Biology and Life History of the Coastal Stock of Pacific Whiting, *Merluccius productus*

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Introduction

Research on the life history and biology of the coastal stock of Pacific whiting, *Merluccius productus*, has been conducted since the development of the foreign trawl fishery in the mid-1960's. Insights gained from these studies have been reviewed by Nelson and Larkins (1970) and Bailey et al. (1982). This review provides an updated summary of the information on the biology and life history of the coastal stock of Pacific whiting.

Distribution and Migration

Four major spawning stocks of Pacific whiting have been identified. Of the four, the coastal stock off California, Oregon, Washington, and British Columbia is the most abundant and widely distributed. Other spawning stocks occur in central Puget Sound, the Strait of Georgia, and off the west coast of southern Baja California. The latter stock has been referred to as the dwarf variety by Vrooman and Paloma (1977). The coastal stock is distributed primarily over the continental shelf and slope from central Baja California in the winter (spawning) months to Queen Charlotte Sound during the summer (feeding) period.

The original hypothesis about the annual migration of the coastal stock still holds today. Alverson and Larkins (1969) developed it on the basis of Soviet fishing information, egg and larval distribution, and resource survey data. These authors proposed that after spawning off California and Mexico during the winter, adult whiting move northward to feed during the summer from northern California to Queen Charlotte Sound (Fig. 1).

Subsequent studies have added considerable detail to knowledge about the distribution and migration of coastal whiting. Ermakov (1974), for example, noted that the largest individuals tend to make the longest northerly migrations. Similarly, Dark

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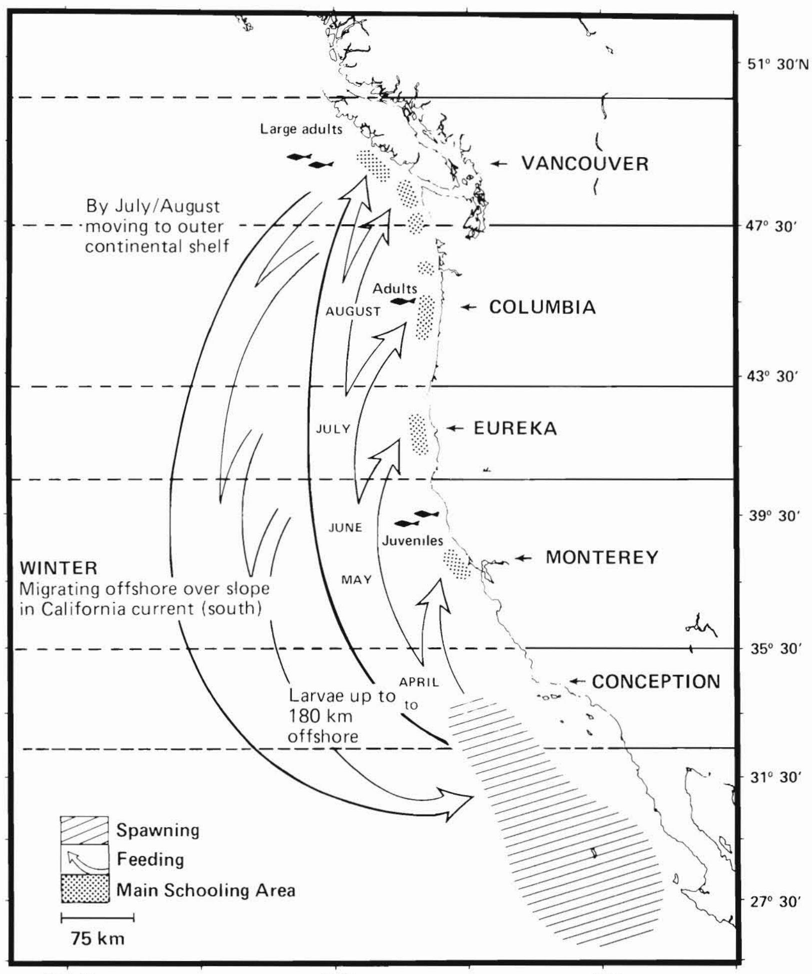

Figure 1.—Migratory patterns of Pacific whiting (from Bailey et al., 1982).

et al. (1980) reported that juvenile whiting are concentrated mainly off central California and southward.

