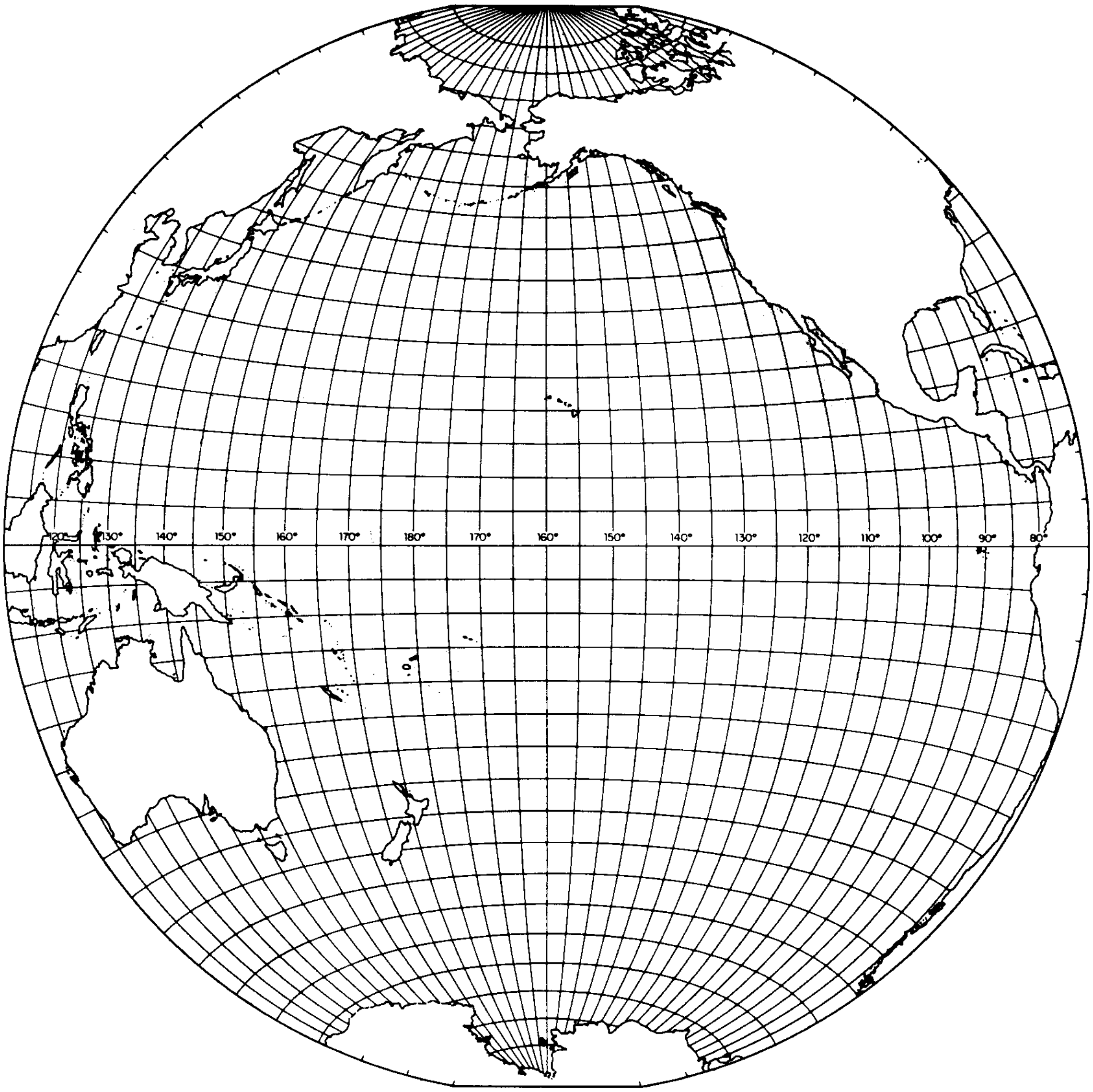

California Cooperative Oceanic Fisheries Investigations

Reports

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UNIVERSITY OF CALIFORNIA, SCRIPPS INSTITUTION OF OCEANOGRAPHY
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Part I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE

The CalCOFI Committee is pleased to report that the research, monitoring, and advisory roles of the CalCOFI program continued into 1992. The California Department of Fish and Game at Long Beach, and the Southwest Fisheries Science Center, NOAA, and the Scripps Institution of Oceanography, UCSD, both located in La Jolla, continue to cooperate in evaluating the status of stocks and the condition of the California Current ecosystem. We have begun new research initiatives, forming new alliances and making new management arrangements.

The California sardine population slowly continues to recover. The third annual workshop involving state, federal, and industry biologists was convened by the California Department of Fish and Game (CDFG) to examine sardine assessment procedures and management options. Participants used CalCOFI collections of sardine eggs and larvae, aerial survey data from fish spotters, and fishery landing data to estimate the spawning biomass of sardines. The consensus estimate was 385,000 short tons. As a result, CDFG set the 1992 directed fishery quota at 20,500 tons, nearly double the quota for last year, and the largest harvest allowed since the recovery began. The 1992 fishery has been slow, however, partly because of financial problems in the industry.

The symposium of the 1991 CalCOFI Conference focused on the recovery of the sardine. The proceedings of that symposium appear in this volume, and offer new insights into the mechanisms governing the variability of sardine populations, historic and prehistoric population sizes, and current assessment and management tools.

The reduction fishery for northern anchovy has stopped. Although U.S. fish meal production averages about 250,000 MT annually, anchovy prices and biomass since 1982 have not generated enough earnings to cover the cost to California fishermen.

In late 1991 signs of an incipient El Niño Norte became apparent. By the end of March 1992 it was clear that a large perturbation was in progress. The January 1992 sea height at Scripps Pier in La Jolla was the second highest in the 68-year record; the February, March, and April sea heights set new monthly mean records. In addition, the Scripps Pier monthly mean sea-surface temperature for April set a new 76-year high of 19.00°C (3.46°C above the mean). SIO and NOAA vessels working north of Point Arenas in March reported a strong northward-flowing countercurrent and little or no active coastal upwelling. They also observed low chlorophyll concentrations and low zooplankton abundances, implying a possible diminution of the biomass at the lower end of the pelagic food chain. During the April CalCOFI cruise scientists aboard R/V *David Starr Jordan* measured the temperature and salinity field across the California Current at various latitudes. The data show a positive temperature anomaly in the first 100 km offshore to a depth greater than 300 m. The positive anomaly continued in the upper 100 m as far as 650 km offshore, a significant redistribution of heat. At this writing, it is still too early to catalogue the biological response to this event, or even to evaluate its magnitude. Anecdotal and observational information will be collected throughout this year and reported at the November CalCOFI Conference and in next year's *CalCOFI Reports*.

El Niño events affect our understanding of changes related to possible global warming. A hypothetical effect of global change is increased ultraviolet radiation (UVB). A new NOAA project called BURNM studies the survival of anchovy larvae under various intensities of irradiation, using biochemically based estimates of UVB damage to the DNA of larval anchovy.

NMFS and CDFG embarked on several cooperative efforts this year. Cruises aboard the R/V *Mako* and NOAA ship *David Starr Jordan* were designed to evaluate the performance and effectiveness of a rope trawl for capturing adult sardines and mackerel. Scientists from NMFS-Pacific Fisheries Environmental Group, Moss Landing Marine Laboratories, and the CDFG made several cruises to assess halibut stocks in the southern California region, using an "area-swept" technique.

The working relationship between NMFS and SIO, long a strong feature of the CalCOFI program, was further strengthened by the development of a Joint Institute for Marine Observation. John Knauss, Under Secretary for Oceans and Atmosphere, and Edward Frieman, Director of SIO, signed the memorandum of understanding establishing the institute in November 1991. The institute will serve as a research center for collaboration between NOAA and Scripps scientists.

Another cooperative venture was the two-ship operation involving UCSD's R/V *New Horizon* and NOAA's ship *David Starr Jordan* in a project called FORAGE (Fishery Oceanography Research and Groundfish Ecology). The object of this effort is to determine the relationship between the successful return and settlement of juvenile groundfishes on the continental shelf and the dynamics of mesoscale features such as eddies and jets.

A team of federal and state biologists, economists, and statisticians is developing a federal fishery management plan for coastal pelagic species (sardine, Pacific mackerel, jack mackerel, and northern anchovy). The plan is necessitated by the recent increase in the sardine population, and because factory trawlers from the Pacific Northwest are considering fishing for coastal pelagic species in federal waters, where no management plan is in place. Implementation of the plan, scheduled for 1993, will shift responsibility for sardine, Pacific mackerel, and jack mackerel from state to federal agencies.

The Committee will miss Rick Klingbeil, a member for the last five years and an alternate long before. Patricia Wolf has been appointed as the new CDFG representative, after having served an excellent two-year stint as CalCOFI coordinator.

The Committee also acknowledges the retirement of two senior CalCOFI investigators: Joseph L. Reid and Edward Brinton. Joe's research on the physical oceanography of the North Pacific Ocean has significantly enhanced our understanding of the coupling between the California Current system and other currents and water masses. Joe was director of the Marine Life Research Group (the SIO component of CalCOFI) from 1974 to 1987, and a member of the Committee for the same period. His quiet tenacity arguably kept Scripps in CalCOFI. Ed's encyclopedic knowledge of the taxonomy, ontogeny, and zoogeography of euphausiids helped him understand such phenomena as changes in boundaries associated with El Niño events, and semi-isolated populations within the Southern California Bight region. Both Ed and Joe continue their research, on California Current euphausiids and on the deep circulation of the world's ocean, respectively.

We wish to thank the officers and crews of the CDFG's R/V *Mako* and of the F/V *Good News*, the University of California's R/V *New Horizon*, and the NOAA ship *David Starr Jordan* for their continued excellent support of the CalCOFI mission. These research platforms are essential to the continuity of CalCOFI time-series studies as well as to experimental work arising from the long-term observations.

We also wish to thank *CalCOFI Reports* editor Julie Olfe and Spanish language editor Jesús Pineda for another excellent volume of *CalCOFI Reports*. Our deep appreciation goes to our colleagues who served as reviewers and editorial consultants for this volume: Angeles Alvariño, Pablo Arenas, Louis Botsford, Edward Brinton, Daniel Cayan, Thomas Crowley, Rick Deriso, John Govoni, George Hemingway, Anne Babcock Hollowed, Larry Jacobson, Dan Kimura, Alec MacCall, Gordon McFarlane, Geoffrey Moser, Ashley Mullen, Michael Mullin, Richard Parrish, Immants Priede, Kurt Schaefer, Paul Smith, Gary Stauffer, and Elizabeth Venrick.

The CalCOFI Committee:
Izadore Barrett
Michael Mullin
Patricia Wolf

REVIEW OF SOME CALIFORNIA FISHERIES FOR 1991

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Total landings of fishes, crustaceans, echinoderms, and mollusks decreased 8% from 1990. This is the third consecutive year that California has experienced a decline in total landings. The 1991 landings exceeded the 1985 low by only 2%, and are 27% below the last ten-year average.

Pelagic wetfish landings increased 4% from last year, marking a return from last year's decline to the upward trend that began in 1985. Squid and sardine landings increased, but Pacific and jack mackerel landings declined (table 1).

Groundfish landings decreased slightly. Landings of Dover sole and Pacific whiting increased, while all other species remained the same or decreased. California halibut landings increased from the ten-year low in 1990.

Landings of swordfish declined for a second year, to the lowest catch in nine years. Shortfin mako shark landings decreased considerably from last year, while common thresher shark landings increased to the highest level since 1986.

The red sea urchin fishery continued to be a major California fishery. Although landings in northern and southern California dropped, the value of the catch reached a record high. Dungeness crab landings increased dramatically.

Both the numbers of anglers and the sport catch declined in 1991, although developing warm-water conditions may improve the sport catch in southern California. Albacore landings were the lowest on record.

PACIFIC SARDINE

In July 1990, the California Department of Fish and Game (CDFG) conducted a survey to assess the spawning biomass of the Pacific sardine (*Sardinops sagax*). The egg production area method (EPAM) was used to determine if the observed spawning area exceeded the critical spawning area of 2,300 nautical miles^2 (n.mi.^{2}), which is considered indicative of a 20,000-ton spawning biomass. The observed spawning area of 1,480 n.mi.^{2} was 62% smaller than the area observed in 1989, and 35% smaller than the 2,300-n.mi.^{2} critical spawning area. The decrease in observed spawning may have been due to warm

TABLE 1
Landings of Pelagic Wetfishes in California (Short Tons)

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Pacific herring	Market squid	Total
1971	149	44,853	78	29,941	120	15,759	90,900
1972	186	69,101	54	25,559	63	10,800	105,763
1973	76	132,636	28	10,308	1,410	6,031	150,489
1974	7	82,691	67	12,729	2,630	14,453	112,577
1975	3	158,510	144	18,390	1,217	11,811	190,075
1976	27	124,919	328	22,274	2,410	10,153	160,111
1977	6	111,477	5,975	50,163	5,826	14,122	187,569
1978	5	12,607	12,540	34,456	4,930	18,899	83,437
1979	18	53,881	30,471	18,300	4,693	22,026	129,389
1980	38	47,339	32,645	22,428	8,886	16,957	128,293
1981	31	57,659	42,913	15,673	6,571	25,915	148,762
1982	145	46,364	31,275	29,110	11,322	17,951	136,167
1983	388	4,740	35,882	20,272	8,829	2,001	72,112
1984	259	3,258	46,531	11,768	4,241	622	66,679
1985	653	1,792	38,150	10,318	8,801	11,326	71,040
1986	1,283	2,105	45,503	12,209	8,405	23,454	92,959
1987	2,309	1,595	45,890	13,055	9,258	22,028	94,135
1988	4,172	1,618	47,278	11,379	9,721	41,040	115,208
1989	4,308	2,700	39,825	21,820	10,134	45,076	123,863
1990	3,103	3,536	41,134	5,460	8,938	31,357	93,528
1991*	8,543	4,238	34,124	1,868	7,945	40,529	97,247

*Preliminary

water in the Southern California Bight before the survey.

After a review of the status of the sardine, including various sources of information in addition to the CDFG survey, participants at a sardine management workshop in September 1990 estimated the adult sardine population to be 100,000 tons. As a result, a 2,499-ton directed quota (based on a 5% harvest guideline, which included a 3,000-ton reserve for incidental take) was opened in January 1991. This was the sixth consecutive year that a directed sardine fishery was allowed since the moratorium went into effect in 1974, and was the first time since 1986 that the directed fishery quota exceeded 1,000 tons.

The 2,499-ton quota was divided between northern California (one-third reserved for landings north of San Simeon Point; figure 1) and southern California (two-thirds reserved for landings south of San Simeon Point). This was a change from the 20%/80% allocation scheme in effect in 1989 and 1990, and resulted from legislation passed in the last year. In addition to the directed fishery and the 3,000-ton reserve for incidental take, there was a 350-ton quota for live bait (opened January 1, 1991) and a 250-ton quota for dead bait (opened March 1, 1991).

The southern California allocation of the directed fishery opened on January 6, 1991. In an effort to minimize landings in excess of the quota, the southern directed fishery was open for one day (24 hours) per week until the quota was taken. A total of 1,879 tons was landed against the 1,667-ton quota during two 24-hour fishing periods, and the fishery was closed on January 14, 1991.

During February, the CDFG reexamined the information developed at the workshop and considered comments received at a meeting with industry representatives. Several series of data suggested that the sardine resource had shown net annual increases of 30% to 40% during recent years, even with annual harvest levels of at least 5% and perhaps as high as 10%. As a result, the CDFG increased the 1991 harvest level to 10%, or 10,000 tons, since this harvest level would allow the sardine population to continue to grow. The revised harvest level resulted in a 6,150-ton directed fishery quota, with 4,100 tons allocated to southern California and 2,050 tons allocated to northern California. The dead bait quota was increased to 500 tons (as specified in current regulations); the live bait quota remained at 1,000 tons; and the incidental reserve remained at 3,000 tons.

The take of sardines in the live bait fishery, as estimated from logs submitted by fishermen, amounted to 300 tons. Most of the sardines landed as bait were caught from July through November. Live bait fishermen reported a decrease of large sardines in 1991 compared to 1990.

The southern California directed fishery opened again on March 4, 1991, with an additional 2,434-ton quota. The fishery was closed on March 25, with 2,636 tons landed during four 24-hour periods. A total of 28 boats participated in the January and March fisheries, and made 114 landings. Most of the catch consisted of pure loads of sardines, and was canned for human consumption.

The northern California directed fishery opened on August 1, 1991, and remained open until the end of the year. Unlike the southern California fishery, the northern California fishery had no landing restrictions. A total of 977 tons was landed against the 2,050-ton allocation. Approximately half of the 41 landings consisted of pure loads of sardines, and four boats made most of the landings.

Current law allows a 250-ton dead bait quota when the directed fishery quota is less than 2,500 tons, and increases the dead bait quota to 500 tons when the directed quota is 2,500 tons or greater. This dead bait quota is allocated among three geographic areas: 376 tons are reserved for landings south of San Simeon Point; 62 tons are reserved for landings between San Simeon Point and Pescadero Point; and 62 tons are reserved for landings north of Pescadero Point.

The southern California dead bait fishery was closed on April 8, 1991, with 424 tons landed during one 24-hour fishing period. Most of the catch consisted of pure loads of sardines. The central California dead bait fishery was closed on May 24, with 70 tons landed. No landings were made against the northern California dead bait allocation in 1991.

The tolerance limit for sardines landed incidentally in the mackerel fishery remained at 35% by weight throughout the year. Incidental landings of sardines totaled 1,295 tons, and represented 3% of the total mackerel catch. This was similar to 1990 (2.9%), but less than in 1989 (4.5%). Although the 1991 proportion of sardines in mackerel landings was similar to 1990, the total amount of sardines landed incidentally in 1991 decreased 12% from 1990 because of a 23% decrease in total mackerel landings.

In October 1991, the CDFG estimated that only 1,000 of the 3,000 tons of sardines initially reserved for the annual incidental take would be landed by the end of the year. As a result, the remaining 2,000 tons were made available as a directed fishery. This quota was allocated and managed similarly to the directed fisheries in January and March. The southern California allocation (1,333 tons) was opened on

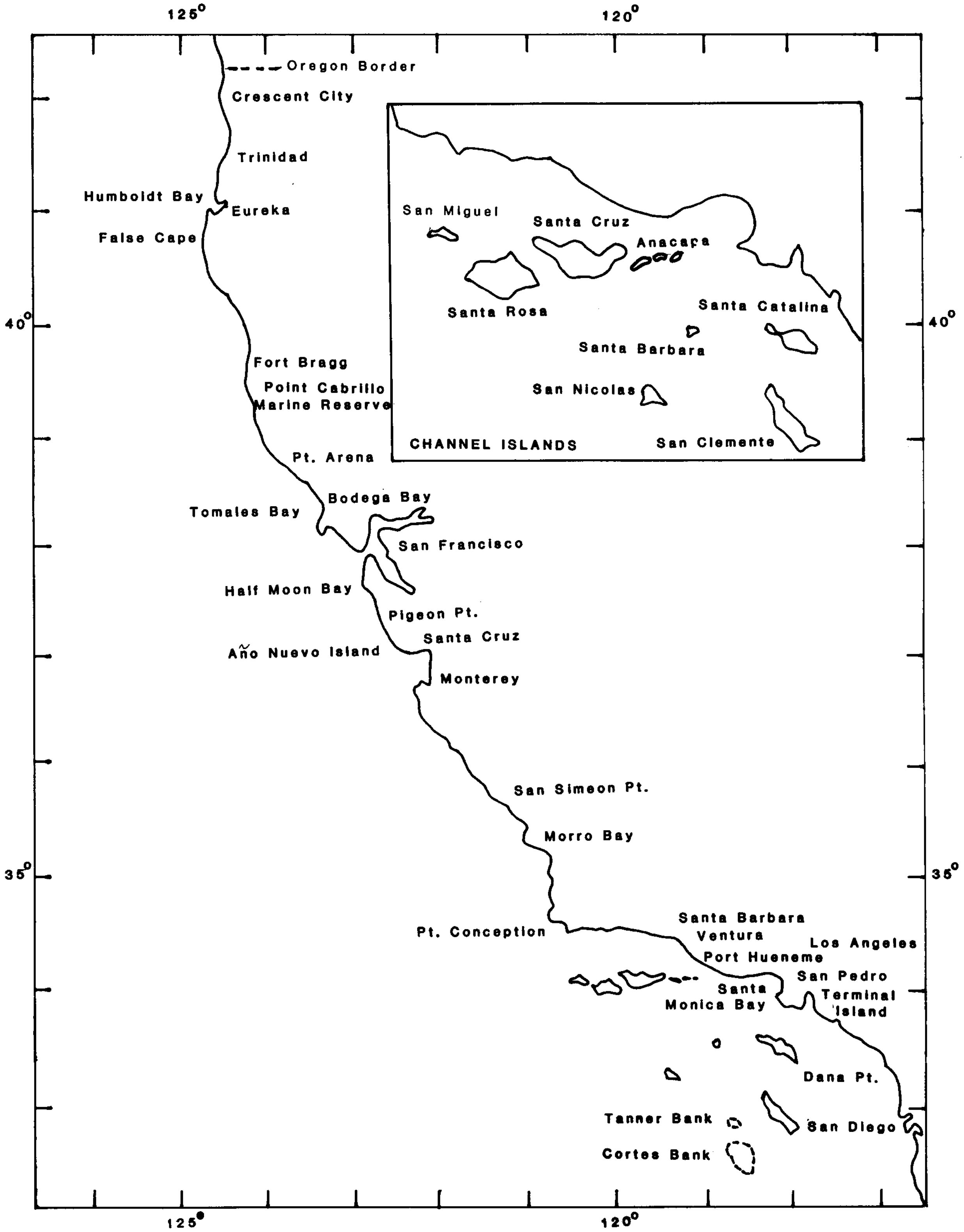

Figure 1. California ports and fishing areas.

October 27. A total of 1,232 tons were landed in two 24-hour fishing periods, and the fishery was closed on November 4. There were no additional landings made against the northern allocation.

The total 1991 landings of sardines from all sources (directed, dead bait, live bait, and incidental) was 8,543 tons (table 1), an increase of almost 200% over the total 1990 sardine take. The increase in 1991 was due to the increased directed quota. As in 1990, sardines landed in 1991 were canned for human consumption and pet food, and were used for dead bait.

In June 1991, the CDFG conducted an EPAM survey to evaluate the sardine spawning biomass. The survey covered the waters off southern California from Point Conception to the Mexican border, from close to shore to as far out as 200 miles. The observed spawning area of 3,840 $n.mi.^2$ was 2.6 times larger than the area observed in 1990, and 4% larger than the area observed in 1989. With the exception of 1990, the size of the sardine spawning area as estimated by CDFG surveys has increased steadily since the surveys were begun in 1985. During 1991, sardines spawned in patches southwest of San Clemente Island, and in smaller concentrations along the coast from Santa Barbara to Dana Point. The observed spawning area indicated an adult population well above the 20,000-ton critical level.

