific hake (*Merluccius productus*). Rapp. P-v. Cons. Réun. Int. Explor. Mer 161:87-89.
- Vrooman, A.M., and P.A. Paloma. 1977. Dwarf hake off the coast of Baja California. Calif. Coop. Oceanic Fish. Invest. Rep. 19:67-72.
- Wooster, W.S., and J.H. Jones. 1970. California Undercurrent off northern Baja California. J. Mar. Res. 28:235-250.
- Wyllie, J.G. 1967. Geostrophic flow of the California Current at the surface and at 200 meters. Calif. Coop. Oceanic Fish. Invest. Atlas 4.
- Zweifel, J., and R. Lasker. 1976. Prehatch and posthatch growth of fishes—a general model. Fish. Bull., U.S. 74:609-622.