Ermakov (1974) also commented on the intraseasonal movement of the adult fish. Using data collected from the Soviet fishing fleet during 1965-69 and from associated research cruises, he reported that large, spawned-out individuals of the type observed off San Francisco in early March gradually began to appear in an area 111.2 km (60 n.mi.) north within a few weeks. By the third week in April, large whiting were showing up off Oregon and Washington. The largest individuals usually arrived first and were followed by the smaller ones. Schools of large whiting first appeared off Vancouver Island in late May. The lead schools migrated at a rate of 5.5-11.1 km (3-6 n.mi.) per day. With respect to the inshore-offshore distribution of adult whiting, Ermakov reported that during the spring, schools off Oregon, Washington, and California are generally found over the continental slope but not over the shelf. In June they begin to move shoreward over the shelf to depths of 90 m (50 fathoms) or less. Few remain over the slope during July or early August until the schools begin their return (spawning) migration by moving westerly over the slope and eventually southward by early September. Most have departed by fall. Bailey et al. (1982) add that the southward migration may be triggered by the shift of the wind direction in the fall and the appearance of the Davidson Current.

Beamish and McFarlane (1985) report that the migration of whiting in and out of the Vancouver area is quite variable. In general, large quantities are present from mid-June until October, although fishable concentrations have been reported there as early as April and as late as November. They also note that males arrive off Canada later than females and depart earlier.

Whiting undertake strong diurnal migrations while on the feeding grounds, apparently in response to the vertical migrations of euphausiids, their primary food. During the day the schools are densely concentrated between 100 and 250 m. Daytime schools are composed of fish of similar size that move slowly in random directions. At sunset the schools begin to disperse and rise toward the surface. At night (2200-0300 h) they are scattered from near the surface to 20 m, moving quickly toward the bottom at dawn. Diurnal migration diminishes as fall approaches (Ermakov, 1974). Dark et al. (1980) report that there is no relation between fish size and school depth during the feeding season.

Reproduction

Information on the spawning biology of coastal whiting is limited because of the difficulty of locating adult schools in the spawning areas. Unlike the dense layers of spawning adults found in the Strait of Georgia stock (Thompson and McFarlane, 1982), spawning schools of coastal whiting are apparently dispersed over a wide area of the continental slope from central California to northern Baja California.

The few observations that have been made were reviewed by Bailey et al. (1982). Erich et al. (1980) and Stepanenko[1,2] reported spawning schools out to 400 km off California. During the 1979 U.S.-U.S.S.R. cooperative ichthyoplankton survey of the California Current system, Stephanenko found two dense spawning schools of whiting 220-330 km (120-160 n.mi.) off central California at lat. 35°45′N. These schools were in a dense layer at 100-200 m and extended for 7.8 km (4.2 n.mi.). One was found in the evening and the other at midnight—both in early February. In 1980, three groups of dense spawning schools were found at 340-400 m. These were spotted between 1300 and 2100 h in late February, 220-370 km (120-200 n.mi) offshore at lat. 31°00′N. The schools were from 1.6 to 16 km long.

Generally, what knowledge there is about the spawning of Pacific whiting has been deduced from the California Cooperative Oceanic and Fisheries Investigations (CalCOFI) egg and larval surveys. These surveys show that whiting larvae are abundant from December through April within 400 km of the coast from central California to northern Baja California. Bailey et al. (1982) used the peak occurrences of whiting eggs and small larvae to pinpoint January and February as the peak spawning months. They found the majority of eggs and small larvae (2-3 mm) off central California over the areas of the continental slope with bottom depths ranging from 130 to 500 m. Off southern California, with its many eddy currents and varied bottom topography (alternating deep basins and islands or banks) eggs and larvae are distributed out to 400 km from shore. Whiting eggs and small larvae (<8 mm) appear to aggregate at the 40-100 m depth interval near the base of the thermocline or mixed layer (Ahlstrom, 1959; Bailey, 1982). Because spawning occurs at depths of 130-500 m, it must be assumed that eggs ascend in the water column to a level of neutral buoyancy.