In October 1991 the third annual workshop on sardine management was held by the CDFG and attended by state, federal, and fishing-industry biologists. The 1991 population of adult sardines was estimated to range between 275,000 and 495,000 tons, with an average estimate of 385,000 tons. This estimate was derived from various sources, including the occurrence of sardine eggs and larvae in CalCOFI surveys, observations of sardines by aerial fish spotters, CDFG spawning area surveys, and catch and age data from historical and current sardine fisheries. A total harvest level of 10% was recommended. This is similar to the 1991 harvest level, except that the sardine catch by Mexico was not considered in setting U.S. quotas for 1991. In contrast, 13,500 tons were subtracted from the 1992 total harvest of 38,500 tons, to account for the expected Mexican catch. As a result, the total U.S. harvest for 1992 was set at 25,000 tons, including 500 tons for dead bait, 1,000 tons for live bait, a 3,000-ton incidental reserve, and a directed fishery quota of 20,050 tons.

Legislation (AB 173) was enacted in July 1991 to reestablish the procedures for setting the tolerance limit for sardines caught incidentally with mackerel. A sunset clause eliminated this section of the Fish and Game Code in January, but the 35% tolerance remained in effect during the interim. AB 173 also eliminates the sunset clause pertaining to the 350-ton live bait quota and the use of bait nets to take sardines in Santa Monica Bay, and allows the CDFG to increase the live bait quota provided the increases do not affect the recovery of the sardine resource. The bill also allows sardines taken as dead bait to be sold to commercial fishermen; previously, sardines taken under the dead bait quota could be used only by sport fishermen.

PACIFIC MACKEREL

At the start of 1991, there were 28,954 tons of Pacific mackerel (*Scomber japonicus*) already landed towards the total for the 1990–91 fishing season (July 1 through June 30). There were no quota restrictions, since a preliminary estimate indicated that the biomass was well above 150,000 tons. Current legislation allows an open fishery when the biomass exceeds 150,000 tons.

Landings during the first quarter of the year totaled 7,136 tons and were higher than in 1990, despite the availability of squid (*Loligo opalescens*) and the directed sardine fishery in January and March. Individual fish in the catch tended to be large.

Landings decreased during April and May. One cannery issued no orders in April and closed down for three weeks in May. As a result, most of the fleet remained in port. Pacific mackerel landings increased at the end of May and were high during June. Second quarter landings totaled 7,976 tons, with the majority (7,044 tons) landed in June.

The 1990–91 season ended on June 30, 1991, with a total catch of 44,066 tons of Pacific mackerel, a 60% increase over the 1989–90 season. Jack mackerel (*Trachurus symmetricus*) landings in the mackerel fishery totaled 3,839 tons for the 1990–91 season. The species composition of the total statewide mackerel landings was 89% Pacific mackerel, 8% jack mackerel, and 3% Pacific sardine. During the 1989–90 season, when jack mackerel made up an unusually large proportion of the catch, the species composition was 55% Pacific mackerel, 40% jack mackerel, and 5% Pacific sardine. Landings in northern California made up 5% of total statewide landings, up considerably from 0.3% during the 1989–90 season, and the highest proportion since northern California landings contributed 6% to the total in 1985–86.

The 1991–92 season opened on July 1, 1991, with no quota restrictions, since the total biomass was estimated to be 192,000 tons. In fishery samples from January to June 1991, the 1990 year class made up 36% of the landings, and the 1989 year class made up 13%. From July to December 1991, these two year classes made up 44% and 3% of the landings, respectively. Landings of Pacific mackerel during the first two months of the third quarter were lower than in the previous year. Several seiners searched for bluefin tuna during August. Landings increased during September and were comparable to landings in September 1990. A total of 9,651 tons was landed during the third quarter.

During October, landings were low, partly because the directed sardine fishery reopened, and effort was also directed toward squid during the last two weeks of the month. Landings increased during November, despite the directed sardine fishery during the first week of the month. December landings were higher than in 1990, even though one cannery closed for two weeks because of financial problems. In the fourth quarter 9,361 tons were landed. By year's end, 19,012 tons of Pacific mackerel had been landed towards the 1991–92 season catch. This is about 80% of the last five-year average for midseason landings. Pacific mackerel landings for 1991 totaled 34,124 tons (table 1), down 17% from 1990 landings, and 22% lower than the average landings for the previous five years. Jack mackerel landings in the mackerel fishery totaled 1,868 tons in 1991. An apparent decline in the Pacific mackerel population over the last five years, warm water conditions (which tend to displace Pacific mackerel to the north), and the financial difficulties of a major southern California processor contributed to low landings.

NORTHERN ANCHOVY

Landings of northern anchovy (*Engraulis mordax*) for reduction purposes in 1991 were limited primarily by poor market conditions, although landings were the highest since the 1983–84 season (table 2). California processors offered $30 to $50 per ton for anchovy, but most fishermen directed their effort to other fisheries. The 1990–91 season closed on June 30, 1991, with 1,143 tons landed against a reduction quota of 128,088 tons (116,200 metric tons [MT]). Of the total catch, 943 tons were landed under the northern permit area quota (10,000 tons), and 200 tons under the southern permit area quota (118,088 tons).

The reduction fishery in Mexico slowed in 1991, partly because Zapata Company, a primary reduction processor in Ensenada, went out of business. Mexican biologists also attributed the fishery decline to weak demand and a reduced anchovy population, probably a result of changing environmental conditions and heavy fishing.

TABLE 2
Anchovy Landings (Short Tons) for Reduction

Season	Southern area	Northern area	Total
1967–68	852	5,651	6,503
1968–69	25,314	2,736	28,050
1969–70	81,453	2,020	83,473
1970–71	80,095	657	80,752
1971–72	52,052	1,314	53,366
1972–73	73,167	2,352	75,519
1973–74	109,207	11,380	120,587
1974–75	109,918	6,669	116,587
1975–76	135,619	5,291	140,910
1976–77	101,434	5,007	106,441
1977–78	68,467	7,212	75,679
1978–79	52,696	1,174	53,870
1979–80	33,383	2,365	35,748
1980–81	62,161	4,736	66,897
1981–82	45,149	4,953	50,102
1982–83	4,925	1,270	6,195
1983–84	70	1,765	1,835
1984–85	78	0	78
1985–86	0	1,595	1,595
1986–87	0	42	42
1987–88	0	122	122
1988–89	0	258	258
1989–90	157	32	189
1990–91*	200	943	1,143

*Preliminary

A U.S. total of 3,095 tons of anchovy was landed for nonreduction use in 1991. This represents a 12% decrease from the previous year, and may have been partly due to the presence of domoic acid, a toxin that causes amnesiac shellfish poisoning, in anchovy in 1991.

The production of domoic acid has been attributed to two commonly occurring diatoms, *Nitzschia pungens* and *Nitzschia pseudoseratia*. In September several pelicans in Monterey Bay died apparently as a result of high levels of domoic acid. Subsequent investigations by the U.S. Food and Drug Administration revealed toxin levels in some anchovy viscera that were well above established safety standards. As a result, harvesting of anchovy for human consumption was prohibited from November 1, 1991, to January 1, 1992, and shipments of anchovies from Monterey Bay and San Pedro were subject to an embargo.

The anchovy live bait catch was 5,555 tons in 1991, an increase of 4% from 1990. California bait haulers were able to meet demand throughout the season and considered 1991 a good year. Total anchovy landings during 1991, including reduction and nonreduction, but excluding live bait, totaled 4,238 tons (table 1).

National Marine Fisheries Service biologists estimated the 1991 spawning biomass of northern anchovy to be 287,700 tons (261,000 MT) and the total biomass to be 292,112 tons (265,000 MT). Since the spawning biomass estimate is below the 300,000-MT minimum level required for a reduction quota by the Anchovy Fishery Management Plan, no take for reduction purposes is allowed during the 1991–92 season. The nonreduction harvest allocation was set at 5,201 tons (4,900 MT), with an unspecified amount for use as live bait.

MARKET SQUID

Market squid (*Loligo opalescens*) landings in 1991 were 40,529 tons (table 1): 31,516 tons (77.8%) were from the southern California fall-winter fishery, 7,389 tons (18.2%) from the central California (Monterey Bay area) spring-summer-fall fishery, and 1,624 tons (4.0%) from north of the Monterey Bay area (table 3). The 1991 total landings increased 29% from the 31,357 tons landed in 1990. Southern California landings were 40% higher; landings in the Monterey Bay area were 15% lower; and landings from north of Monterey Bay were up dramatically from the 143 tons landed in 1990. The total ex-vessel value was approximately $5.6 million, 30% above the $4.3 million earned in 1990.

Prices continued to fluctuate during the year and compared to the previous year. In 1991, prices in southern California remained lower than those paid in central and northern California. Southern California prices ranged from $40 to $140 per ton and averaged about $120 per ton. This was down from the 1990 range of $110 to $150 per ton and the average of $130 per ton. Monterey Bay prices ranged from $200 to $300 per ton and averaged about $209. Prices in 1990, by comparison, ranged from about $130 to $200 per ton and averaged about $160. In northern California, 1991 prices ranged from $60 to $300 per ton and averaged about $212 per ton.

TABLE 3
California Market Squid Landings (Tons)

Year	Monterey	Southern California	Other	State total
1970	4,314	7,982	0	12,296
1971	8,323	7,435	trace	15,758
1972	6,129	3,950	0	10,079
1973	620	5,410	0	6,030
1974	7,248	7,205	0	14,453
1975	2,495	9,316	trace	11,811
1976	2,511	7,462	0	9,973
1977	2,234	11,887	1	14,122
1978	10,326	8,571	trace	18,897
1979	14,183	7,842	1	22,026
1980	7,856	9,100	1	16,957
1981	14,134	11,779	2	25,915
1982	11,670	6,276	5	17,951
1983	542	950	509	2,001
1984	431	84	107	622
1985	4,202	7,039	85	11,326
1986	6,049	16,488	917	23,454
1987	5,269	16,665	94	22,028
1988	5,329	34,634	426	40,389
1989	7,877	37,195	4	45,076
1990	8,728	22,486	143	31,357
1991*	7,389	31,516	1,624	40,529

*Preliminary

Frozen squid for human consumption continued to supply the major market, with most exported to European countries and Japan. Some squid was sold fresh or for use as dead and live bait. The squid live bait fishery is centered in southern California, and in 1991 approximately 158 tons were caught. This represents about 3% of southern California's multispecies live bait fishery. In Monterey Bay, one boat began fishing for squid for live bait in late 1991.

Most 1991 southern California landings were made in two ports: Port Hueneme and San Pedro. Approximately 17,000 tons (54% of the southern California total) were landed in Port Hueneme, and approximately 10,300 tons (33%) in San Pedro. A third port, Terminal Island, received about 2,700 tons (8%). Landings in Port Hueneme were high, mainly because several large boats from Monterey fished around the Santa Barbara Channel Islands and landed squid at Port Hueneme. This squid was trucked to dealers in the Monterey Bay area for processing.

Squid were consistently larger in 1991 than in 1990. A possible reason for the decreased southern California landings in 1990 was because small squid, averaging over 15 per pound, were common throughout the area during much of the latter part of the season. Some dealers had difficulty marketing these small squid and set trip limits for their boats, or stopped buying squid altogether. In 1991, much larger squid dominated the catches, resulting in increased demand and increased landings.

In 1991 the squid season in the Monterey Bay area was unusual. Typically, squid appear on the spawning grounds in catchable quantities beginning April. In some years (most recently 1981, 1985, and 1989) small catches have been made as early as March. In 1991, however, the fishery had its slowest start since commercial squid landing records began in 1916. Fewer than 500 pounds were landed from January to May. In June, fishermen landed approximately 30 tons, and in July they landed about 440 tons. In August fishermen brought in just over 1,400 tons, and September's landings exceeded 4,000 tons, making that month one of the highest on record.

Most of the squid landed in Monterey Bay ports are traditionally caught in southern Monterey Bay. However, roughly 70% of the squid landed in August and September was caught north of Santa Cruz near Año Nuevo Island (figure 1). This area has been fished only sporadically since the 1983–84 El Niño period. During late September and October, most of the catches again came from the traditional fishing grounds in the southern part of the bay. Many fishermen and processors felt that the availability of squid in the Año Nuevo Island area caused the 1991 Monterey Bay area squid season to be good, rather than only fair. The 1991 total landings of 7,389 tons were higher than the previous 20-year average of 6,213 tons.

The use of attracting lights has been controversial since this practice was first approved for southern Monterey Bay in 1989, and disputes among squid fishermen over their use continued throughout the season. Fishermen opposed to the lights believe that they disrupt spawning, and that small boats cannot compete with large boats with large light systems. Those who favor lights claim that lights allow them to use shallower nets that can be fished off the bottom, thus protecting squid eggs attached there. They also point out that fishermen in southern California and elsewhere have used lights for years without any apparent adverse effects on the squid resource and spawning.

The 1991 landings of 1,624 tons of squid at ports north of Monterey Bay were 77% greater than the previous highest annual landings of 917 tons in 1986. Approximately 91% (1,403 tons) of the 1991 northern California total was landed in Half Moon Bay. Most of this squid was landed in July, August, and September, and was caught in the Año Nuevo Island area (figure 1).

PACIFIC HERRING

Annual statewide landings for the 1991 roe herring fishery (*Clupea harengus*) were 7,945 tons, an 11.1% decrease from 1990 (table 1). Statewide landings for the 1990–91 season (November to March) totaled 7,936 tons. San Francisco Bay gill net permittees landed 5,832 tons, 443 tons short of the 6,274-ton quota. Round haul permittees fishing in San Francisco Bay landed only 1,909 tons, which was 675 tons less than their quota. Bodega Bay permittees landed 95 tons (200-ton quota); Humboldt Bay permittees landed 63 tons (60-ton quota); and Crescent City permittees landed 36 tons (30-ton quota). Ex-vessel prices ranged from $750 to $1,000 per ton for 10% roe-recovery herring and were low because of a weak Japanese market at the end of 1991.

San Francisco Bay roe-on-kelp permittees had a very difficult 1990–91 season. They processed only 48 tons (144-ton-quota) of roe-on-kelp, with an estimated ex-vessel value of $1 million. Fishermen attributed the low landings to patchy spawns and unpredictable spawning behavior.

Spawning biomass estimates were determined for San Francisco, Tomales, and Humboldt bays. Both hydroacoustic and spawn deposition surveys were employed in San Francisco Bay, but only spawn deposition surveys were used in the remaining bays. The 1990–91 season estimate for San Francisco Bay was 51,000 tons, a 21% decline from the 1989–90 season. Tomales Bay and Bodega Bay herring are managed as one stock; therefore the total spawning biomass of 874 tons included 95 tons of Bodega Bay landings missed by the survey. This total spawning biomass is 10.6% higher than the 1989–90 season estimate of 790 tons. The first spawning deposition survey in Humboldt Bay since 1976 estimated a spawning biomass of 400 tons, compared with previous estimates by independent researchers of 372 tons in 1974–75, and 242 tons in 1975–76.

This was the fourth consecutive poor season in Tomales Bay. Although the Tomales Bay herring population appears to be depressed, the age structure of the sampled catch has remained relatively stable and does not seem to reflect a declining population. Drought conditions have persisted for five years, however, and low freshwater runoff into Tomales Bay may be the primary reason why herring have not spawned in the bay at historic levels.

Results of young-of-the-year (YOY) trawl surveys in San Francisco Bay suggest a weak 1991 year class. Relatively few YOY herring were collected in midwater trawl tows at stations located throughout the bay. This is the second consecutive poor year class and may be due to abnormal oceanic conditions.

GROUNDFISH

California's 1991 commercial groundfish harvest was 35,763 MT, with an ex-vessel value of approximately $27.13 million. All-species landings decreased approximately 8%, or 3,086 MT, from 1990 (table 4). Rockfish (*Sebastes* spp.), Dover sole (*Microstomus pacificus*), sablefish (*Anoplopoma fimbria*), Pacific whiting (*Merluccius productus*), and thornyheads (*Sebastolobus* spp.) were the principal species harvested in 1991. Landings of Dover sole and Pacific whiting increased, while landings of other species or species groups either remained the same or declined.

Fishing effort in the Washington-Oregon-Cali-

TABLE 4
California Groundfish Landings (Metric Tons)

Species	1990	1991	Percent change
Dover sole	6,419	7,726	20
English sole	912	812	−11
Petrale sole	691	735	6
Rex sole	570	621	9
Other flatfish	1,429	880	−38
Widow rockfish	1,975	1,201	−39
Other rockfish	11,019	9,708	−12
Thornyheads	5,391	2,864	−47
Lingcod	1,118	786	−30
Sablefish	3,531	3,308	−6
Pacific whiting	5,519	6,893	25
Other groundfish	275	229	−17
Total	38,849	35,763	−8

fornia (WOC) area was higher in 1991 than in 1990. The largest increase in effort occurred in the trawl fishery, when 13 trawler/processors and three motherships from Alaska came south to fish for Pacific whiting. There was also a large influx of displaced salmon trollers to the groundfish fishery because of shortened salmon seasons.

Incidental catch of salmon by the whiting fleet was of special concern to the Pacific Fishery Management Council (PFMC) because of area closures and severe quota reductions in salmon fisheries off southern Oregon and northern California. An estimated 6,280 salmon were taken in the WOC area, resulting in an overall by-catch rate of 0.032 salmon per ton of whiting. On average, salmon bycatch was lower than the target rate of 0.05 salmon per ton of whiting established by the PFMC and trawl industry. The incidental rockfish catch in the WOC area was 1,536 MT, nearly all of which was discarded.

The general distribution of 1991 California landings among gear types was similar to last year. Bottom and midwater trawl landings dominated the statewide groundfish catch and contributed 78.9% of total landings in 1991, up slightly from 77.4% in 1990. The trap component dropped slightly, from 1.9% in 1990 to 1.2% in 1991, and setnet landings decreased from 8.3% to 5.9%. The line portion of the catch was 14% of the California groundfish harvest in 1991, up from 6.6% in 1989 and 12.4% in 1990.

Various quotas, harvest guidelines, and trip limits were used in 1991 to limit the total harvest of species or species groups in order to meet the PFMC objective of a year-round groundfish fishery. The PFMC established a widow rockfish harvest guideline of 7,000 MT for the WOC area in 1991. This was 20% (1,800 MT) less than the 1990 quota (8,800 MT) and represents a considerable decrease from the 1989 quota (12,400 MT). Trip limits were 10,000 pounds per week or 20,000 pounds per two-week period. On September 25, a 3,000-pound trip limit was implemented to further restrain landing rates. The widow rockfish catch in 1991 totaled 6,932 MT in the WOC area, and was 1% under the quota. California landings were 1,201 MT, 17% of the WOC total.

Sablefish management in the WOC area during 1991 was similar to 1990. After a native American tribal allotment of 300 MT was deducted from the harvest guideline, 8,600 MT of sablefish were allocated between trawl and nontrawl in a 58%:42% ratio. The nontrawl season opened on January 1 with a 1,500-pound trip limit, and unrestricted fishing began on April 1. The April 1 opening was intended to coincide with the sablefish season opening in Alaska to reduce fishing effort in the WOC area, but the Alaska season did not open until May 15. Many longline vessels, particularly from Washington, participated in both the Alaska and WOC sablefish fisheries. Nontrawl landings in April 1991 were four times the 1985–89 average April landings of 392 MT. This pulse of effort shortened the season substantially, and a 500-pound trip limit was established on May 24. Last year a 500-pound trip limit was not set until June 24, and that limit was raised to 2,000 pounds in October to allow the entire nontrawl quota to be taken. The 1991 nontrawl season closed on July 1. An emergency action to allow continued incidental and low-level catches under a 300-pound daily trip limit was recommended by the PFMC in July, but was not implemented until September 30. The total catch of sablefish by nontrawlers in 1991 was 4,522 MT, and exceeded the nontrawl quota by 25%. California landings (1,167 MT) accounted for 26% of the nontrawl total. WOC-area sablefish landings by trawl gear were 4,918 MT, about 1% less than the trawl allocation. California landings (2,141 MT) accounted for 44% of the trawl total.

The deepwater complex (sablefish, Dover sole, and thornyheads) was managed in 1991 by a weekly trip limit of 27,500 pounds. The first thornyhead stock assessment was conducted, resulting in a harvest guideline of 7,900 MT for this species, and a weekly trip limit of 7,500 pounds within the overall weekly limit for the deepwater complex. The sablefish component of the deepwater complex was limited to 1,000 pounds per trip, or 25% of the deepwater complex, whichever was greater.

Thornyhead landings were 6,536 MT, down sharply from the 10,126 MT landed in 1990, primarily because of more restrictive management and weak market demand. This declining trend was evident by midyear, and in response the Council increased the weekly trip limit to 12,500 pounds on July 31. Despite the increased trip limit, total landings were less than the harvest guideline. California landed 2,864 MT, 44% of the WOC thornyhead catch. The 1991 coastwide catch of Dover sole was 18,203 MT, an increase of 2,408 MT from the previous year, primarily as a result of increased market demand. California landings (7,726 MT) constituted 42% of total WOC-area Dover sole landings.

For the area south of Coos Bay, Oregon, the PFMC set the trip limit for the *Sebastes* complex (rockfishes other than widow) at 25,000 pounds, with no restriction on trip frequency. The PFMC also established a 1991 harvest guideline of 1,100 MT for bocaccio rockfish (*Sebastes paucispinis*) and restricted the take of bocaccio to 5,000 pounds of the allowable 25,000 pounds of rockfish per trip. Landings of the *Sebastes* complex in California dropped from 11,019 MT in 1990 to 9,708 MT in 1991. This total included nearly 1,300 MT of bocaccio. The combined commercial and recreational bocaccio catch in 1991 was 1,500 MT.

A limited entry plan for groundfish was adopted by the PFMC in 1991 and has been submitted to the National Marine Fisheries Service for approval. The plan is tentatively scheduled for implementation on January 1, 1994. The plan includes all trawl vessels, and any longline or pot vessel with minimum landings (as yet undetermined) in the limited entry system. The PFMC also determined that the section of the California public initiative (Proposition 132) prohibiting the take of rockfish with gill nets in the Exclusive Economic Zone (EEZ; 3 to 200 miles from shore) was inconsistent with the Magnuson Fisheries Conservation and Management Act. As a result, the commercial take of rockfish with gill nets in the EEZ is still allowed.

PACIFIC WHITING

The combined U.S. and Canadian coastal Pacific whiting (*Merluccius productus*) harvest for 1991 was 316,000 MT. The total catch exceeded the 228,000-MT quota by 39%, and is the largest whiting harvest on record. The U.S. portion of the catch in 1991 was approximately 218,000 MT: 197,000 MT were taken by at-sea processors, and 21,000 MT went to shore-based processors.

In 1991 an estimated 63% (116,000 MT) of the total U.S. coastal whiting harvest that was processed at sea was captured off California. California shore-based landings were 6,893 MT, an increase of 25% over the 5,519 MT landed in 1990 (figure 2).

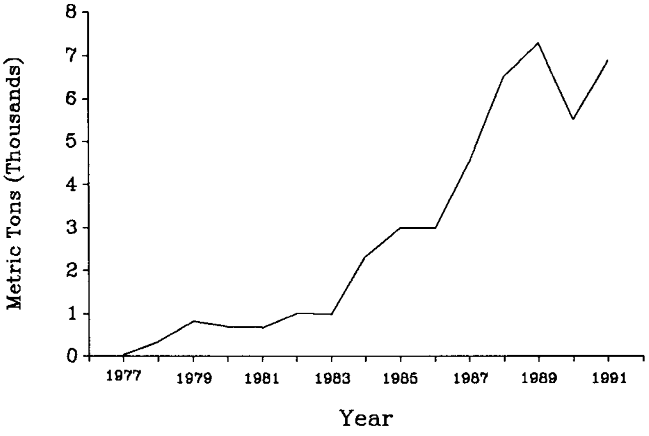

Figure 2. California landings of Pacific whiting, 1977–91.

The California total accounted for one-third of all shore-based whiting landings in Washington, Oregon, and California in 1991. Five midwater trawl vessels, fishing off Eureka and Crescent City, caught most of the California shore-based harvest.

The U.S. fishery for coastal Pacific whiting became exclusively domestic in 1991. U.S. at-sea processing vessels, which typically operate in the Gulf of Alaska and Bering Sea and are capable of high production, displaced foreign processors off the West Coast. Domestic processing capability in 1991 greatly exceeded the 228,000-MT quota for whiting, and allocation of the quota between trawler-processor vessels and trawl vessels that could deliver to either at-sea or shore-based facilities was necessary.

The fishery for Pacific whiting has depended heavily on the declining 1980, 1984, and 1987 year classes. The U.S. harvest is expected to decline below 200,000 MT unless a strong year class of whiting occurs.

DUNGENESS CRAB

California Dungeness crab (*Cancer magister*) landings during the 1990–91 season totaled 12.0 million pounds, an increase of 7.4 million pounds (261%) from the previous season's landings of 4.6 million pounds.

The season opened in northern California on December 1, 1990, with an ex-vessel price of $1.50 per pound — $0.25 per pound higher than the 1989–90 season. The northern California ports of Crescent City, Trinidad, Eureka, and Fort Bragg (figure 1) received 5.5, 1.2, 3.6, and 0.3 million pounds, respectively, from 340 vessels, for a total of 10.6 million pounds. This was 6.88 million pounds more than the catch of the previous season.

The San Francisco area Dungeness crab season opened on November 14, 1990, with the price set at $2.10 per pound. Season landings totaled 1.25 million pounds, an increase of 0.52 million pounds from the 1989–90 season. Landings for Bodega Bay were 0.55 million pounds; San Francisco, 0.44 million pounds; and Half Moon Bay, 0.26 million pounds. Sixty-seven percent of the catch was taken in November and December. Approximately 114 boats participated in the fishery.

The ports of Monterey and Morro Bay contributed 0.12 million pounds to the statewide total, slightly more than the 0.10 million pounds landed in the 1989–90 season.

In 1989 the Pacific States Marine Fisheries Commission received a federal grant to help resolve crab industry issues of coastwide concern. As a result, a tristate (Washington, Oregon, and California) Dungeness crab committee of fishermen, processors, and state agency advisors was formed in 1990. The committee identified four issues for consideration: (1) the occurrence of soft-shell crabs at the beginning of the season, (2) soft-shell crabs during the season, (3) "groundlining" of crab traps (traps attached by a line), and (4) a limited entry fishery. Soft-shell crabs are less marketable, and the committee agreed that when soft-shell conditions occur (typically in Washington and Oregon), the season opening should be delayed until the conditions improve. Groundlining of crab traps causes gear conflicts with vessels trawling with bottom nets, but the committee was unable to resolve this issue. Most committee members recommended a limited-entry fishery, with eligibility restricted to fishers or vessels that participated in the fishery before September 15, 1991.

Local meetings were held in ports from Eureka, California, to Westport, Washington, to discuss these issues with fishermen and processors. A coastwide questionnaire to all crab fishers revealed that 61.6% of the respondents favored a study of possible limited entry programs and establishment of an eligibility cutoff date.

PACIFIC OCEAN SHRIMP

Statewide landings of Pacific Ocean shrimp (*Pandalus jordani*) for the 1991 season totaled 10.2 million pounds, an increase of 18.4% over the 8.7 million pounds landed in 1990 (figure 3). The 1991 season landings were the fifth largest since the beginning of the fishery in 1952. There were only two areas of production in 1991: Area A (Oregon border to False Cape), which accounted for 99% of the catch, and Area B-1 (False Cape to Point Arena) (figure 1). Area C (Pigeon Point to the Mexican border) reported no catch for the second straight year.

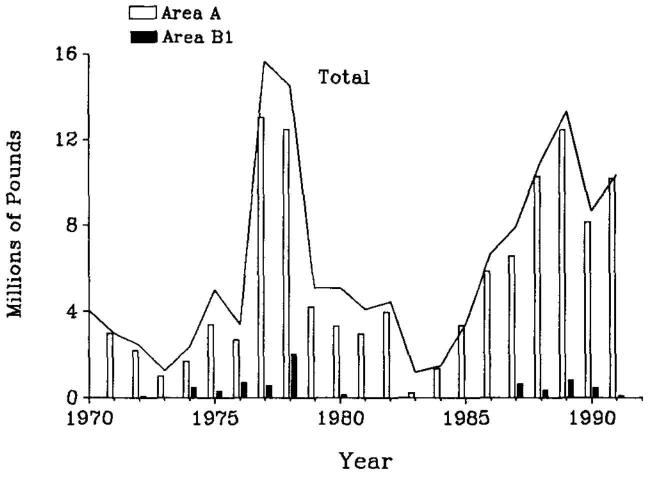

Figure 3. California landings of Pacific ocean shrimp, 1970–91. Total includes landings from Area C.

The season opened on April 1 with an ex-vessel price of $0.54 per pound. On May 28 the price increased slightly to $0.60 per pound; in late July it dropped to $0.53 per pound, where it remained. Shrimp landings in Area A ports reached 10.2 million pounds, an increase of 25% from the 8.16 million pounds landed in the previous season. Of total Area A landings, 9.56 million pounds were caught in Area A waters; 450,000 pounds were taken off Oregon; and 190,000 pounds were caught in Area B-1.

Eighty-six trawl vessels (54 single-rigged and 32 double-rigged trawlers) delivered shrimp to Area A ports during 1991, an increase of 29 boats from 1990, and the largest fleet on record to make deliveries in Area A. Single-rigged vessels had an average catch rate of 342 pounds per hour, a 2% decrease from the previous year; double-rigged vessels averaged 556 pounds per hour, a 12% decrease.

The biological characteristics of the 1991 catch were similar to those observed during 1980–89, in contrast to the anomalous size and age composition noted in 1990. One-year-old shrimp constituted 85.7% of the 1991 catch, compared to 18.8% in 1990 and the 1980–89 average of 80.5%. Female shrimp made up only 7.1% of the catch, compared to an average of 17.1% during the 1980–89 period. The count per pound averaged 113 shrimp (the legal maximum is 160 per pound).

Area B-1 shrimp landings were 137,000 pounds, down 74% from the 519,000 pounds landed in 1990. Over 95% of the catch was landed during the first month of the season. Thirty-four landings, a decrease of 53% from 1990, were made by six single-rigged trawl vessels. These vessels caught an average of 364 pounds per hour, a decrease of 17% from last season. One-year-old shrimp were less abundant in Area B-1, constituting 25% of the sampled catch in April and 51% in August. As a result, fishermen landed exceptional counts of 85 shrimp per pound in April and 110 shrimp per pound in August. Ex-vessel price trends were the same as in Area A.

SWORDFISH AND SHARKS

Landings of swordfish (*Xiphias gladius*) in 1991 fell to 1.54 million pounds, a 17% decline from 1990. This was the second consecutive year that landings decreased, and is the lowest catch in nine years (table 5). Harpoon fishermen landed only 123 swordfish, a 70% decline from the previous season; 1991 was the seventh consecutive year of declining catches. The drift gill net catch remained stable at 9,000 fish, although the average size of swordfish was smaller, as evidenced by a decrease in the total weight of the landings.

During the season, 160 gill net permits were issued for taking pelagic sharks and swordfish, and 132 permits were issued for harpooning swordfish. Catch-per-unit-of-effort (CPUE) for gill net gear increased from 1.6 fish per day in 1990 to 2.0 fish per day in 1991, while CPUE for harpoon gear declined from 0.3 fish per day to 0.2 fish per day. San Francisco, Morro Bay, and San Diego continued to receive most of the landings.

Three vessels from San Pedro used longline gear to target swordfish. These vessels were required to fish outside the EEZ, but were able to land their catches in the U.S. with a federal permit.

Common thresher shark (*Alopias vulpinus*) landings increased 64% in 1991 to 756,701 pounds, the highest since 1986. Thresher sharks were landed along the entire California coast—57% in southern California. Market sampling data indicate that this fishery continues to harvest immature fish (average age two years) almost exclusively.

TABLE 5
Landings of Selected Shark Species and Swordfish (Pounds)

Year	Shortfin mako shark	Swordfish	Common thresher shark	Pacific angel shark
1977	19,911	511,388	129,522	366
1978	26,765	2,604,233	302,054	82,383
1979	35,079	586,529	735,726	128,295
1980	154,529	1,197,187	1,805,978	110,037
1981	274,217	1,142,897	1,973,411	268,640
1982	527,006	1,677,020	2,396,960	317,953
1983	322,854	2,601,600	1,722,056	351,344
1984	239,687	4,429,540	1,662,587	632,937
1985	225,535	5,196,685	1,540,770	1,237,810
1986	473,608	3,845,932	606,583	1,241,130
1987	602,718	2,741,015	525,076	940,187
1988	488,136	2,484,428	549,516	487,278
1989	388,322	2,850,734	649,174	268,252
1990	576,428	1,871,540	461,606	250,850
1991*	331,216	1,541,333	756,701	181,553

*Preliminary

Shortfin mako shark (*Isurus oxyrinchus*) landings were just over 331,000 pounds, a decrease of 43% from last year (table 5). The drift gill net fishery accounted for 67% (220,703 pounds) of this total; the remaining 33% (110,513 pounds) was taken by the experimental drift longline fishery. The California Fish and Game Commission approved continuing the experimental drift longline fishery for shortfin mako sharks, and established a limited season, a 175,000-pound quota, and a limited number of permittees. The drift longline catch, down 37% from last year and only 63% of the season quota, was limited in part by unfavorable market conditions. Drift longline length-frequency data indicate that the catch consisted of immature fish (one-, two-, and three-year-olds).

Landings of Pacific angel shark (*Squatina californica*) were a dismal 181,553 pounds. This represents a decline of 28% from last year, and is the lowest catch in 11 years. A low ex-vessel price, reduced availability, and the minimum size limit contributed to the low landings. As in the past, the Santa Barbara–Ventura area was the major fishing location (figure 1).

CALIFORNIA HALIBUT

California halibut (*Paralichthys californicus*) landings in 1991 were 469 MT, an increase of 12% from the 419 MT landed in 1990 (figure 4). Over 56% of the total landings were made south of Point Conception, mostly in the Santa Barbara area (table 6). Nearly 44% of the catch occurred north of Point

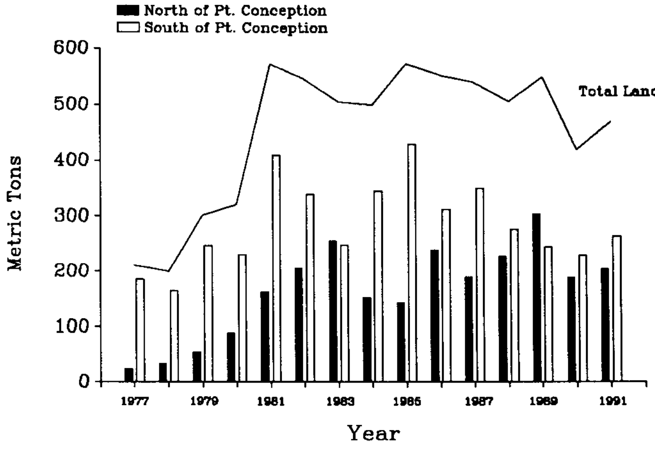

Figure 4. Landings of California halibut, 1977–91.

TABLE 6
1991 California Halibut Landings by Area

Area	Metric tons	% of total
Eureka	4.2	.9
San Francisco	116.8	24.9
Monterey	25.7	5.5
Morro Bay	58.3	12.4
Santa Barbara	155.8	33.2
Los Angeles	74.0	15.8
San Diego	34.1	7.3
Total	468.9	100.0

Conception, which was similar to 1990. The San Francisco area accounted for nearly a quarter of all halibut landings.

The highest monthly landings of California halibut in 1991 were made from June through August, although fishing in January and February was also productive. Entangling nets captured 50% of all halibut taken, followed by trawl (32%), miscellaneous and unspecified gears (10%), and hook and line (8%).

Most of the halibut caught by trawl were taken off central and northern California, whereas most of those caught in entangling nets were taken off southern California. Ex-vessel prices ranged from $1.00 to $3.50 per pound, with an average price of $2.38 per pound. The total value of 1991 landings was estimated at $2.5 million, compared to $2.2 million in 1990.

ALBACORE

In 1991, albacore (*Thunnus alalunga*) landings in California totaled 750 tons. This was a 27% decrease from the 971 tons landed in 1990, and only 9% of the 25-year average (7,573 tons; figure 5). The number of California boats that participated in the 1991 fishery decreased 15% from 1990. Fishing success was poor compared to past years, with only 47 out of 133 boats landing more than one ton of albacore during the season.

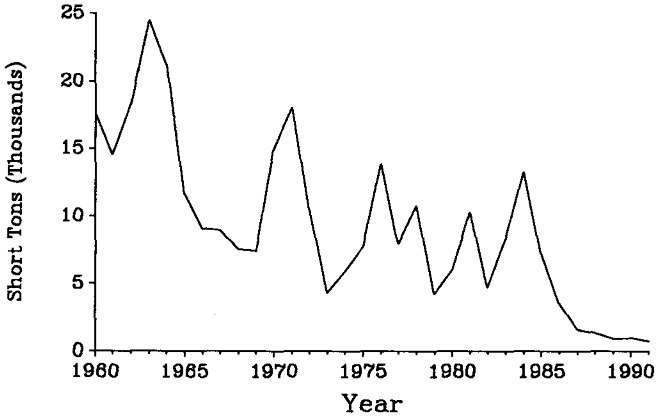

Figure 5. California landings of albacore, 1960–91.

The 1991 season started in mid-July off the Washington coast and progressed north to the Queen Charlotte Islands, Canada. By the end of September, the weather had forced many smaller vessels south, where they fished 100 to 150 miles off the Oregon coast. During October, schools of small albacore were reported 100 miles off the northern California coast. Fishing declined, however, because of the low price for small fish, and most vessels quit for the season.

For those boats that remained active, fishing improved off the California coast from October to November, with vessels making 2- to 3-day trips out of Eureka, Monterey, Morro Bay, and Ventura. The California fleet landed three-year-old (64 cm) and four-year-old (77 cm) fish in August and September, but mostly two-year-old fish (55 cm) were landed towards the end of the season. Vessels averaged about 100 fish per day. The sport fishery was poor and similar to the past few years, with 976 fish (average weight of 14 pounds) caught near San Diego, Los Angeles, Morro Bay, and San Francisco.

The 12th Northern Pacific Albacore Workshop in Shimizu, Japan, was attended by representatives of the California Department of Fish and Game and the National Marine Fisheries Service, Southwest Fisheries Science Center. The status of the international albacore fishery over the last ten years, and the future of the fishery were among the topics discussed.

Pan Pacific cannery and the Western Fishboat Owners Association (WFOA) did not agree on a price for albacore until September. The price was set at $1,700 per ton for fish heavier than 9 pounds and $1,000 per ton for lighter fish. The WFOA also agreed to pay a $100-per-ton shipping fee for fish landed at buying stations. The delay in setting a price was caused by a glut of albacore on the world market. Fishermen selling their catch directly to the public received $1.00 to $1.50 per pound.

The 1991 season was the worst on record. Several factors contributed to poor albacore fishing, including the delay in setting a price, and the relatively low prices of the last few years. The general perception among albacore fishermen that international efforts have failed to effectively regulate the Asian drift-net fishery, and their concern about the effect of that fishery on albacore also contributed to a decreased interest in fishing. An apparent shift in the migration path has moved albacore into northern Pacific waters, thus shifting effort and landings away from California. In addition, the albacore population on both sides of the Pacific seems to be declining, as evidenced by the lack of three- and four-year-old fish. These fish previously made up most of the commercial catch.

RIDGEBACK AND SPOT PRAWN

Ridgeback prawn (*Sicyonia ingentis*) are fished commercially with trawl nets. Ridgeback may be trawled by permit from October 1 through May 31. An incidental catch of 50 pounds is allowed during the closed season. Preliminary landings for 1991 totaled 129,000 pounds, 42% more than the decade's low catch of 91,000 pounds in 1990 (figure 6). Most of this year's catch came from the Santa Barbara Channel. The average ex-vessel price was $1.25 to $1.35 per pound.

The spot prawn (*Pandalus platyceros*) is a large shrimp, and commands a higher price than the ridgeback. Spot prawn were caught with traps until the mid 1970s, when trawl nets became the primary gear. Because of an increasing demand for live product, traps have again become preferred.

Spot prawn may be trawled by permit from February 1 through October 31. During the closed period, an incidental catch of 50 pounds is allowed. Trawling in 1991 took place in the Santa Barbara Channel. By trap, spot prawn may be harvested year-round, except for a 5-fathom restriction from Point Conception south to the southern boundary of Ventura County (figure 1). San Clemente and San Nicolas islands have become favored trapping areas. Preliminary landings for 1991 were 305,000 pounds, just 4% lower than last year. Ex-vessel prices ranged from $3.50 (dead) to as much as $6.00 (live) per pound.

SEA URCHIN

The California commercial red sea urchin (*Strongylocentrotus franciscanus*) fishery continued to be among the most important fisheries in the state. Preliminary landings for 1991 reached 41.5 million pounds (figure 7), and were valued at a record $30 million, despite an actual 8% decline in landings from the previous year. Landings dropped in the south from 27 to 24.7 million pounds (9% decline), and in the north from 18.3 to 16.8 million pounds (8% decline). Among the major northern ports, Fort Bragg (figure 1) registered the most severe reduction in landings, from 13.8 million pounds in 1989 to 4.9 million pounds in 1991. Despite more restrictive regulations enacted in northern California in 1990, including a complete July closure and an increase in the minimum size limit (test diameter) to 3.5 inches, Bodega Bay landings increased from 4.0 million pounds in 1989 to 5.4 million pounds in 1991. This increase was partly attributable to an influx of urchin vessels to the Bodega Bay area as Fort Bragg area stocks declined.

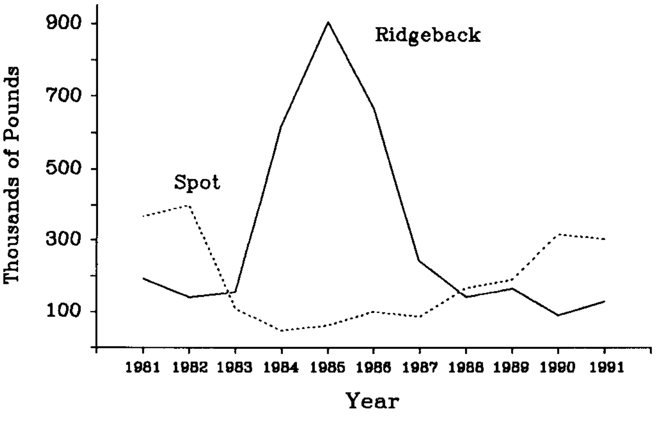

Figure 6. California landings of ridgeback and spot prawn, 1981–91.

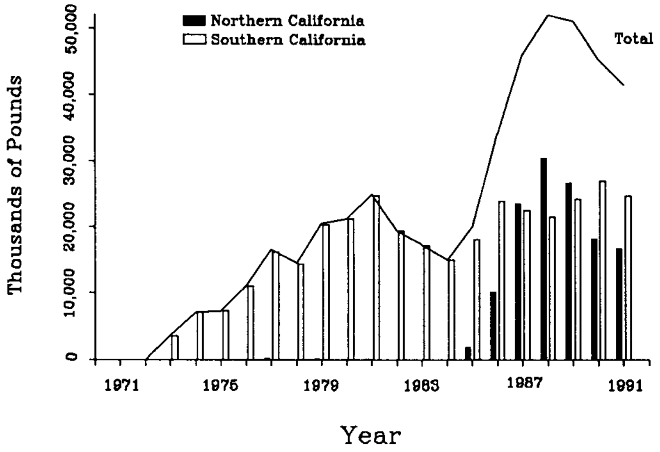

Figure 7. California landings of sea urchins, 1971–91.

Divers harvest sea urchins using conventional hookah gear, consisting of a low-pressure compressor that feeds air through a hose to the diver's mouthpiece regulator. Harvesting takes place in water 5 to 100 feet deep, with most effort expended at 20 to 60 feet. Analysis of southern California logbook data for 1991 (through October) showed a mean CPUE of 288 pounds per hour, compared to 293 pounds per hour for 1990. This decrease represents a continuing trend over the past few years. Although mean CPUE remained higher in northern California, CPUE in Fort Bragg and Point Arena declined dramatically—about 40% from 1989 to 1991.

The final year of a three-year northern California survey, designed to gather information for more effective management of the fishery, was completed in 1991. Size-frequency distributions and relative abundances were determined at fished and unfished sites in the Fort Bragg vicinity. Mean densities at Point Cabrillo Marine Reserve fluctuated from 5.4 red urchins/m^2 to 7.0/m^2 during summer surveys conducted from 1988 to 1991. Commercially fished sites declined from a high of 2.2 red urchins/m^2 in 1988 to just 0.3/m^2 in 1991.

Current management regulations include a 3.0-inch (76-mm) minimum size limit in southern California and a 3.5-inch (89-mm) minimum for northern California. Market sampling continued statewide in 1991, although it was interrupted for part of the year because of decreases in the state budget. The mean size of harvested red urchins in the north was 107 mm. In southern California, the mean size was 92 mm during the second half of 1991, when sampling was done.

During 1991, a review of how regulations are affecting the sea urchin resource was initiated, as required by the California Environmental Quality Act. Additional fishery restrictions are under consideration for 1992, partly in response to a continuing shift of effort to southern California.

RECREATIONAL FISHERY

The California commercial passenger fishing vessel (CPFV) fleet is capable of exploiting any sportfish resource in ocean waters from Mexico to Canada. Although the fleet generally does not fish north of the Oregon border, considerable activity takes place in Mexican waters, where most fishing is done off northern Baja California, and some as far as 800 miles south of Cabo San Lucas, Baja California. Without access to Mexico, catches of semitropical species such as yellowtail (*Seriola lalandei*) and yellowfin tuna (*Thunnus albacares*) (table 7) would be significantly reduced, since California is the northern edge of their ranges.

The CPFV fleet was adversely affected by environmental conditions during 1991. Abnormally cool water during the summer resulted in fewer passengers and lower catches south of Point Conception (figure 1). This was especially true for CPFVs operating out of San Diego, since few yellowtail or yellowfin tuna were available in waters off northern Baja California. North of Point Conception, salmon (*Oncorhyncus* sp.) anglers were affected by the drought. Fishing was poor in both Monterey and San Francisco, where most salmon angling takes place. However, a few lucky anglers from Fort Bragg north did experience good fishing because of coho salmon produced in Oregon.