Female whiting in the coastal stock mature at 40 cm (16 inches) or more and at weights greater than 0.4 kg (0.9 pounds) (Best, 1963; Dark, 1975). These minimum sizes are achieved by some 3-year-old fish and most 4-year olds. MacGregor (1971), on the other hand, did find mature females as small as 12.5 cm and 22.2 cm off southern and central Baja California, respectively. It is likely, however, that the smaller fish in these samples were from the so-called "dwarf" stock rather than from the coastal stock.

Because of the scarcity of the samples and the variability of the

[1]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. manuscr. Pacific Scientific Research Institute of Fisheries and Oceanography (TINRO), Vladivostok, U.S.S.R.

[2]Stepanenko, M. A. 1981. Assessment of stocks and reproduction conditions of some commercial fish off the Pacific Coast of North America in 1980. Unpub. manuscr. Pacific Scientific Research Institute of Fisheries and Oceanography (TINRO), Vladivostok, U.S.S.R.

Table 1.—Values of growth parameters for whiting estimated by Dark (1975) and Francis (1983) for the von Bertalanffy growth model and the length-weight relationship for length measured in cm and weight in kg.

Analysis and growth parameter	Dark (1975) Male	Dark (1975) Female	Dark (1975) Male & Female	Francis (1983) Male & Female
von Bertalanffy				
l (cm)	56.29	61.23	60.85	55.40
k	0.30	0.30	0.30	0.26
t_0	0.20	0.01	0.03	1.61
Length-weight relationship				
a	0.00003468	0.00002044		0.00001815
b	2.55618	2.69509		2.73343

Table 2.—Average length and weight of female and male Pacific whiting from the offshore stock for ages 1.0-13.3 years derived for growth equations given by Dark (1975).

	Females				Males			
	Average fork length		Average weight		Average fork length		Average weight	
Age	in	cm	lb	kg	in	cm	lb	kg
1.0	6.1	15.4	0.07	0.032	6.1	15.4	0.08	0.038
2.0	11.0	28.0	0.36	0.163	10.6	26.9	0.35	0.157
3.3	16.2	41.2	1.01	0.460	16.6	42.2	1.09	0.496
4.3	18.2	46.2	1.38	0.626	17.6	44.6	1.26	0.570
5.3	19.0	48.2	1.55	0.704	18.7	47.6	1.49	0.675
6.3	19.8	50.3	1.73	0.786	19.6	49.7	1.65	0.751
7.3	20.4	51.8	1.88	0.854	20.0	50.9	1.76	0.798
8.3	21.4	54.3	2.13	0.967	20.6	52.3	1.89	0.857
9.3	22.4	57.0	2.43	1.102	21.6	54.8	2.12	0.964
10.3	23.2	58.9	2.66	1.207	22.2	56.4	2.29	1.041
11.3	23.2	59.0	2.67	1.211	22.0	55.9	2.24	1.015
12.3	24.0	60.9	2.91	1.320				
13.3	24.3	61.8	3.03	1.374				

observations, the fecundity of coastal whiting is not well defined. MacGregor (1966) and MacGregor (1971) examined 50 females collected off Baja California. For females collected off northern Baja California (and presumably of the coastal stock), he found that mature ovaries contained from 83 to 556 eggs in the advanced stage of development per gram of body weight (average 197 eggs per gram of body weight). The data were too limited, however, to predict rates of change in the number of eggs per unit weight for the larger females, although this information is available for the Strait of Georgia stock[3]. According to MacGregor (1966), and MacFarlane and Beamish (1985), Pacific whiting spawn only once per season.