TABLE 7
1991 Commercial Passenger Fishing Vessel Catch

Species/species group	Thousands of fish	Rank
Rockfish	2,015	1
Barred sand bass	484	2
Pacific mackerel	442	3
Kelp bass	317	4
Sculpin	180	5
Barracuda	176	6
Pacific bonito	118	7
Halfmoon	92	8
Salmon	54	9
Ocean whitefish	49	10
Lingcod	49	11
Sheephead	42	12
White croaker	16	13
Yellowtail	14	14
Flatfish (misc.)	11	15
Yellowfin tuna	11	16
Pacific hake	6	17
Skipjack	6	18
California halibut	6	19
Blue shark	5	20
Others	40	—
Total	4,133	

A total of 651,000 anglers on CPFVs landed 4.133 million fish in 1991 (table 7). The catch declined 13%, and the number of anglers declined 15% from 1990. Barred sand bass (*Paralabrax nebulifer*; up 14%) sculpin (*Scorpaena guttata*; up 12%), halfmoon (*Medialuna californiensis*; up 91%) and ocean whitefish (*Caulolatilus princeps*; up 10%) were the only species in the first ten ranks to show increased landings from 1990. Species among the first ten ranks with lower landings in 1991 were rockfishes (down 11%), Pacific mackerel (down 6%), kelp bass (*Paralabrax clathratus*; down 30%), barracuda (*Sphyraena argentea*; down 10%), Pacific bonito (*Sarda chilensis*; down 55%), and salmon (down 41%).

Three semitropical species showed the most dramatic declines in the CPFV landings. The dolphinfish (*Coryphaena hippurus*) catch dropped 96% in 1991 from a record high of 31,548 fish in 1990. The yellowfin tuna catch decreased by 77%, and yellowtail landings decreased by 80%.

An El Niño event developed in the eastern Pacific in late 1991. If warm water conditions persist and spread north, CPFV angling could significantly improve in southern California. However, there does not appear to be any environmental event that could immediately restore fishing in northern California.

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J. O'Brien, swordfish/shark
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D. Thomas, groundfish
G. Walls, anchovy
P. Wolf, editor

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Part II

SYMPOSIUM OF THE CALCOFI CONFERENCE

Lake Arrowhead, California

October 23, 1991

A DECADE OF RECOVERY OF THE PACIFIC SARDINE

RECONSTRUCTION OF THE HISTORY OF PACIFIC SARDINE AND NORTHERN ANCHOVY POPULATIONS OVER THE PAST TWO MILLENNIA FROM SEDIMENTS OF THE SANTA BARBARA BASIN, CALIFORNIA

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ABSTRACT

We present a composite time series of Pacific sardine and northern anchovy fish-scale-deposition rates developed from the anaerobic varved sediments of the Santa Barbara Basin off southern California. These series were constructed by integrating and adding to the data sets developed by Soutar and Isaacs and cover the period from A.D. 270 through 1970. We offer these series as a current best estimate of the sardine and anchovy scale-deposition rates and point out the sources and ranges of uncertainty remaining in the data. This includes providing a detailed analysis to determine the strength of the signal compared to the noise in scale-deposition rates.

We also recalibrate the scale-deposition data using available population estimates; we use this recalibration to hindcast the variability in sardine and anchovy stocks through almost 2000 years. Spectral analysis of the scale-deposition series shows that sardines and anchovies both tend to vary over a period of approximately 60 years. In addition, the anchovies fluctuate at a period of 100 years. The anchovy and sardine series show a moderate correlation over long time scales of several centuries or more; the correlation of shorter-period components in the time series is virtually nil. The scale-deposition record shows nine major recoveries and subsequent collapses of the sardine population over 1700 years. The average time for a recovery of the sardine is 30 years. A recovery is defined as an increase from less than one to over four million metric tons of biomass. We find that the current recovery is not unlike those of the past in its rate or magnitude.

RESUMEN

Presentamos series de tiempo de las tasas de depositación de escamas de la sardina del Pacífico y de la anchoveta norteña obtenidas de los sedimentos laminados anaeróbicos de la cuenca de Santa Barbara, al Sur de California. Estas series fueron construidas al integrar y completar los datos de Soutar e Isaacs e incluyen de 270 a 1970, D.C. Ofrecemos éstas series como la mejor estimación a la fecha de las tasas de depositación de escamas de sardinas y anchovetas y subrayamos las fuentes y rangos de incertidumbre quedando en los datos. Se incluye un análisis detallado para distinguir entre la fuerza de la señal respecto al ruido en las tasas de depositación de escamas.

También ofrecemos una recalibración de los datos de depositación utilizando estimaciones disponibles de la abundancia de la población. Utilizamos esta recalibración para estimar la variabilidad de los stocks de sardinas y anchovetas durante casi 2000 años. El cálculo del espectro de las series de depositación muestran que tanto las sardinas como las anchovetas tienden a variar con un periodo de aproximadamente 60 años, mientras que por otro lado las anchovetas fluctúan con periodo de 100 años. Las series de anchovetas y sardinas muestran una correlación mediana en escalas temporales de siglos o mayores, mientras que la correlación en periodos más cortos es virtualmente nula. El registro de depositación de escamas muestra que durante 1700 años la población de sardinas tuvo nueve recuperaciones principales seguidas de nueve colapsos. El tiempo promedio de recuperación de la sardina es de 30 años; se define recuperación como un incremento en la biomasa de menos de uno a más de cuatro millones de toneladas. Encontramos que el proceso de recuperación actual es similar a los del pasado en su tasa y magnitud.

INTRODUCTION

Traditional efforts to determine the fundamental time scales, and the sources, of variability in population sizes of Pacific sardine and other small pelagic fishes of the California Current are hindered because these stocks expand and contract over periods of several decades or longer. After roughly 60 years of annual biomass estimates for the Pacific sardine, fisheries scientists are able to describe only one major oscillation in its abundance. This oscillation appears to be nearing completion as the current sardine recovery gets well under way.

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[1] Manuscript completed while a visiting scientist at the Marine Life Research Group, Scripps Institution of Oceanography, University of California, San Diego.

Fortunately, the annually layered (varved) sediments in the Santa Barbara Basin off southern California provide a natural historical record of pelagic fish populations (Soutar 1967). Not only does the Santa Barbara Basin underlie a portion of the spawning grounds of the Pacific sardine and northern anchovy, but also anaerobic conditions below sill depth preserve fish scales within a much more detailed chronological framework than is normal for marine sediments. Because they prevent the homogenization of sediments that results from mixing by benthic animals, anaerobic conditions produce a yearly memory of processes in the pelagic ecosystem.

Soutar and Isaacs (1969) developed time series of fish-scale counts for small pelagic species including the Pacific sardine and northern anchovy; these series were based on the analysis of a piston core from the Santa Barbara Basin and extend back over nearly two millennia. After developing these long time series, Soutar and Isaacs turned their attention to constructing shorter series covering the 160 years from 1810 through 1970. These series were based on a much expanded and therefore more reliable data base of four box cores (Soutar and Isaacs 1974). Development of these high-quality time series of scale-deposition data into the twentieth century also made it possible to compare and integrate the paleoecological record with direct estimates of population biomasses.

These data constituted the first continuous time series of fossil fish and offered a picture of variability over periods significantly greater than a century. Sequences of fossil scales have since been constructed from the slope sediments off Peru (DeVries and Pearcy 1982) and for the Benguela margin off West Africa (Shackleton 1986). But the lack of well-developed, continuously varved records in these places has so far prevented the reconstruction of time series to equal the quality of those from the Santa Barbara Basin. An overriding lesson from the Santa Barbara records is that in the past both sardines and anchovies experienced large natural fluctuations which were clearly unrelated to fishing, and that abrupt natural declines, similar to the collapse of the sardines during the 1940s, are not uncommon.

An obvious shortcoming in the study by Soutar and Isaacs (1969) is that the very small area sampled by a single piston corer (7.6-cm diameter) is used to represent scale deposition over the entire basin. Another constraint on their results derives from the uncertainty in the underlying chronology due to imperfect preservation of the annually deposited layers over the entire length of the record. One of the goals of this paper is to provide improved composite time series of sardine and anchovy scale deposition covering most of the past two millennia. We developed these new time series by integrating data from a second piston core with the original data presented by Soutar and Isaacs (1969), and by substituting the box core data for the upper portion of the two piston cores. The new sardine and anchovy series provide significantly more reliable estimates of the scale-deposition rates (SDR's) and are now presented as a continuous record from approximately A.D. 300 through 1970. The evolution of the improved SDR series is documented in the following section, along with a description of the efforts to achieve a more accurate chronological base for the series.

A second goal of this paper is to examine the quality and inherent limitations of the composite sardine and anchovy time series constructed by averaging information from the two piston cores. We have made a detailed analysis of the strength of the SDR signals relative to the noise that tends to obscure the information in which we are interested. This analysis is presented in the section "Signal-to-Noise Ratios in Scale-Deposition Rates," which documents the range of uncertainty in the SDR values and evaluates our current effort to provide reliable series for hindcasting the changes in fish populations. How the SDR series can be used to describe past variability in the sizes of sardine and anchovy stocks is illustrated in the section "Hindcasting Population Sizes from Scale-Deposition Rates."

Our final goal is to describe the principal time scales over which the variability occurs in the SDR series and to apply this information to a historical analysis of the inferred recoveries and collapses. This goal is met in the sections "Time Scales of Variability in the SDR Series" and "Recoveries and Collapses of the Pacific Sardine." We also compare past recoveries with the current one.

RECONSTRUCTING THE TIME SERIES OF SCALE-DEPOSITION RATES

The essential foundation for reconstructing any time series from the sediment record is the chronology assigned to a sediment column. Detailed radiometric dating of the modern laminated sediments in the Santa Barbara Basin with ^{210}Pb and ^{228}Th/^{232}Th has demonstrated that the light-dark lamina pairs are annually deposited varves (Koide et al. 1972; Soutar and Crill 1977; Bruland et al. 1981). Varved sediments began to form in the Santa Barbara Basin as early as 8000 years ago and have provided a much more detailed chronological framework for reconstructing paleoecologic and climatic histories than is normally available from ocean basin and margin sediments (Soutar and Isaacs 1969; Soutar and Crill 1977; Heusser 1978; Pisias 1978).

The varve sequence of the anaerobic sediments of the Santa Barbara Basin is not continuous over the past 8000 years but is occasionally degraded by bioturbation and interrupted by turbidite deposition of centimeter-scale homogenous layers (Fleisher 1972; Soutar and Crill 1977; Schimmelmann et al. 1990). Although varve preservation for the past 2000 years is mostly good to excellent, episodes of bioturbation have disrupted the lamina sequence in varying degrees from negligible to complete erasure of the varve structure. These disturbances cover stratigraphic intervals of less than one to over many centimeters. Extending the annual chronology through these intervals (by interpolating sedimentation rates) leaves an inherent uncertainty proportional to the thickness of the interval, which accumulates downcore as more problem intervals are encountered. We now estimate the overall uncertainty to be approximately 50 years around the year 1000, which translates to roughly 5% over the length of the series. This estimate is based on comparisons of the SDR series to available high-resolution proxy records of climate change such as the tree rings of California bristlecone pines (LaMarche 1974). These comparisons suggest a possible chronological offset of 50 years near the midpoint of the series.

Soutar and Isaacs (1969) presented a time series (of continuous 10-year sample blocks) of fish-scale counts through the past 1800 years for the Pacific sardine, northern anchovy, Pacific hake, and a group of undifferentiated species including lampfish, saury, jack mackerel, and others. These series were developed from analyses of a 2.5-m core retrieved by a standard Kullenberg piston corer with 7.6-cm-diameter barrel. The location of this core is shown in figure 1 as core site 214 in the east-central basin area. Recently we combined results from the analysis of a second piston core from site 224 (figure 1) with the original series from site 214. Continuous records of the laminar varve structures in cores 214 and 224 were made by X-radiography of longitudinal slabs cut from the outside of the core. After identifying and matching the varve sequences from the radiographs of both cores, we assigned calendar dates to the varve record by counting from surface ages of box cores that correlated to the upper sections of the piston cores.

Cores 214 and 224 were continuously sampled at 1-cm intervals for wet sieving and separation of the

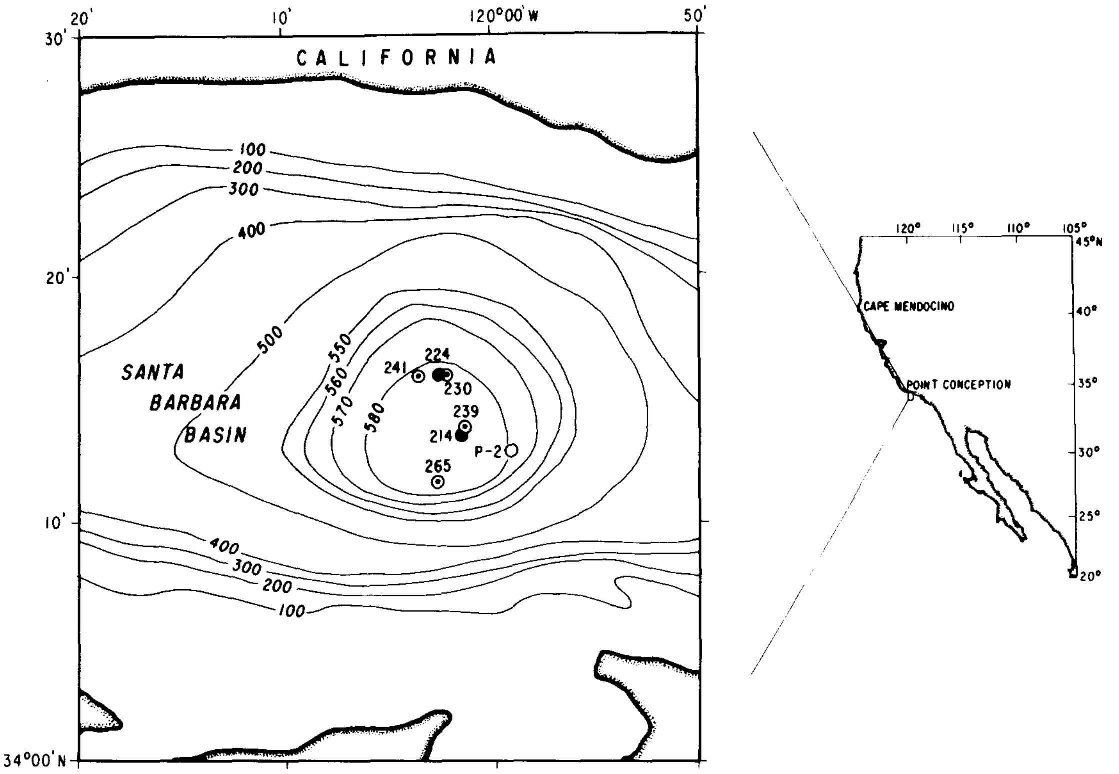

Figure 1. Locations of cores within the Santa Barbara Basin referred to in text. *Dark circles* are piston core sites (214 and 224) used to construct figures 2 and 3; *open circle* is piston core dated with tree-ring correlations (core P-2). *Circles with dots* are box cores (230,239,240,265) used to construct the short time series by Soutar and Isaacs (1974), which has been added to the series from the piston core sequence to obtain the series in figure 4.

fish debris (Soutar and Isaacs 1969). The time periods represented by the 1-cm subsamples range from 4 to 20 years, depending on the rate of sedimentation. Sampling based on depth downcore (the 1-cm slices) rather than on uniform varve (time) intervals results in only a slight loss of accuracy. The fish-scale counts with respect to depth were converted to scale-deposition rates over time (SDR's) by interpolation across the subsample thicknesses in order to adjust the values to 10-year intervals. To identify the scales we used a reference collection taken from fish caught off California and Baja California.

Figures 2 and 3 compare the time series reconstructed from cores 214 and 224 for the sardine and anchovy. It is important to note that the chronology used in these figures represents a preliminary stage of development, based solely on varve counts from X-radiographs and therefore subject to the necessary interpolation and bridging of poorly preserved and nonvarved intervals. Note also that the uppermost value plotted in figures 2 and 3 is from the interval 1800–1810. Because of the disturbance and loss of surface material associated with piston coring, it is prudent to disregard the uppermost section of the piston core. For a continuous record into the twentieth century, the period above 1810 is covered by the series developed by Soutar and Isaacs (1974) from the box cores at locations shown in figure 1.

Chronological uncertainty in varve sequences of the Santa Barbara Basin can be reduced by cross-correlating sequences of varve thicknesses to tree-ring widths because they are linked through rainfall in southern California (Soutar and Crill 1977; Schimmelmann et al. 1990). Cores 214 and 224 have not been directly dated by this method, but rather have been compared indirectly by correlation to a third piston core (P-2 in figure 1), for which the varve stratigraphy has been anchored with dates centered around 1405 and 770. Byrne et al. (in press) compare ring-widths of San Jacinto bigcone spruce (*Pseudotsuga macrocarpa*) from a 30-year interval (1391–1422) to the sequence of varve thicknesses to derive the best match from a lagged cross-correlation. The lower anchor point in core P-2 was obtained by cross-correlating the varve sequence to an 80-year tree-ring series (728–808) developed from *Pinus flexilis*. The *P. flexilis* series, however, is not as strongly correlated to varve thicknesses as are the *P. macrocarpa* series, and the lower anchor date is con-

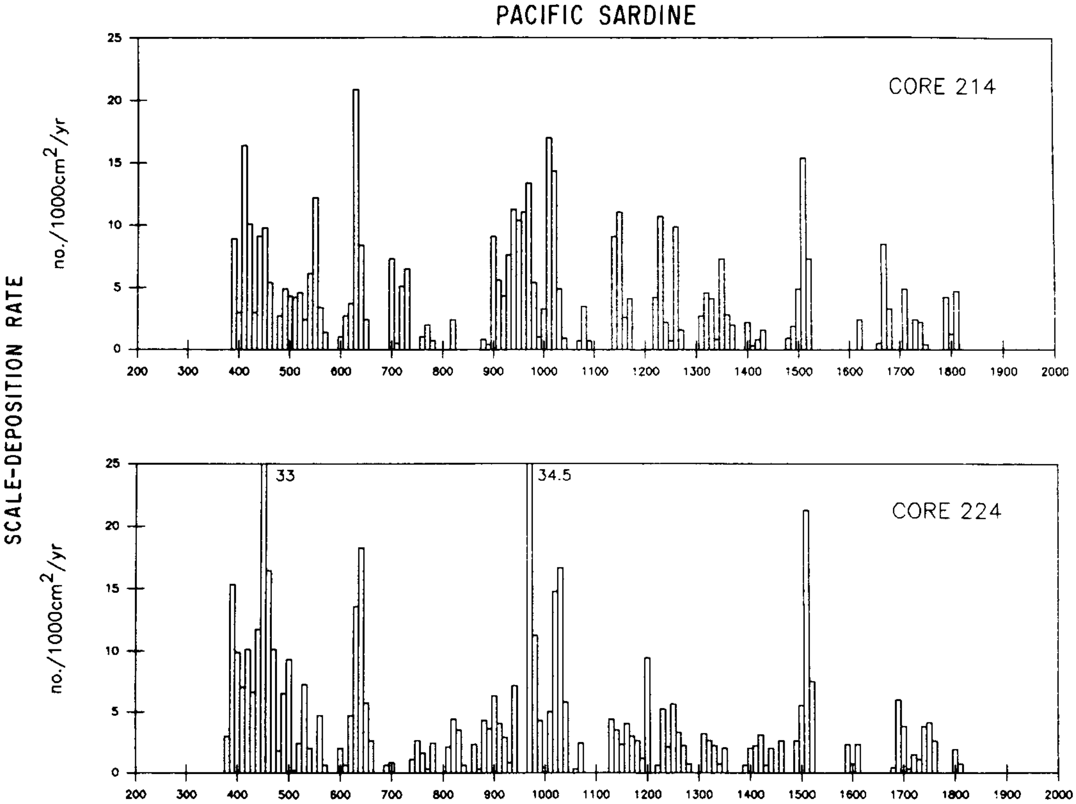

Figure 2. Original time series of scale-deposition rates for the Pacific sardine reconstructed at 10-year intervals from analysis of piston cores 214 and 224 from the Santa Barbara Basin (core sites in figure 1). The series is based on preliminary chronology; compare to figure 4. Scale-deposition rates are given as mean annual values for each 10-year period.

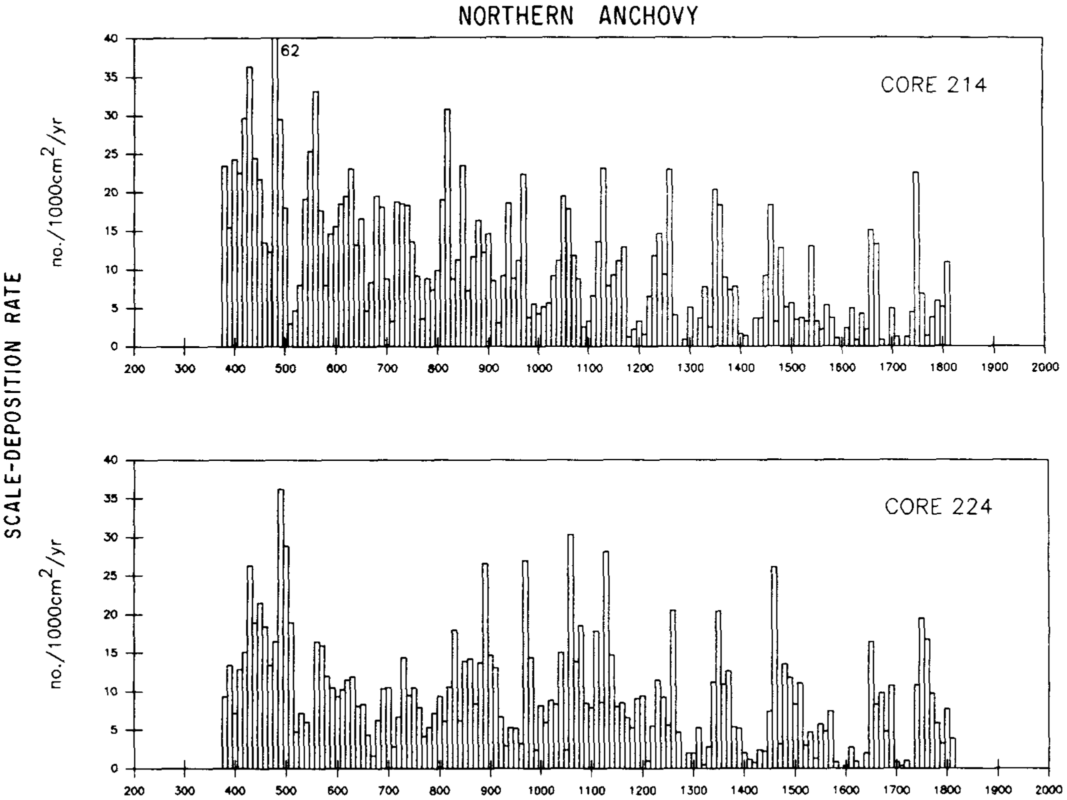

Figure 3. Original time series of scale-deposition rates for the northern anchovy reconstructed at 10-year intervals from analysis of piston cores 214 and 224 from the Santa Barbara Basin (core sites in figure 1). The series is based on preliminary chronology; compare to figure 4. Scale-deposition rates are given as mean annual values for each 10-year period.

sidered less reliable than the upper anchor date (J. Michaelsen, UC Santa Barbara, pers. comm.).