Growth

Growth of Pacific whiting has been studied on the basis of changes in the average length and weight at age, with age having been determined from ring counts on the fish's otoliths. This method has been found by Dark (1975), Beamish (1979), and Beamish (1981) to be reasonably accurate through the first 11 years of life—the period when the bulk of the growth accrues.

The standard von Bertalanffy growth model and length-weight relationship have been presented by Dark (1975) and Francis (1983) as follows:

$$l_t = L_\infty (1 - e^{-k(t-t_0)}), \text{ and}$$

$$w = al^b$$

where

l_t and w = body length at age (t) and body weight;

L_∞, k, and t_0 = the von Bertalanffy parameters for maximum length, growth rate, and age at zero length; and

a and b = regression coefficients for length-weight relationship.

Estimates of the growth parameters given by Dark (1975) and Francis (1983) are summarized in Table 1. In general, the relationships derived by both authors coincide for the major group of fish and diverge only at the extremes of the age and length ranges. Average length, in inches and centimeters, and average weight, in pounds and kilograms, estimated by parameter values given by Dark (1975) are listed in Table 2 for fish between 1.0 and 13.3 years of age.

The growth pattern described by Dark (1975) showed that whiting reach about 70-75 percent of their maximum length and about 50 percent of their maximum weight by 4.3 years (the age at which whiting begin to mature sexually). He also found that mature females were about 1 inch (2.5 cm) longer than males of the same age. The differential growth between males and females was not apparent before 4.3 years. Considered in conjunction with the longer migrations of larger fish, the larger size of mature females would tend to explain the preponderance of females in the northern areas of the summer feeding grounds described by Beamish and McFarlane (1985). Average maximum sizes reported by Dark (1975) are about 56 cm (22 inches) and 1 kg (2¼ pounds) for males and 61 cm (24 inches) and 1⅓ kg (3 pounds) for females. Females have been observed up to 81 cm (32 inches) and 2¼ kg (5 pounds). Length at age is variable between year classes. Dark found the slowest growth rate for the large 1961 year class, which suggests density-dependent growth.

Francis (1983) examined within-year growth in terms of both length and weight and found both to be seasonal, with fish growing during the summer feeding season and then ceasing to grow (actually losing 5-10 percent of their weight) during the winter spawning period. Weight loss can be attributed to energy expended in the migratory and reproductive processes. The seasonal growth pattern reported by Francis for coastal whiting is similar to that observed in the Strait of Georgia stock (McFarlane and Beamish, 1985).

Mortality

Estimates of annual instantaneous

[3]G. A. McFarlane, Pacific Biological Station, Nanaimo, B.C., V9R 5K6, Canada. Pers. commun., 1982.

Table 3.—Estimates of annual instantaneous mortality rates of Pacific whiting (from Bailey et al., 1982).

Investigators	Males	Females	Both sexes
M: Natural mortality			
Tillman (1968)	0.72	0.62	$\bar{x} = 0.67$
Nelson and Larkins (1970)			0.56
Efimov (1974)[1]			0.35
PFMC[2]			0.30-0.60
Jackowski (1980)[3]			0.30
Erich et al. (1980)			0.56
Low (1978)[4]			0.50
Francis (1983)			0.19-0.86 (variable age-specific natural mortality
F: Fishing mortality			
Efimov (1974)[1]			0.30
Erich et al. (1980)			0.67
Z: Total mortality			
Efimov (1974)[1]			0.65
Erich et al. (1980)			1.23

[1]Efimov, Y N. 1974. The size of stocks and status of fishery of Pacific whiting. Unpubl. manuscr. Pacific Scientific Research Institute of Marine Fisheries and Oceanography (TINRO), Vladivostok, U.S.S.R.
[2]Pacific Fishery Management Council. 1980. Pacific coast groundfish plan. Draft rep. Pacific Fishery Management Council, 526 S.W. Mill St., Portland, OR 97201
[3]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. manuscr. presented at the U.S.-Poland bilateral meetings, 1980.
[4]Low, L. L. 1978. Hake natural mortality and yield potential. Unpubl. manuscr. Northwest and Alaska Fisheries Center, NMFS, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