Figure 4 is a plot of the two composite time series of scale-deposition rates for the Pacific sardine and northern anchovy constructed by averaging the species SDR data from cores 214 and 224. Piston core P-2 (Byrne et al., in press) has been used as a chronological reference to adjust the original chronologies of cores 214 and 224 underlying the time series plotted in figures 2 and 3. The chronological adjustment to the fish-scale data in figure 4 was made by altering the calendar dates between the lower end of the series and the year 1100 in the original varve chronologies of figures 2 and 3. The chronology used for the interval 1100–1810 in the series of figure 4 is identical to that used in figures 2 and 3, whereas the lower end of the series in figure 4 is assigned an age 60 years younger than the original date. We completed this adjustment by compressing the data to fit into the decreased number of years by linear interpolation across the entire interval. This has a cumulative effect on the SDR values toward the lower end of the series as the chronological offset from the adjustment increases toward the maximum at the end of the record. When we take these adjustments into account, we can see the sardine and anchovy SDR series of figure 4 as the averages of the series in figures 2 and 3.

Values covering the period from 1810 through 1970 in figure 4 are based on the work published by Soutar and Isaacs (1974). These records were developed from four undisturbed, large-area (20 × 20 cm) box cores well distributed over the floor of the basin (figure 1; core sites 241, 230, 239, and 265). The chronology is very well constrained for the period of well-defined varve layering between 1860 and 1970, but less so for the period 1810–60, during which the sediments were subject to increased bioturbation, which somewhat degraded the laminar structure. Radiometric dating by ^{210}Pb and ^{228}Th/^{232}Th also provides a solid backup to the varve chronology above 1870. Scale-deposition rates were determined by sampling 5-year intervals down four longitudinal slabs (surface areas for each slab approximately 40 cm^2) from each of the four box cores.

Figure 5 shows the total area of depositional surface, plotted against calendar years, which has been sampled in the process of reconstructing the time series of scale-deposition rates in figure 4. The ex-

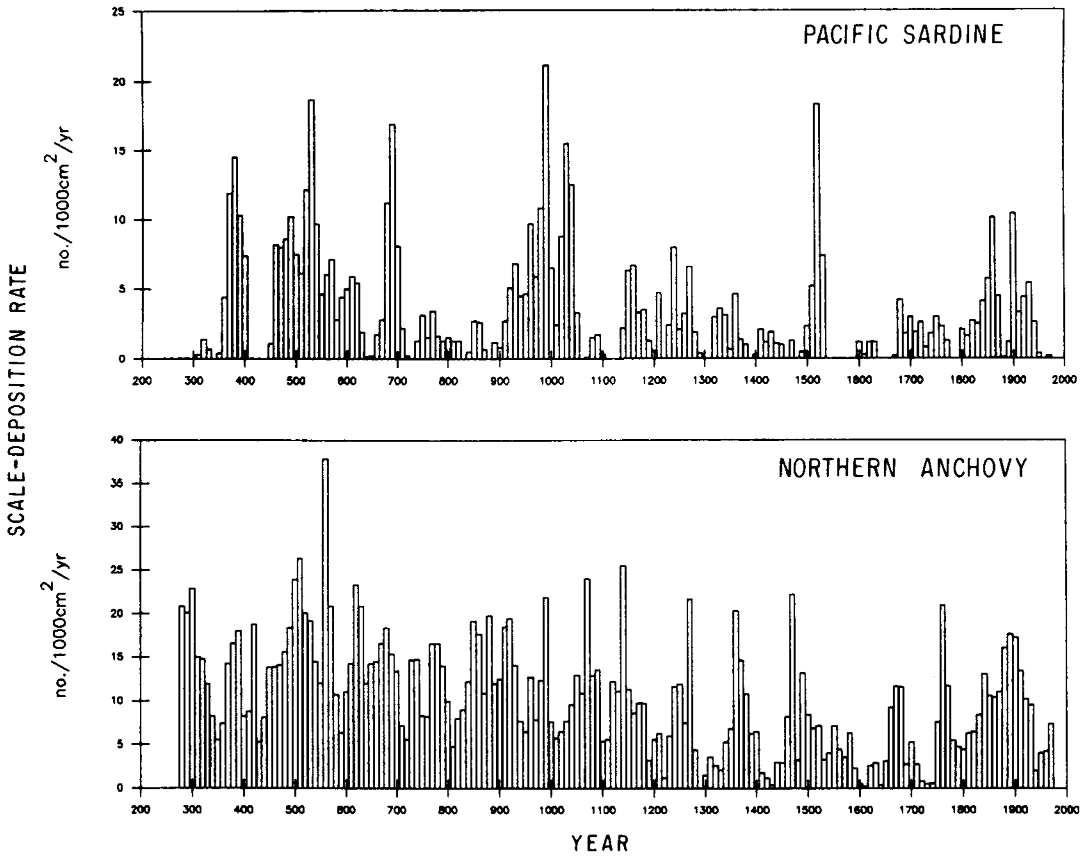

Figure 4. Composite time series of the Pacific sardine and northern anchovy scale-deposition rates developed by averaging across piston cores 214 and 224 (for the interval A.D. 270–1810; see figures 2 and 3) and by adding series developed from box cores 241, 230, 239, and 265 (for the interval 1810–1970). Note that the chronology used for these two time series is different (below A.D. 1100) from that of the original series in figures 2 and 3; it has been revised by correlation of varve chronostratigraphies from cores 214 and 224 to piston core P-2. Also note that 10 data points not plotted on figures 2 and 3 have been added to the beginning of figure 4.

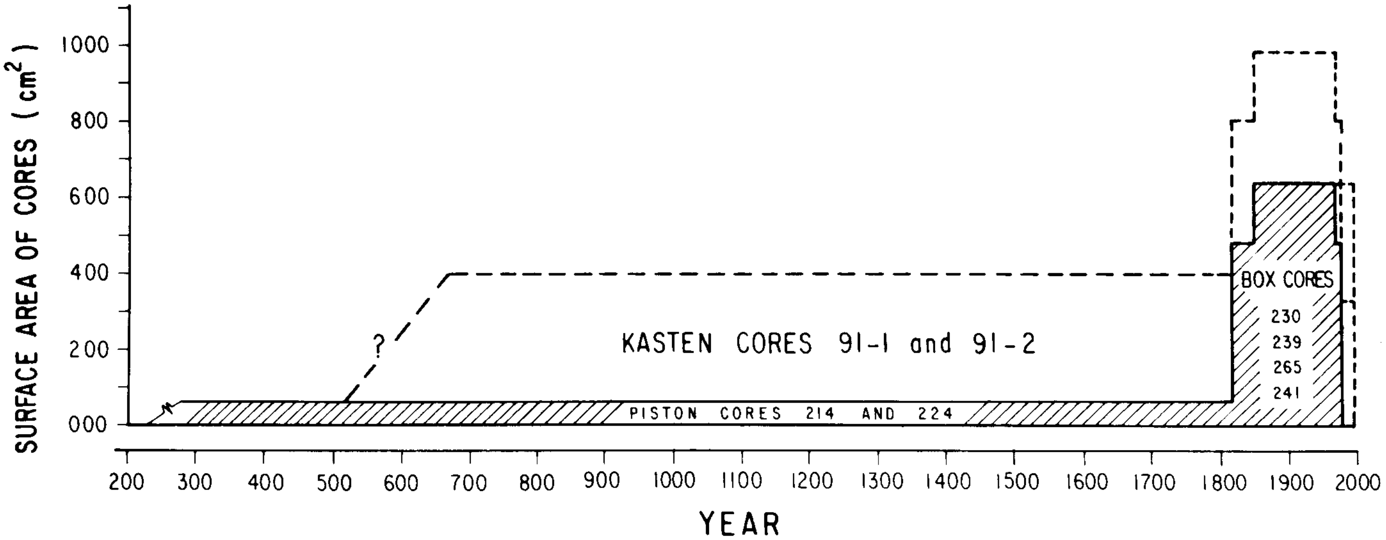

Figure 5. Diagram of the cumulative area of depositional surface sampled by the cores marked on location map in figure 1, plotted as a function of estimated calendar time sampled. *Hatched area* corresponds to the cores used to construct the sardine and anchovy SDR time series in figure 4. *Open area* represents the amount of material made available for future analysis by the recent recovery of two Kasten cores and two box cores from the Santa Barbara Basin.

panded data base for the period after 1810, obtained from the four box cores, should provide a much better averaged estimate of the SDR series than the data prior to 1810, which is based on the two small-diameter piston cores. We are now taking measures to expand this narrow data base. During 1991 we collected two high-quality Kasten cores, whose combined depositional surface areas are plotted in figure 5. These Kasten cores retrieved approximately 2.6 m of material and certainly reach at least 1500 years into the past.

Another important consideration bearing on the quality of the fish-scale numbers as a proxy record of populations is the extent to which diagenetic processes may have destroyed the buried scales. Evidence from both the stratigraphic distribution of scales and the interstitial water chemistry of the Santa Barbara Basin sediments indicate that degradation after deposition is negligible. Sholkovitz (1973) showed that the production of dissolved phosphate in the interstitial waters downcore is totally accounted for by decomposition of organic matter. This means that there is no "excess" phosphate present in the Santa Barbara Basin sediments to indicate dissolution of fish debris (as opposed to organically bound phosphorus) such as apparently does occur in sediments of the Peruvian margin (Suess 1981). The distribution of scales at depth also indicates that postburial degradation is not important, since there is no trend of decreasing scale numbers at depth for either sardines or anchovies in piston cores 214 and 224 (figures 2 and 3); on the contrary, there are clear tendencies toward increased SDR values downcore for both species in both cores.

SIGNAL-TO-NOISE RATIOS IN SCALE-DEPOSITION RATES

One of the most important questions regarding the use of fossil fish scales to hindcast population sizes addresses the reliability of the SDR values as indices of abundance. Part of this concern arises from our uncertainty about how well a single piston core represents the variability in scale deposition over the basin. A preliminary answer lies in comparing the time series of sardine and anchovy data from piston cores 214 and 224 plotted in figures 2 and 3. This comparison allows us to begin to characterize how well a "true" signal of the regional, or basin-wide, scale-deposition rate is visible above the noise induced either from sampling or from natural processes.

Note that this analysis does not specifically identify chronological error; rather we assume *a priori* a perfect "chronological" alignment among the time series analyzed. Therefore we must first obtain as good a match between the varve chronostratigraphies as possible. This produces a verifiable stratigraphic alignment between the two cores, but does not insure accurate agreement with calendar time. This is the case for the time series in figures 2 and 3. The varve stratigraphies matched one another, but the chronology by varve counting was subsequently modified below A.D. 1100 after comparison to core P-2. However, the chronological error does not alter the results of a signal-to-noise analysis, because the error is consistent in both cores.

The simplest means for an initial comparison are linear correlations among the sardine and anchovy data series from cores 214 and 224. The results of these correlations are given in table 1. We adjusted the significance levels of the correlation coefficients for the effects of autocorrelation within each of the series by calculating the reduced degrees of freedom for each correlation pair from the "integral time scales" as described in Enfield and Allen (1980). It is interesting that correlation between cores 214 and 224 for the sardines ($R = 0.53$) is the same as the between-core correlation for the anchovies ($R = 0.54$). These are respectable (and significant) correlations, although they indicate that the variance shared between cores for each species (R^2) does not exceed 30%.

Comparison of the above correlations with correlations between the two species in the same core and from different cores is also instructive: the correlation of the sardine series from core 214 with the anchovy series from 224 is virtually nil ($R = 0.16$; $R^2 = 0.03$), whereas correlation of the sardine series from core 224 and the anchovy series from the same core is significant, with a modestly high value of $R = 0.37$ ($R^2 = 0.14$). The fact that only about 30% of the variance is shared between series of the same species from the two cores indicates that the data in figures 2 and 3 must contain a substantial quantity

TABLE 1

Correlation Matrix of the Time Series of Pacific Sardine and Northern Anchovy from Cores 214 and 224

	Anchovy 214	Anchovy 224	Sardine 214	Sardine 224
Anchovy 214		0.54	0.26	0.24
Anchovy 224	(65) .001		0.16	0.37
Sardine 214	(80) .05	(92) .20		0.53
Sardine 224	(77) .05	(92) .001	(95) .001	

Note: Correlation coefficients (R) are shown above the diagonal. Levels of significance (α) and the reduced degrees of freedom (shown in parentheses) obtained from the "integral time scales" of the correlation pairs (see text) are given below the diagonal. Length of all series is $N = 144$.

of uncorrelated noise. Conversely, the shared signals are clearly detectable by the correlations.

Determining the actual ratio of the signal to noise in the SDR data of figures 2 and 3 can be approached by a two-way analysis of variance performed separately for the sardine and anchovy SDR series of the two piston cores in order to distinguish among the different sources of variability. Comparison of the sardine or anchovy SDR series from the two cores follows an experimental design (Griffiths 1967; chap. 19) in which each observation $x_{i,j}$ can be expressed by the linear model

$$x_{i,j} = \mu + \alpha_i + \beta_j + \epsilon_{i,j}$$

indicating that any observation of the two series comprises an estimate of the overall mean value μ, plus a contribution from the effect of downcore variability α_i (this is the time-dependent *signal* in which we are interested), plus a contribution from the effect of β_j associated with the difference between the j core sites (a consistent difference through time in deposition of fish scales from one site to the next), plus a contribution from random "errors", ϵ_{ij} (the undifferentiated between-core and downcore *noise*), occurring among the i samples down each core. Note that this design assumes there is no "interaction" (dependence) between the downcore, temporal variability and the between-core, spatial variability (i.e., $\alpha\beta_{ij} = 0$). This assumption is necessary because we lack the replicate subsamples within each core to estimate any effect from $\alpha\beta_{ij}$ (Griffiths 1967; chap. 19).

Table 2 displays the results of the two-way ANOVA for the sardine data; the same information for the anchovy data is given in table 3. These tables

TABLE 2

Results of the Two-Way Analysis of Variance on the Sardine SDR Series from Cores 214 and 224 Plotted in Figure 2

No. of items	Source of variation	d.f.	Sum of squares	Mean square
a = 144	Downcore signal	143	5221.372	36.5103 $(b\sigma_\alpha^2 + \sigma_\epsilon^2)$
b = 2	Between-core effect	1	6.037812	6.03781 $(a\sigma_\beta^2 + \sigma_\epsilon^2)$
	Noise	143	1692.447	11.8353 (σ_ϵ^2)
ab = 288	Total	287	6919.857	

Ratios of mean square value of the downcore signal and the between-core effect to the mean square value of noise	Observed F				Test statistic $F_{.05}$
Downcore signal : noise (143 d.f. : 143 d.f.)	$\frac{36.51}{11.84}$	=	3.08	>	1.32
Between-core effect : noise (1 d.f. : 143 d.f.)	$\frac{6.04}{11.84}$	=	0.51	<	3.91

TABLE 3

Results of the Two-Way Analysis of Variance on the Anchovy SDR Series from Cores 214 and 224 Plotted in Figure 3

No. of items	Source of variation	d.f.	Sum of squares	Mean square
a = 144	Downcore signal	143	14512.07	101.4830 $(b\sigma_\alpha^2 + \sigma_\epsilon^2)$
b = 2	Between-core effect	1	140.4209	140.4209 $(a\sigma_\beta^2 + \sigma_\epsilon^2)$
	Noise	143	4558.724	31.8792 (σ_ϵ^2)
ab = 288	Total	287	19211.21	

Ratios of mean square value of the downcore signal and the between-core effect to the mean square value of noise	Observed F				Test statistic $F_{.05}$
Downcore signal : noise (143 d.f. : 143 d.f.)	$\frac{101.48}{31.88}$	=	3.18	>	1.32
Between-core effect : noise (1 d.f. : 143 d.f.)	$\frac{140.42}{31.88}$	=	4.40	>	3.91

show the partitioning of the total variance by the analysis into the mean square values associated with three sources of variability: the downcore, temporal signal ($b\sigma_\alpha^2 + \sigma_\epsilon^2$); the constant between-core difference ($a\sigma_\beta^2 + \sigma_\epsilon^2$); and the unexplained noise (σ_ϵ^2).

The significance of contributions from the downcore signal and the between-core difference versus the unassigned noise is found by comparing their respective mean square values through a variance ratio *F* test (Griffiths 1967; chap. 19). Using the *F* statistic we can test the hypotheses

(1) H_o: The variance of the noise is equivalent to the downcore signal ($\sigma_\alpha^2 = \sigma_\epsilon^2$), against

H_a: The variance of the downcore signal is significantly greater than that of the noise ($\sigma_\alpha^2 > \sigma_\epsilon^2$)

and

(2) H_o: The variance of the noise is equivalent to the between-core effect ($\sigma_\beta^2 = \sigma_\epsilon^2$), against

H_a: The variance of the between-core effect is significantly greater than that of the noise ($\sigma_\beta^2 > \sigma_\epsilon^2$).

Table 2 shows that for the sardine data the first null hypothesis above can be rejected; the observed value of *F* (3.08) is greater than the tabulated value (1.32) at the 95% level of confidence. Therefore, the ANOVA does clearly distinguish between the downcore signal and the undifferentiated noise. The mean square value of the signal is threefold that of the noise. This is substantially more than is needed to reject the first null hypothesis.

Table 2 further shows that the second null hypothesis above cannot be rejected; the observed value of *F* (0.51) is considerably less than the tabulated value (3.91) at the 95% level. This means that the ANOVA cannot detect a between-core effect above the noise. There appears to be no significant consistent difference in deposition of sardine scales between cores 214 and 224.

Table 3 shows that both null hypotheses are rejected in the analysis of the anchovy series. Therefore, the ANOVA does also clearly distinguish a regional downcore signal above the residual temporal-spatial noise in the anchovy data. Like the downcore sardine signal, the anchovy signal is three times that of the noise. However, in contrast to the sardine ANOVA, we find here a measurable difference in anchovy scale deposition between cores 214 and 224. Although this suggests some pattern of nonuniform deposition of anchovy scales within the basin, we cannot determine the spatial scale of this suggested variability (is it basinwide or does it occur, for example, over small distances of centimeters to meters?) or distinguish any temporal-spatial interaction. This result stresses the need for multiple-site sampling within the basin using coring devices that retrieve surface areas large enough to allow for replicate determinations within each core (cf. figure 5).

HINDCASTING POPULATION SIZES FROM SCALE-DEPOSITION RATES

Another major concern over the value of SDR's for estimating population sizes is how sensitive the "true" basin-wide SDR signal is to changes in regional abundance (density) of fish. One of the major accomplishments by Soutar and Isaacs (1974) was to demonstrate that the rates of fish-scale deposition in the Santa Barbara Basin provide reasonable indices to changes in the population biomasses, particularly for sardines and anchovies in the California Current. Their comparison of SDR's to biomass was based on a 5-year sample resolution obtained from the analysis of the box cores.

Soutar and Isaacs (1974) were able to establish a relationship between SDR values and the six 5-year averages of available annual estimates of the total sardine population from 1932 to 1960 obtained by Murphy (1966). They also found an exceptionally good relationship between sardine SDR and the biomass of fish younger than 2 years old, consistent with the observation that most of the scales (greater than 90%) found in the sediments were from fish less than 2 years old. This indicates that scale deposition is sensitive to the density of fish in the immediately overlying water column. The relationship between the scales and the biomass of the 2-year-old and older fish was diminished but still clearly significant, and demonstrated that the Santa Barbara SDR's are also proportional to the adult biomass off California and northern Baja California. Thus the response of the SDR's to the larger population biomass appears to occur through an indirect relationship between the numbers of younger fish inhabiting the area inshore over the Santa Barbara Basin and the total adult populations over their respective ranges.

It is now possible to recalibrate the sardine SDR data to biomass estimates by using revised population estimates for the years 1945–65 presented by MacCall (1979), coupled with Murphy's (1966) estimates for 1932–44, and by assuming that the population had shrunk to under 20,000 metric tons (MT) after 1964. This provides an improved series of biomass estimates, and we gain two more data points than were available to Soutar and Isaacs (1974) for the sardine SDR's. The upper diagram in figure 6 is a scatter plot of the biomass of sardines as a function of the 5-yr averages of SDR's. The population estimates used in figure 6 represent the spawning biomass of adults 2 years old and older.

Our regression of the sardine SDR with the revised population estimates yields a lower zero crossing than that obtained by Soutar and Isaacs (1974). This slightly improves the definition of population sizes where zero scale counts occur. Their zero crossing (MT of biomass at zero observed flux of scales) is approximately 700,000 MT compared to approximately 400,000 MT in figure 6.

The regression of anchovy-scale data versus biomass estimates is presented in the lower plot of figure 6. This analysis is based on data tabulated from Smith (1972), and includes two more data points than used in Soutar and Isaacs' (1974) comparison; we have added averages from two 5-year periods based on estimates of only two years of surveys (1940–44) and of four years (1965–69). This is done to gain more degrees of freedom but also adds more scatter to the earlier regression. Another important difference between this recalibration and that given by Soutar and Isaacs (1974) for the anchovy is the dramatic reduction in annual biomass estimates (see Smith and Moser 1988) as a result of work by Lo (1985) and Methot and Lo (1987). The implication of this work is that the spawning biomass estimates derived by Smith (1972) are now considered to be approximately four times too large (Smith, pers. comm.). Therefore we have reduced these values accordingly to compute the regression of anchovy biomass against the SDR data shown in the lower plot of figure 6.

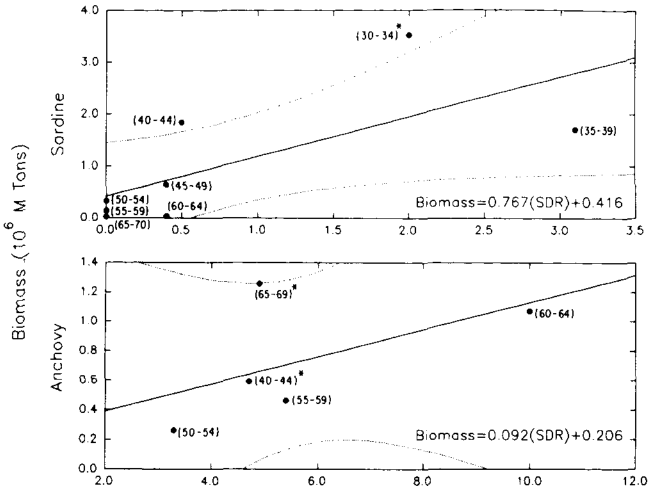

Figure 6. Linear regression of population biomass estimates of 2-yr-old and older Pacific sardine and northern anchovy (5-year averages) against the scale-deposition rates from the Santa Barbara Basin given by Soutar and Isaacs (1974). Sardine population estimates are from Murphy (1966; values from 1930 to 1944) and MacCall (1979; from 1945 to 1964). Anchovy population estimates are for the same years as in Soutar and Isaacs (1974) but with values strongly revised downwards (see Smith and Moser 1988). *Curved lines* show the 95% confidence interval around the regression line. Parenthetical numbers at data points refer to years of that pentad; the pentads marked by asterisks indicate population estimates based on less than 5-year averages for that pentad.