rates of natural mortality (M) have been derived by a number of authors (Table 3). Two factors tend to introduce variability to the estimates. First is the differential rate of migration, hence the segregation of the various size groups during the summer. This makes it difficult to obtain representative samples of the overall population. Second is the wide fluctuation in annual recruitment. Nonetheless, most values of (M) fall between 0.30 and 0.67, implying that between 26 and 49 percent of adult whiting would die each year of natural causes if there were no fishing. Although an intermediate value ($M = 0.45$) constant throughout the life span is frequently used in population models for Pacific whiting, Francis (1983) considered it probable that factors such as spawning stress make it likely that natural mortality increases with age. He assumed, therefore, that natural mortality increases 10 percent with each additional year of age and proceeded to compute age-specific values of (M) ranging from 0.19 for age 3 fish to 0.86 for age 11 fish.

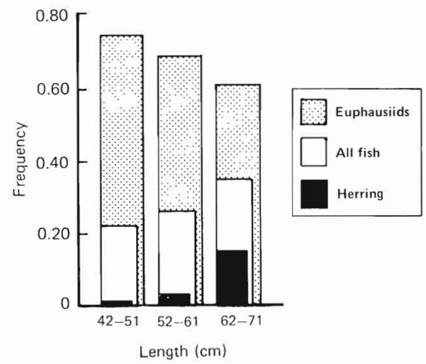

Figure 2.—Frequency of occurrence of prey types in different Pacific whiting size classes off Vancouver Island (data from Outram and Haegel, 1972; figure from Bailey et al., 1982).

Feeding Behavior

Several authors have contributed information on the feeding behavior of Pacific whiting. Livingston and Bailey (1985) have reviewed the role of the species both as a predator and as a prey item throughout its life history. As juveniles and adults, whiting feed on euphausiids, fish, shrimp, and squid during the spring, summer, and fall. Apparently, mature individuals do not feed during the spawning season (Tillman, 1968). Alton and Nelson (1970) reported that during the growth season, whiting feed at night near the surface. From stomach samples collected over a 15-h period beginning in the early evening, Livingston (1983) found stomachs fullest at 1800 h (the first hour of sampling). With the exception of a minor peak at 0300 h, stomach fullness generally decreased after 1800 h until it increased again at 0900 h, the last hour of sampling. The peaks at 1800 h, 0300 h, and 0900 h coincided, it was noted, with the times during which whiting and euphausiids occur together in the water column in the greatest concentrations—near bottom in the evening and morning and near the surface after midnight. The daily ration of adult whiting has been estimated to be 0.71-1.09 percent body weight/day by Francis (1983) and as high as 2.5 percent by Livingston (1983).

The species composition of the diet varies with size, age, and geographic location. Generally, euphausiids make up 80-90 percent of the food items but decrease in importance for larger fish on their northward migration (Fig. 2). Fish make up an increasing percentage of the food as the whiting grow larger. When schools of adult and juvenile whiting occur together off northern California in the summer, adults may feed on the juveniles (Bailey et al., 1982). Other fish that are important food items for whiting are Pacific sand lance, *Ammodytes hexapterus*; Pacific herring, *Clupea harengus pallasi*; and deep-sea smelt, *Bathylagus* spp. (Outram and Haegele, 1972). Gotshall (1969) found that shrimp made up 50-60 percent of the stomach contents of samples taken off northern California in spring and summer. Other studies, however, have not revealed shrimp to be as important in the diet.

Recruitment

Young whiting are recruited to the exploitable stock at ages 3-6, beginning with age 3 fish off northern California. Recruitment to the summer fishery off Oregon and Washington is nearly complete for 5-year-olds. Beamish and McFarlane (1985) found that recruitment to the fisheries off Vancouver occurred at ages 5 and 6. Since the development of the whiting fishery, the harvest has been dominated by a number of large year classes. Dark (1975), Bailey (1981), Francis and Hollowed (1985), and Beamish and McFarlane (1985) report that the 1961, 1970, 1977, and 1980 year classes were strong and that the 1960, 1967, and 1973 year classes were moderately strong.

The biological and environmental factors influencing the recruitment of whiting, first described by Bailey (1981), are considered in detail by Bailey and Francis (1985). Bailey found that the years producing strong year classes were correlated with the presence of strong onshore ocean currents. These conditions are associated with weak upwelling and warm coastal sea-surface temperatures. He reasoned that poor recruitment resulted from a low rate of survival of the larvae which had been transported offshore by coastal upwelling currents which, in turn, were created by north winds blowing along the shore.

Abundance

The primary method for measuring the abundance of the coastal whiting stock has been by trawl-acoustical surveys off the continental slope and shelf from central California to Vancouver Island. Surveys by the Northwest and Alaska Fisheries Center produced biomass estimates of 445,000 metric tons (t), 1,129,000 t, and 1,537,000 t for the years 1975, 1977, and 1980, respectively (Bailey et al., 1982; Nelson and Dark, 1985). The large increase in 1980 was attributed to the high abundance of juveniles from the strong 1977 year class that was found off central California.

Similar surveys have been conducted by Soviet researchers since 1967. The results of these surveys, which appear in unpublished manuscripts submitted at the annual U.S.-U.S.S.R. bilateral meetings, were summarized by Bailey et al. (1982). Soviet estimates of biomass averaged 1,360,000 t for 1967-73, and were 1,400,000 t and 1,860,000 t for 1974 and 1975, respectively. The Soviets made two surveys in 1978. Biomass estimates were 770,000 t on the basis of the early summer survey and 1,470,000 t for the late summer survey. Similarly, the 1979 estimates were 2,870,000 t and 1,200,000 t based on their July-August and August-September surveys, respectively. These large intra-annual differences more likely reflect differences in the distribution and availability of the fish along the coast, differences in the areas surveyed, and variations in the effectiveness of the echo sounding equipment rather than actual changes in the stock biomass.

Francis (1983) estimated the biomass of the coastal whiting stock for 1973-80 using age composition data from the commercial fishery in a cohort analysis. Allowing for varying regimes of seasonal growth and natural mortality, his biomass estimates for fish age 3-11 averaged 1,253,000 t annually. Biomass peaked at 1,450,000 t in 1976 and again in 1980 as a result of the recruitment of 3-year-olds from the strong year classes of 1973 and 1977.

Another source of biomass estimates is the series of CalCOFI surveys to assess the pelagic spawning products of fish populations within the California Current region since 1951. The Pacific whiting has been one of the dominant species sampled in these surveys. For the past decade, cooperative surveys between the United States and the Soviet Union have been directed specifically at measuring the abundance of whiting larvae during the months of peak spawning.

Ahlstrom (1968) was the first to derive estimates of the biomass of the coastal whiting stock. Using the relative abundance of whiting and jack mackerel, *Trachurus symmetricus*, larvae as a basis, he estimated the biomass of coastal whiting at 1,800,000-3,600,000 t. In more recent years Soviet scientists have used information obtained on the cooperative U.S.-U.S.S.R. ichthyoplankton surveys to develop biomass estimates for presentation at the annual bilateral meetings[1,2,4,5]. These estimates are generally about double those based on trawl-acoustic surveys, but are similar to the estimates obtained by Francis (1983) where he assumed a constant natural mortality rate.

Bailey et al. (1982) asserts that estimates of the spawning biomass of whiting derived from egg and larval surveys are likely to be biased and imprecise because 1) fecundity estimates are weakly based, 2) the mortality rate of eggs and larvae is poorly defined, and 3) the number of stations surveyed during the spawning season is relatively small considering the extremely patchy distribution of the eggs and larvae in the ocean.