Using the regression equations shown in figure 6, we have transformed the SDR values of sardines and anchovies of figure 4 into units of biomass in figure 7. The regression of biomass against SDR values accounts for approximately 50% of the variance in the biomass of the sardine population and 31% of the variance in the anchovy population. The envelopes around the regression line in the scatter plots of figure 6 indicate the region in which 95% of the hindcast values are expected to fall.

The sardine hindcasts estimate the biomass between Punta Baja in Baja California and a point near Monterey, California (based on the area surveyed for the estimates obtained by MacCall [1979]). This corresponds to the "northern" sardine stock defined by Radovich (1981). The hindcasts of anchovy population are based on the estimates (Smith 1972) that include both the "central" and "southern" stocks of northern anchovy as defined by Vrooman et al. (1981). Thus the anchovy hindcasts in figure 7 refer to the adult biomass inhabiting inshore and offshore areas between roughly San Francisco, California, and Cabo San Lucas, Baja California.

TIME SCALES OF VARIABILITY IN THE SDR SERIES

Despite uncertainties in the varve chronology and the SDR estimates of population biomass, these records are valuable tools for exploring the variability occurring over time scales of several decades through several centuries. Figure 8 shows the variance spectra for the sardine and anchovy data after removal of long-term linear trends over the full length of both series. The spectral estimates have been smoothed by filtering with a cubic spline fit. The original sample resolution of 10-year intervals does not permit us to consider periods shorter than 20 to 30 years; to be completely safe we focus only on periods longer than 50 years.

In describing the time scales of variability, we distinguish between low-frequency variability and high-frequency variability based on the spectral characteristics of both the sardine and anchovy SDR

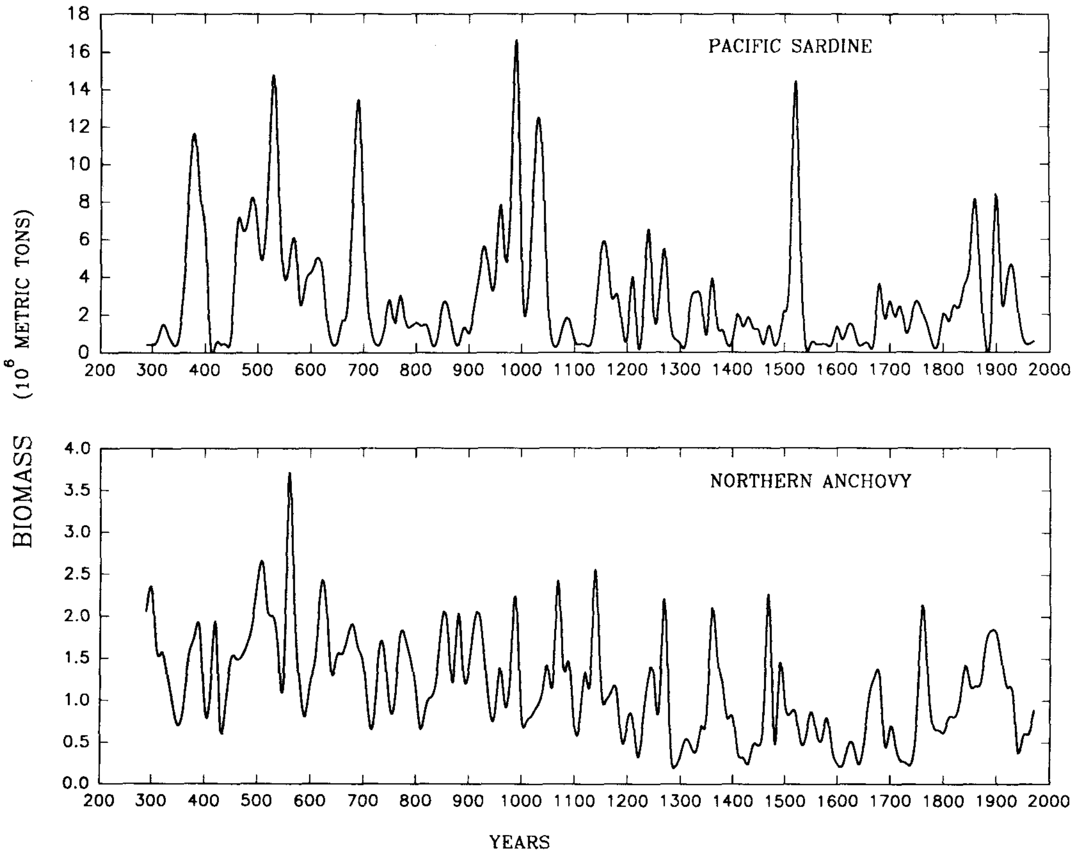

Figure 7. 1700-year hindcast series of Pacific sardine and northern anchovy biomasses off California and Baja California obtained by conversion of SDR data in figure 4 to units of biomass with the regression equations in figure 6.

series. For convenience we use the period of 150 years as a naturally occurring boundary between the high and low frequencies.

One noteworthy difference between spectra of the sardine and anchovy SDR data is the considerable variance centered around the 480- and 160-year periods in the sardine series. This appears to reflect low-frequency clumping in the sardine record, which does not appear in the anchovy record.

At the higher frequencies (periods shorter than 150 years), both the sardine and anchovy show peaks at nearly the same positions but with different levels of relative importance (near 60 years, between 70 and 80 years, and between 100 and 110 years). The 102-year peak dominates the spectrum of the anchovy data (figure 8); this reflects the strong regular organization of maximum and minimum values in the anchovy data of figure 4. In comparison, the 106-year peak in the sardine series is very weak. (The one-year precision in the position of spectral peaks is an artifact of calculation, since the sample resolution is only 10 years; thus peaks at 102 and 72 years should be rounded to 100 and 70 years, for example.)

We have separated the low-frequency variability (periods > 150 years) from the original sardine and anchovy series using a low-pass Spencer's 21-term filter (Statistical Graphics Corp. 1989) to produce the smooth curves through the original data points plotted in figure 9. Subtracting the deviations of the original from the filtered data gives us the time series of "residuals" plotted in figure 10. These are the extracted high-frequency components of the variance from the sardine and anchovy SDR series of figure 4, emphasizing periods in the range of 50 to 100 years. The spectra of the residual series (figure 11) allow us to view the relative importance of the shorter periods without interference from the low-frequency components.

The 57-year peak is more strongly emphasized (with respect to the other dominant peaks) in both the sardine and anchovy spectra of figure 11 than in figure 8. Figure 11 also clearly shows that the approximate 100-year peak for the anchovies is not present in the sardine data. The importance of the 100-year peak in the anchovy spectra of figure 11 is also diminished compared to its expression in figure

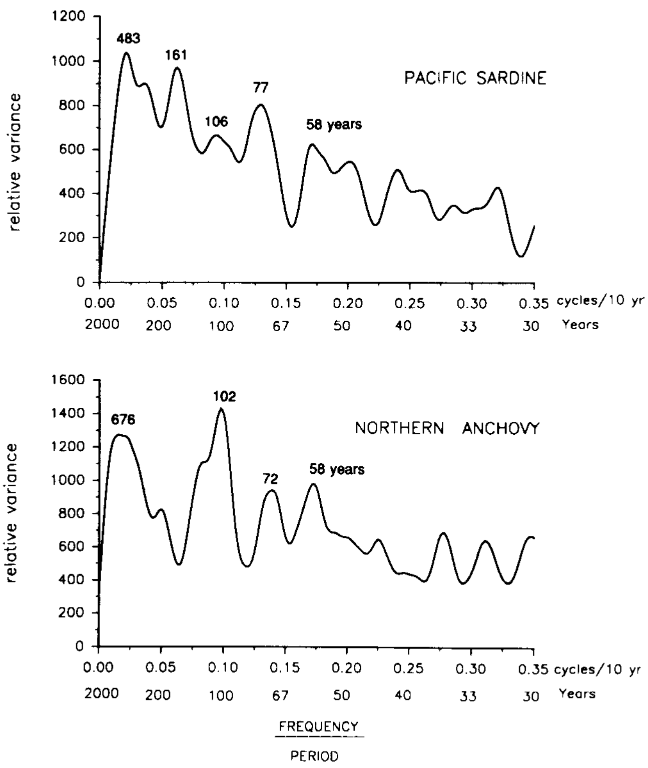

Figure 8. Smoothed power spectra of the scale-deposition rates of the Pacific sardine (*top*) and northern anchovy (*bottom*) that are plotted as time series in figure 4. Concentration of variance in specific frequency bands is identified with the corresponding time period, at the center of the spectral peaks.

8, reflecting a contribution of low-frequency variability to this peak in figure 8. We also see that both the importance and the offset between the 76-year (sardine) and 72-year (anchovy) peaks is maintained in figure 11.

Finally, it is important to point out that the correlation between the sardine and anchovy residuals of figure 10 ($R = 0.20$) is markedly lower than that for the original unfiltered series ($R = 0.33$) of figure 4, and much less than for the smoothed low-frequency data of figure 9 (which is $R = 0.56$). This important distinction has not been made in previous discussions of scale-deposition rates (e.g., Soutar and Isaacs 1974; Lasker and MacCall 1983; or Rothschild 1986). All these authors have remarked on the positive correlation, albeit weak, between the sardine and anchovy series. This positive correlation appears to be a response to the low-frequency components, and is negligible for periods less than 150 years. Cross-correlation of the two residual series of figure 10 also shows that there is no clear lag structure between the high-frequency components of the sardine and anchovy series (i.e., correlation is greatest at zero lag). Therefore the correlation is not simply reduced because of a consistent phase shift between the residual series.

RECOVERIES AND COLLAPSES OF THE PACIFIC SARDINE

The nature of fluctuations in the Pacific sardine population is particularly interesting as a background for better understanding the current recovery. The long records of sardine and anchovy SDR's allow us to examine the rise and fall of these populations as a series of collapses and recoveries. We can create a more visually concise record of the history of major declines and recoveries of the Pacific sardine by reducing the magnitudes of the sardine SDR values of figure 4 into four selected ranges: 0 scale deposition; ≤ 1 scale/10^3 cm^2 yr^{-1}; 1–5 scales/10^3 cm^2 yr^{-1}; and ≥ 5 scales/10^3 cm^2 yr^{-1}. The bottom plot of figure 12 is the simplified time series that corresponds to the new succession of clipped values obtained by expressing the data with these four categories. The estimated levels of biomass corresponding to these categories are given below the plot.

To establish a basis for examining population recoveries and declines, we define recovery and collapse in ways compatible with the record of scale deposition, and useful as a guide to past population behavior. We thus define recovery as a population expansion starting from less than or equal to approximately one million MT (from ≤ 1 SDR unit $\approx 1.2 \times 10^6$ MT) and climbing to a level equal to or greater than approximately four million MT (to ≥ 5 SDR units $\approx 4.2 \times 10^6$ MT). We chose a target biomass of four million MT or greater to represent a major recovery because that is the total biomass thought to have been present in the northern and southern subpopulations during the mid-1930s, when the fishery was at its peak of production (although the maximum biomass present before 1930 was considerably higher; Smith 1978). This level of biomass is also conveniently approximated by an SDR value of ≥ 5 units. The level of biomass chosen to represent the initial value at the beginning of a recovery (between near zero and roughly one million MT; approximated by the SDR values of ≥ 0 units and ≤ 1 unit) encompasses a very large range, but the sensitivity of the SDR values to low biomass values does not presently allow for greater precision. Collapses are defined as sustained population decreases from biomass levels starting above roughly four million MT and falling to one million MT or less.

Based on our definitions above, we recognize nine major recoveries and nine subsequent collapses of the sardine population off California in the past 1700 years. Eight recoveries begin from 0 SDR values (equivalent to $\leq$400,000 MT), with one recovery

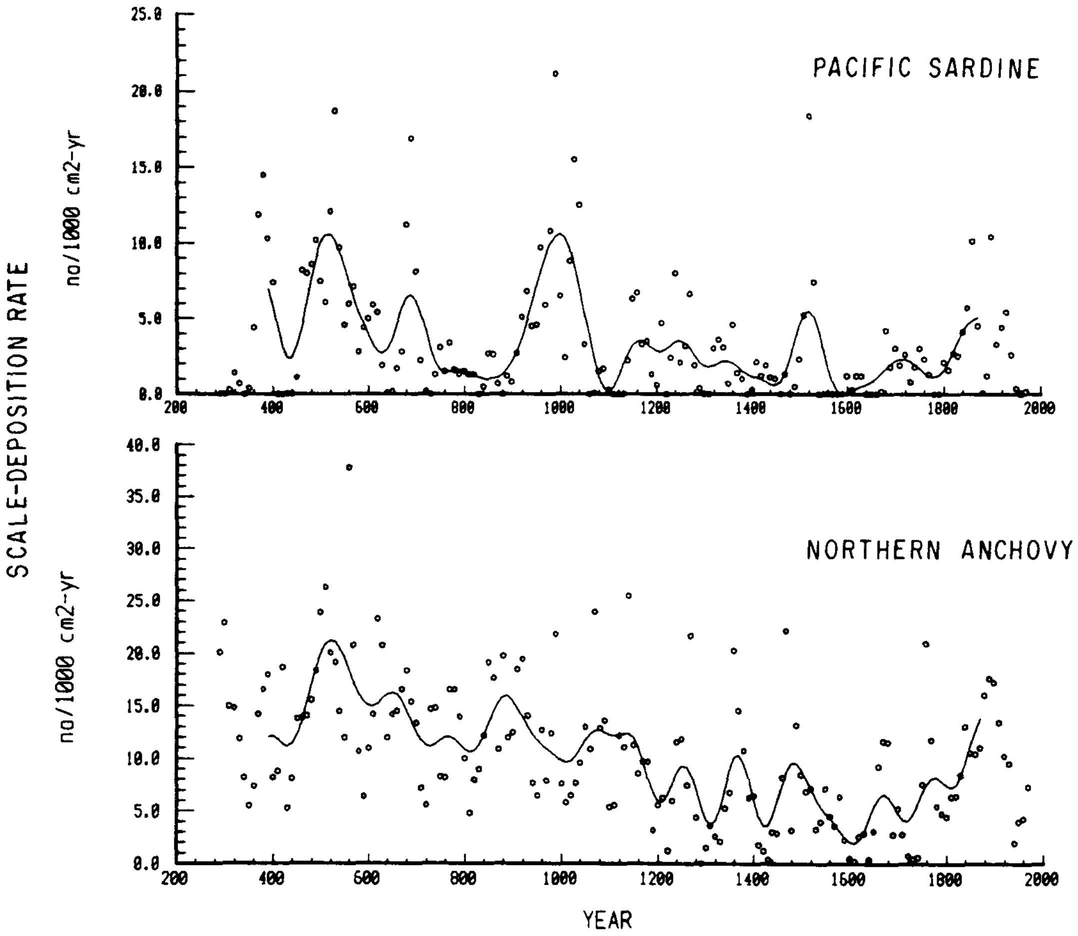

Figure 9. Extraction of the low-frequency variability (*continuous lines*) from the original data points (*circles*) of the Pacific sardine and northern anchovy SDR plots in figure 4. The continuous lines were obtained by low-pass filtering (using a 21-term Spencer filter); this effectively removes all periods longer than approximately 150 years from the original data (see figures 10 and 11).

starting from an initial value of $\leq 1.2 \times 10^6$ MT (≤ 1 SDR unit). Each interval of recovery and collapse is plotted in the upper part of figure 12.

The length of a recovery or decline is measured in decades because this is the smallest unit of time associated with our fish-scale chronology. We include as the initial decade of a recovery, for example, the first decade with a value of ≤ 1 SDR unit succeeding a decade of 0 SDR value; the final decade of the recovery is the first one in which a value of ≥ 5 SDR units occurs. Measured in this way (the temporal resolution is one decade) the recoveries range in length from 20 through 70 years, with an average duration of 36 years. The collapses range from 20 through 50 years, and average 30 years. Only two of the recovery events lasted for over 30 years; the longest of these lasted about 140 years. The upper plot in figure 12 indicates that most recoveries were followed relatively soon by collapses. Figure 12 also allows us to roughly compare the rate of the fishery-impacted decline during the 1940s with the average rate of declines through the past.

The rapid expansions of population size during the nine recoveries in figure 12 suggest that we can characterize an average recovery using the equation for simple exponential growth (neglecting, for now, the effects of density-dependence upon growth). Assuming a nominal prerecovery biomass of 10,000 MT and unrestrained exponential growth for the averaged 36-year period of a recovery, we determine a rate of population increase by substituting the average length of recovery (t = 36 years) and the post-recovery biomass ($N_{35} = 4.2 \times 10^6$ MT) into the equation

$$N_t = N_0 e^{rt}.$$

The rate of population growth for this period is then found to be $r = 0.17$ yr^{-1}, or approximately 17% per year. At t = 15 years after initiation of the recovery,

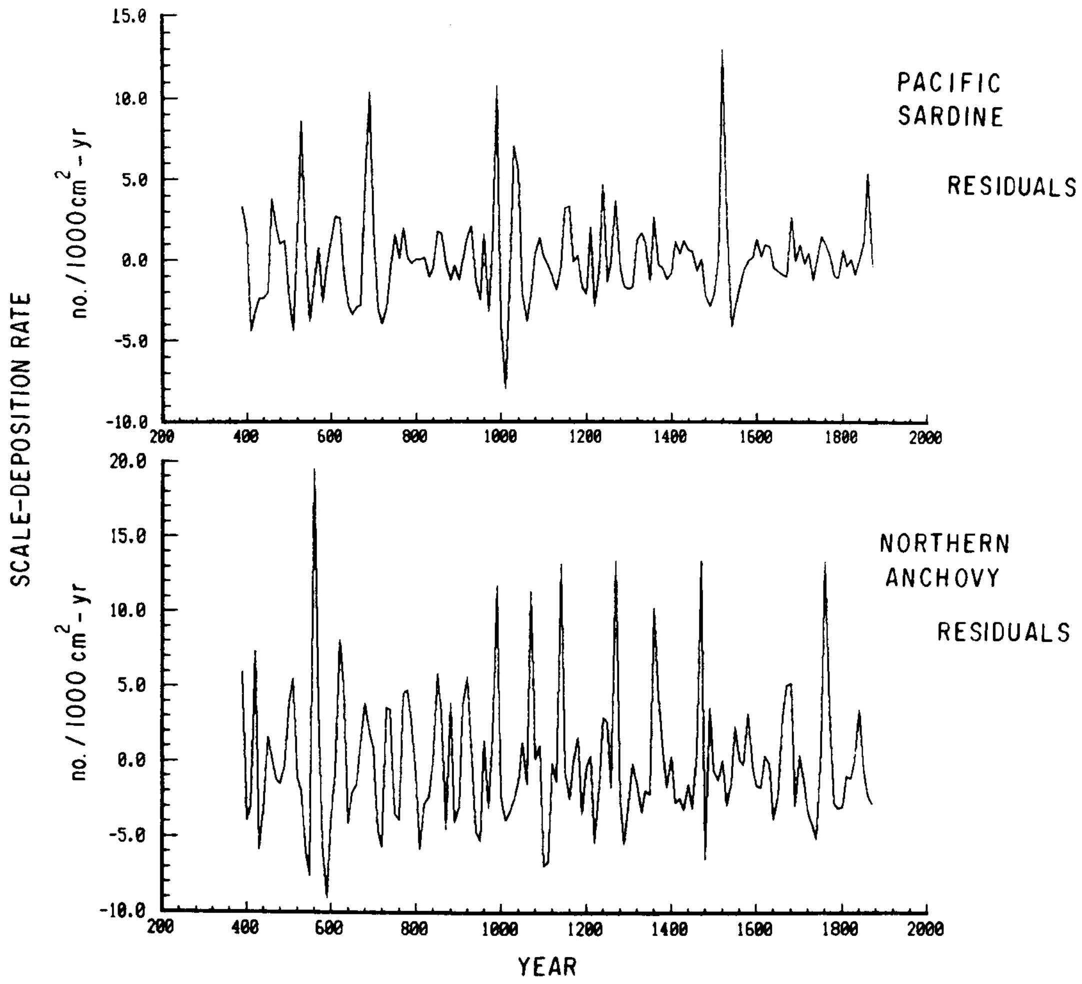

Figure 10. High-frequency components of variability in the Pacific sardine and northern anchovy SDR time series from figure 4. These values are the deviations (residuals) of the original data points from the smoothing function plotted in figure 9. Subtracting the original data from the filtered series leaves the high-frequency residuals containing variance with periods shorter than 150 years (see figure 11).

with this rate of increase, the population biomass would have grown to $N_{15} = 128{,}070$ MT.

We can test whether or not the characteristics of recoveries reconstructed from the scale-deposition rates are reasonable by comparing the above results to estimates for the present recovery of the Pacific sardine. Information presented by Barnes et al. (1992) indicates that the current recovery has been under way since the late 1970s—i.e., for approximately 15 years. The 1990 spawning biomass is estimated between 100,000 and 400,000 MT, and the rate of population increase since the early 1980s at around 30% per year. These figures are somewhat higher than we have obtained using the average-length recovery of 36 years as a guide. But they are very similar to the results we obtain by assuming a shorter recovery time of 25 years, which lies within the range observed for the nine recoveries described in figure 12.

Changing the recovery period to 25 years with the same initial and final biomass levels (10×10^3 and 4.2×10^6 MT) yields a growth rate of 24% per year. The biomass at 1990 ($t = 13$ years), predicted from the exponential growth equation, is then $N_{13} = 231{,}224$ MT. This exercise suggests that the current recovery of the Pacific sardine is occurring somewhat faster than an average, or canonical, recovery, but falls comfortably within the range of values for recoveries that can be derived from the SDR data.

DISCUSSION AND CONCLUSIONS

Although the Pacific sardine and northern anchovy have supported major fisheries off California during the twentieth century, volatility in these stocks has made them notoriously difficult to manage. Their boom-and-bust history has been attributed, in varying degrees, to overintensive fishing,

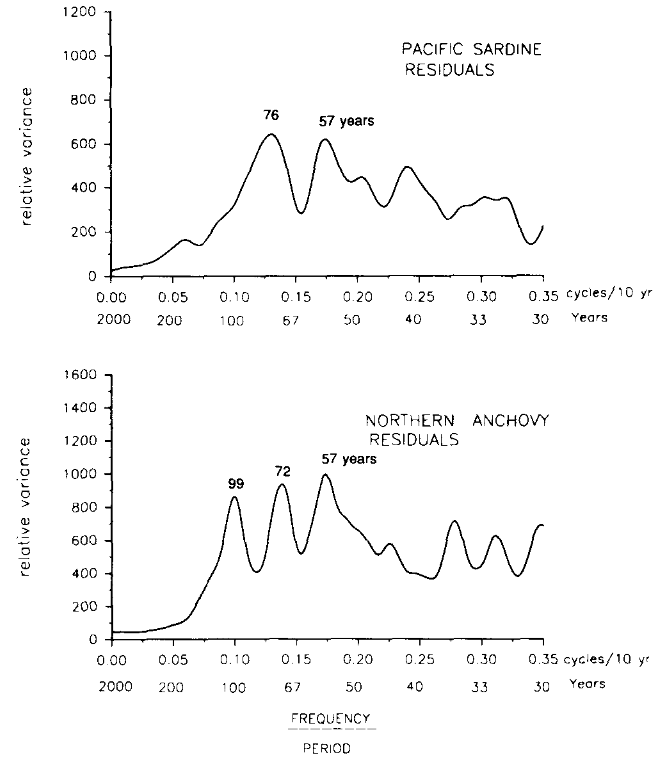

Figure 11. Power spectra of the isolated high-frequency components (residuals) of the Pacific sardine and northern anchovy SDR time series from figure 10. Major spectral peaks are identified with the corresponding time period. Note the abrupt cutoff of variance at periods longer than approximately 150 to 200 years.

biological interaction within and among species, and environmental controls associated with large-scale climatic change. The perspective provided by our improved 1700-year reconstruction of scale-deposition rates in figure 4 should provide critical insights needed to unravel the sources of variability in these fish stocks.