These limitations notwithstanding, the surveys have provided two indices of the biomass of spawning whiting. First is the density of larvae within the survey area expressed as number of larvae/10 m^2 of sea surface area. This index is taken to be indicative of the density of the spawning biomass. Second is the percentage of the occupied stations that contain whiting larvae. This measures the expanse of the spawning area. Both indices can be influenced by the timing of the surveys and the geographic areas covered. Timing has varied over the years, but generally the surveys have covered a 30-day period between mid-January and 1 March. For the first 25 years of the CalCOFI surveys, stations were sampled from San Francisco (lat. 38°N) to central Baja California (lat. 25°N). In recent years the majority of these surveys of whiting larvae have been restricted to the regions north of San Diego (lat. 32°N).

The indices of abundance derived from the larvae surveys (Table 4) can be used to evaluate the status of the coastal stock of Pacific whiting from 1951 to 1984. First, there are indications that abundance was higher in the middle years of the 1950's than at the beginning or at the end. Then, following a prolonged period of low abundance, the stock increased in the mid-1960's. This coincided with the maturity of the dominant 1961 year class and the buildup of the foreign fisheries which might have been expected to reduce the abundance of eggs and larvae in subsequent years. This, however, was not the case as the surveys revealed high levels of abundance for the years 1972-1980, with the isolated exception of 1976 when the survey revealed a precipitous decline in larvae. Not only were larvae scarce in 1976, but they were found within only a small area. This suggests that the area used for spawning in 1976 was itself greatly reduced.

The low index values for 1976

[4]Stepanenko, M. A. 1979. Estimates of spawning biomass and reproductive conditions of Pacific hake and California anchovies in 1978. Unpubl. manuscr., Pacific Scientific Research Institute of Fisheries and Oceanography (TINRO), Vladivostok, U.S.S.R.

[5]Stepanenko, M. A. 1981. Assessment of stocks and reproductive conditions of Pacific hake and California anchovy in 1981. Unpubl. manuscr., Pacific Scientific Research Institute of Fisheries and Oceanography (TINRO), Vladivostok, U.S.S.R.

proved, however, to be a 1-year phenomenon, as the index values increased sharply in 1977 and remained very high through 1980. This reflects the continued influence of the large 1970 and 1973 year classes. The extremely low levels of abundance of larvae in 1982 and 1983 suggest that the contribution of the 1977 year class (which was strong according to Bailey and Francis (1985) and Beamish and McFarlane (1985)) has been much lower than expected. It is not known whether the scarcity of larvae in 1982 and 1983 (and 1976) was caused by an unexpected reduction of the respective spawning biomasses, by impaired spawning of normal-sized spawning populations, by poor survival of eggs and larvae from normal-sized spawning populations, by displacement of eggs and larvae from the survey area, or by a combination of these and other possible factors. That the extremely low indices of larvae can be the first signal of an impending year-class failure is supported by the work of Bailey and Francis (1985) who reported that recent age composition samples from the commercial fishery indicate that the 1976 year class is practically nonexistent.

Table 4.—The CalCOFI time series of Pacific whiting spawning biomass indices based on the occurrence of whiting larvae in the ichythoplankton, 1951-84[1].

Year	Percentage of positive stations	Number of larvae/10m²	Survey months
1951	23	32	Jan.-Feb.
1952	30	86	" "
1953	44	109	" "
1954	54	55	" "
1955	75	158	" "
1956	52	216	" "
1957	44	216	" "
1958	55	83	" "
1959	45	52	" "
1960	43	30	" "
1961	31	34	January
1962	48	77	"
1963	57	65	"
1964	49	26	"
1965	49	63	"
1966	52	170	Jan.-Feb.
1968	54	270	January
1969	49	91	Jan.-Feb.
1972a	31	67	" "
1972b	57	406	March
1975a	36	252	January
1975b	54	434	March
1976	16	68	February
1977	76	321	March
1978	70	461	"
1979	84	550	"
1980	56	485	Feb.-Mar
1981	44	136	February
1982	26	18	Jan.-Apr
1983	28	10	Feb.-Apr
1984	35	175	Feb.-Mar

[1]Sources:

Stauffer, G. D., and P. E. Smith. 1977 Indices of abundance of Pacific hake from 1951 to 1976. Southwest Fish. Cent. Admin. Rep. LJ-77-2. Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, LaJolla, CA 92038.

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