We caution, however, that these data are still based on a relatively small area of depositional surface with respect to the density of scales (particularly those of the sardine) found in the sediment. The area of the two piston cores (214 and 224) constitutes roughly 10% of that of the four box cores (see figure 5) used for the uppermost section (Soutar and Isaacs 1974). Our analysis of the signal-to-noise ratios indicates a need for further sampling of the long time series to capture the complete range of variability of SDR's over the basin. This means recovering the upper 2–3 m of sediment with devices such as box-type Kasten corers, which sample an effective area of 100 cm^2 or greater. This is particularly important to permit replicate sampling of multiple cores to distinguish possible "interaction" between spatial and temporal variability in SDR values over the basin.

In addition to a clean and verifiable signal in the SDR's, chronological accuracy is the other crucial ingredient for reconstructing the series of SDR values in figure 4. Although we believe the chronology

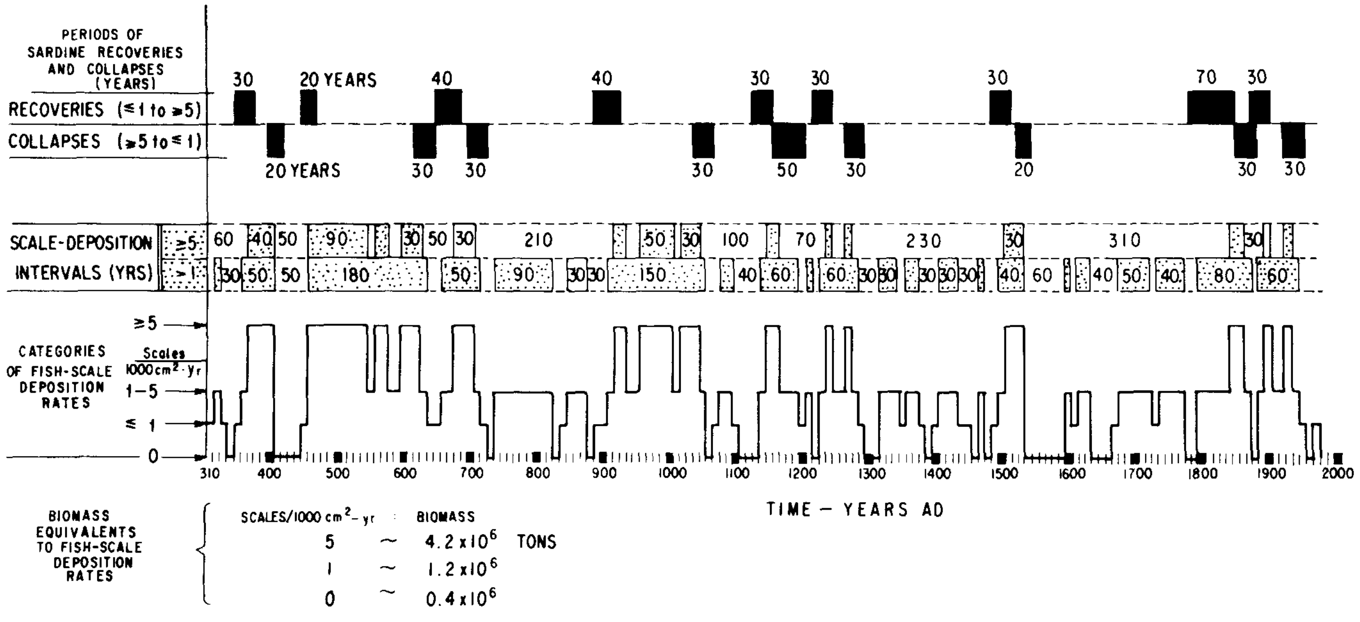

Figure 12. Pacific sardine SDR data from figure 4 plotted according to four selected ranges of values. The continuously varying curve of figure 4 has been transformed into a step function (*lower plot*), which takes on the values of 0 scale deposition; ≤1 scale/10^3 cm^2 yr^{-1}; 1–5 scales/10^3 cm^2 yr^{-1}; or ≥5 scales/10^3 cm^2 yr^{-1}. Biomass levels equivalent to these SDR values are listed at the bottom of the lower plot. The nine periods of recoveries and collapses of the sardine population inferred from the SDR time series are plotted above as darkened blocks corresponding to increases from ≤1 to ≥5 SDR units and declines from ≥5 SDR to ≤1 SDR units.

supporting figure 4 is a substantial improvement from figures 2 and 3, another similar adjustment may still prove necessary. Ultimately the desired accuracy necessary to solidly anchor the varve chronology to calendar time must be sought through independent, detailed radiometric dating. This has not been pursued so far because of the poor precision of available radiometric techniques applied to ocean sediments less than 2000 years old. However, we are now involved in an effort to provide an independent radiocarbon chronology using high-precision AMS techniques on sources of terrestrial carbon in the varved sediments.

The relationship between the SDR data and modern population estimates (figure 6) gives us a means to hindcast the estimates of population biomasses over the past 1700 years (figure 7). The accuracy of this hindcast is, however, limited not only by chronological uncertainty but also by the uncertainty evident in calibration of the SDR values. An important goal of future work will be to upgrade this calibration by appending data from recent decades (during which the population sizes of sardines and anchovies have changed substantially) to the data of figure 6 through further box coring.

Development of the long time series of SDR's in figure 4 has enabled us to begin an exploratory analysis of the decadal-through-centennial time scales of variability in the sardine and anchovy populations. To begin, we have separated the variance of the fish-scale series into its higher-frequency versus lower-frequency components using a period of about 150 years as a convenient natural boundary. In the high-frequency part of the spectra, both anchovies and sardines fluctuate at a period of approximately 60 years. Conversely, a 100-year period is very important in the anchovy data, but is completely missing in the sardine spectrum. At lower frequencies the anchovies appear to fluctuate with a longer period (680 years) than do the sardines (480 years).

We find that the weak positive correlation between the sardine and anchovy series (noted by Soutar and Isaacs [1974] for the period of 1810–1970) is carried by the low-frequency component of the variances (periods of 150 years and longer; cf. figures 9 and 10). This is an important observation, since the weak positive correlation between these two species has been used to question Murphy's (1966) suggestion that replacement of the sardines by anchovies in the California Current implied a competition for food resources (Radovich 1981).

Lasker and MacCall (1983) suggested that the weak correlation signified a parallel response to large-scale environmental change. Their explanation seems quite reasonable for very-long-period change, but perhaps not so much for periods less than 150 years. For example, the lack of any lagged cross-correlation of the high-frequency variability of sardines and anchovies indicates that there is no consistent phase shift associated with the 60-year period exhibited by both species. This appears to be as consistent with a hypothesis for competition or some other biological interaction as with a hypothesis for mediation through environmental change. We are presently using our analysis of the time scales of variability to search for evidence or suggestions of the sources of the variability.

Lumping all the sardine SDR data into four categories of increasing magnitude (figure 12) provides a simplified version of the population's overall variability through time. We perceive a tendency toward two alternating long-lived regimes of SDR's due to the general clustering of the high values (≥5 SDR units; encompassing over 25% of the record) and a persistence of the intermediate values (1–5 SDR units; 41% of the record). These two long-term regimes (200 years and greater) are interrupted by short-term or abrupt dips in the SDR values, which occur over periods of approximately 30–40 years, reflecting the 60–80-year periods shown in figures 8 and 11. The general persistence and abrupt shifts in biomass levels in figure 12 may reflect two alternating states in habitat suitability during the last 2000 years.

Finally, our analysis of the history of scale deposition in the Santa Barbara Basin provides a useful perspective on the current recovery of the Pacific sardine. We find that this recovery is not unlike those of the past in its rate, magnitude, and overall evolution (figure 12). Neither was the sardine collapse that began in the 1940s unlike earlier collapses. This does not necessarily mean, however, that the current cycle of collapse and recovery has no relation to the application/release of fishing pressure, or change in ocean climate, or both. What we infer is (as well as we can determine from the resolution of a 10-year sampling window) that the rates and magnitudes of the recoveries and the collapses can generally be described by relatively few parameters. This suggests that even though the causes, and perhaps the mechanisms, may vary for different recoveries or collapses, the sustained reproductive consequences (success for recoveries and failure for collapses) are similar from one event to another.

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LIFE-STAGE DURATION AND SURVIVAL PARAMETERS AS RELATED TO INTERDECADAL POPULATION VARIABILITY IN PACIFIC SARDINE

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ABSTRACT

Surveys in the Southern California Bight have shown rapid increases in the spawning rate of Pacific sardine over the past decade. We found simple deterministic population models to be useful for examining the rates of change observed in the sardine population. We first describe the "best guess" parameters of an equilibrium sardine population with the Leslie matrix model. From this we determine that small changes in annual mortality rate of the O-group impose high rates of change in the population. We then erect a Lefkovitch matrix model, which uses life stages rather than ages, to emphasize the parameters of the early life stages. From this study, we can specify the range of growth rates and the changes in survival rates for each developmental stage, as well as the adult parameters required to evaluate the observed rates of change.

Changes in egg production rates imply important changes in the sardine population. Therefore, examination of these rates of change can offer insight into the frequency and precision of population assessment and recruitment prediction required for effective management of fisheries on sardines and other stocks.

RESUMEN

Reconocimientos en la Cuenca del Sur de California han revelado que en la década pasada la tasa de desove de la sardina del Pacífico mostró un incremento pronunciado. Encontramos que modelos poblacionales deterministas simples son útiles para investigar las tasas de cambio observadas en poblaciones de sardinas. Describimos primero los parámetros que juzgamos mas atinados de una población de sardina en equilibrio con un modelo de matrices de Leslie; determinamos que pequeños cambios en la tasa de mortalidad anual del grupo de edad cero producen altas tasas de cambio en la población. Continuamos con la elaboración de un modelo de matrices de Lefkovitch, que al considerar fases vitales en vez de edades, hace hincapié en los parámetros de los estadios vitales tempranos. A partir de este estudio, podemos especificar el rango de las tasas de crecimiento, los cambios en las tasas de sobrevivencia para cada fase de desarrollo y los parámetros de los estadios adultos requeridos para evaluar las tasas de cambio observadas.

Cambios en las tasas de producción de huevos llevan consigo cambios importantes en la población de sardinas. Consecuentemente la investigación de tales tasas podría ayudar a discernir la frecuencia y precisión de la evaluación de la población, así como la predicción del reclutamiento, elementos requeridos para un manejo efectivo de las pesquerías de sardinas y otros stocks.

INTRODUCTION

The current recovery of Pacific sardine was predicted by Murphy (1967) based on a deterministic population model, and by Lenarz (1971), who used a stochastic model and incorporated autocorrelation of recruitment success. Records of the Pacific sardine fishery begin in the late 1800s (Schaefer et al. 1951), with small catches being used for bait in the rockfish fishery, and for canning. During World War I the fishery grew continuously at a rate of about 14% per year, doubling every five years. Brief deviations from the growth of the fishery were largely attributed to economic factors (Schaefer et al. 1951). The catch was chiefly landed in California, but fisheries extended northward to British Columbia.

The growth rate of the fishery slowed after the mid 1930s, and a succession of collapses began in 1945–47. California landings fell below the 1916 values in the 1961–62 season (Ahlstrom and Radovich 1970), where they have remained through 1991. California legislation in 1967 and 1973 prohibited the landing of sardines for any purpose and prevented the sale of incidental catches. The 1973 legislation stipulated that a 1,000-ton fishery could start as soon as the spawning biomass exceeded 20,000 tons; thus a small fishery began in 1986 and continues to grow (Wolf et al. 1987).

There has been relatively little directed research on the Pacific sardine population off California since the decline of the 1960s; most of the research was reviewed by Ahlstrom and Radovich (1970). Smith (1972) updated and revised Ahlstrom's (1966) egg and larval time series. MacCall (1979) updated and revised Murphy's (1966) population data. Soutar and Isaacs (1974) augmented the record of sardine and other fish scales in the anaerobic varved sediments off California and added a record from Baja California (Soutar 1967; Soutar and Isaacs 1969). Lasker (1970) estimated the use of zooplankton energy by the historical sardine population.

The recovery of the sardine population was first detected in 1979, through surveys by the Ichthyoplankton Coastal and Harbor Studies in waters shallower than 40 meters off Santa Monica Bay, Palos Verdes, and Seal Beach in southern California. These bimonthly field studies were sponsored by the Southern California Edison Co. and NOAA Sea Grant and were staffed by the Los Angeles County Museum and the Institute for Marine and Coastal Studies of the University of Southern California (Brewer et al. 1980; Brewer and Smith 1982; Lavenberg et al. 1987). Wolf and Smith (1985, 1986) estimated the spawning biomass from the spawning area in 1985.

Sardine and anchovy fisheries constitute a relatively large fraction of the fluctuations in global catch (Murphy 1977; Smith 1985; Lluch et al. 1989). Although variations in recruitment are large for sardine and anchovy stocks, the major changes appear to be long term. Thus the "overfishing problem" is complicated by the "recruitment problem" and the "regime problem."

In the near future we plan to issue a series of matrix models for schooling coastal pelagic fishes. This paper concerns the relationship between population parameters and observed rates of change in the sardine population. We also plan to produce papers on the sensitivity of sardine and anchovy population size to changes in parameters based on Smith (1985) and Smith, Lo, and Butler (1991). In addition, we plan to compare the errors of estimation of the abundance of life stages with interannual changes in population size.

In this paper we use the recent remarkable increases in Pacific sardine egg abundance off southern California to pose questions about the causes of the increase. Is the current increase due to migration of sardine stocks from other habitats to the southern California area? How does the increase of spawning off southern California compare to the increase off Japan? Is the increase due merely to the fishing moratorium? Has the increase resulted from the decline in natural predators? Have other population parameters changed? Can normal fluctuations in recruitment rates be detected in time to improve fisheries management? Can critical changes in the recruitment rate be predicted from observations of the physical and biological environment of the sardine?

It is the purpose of this paper to explore some characteristics of Pacific sardine with respect to the observed changes in population size. We have prepared similar estimates for the northern anchovy (Smith 1985; Smith et al. 1991). First we postulate values for stage survival, growth, and reproduction parameters. We then determine which features of the population are most likely to control the sardine's reproductive success. Lastly, we describe the related features of the biological and physical environment. Although there are serious reservations surrounding the use of the simple Leslie (1945) and Lefkovitch (1965) matrix models for projecting population (Caswell 1989; Seber 1973), tractable methods have been developed for evaluating and extending these models (DeRoos et al. 1992). For this stage of our research, we chose the simplicity and flexibility of the Leslie (Vaughn and Saila 1976) and Lefkovitch (Crouse et al. 1987) matrix models.

METHODS

Abundance estimates for sardine eggs arise from quantitative techniques that were established in 1938 (Sette and Ahlstrom 1948) and that have not changed with respect to sardine eggs since then. Sardine population parameters have been selected from Butler (1987). Where values are missing for sardine, we used analogous parameters for the same stage of anchovy (Smith 1985; Lo 1986; Lo et al. 1989; Smith et al. 1991).

The egg time series, from representative surveys selected from 1957 to 1991, is shown in table 1, which lists the number of sardine eggs of all ages per 10 square meters of sea surface between CalCOFI line 76 (at times called 77 or 76.7) and line 94 (usually called 93 or 93.3). Data from all tows taken from January to June at CalCOFI stations 26 to 70 were used. Surveys were conducted from two to five times in the six-month period. The maximum number of stations was 293 in 1975; the minimum number was 77 in 1990 and 1991. The data reported in table 1 represent two series of egg abundances on the decadal scale with relatively even rates of decline (1957–69) or increase (1975–91).

Scale-deposition rates from the fossil record in the Santa Barbara Basin (Soutar and Isaacs 1974; Smith 1978; Smith and Moser 1988) are shown in table 2. A Velleman nonparametric, robust, resistant smoother (Velleman 1980; Velleman and Hoagland 1981; Min-

TABLE 1
Time Series of Sardine Eggs off Southern California

Year	Eggs per 10 m^2 sea surface
1957	22.65
1958	69.02
1959	143.85
1960	95.36
1961	12.85
1962	1.35
1963	11.29
1964	0.61
1965	3.66
1966	1.54
1969	0.27
1972	0
1975	2.43
1978	0.38
1981	0.87
1984	3.47
1985	9.27
1986	3.25
1987	16.14
1988	34.20
1989	53.34
1990	67.29
1991	137.11

TABLE 2
Smoothed Time Series of the Soutar-Isaacs[a] Sardine-Scale Series from the Santa Barbara Basin

Central year	Scale deposition	Smoothed[b] rates	Series
1812	2.44	2.44	R1
1817	2.58	2.58	R1
1822	3.72	2.87	R1
1827	1.29	3.18	R1
1832	5.15	3.42	R1
1837	3.11	3.81	R1
1842	3.74	4.51	R1
1847	7.72	5.64	R1
1852	5.11	6.70	R1
1857	15.19	7.07	R1
1862	8.47	5.96	F1
1867	0.62	3.10	F1
1872	0.25	0.71	F1
1877	0.00	0.08	F1
1882	1.00	0.98	R2
1887	1.49	3.30	R2
1892	8.72	5.24	R2
1897	12.08	5.71	R2
1902	4.61	5.50	F2
1907	1.99	5.18	F2
1912	2.99	4.93	F2
1917	5.85	4.72	F2
1922	6.85	4.61	F2
1927	3.99	4.27	F2
1932	1.99	3.22	F3
1937	3.11	1.88	F3
1942	0.50	0.84	F3
1947	0.37	0.29	F3
1952	0.00	0.08	F3
1957	0.00	0.02	F4
1962	0.32	0.00	F4
1967	0.00	0.00	F4

[a] Soutar and Isaacs 1974
[b] Velleman (1980) nonparametric resistant smoother

itab 1989) was used to define secular (long-term) trends and changes in trend. This smoother replaces each value by the median of the values immediately before and after it. Medians of 2, 3, 4, and 5 consecutive values were used in this smoother. Following each median smoother, a weighted running average of each value and the values immediately preceding and following is assembled, with the point value being given twice the weight of the adjacent values. Special methods are used to smooth the ends of the data sequence.

Secular change rates for all time periods were estimated by Marquardt algorithm nonlinear least squares fitted to an exponential function (Saila et al. 1988). We used the same procedure to extract secular rates of change from graphics published by Murphy (1967) and Lenarz (1971). The absence of the actual values in the latter cases should not be an impediment, since the data were based on theory and simulation in both cases.

We used a Leslie matrix of 13 year classes (Leslie 1945; Vaughn and Saila 1976) to estimate the survival rate during the first year of sardine life from the age-fecundity relation (table 3) and the adult survival rates from Butler (1987: table 2). We set the adult annual survival rate at a constant 0.67 (instantaneous mortality rate of 0.4 yr^{-1}) (table 4).

The Lefkovitch matrix also included 13 life stages (Crouse et al. 1987; Smith et al. 1991). Rather than using individual year classes as in the Leslie matrix, we assembled the adult year classes into only 3 stages: early adult, adult, and late adult. The fecundity of the adult stages is derived from the biomass-weighted fecundity of the year classes encompassed by the stages. Daily instantaneous mortality rates and durations (days) of stages are given in table 5. Each rate shown is varied individually while the other rates are held constant. We divided the early

TABLE 3
Sardine Fecundity Schedule

Age	Weight(g)	Eggs/g/batch	Batches/yr[a]	Eggs/female/year
1	52.7	0	0	0
2	93	257	4	95604
3	123	257	8	252888
4	152	257	12	468768
5	170	257	15	655350
6	183	257	17	799527
7	193	257	19	942419
8	202	257	20	1038280
9	205	257	20	1053700
10	205	257	21	1106385
11	205	257	21	1106385
12	205	257	22	1159070
13	205	257	23	1211755

[a] Butler 1987 (postulated by analogy to anchovy) and Smith et al. 1991.

TABLE 4
Projection Matrices of Leslie (1945) and Lefkovitch (1965)

Leslie Age-Based Matrix

$$\begin{matrix} f_0 & f_1 & f_2 & f_3 & \bullet & \bullet & \bullet & f_n \\ p_0 & 0 & 0 & 0 & \bullet & \bullet & \bullet & 0 \\ 0 & p_1 & 0 & 0 & \bullet & \bullet & \bullet & 0 \\ 0 & 0 & p_2 & 0 & \bullet & \bullet & \bullet & 0 \\ 0 & 0 & 0 & p_3 & \bullet & \bullet & \bullet & 0 \\ \bullet & \bullet & \bullet & \bullet & \bullet & \bullet & \bullet & 0 \\ \bullet & \bullet & \bullet & \bullet & \bullet & \bullet & \bullet & 0 \\ \bullet & \bullet & \bullet & \bullet & \bullet & \bullet & \bullet & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & p_{n-1} & 0 \end{matrix}$$

Lefkovitch Size- or Stage-Based Matrix

$$\begin{matrix} p_0 & f_1 & f_2 & f_3 & \bullet & \bullet & \bullet & f_n \\ g_0 & p_1 & 0 & 0 & \bullet & \bullet & \bullet & 0 \\ 0 & g_1 & p_2 & 0 & \bullet & \bullet & \bullet & 0 \\ 0 & 0 & g_2 & p_3 & \bullet & \bullet & \bullet & 0 \\ 0 & 0 & 0 & g_3 & \bullet & \bullet & \bullet & 0 \\ \bullet & \bullet & \bullet & \bullet & \bullet & \bullet & \bullet & 0 \\ \bullet & \bullet & \bullet & \bullet & \bullet & \bullet & \bullet & 0 \\ \bullet & \bullet & \bullet & \bullet & \bullet & \bullet & p_{n-1} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & g_{n-1} & p_n \end{matrix}$$

f is the fecundity per fish per unit of time by age for Leslie matrix and for stage in the Lefkovitch matrix.
p is the probability of survival to the next age for Leslie matrix, and the probability of survival in the stage for the Lefkovitch matrix.
g is the probability of survival and growth into the next stage.

TABLE 5
Postulated Parameters of the Sardine Life Cycle

Stage name	Duration (days)	Instantaneous mortality rate (daily)	Eggs per fish per day
Egg	3	0.3	0
Yolk-sac larva	4	0.3	0
Early larva	11	0.14	0
Late larva	42	0.0556	0
Early juvenile	25	0.0365	0
Juvenile I	100	0.0239	0
Juvenile II	142	0.0140	0
Juvenile III	170	0.0025	0
Juvenile IV	170	0.0021	0
Pre-recruit	175	0.0021	0
Early adult	381	0.00178	169.72
Adult	663	0.00178	462.31
Late adult	2773	0.00178	1258.91

life history of the sardine into the following stages: egg, yolk-sac larva, first-feeding larva, late larva, early juvenile, juvenile I, juvenile II, juvenile III, juvenile IV, and pre-recruit. After we established best estimates for the parameters, we changed the least-known estimates—juvenile I and II—by trial and error to achieve a neutral population growth rate ($\lambda = 1$).

Considering the range of rates of secular change in table 6, we established alternative population growth rates of $\lambda = 0.7$ and $\lambda = 1.3$. We then changed each population parameter, such as individual growth rate or mortality rate, until the population growth rate matched the $\lambda = 0.7$ or $\lambda = 1.3$ value or until the parameter went to zero or an unreasonable value. We manipulated the early life stages, keeping the natural mortality constant at 0.4 yr^{-1} and the fishing mortality at 0.25 yr^{-1}. In this form we would not expect great differences in re-

TABLE 6
Examples of Secular Changes in Sardine Population Size

Category	Time span (years)	r^a	λ^b	References
Theoretical				
Murphy	0–24	0.184	1.202	Murphy 1967
Lenarz	0–16	0.168	1.183	Lenarz 1971
Santa Barbara Basin scales				
Table 2 R1	1810–1860	0.027	1.028	
Table 2 F1	1860–1880	−0.103	0.902	
Table 2 R2	1880–1900	0.088	1.092	
Table 2 F2	1900–1930	−0.009	0.991	
Table 2 F3	1930–1955	−0.099	0.906	
Table 2 F4	1955–1970	−0.335	0.715	
Southern California				
Eggs	1975–1991	0.523	1.687	This paper
Eggs	1957–1969	−0.193	0.824	This paper
Recruits	1932–1964	−0.071	0.931	Murphy 1966 & MacCall 1979
Spawners	1932–1965	−0.108	0.898	Murphy 1966 & MacCall 1979
Benguela Current				
Spawners	1966–1982	−0.245	0.783	Crawford et al. 1983
Humboldt Current				
Spawners	1974–1981	0.126	1.134	Serra 1983
Kuroshio				
Eggs	1970–1978	0.488	1.514	Watanabe 1983

[a] r = annual intrinsic exponential rate of population change.
[b] λ = annual rate of sardine population growth (e^r).

sults from the Lefkovitch stage-and-size-specific matrix and the Leslie age-specific matrix.

RESULTS

The extreme rates of change indicated by all methods of estimating biomass, scale-deposition rates, standing crop of eggs, and virtual population incorporate not only the real rates of change of the population but also errors in the estimation of population levels and changes in age composition. Since many forms of error are multiplicative, the asymmetry in table 6 — i.e., high rates of increase exceed rates of decrease — could either be a characteristic of sardines and anchovies or merely an expression of the errors of estimation. Although we report the maximum and minimum rates of increase as results, we have narrowed the range of subsequent tests of population parameters to explore only the range $\lambda = 0.7$ to $\lambda = 1.3$. The lower λ is somewhat more interesting for fishery management.

The fastest rate of secular increase occurred in the standing crop of eggs. By 1991 there was an average standing crop of 137 sardine eggs per ten square meters. In 1975 the mean concentration of eggs in the same area was fewer than 3 per ten square meters. The average growth rate since 1975 is an instantaneous rate of 0.523 yr^{-1} (SE 0.038). The equivalent λ is 1.687. Even with errors in estimation of values and estimation of slope we would expect this result to be above a λ of 1.3, meaning that the spawning rate was expanding at more than 30% per year. The effects of changed reproductive parameters on estimated biomass are explored below.

The fastest rates of secular decline examined for this paper were in the scale-deposition rate from 1955 to 1970 (table 6), in Namibian sardine (*Sardinops ocellata*) spawners (Crawford et al. 1983), and in Pacific sardine spawners from 1932 to 1964 and recruits in 1965 off southern California (Murphy 1966; MacCall 1979). The California declines approached 20% to 30% per year, and were accompanied by many adults and some juveniles being taken by an active fishery.

Leslie Matrix

The fastest rates of increase cannot be obtained in theory from changing from a fishing instantaneous mortality of 0.25 yr^{-1} to a moratorium (0 yr^{-1}). The fastest population increase expected from a moratorium on fishing is about 20% per year (table 7A). The highest secular rate of increase from the prefishery scale-deposition rates was about 10% per year from 1880 to 1900 (table 6).

TABLE 7

Sardine Life-History Parameters Representing No Population Change, 30% Annual Decline, and 30% Annual Growth

	$\lambda = 1$	$\lambda = 0.7$	$\lambda = 1.3$
A. Leslie matrix (13)			
Fishing mortality	0.25	0.72	<0.0[a]
O-group survival S(1, 0)	6.51E-06	9.90E-07	1.84E-05
O-group mortality Z(yr^{-1})	11.94	13.83	10.91
O-group mortality Z(d^{-1})	0.033	0.038	0.030
Fecundity (batches yr^{-1})	23	3.50	65
Batch fecundity (eggs gm^{-1})	257	39	725
B. Lefkovitch matrix (13)			
Egg (spawn to hatch)			
IMR (d^{-1})	0.3	0.887	0.0003
Duration (d)	3	8.875	0.01
Yolk-sac larva (hatch–4 mm)			
IMR (d^{-1})	0.3	0.7401	0.0752
Duration (d)	4	9.875	1.0089
Early larva (4–10 mm)			
IMR (d^{-1})	0.14	0.2999	0.0582
Duration (d)	11	23.59	4.593
Late larva (10–35 mm)			
IMR (d^{-1})	0.0556	0.0974	0.0341
Duration (d)	42	73.7	25.87
Early juvenile (35–60 mm)			
IMR (d^{-1})	0.0365	0.10665	0.00032
Duration (d)	25	73.52	0.69
Juvenile I (60–85 mm)			
IMR (d^{-1})	0.0239	0.04137	0.014815
Duration (d)	100	173.85	62.56
Juvenile II (85–110 mm)			
IMR (d^{-1})	.0140	0.02623	.00755
Duration (d)	142	268.4	78.51
Juvenile III (110–135 mm)			
IMR (d^{-1})	.002495	.012427	—[b]
Duration (d)	170	996	—
Juvenile IV (135–160 mm)			
IMR (d^{-1})	.0021	0.01201	—
Duration (d)	170	1203	—
Pre-recruit (160–185 mm)			
IMR (d^{-1})	.0021	0.011715	—
Duration (d)	175	1206.5	—
Early adult (185–210 mm)			
IMR (d^{-1})	.0018	0.0064	<0[c]
Duration (d)	381	>3653	<1
Fecundity (d^{-1})	169.6882	—	1108.9
Adult			
IMR (d^{-1})	.0018	0.0066	<0[d]
Duration (d)	663	>3653	<1
Fecundity (d^{-1})	462.2455	—	2145.7
Late adult			
IMR (d^{-1})	.0018	>0.0274	<0[e]
Duration (d)	2773	>3653	<1
Fecundity (d^{-1})	1238.6	—	6595.5

[a] When fishing mortality is 0 (moratorium) $\lambda = 1.214$.
[b] When no value is mathematically possible the symbol — is used.
[c] When fishing mortality is 0, $\lambda = 1.0625$.
[d] When fishing mortality is 0, $\lambda = 1.0725$.
[e] When fishing mortality is 0, $\lambda = 1.0513$.

Variation in O-group mortality rate can effect either a 30% increase or decrease in λ. A decline of this magnitude would result from the first-year survivorship of 9.90×10^{-7} from each egg spawned, or 1 survivor for each 2.8 million eggs spawned. In the absence of fishing, a 30% increase would be expected from a survivorship of 1.84 × 10^{-5}, or 1 survivor per 53,000 eggs. Population stability is achieved with a survivorship of 6.51 × 10^{-6} to the age of one year, or 1 survivor per 307,000 eggs. The instantaneous mortality rate for increase, stability, decrease is 10.91, 11.94, or 13.83 on an annual basis, or 0.030, 0.033, or 0.038 on a daily basis.

Neither of the fecundity rates in table 7 could, with values now perceived as reasonable, cause the rates of increase and decline tested. Of the two fecundity rates, batches of egg spawned per year has somewhat more impact than number of eggs per batch. To achieve the declines observed, the eggs per gram of female would have to drop to 39 from 257 or increase to 725 as a secular change. Fecundities approximating this range have been observed for single females. The number of egg batches per year would have to decline to 3.5 or increase to 65 to cause these extreme changes in sardine population growth rate. There might be only 3.5 spawnings per year if the fishery had removed all of the older spawners, but we are refraining from examining multiple effects in the Leslie model until the parameters are given stochastic ranges and the matrix becomes probabilistic rather than deterministic.

Lefkovitch Matrix

The instantaneous mortality rates, which yield a 30% decline (table 7B), look reasonable for the egg, yolk-sac, and early larva stages. The static rate is a daily exponential instantaneous rate −0.3, −0.3, and −0.14 for the first three stages, and the 30% decline equivalents are −0.887 for eggs, −0.7401 for yolk-sac larvae, and −0.2999 for early larvae. Rate changes of this magnitude for individual stages are probably measurable at sea with existing techniques. Field estimates of instantaneous mortality rates for late larvae through pre-recruits would require equipment that has not yet been designed, and sampling intensity far greater than that now accomplished. With current approaches, the changes in mortality rate in table 7 would probably be undetectable. Similarly, if smaller-parameter changes were distributed among stages, rather than isolated by stage as they are in this simulation, the changes might not be detectable from current field sampling practices.

An effective change in duration of the earlier stages would require protracted periods of extremely warm or cold water to explain secular changes in population growth rates. Temperature's effect on age or size of sardines at first maturity (by analogy to anchovy; Methot 1989) could be an important influence on population growth rate. Decreasing population caused by slow growth of late larvae, juveniles, and pre-recruits would be easily detectable by otolith daily growth analysis. Secular increases caused by rapid growth would require sustained growth rates of .5 mm per day or more in the late larvae and 1 mm per day or more in juveniles and pre-recruits to be effective (tables 5 and 7B). The more subtle the effect to be measured, the more expense would be incurred; thus sampling costs and required precision would have to be examined from an economic standpoint. Lenarz (1971) showed that recruitment predictions (and assessments) would not have to be very precise to improve the quality of management for sustained economic yield.

DISCUSSION

The primary finding of this study is that a year-class (Leslie 1945) parameterization of critical population growth rates is not likely to reveal important changes in reproductive success of sardines. Although a stage-based (Lefkovitch 1965) approach requires much ancillary information, some of the earlier stages could provide useful limits on projections of recruitment as well as the usual stock assessment. Another finding is that the rate of increase in the standing crop of eggs cannot be explained by the fishing moratorium alone. We do not have enough information to decide which other factors may have contributed to the current regional increase of sardine eggs; the sustained increase for nearly two decades is as high as any sustained increase measured for sardine stocks, and higher than most.

Is the current increase due to migration of sardine stocks from other habitats to the southern California area?

With present data, we cannot rule out migration of other elements of the sardine species into this area. If the present stock is from a diminished "northern" stock, it probably arose from the remnants ("founders") of a breeding population of less than 2,000 tons. If the present stock arises from a similarly small group migrating into the area, that population too would arise from "founders," and the distinction may be detected genetically. If there is a constant interchange with other populations, the growth in spawning rates may merely represent added migration rates from a larger stock.

How does the increase of spawning off southern California compare to the increase off Japan?

The rate of increase of eggs per unit area is remarkably close to that off the Pacific coast of Japan; any difference could well be negligible.

Is the increase due merely to the fishing moratorium?

The rate of increase in egg abundance, if due entirely to adult biomass and not to increased spawning rates, is too rapid to be explained by the moratorium alone.

Has the increase been caused by a decline in natural predators?

The rate of increase of the sardine population may have been augmented by the decline of anchovy and mackerel in the same area. These species can prey on early stages of sardines. Bird and mammal biomass, and presumably the consumption of juveniles and adults, have increased, however.

Have other population parameters changed?

Warming would tend to decrease mortality of eggs and yolk-sac larvae, in the absence of other effects, by shortening the most vulnerable stages. Warming may accelerate sardine maturation, as it is thought to do for anchovy (Methot 1989). Not enough is known to speculate about how the other stages might be affected by the interactions among temperature-specific growth rate, the lower plankton volumes associated with warm water, and the introduction of exotic tropical predators associated with warming.

Can normal fluctuations in recruitment rates be detected in time to improve fisheries management?

From examining the life table of sardine, one would expect that the possibility of extremely large recruitment successes could be detected in advance, but not assured, by high egg production and high survival of eggs, yolk-sac larvae, and early larvae. The same has been found likely for anchovy (Smith 1985) and hake (Hollowed, this volume). For sardine, this information would be available nearly two years before recruitment to the fishery. Thus it is more likely to be useful than similar information for anchovy, which recruits at an earlier age. The advance warning would be somewhat longer for hake.

The late larvae and juvenile stages of anchovy, sardine, and hake are not well enough known to yield useful information on abundance, and quantitative sampling of these stages is not now practical. Information on growth rates would be very useful for all stages, since there is an interaction between size and mortality. If *growth and survival* rates were known for sardine eggs and larvae, and *only growth* rates were known for late larvae or early juveniles, then recruitment could probably be categorized as "near," "below," or "above" replacement, from existing sea-survey techniques.

Another feature of sardine recruitment is that on the scale of a few years and a few decades, the recruitment in a given year or decade is likely to be similar in sign to the immediately preceding year or decade (Murphy 1966; Lenarz 1971; Smith and Moser 1988); this should yield particularly useful information for stock management following documented recruitment failures even at higher stock sizes.

Can critical changes in the recruitment rate be predicted from observations of the sardine's physical and biological environment?

It does not seem likely that the necessary lists of age structure, fecundity rates, mortality rates, and growth rates at all seasons of the year will be known to sufficient accuracy (Lo 1986). Also, the biological and physical influences of environment have not been sufficiently well related to these population rates to be predicted by simple environmental indices: this is why environmental indices fail to meet the test of time (Lasker and MacCall 1983). For example, offshore transport of sardine larvae at the height of upwelling might be counteracted to some degree by increased food supply for the juveniles. We do not know which areas of the ocean are occupied by juvenile sardines (and juveniles of most of other species); therefore the physical and biological characterization of their immediate environment is not currently possible. Existing knowledge does not warrant consideration of single factors in the life table, let alone interaction among these factors. Current knowledge on the status of other pelagic fish stocks could help interpret the recruitment success of a sardine population (Butler 1991).

CONCLUSION

It should not be inferred from our emphasis on decadal-scale change that we believe that shorter-scale changes in recruitment are unimportant: it may well be that for fisheries management the interannual scale of recruitment is more important than the longer scale. Unfortunately, matrix methods and even life tables are less appropriate at the shorter time scales.

In general, we have found that the rapid apparent growth rate of the stocks of Pacific sardine off southern California is not likely to have resulted from the fishery moratorium alone: other parameters of survival and reproduction are probably acting in concert with the lowered fishing mortality rate if the population conforms to the models used in this study. It is possible that information on egg production and survival in the earliest life stages, together with growth rates of the later life stages before recruitment could contribute to better fishery management.

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THE RECOVERY OF THE CALIFORNIA SARDINE AS RELATED TO GLOBAL CHANGE

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ABSTRACT

California sardine abundance has fluctuated significantly in the past, and the population has remained at either low or high levels for sustained periods longer than a decade. Abundance now appears to be increasing from the low values in the mid 1970s. In a previous paper, evidence that small pelagic fishes from the main fisheries of the world vary synchronously with each other and also with global climatic variations was presented and named the "regime problem." This paper extends that analysis by looking for coherence between interdecadal variations in temperature both at local and global scales, and at variations in California sardine abundance. Possible relationships between this approach and previously presented ones are discussed, including the "recruitment problem" and the "fishery problem." Possible implied mechanisms are also briefly discussed.

RESUMEN

La abundancia de la sardina California ha variado considerablemente en el pasado; la abundancia ha permanecido bajas o altas por periodos sostenidos mayores de una década. En la actualidad, hay indicios de que la abundancia se ha incrementado respecto de los valores bajos de mediados de los 70. En un trabajo previo, se presentó evidencia de que tanto las fluctuaciones climáticas globales como las variaciones de la abundancia de pelágicos menores de las principales pesquerías del mundo occurren simultaneamente, lo que se denominó el "problema del régimen." El presente trabajo extiende el análisis mencionado buscando coherencia, tanto entre las variaciones interdecadales de temperatura a nivel local y global, como en las fluctuaciones de la abundancia de la sardina California. Se discute éste enfoque y sus posibles relaciones con otros que se han presentado, entre los que se incluyen el "problema del reclutamiento" y el "problema de la pesquería." Los posibles mecanismos involucrados también son discutidos brevemente.

INTRODUCTION

In spite of the difficulties of precisely determining the population size, it seems evident that the sardine population off northern Baja California and California has fluctuated widely, with changes of orders of magnitude. Population abundance changed from supporting the most voluminous fishery in North America (reaching some 800,000 MT during its production peak) to a total biomass estimate of less than 5,000 MT (Wolf 1992).

Changes in abundance have occurred over relatively short periods, but the population has remained at either a high or low mode for sustained periods. Recently, the population has been increasing from the low levels of the mid 1970s. The spawning biomass in 1990 may have been as high as 62,000 to 214,000 MT (Barnes et al. 1992). This recovery may be explored through different approaches.

Historically, the first proposed mechanism affecting the abundance of sardine populations was overexploitation of the stocks, or the "fishery problem." The idea is that heavy fishing exerts major predation pressure on the population; this is particularly important if nonspawning fish are affected. This intense pressure has been assumed to severely affect the reproductive capabilities of the species.

It is generally accepted that an intense fishery can at least potentiate the collapse of a population, and perhaps delay its recovery if the population has been severely depleted. When fishery pressure is eliminated, the population is expected to increase, particularly after periods of heavy exploitation. The California sardine remained at low abundance levels from the early 1950s to the late 1970s, but subsequently increased; thus there seems to be a relationship between the recovery and the fishing moratorium imposed since 1967.

However, questions regarding the fishery problem remain. Previous papers presented evidence that the magnitude of the changes in abundance of sardine populations is beyond the mere effect of the fishery (Clark and Marr 1955; Radovich 1982). Moreover, it is well known from scales deposited in marine sediments (Soutar and Isaacs 1969) that the high-low abundance patterns may exist even in the absence of a fishery.

A second approach, the "recruitment problem," stems from the early work of Hjort (1914), and has been postulated by a number of authors. It is based on the assumption that the differential survival of the egg-to-larvae stage determines the amount of recruitment, and thus sardine abundance in following years. Most papers dealing with the subject were reviewed and discussed by Lasker and MacCall (1983), who concluded that despite the specific mechanism proposed by each author, it is the availability of food that determines larval survival.

In a previous paper, Lluch-Belda et al. (1989) presented evidence concerning abundance changes in the main fisheries areas of the world. The data indicate that around Japan and off the west coasts of North and South America the sardine populations are fluctuating in phase, and that the sardine population in a fourth area off South Africa fluctuates out of phase with the Pacific populations. All these fluctuations are also in phase with some large-scale environmental variations. This hypothesis of coherence between sardine abundance and environmental variables has been named the "regime problem" (Alec MacCall, pers. comm.).

The present paper extends the analysis by Lluch-Belda et al. (1989) by relating the temperature regime changes on global and regional scales to the fluctuations of the sardine population off the west coast of North America. Proposed mechanisms relating temperature regimes and California sardine abundance are discussed, as well as possible connections between the regime problem, and the other two approaches — the fishery problem and the recruitment problem.

DATA AND METHODOLOGY

Local California sea-surface temperature (SST) and surface-air temperature (SAT) series from San Francisco (the northernmost recorded area of spawning; Radovich 1982) and San Diego (in the Southern California Bight, the main spawning area) were used. A number of other SST and SAT series from locations covering most of the coast (figure 1; also see figures 2 and 3) were also used to analyze the spatial and temporal coherence. Only the longest and most complete data series were used. All series are from Cayan et al. 1991, and were standardized by expressing the data as anomalies of the monthly averages.

To eliminate secular trends, series were detrended by expressing the data as departures from the least squares fitted line. Data were also smoothed to eliminate high-frequency variability by using the cubic spline procedure in a commercial statistical software package (Graphtool). We consistently used the same smoothing degree (0.5) in all cases. We calculated combined series by averaging the detrended and smoothed local SST (thus obtaining a combined SST series) as well as the SAT (obtaining a combined SAT series).

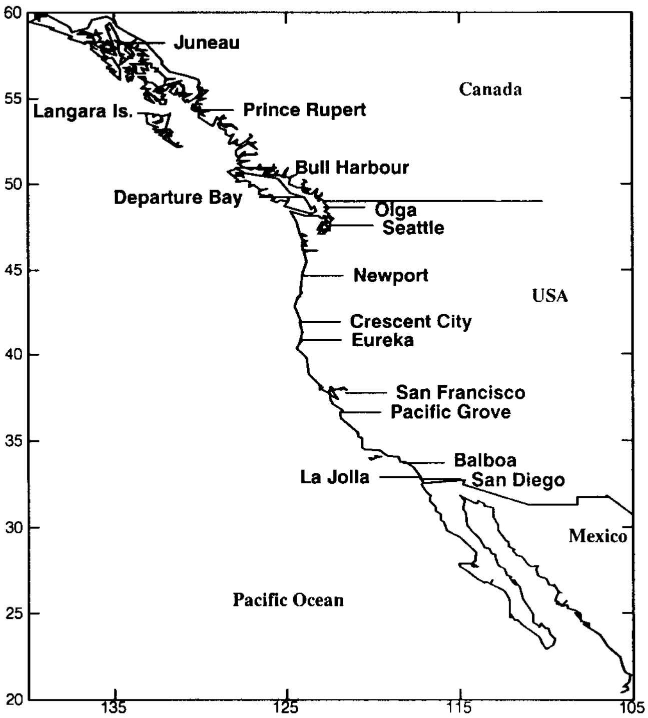

Figure 1. Coastal stations for SST and SAT data.

For a planetary index, we used the global air surface temperature (GSAT) series from Jones and Wigley (1990), as digitized from their figure 1. We used the same criteria for standardizing, detrending, and smoothing the GSAT as for the local SST and SAT series.

A number of indices of sardine abundance have been developed, each with its own limitations. For this paper, we selected three: (1) total landings from the U.S. and Baja California after Radovich 1982; (2) virtual population analysis (VPA) biomass estimates after Murphy 1966 (for the years 1932–44), and MacCall 1979 (for the years 1945–65), complemented with indirect estimates of spawning biomass after Smith 1990 for the years in which VPA estimates are not available; and (3) scales contained in marine sediments after Soutar and Isaacs 1974.

Finally, we used CalCOFI cruise data to obtain the average proportion of positive stations for both sardine eggs and larvae for the area between lines 80 and 100, and from the coast to station 100 of the CalCOFI grid, thus covering the Southern California Bight.

GLOBAL AND LOCAL TEMPERATURE REGIMES

Climatic variation has long been recognized on larger time scales, such as glacial periods. Nowadays, global change on a shorter time scale is a common issue. Recently it has been associated with global warming due to the greenhouse effect, which results from the addition of abnormally high amounts of certain gases to the atmosphere. However, some years ago several climatologists warned about the existence of large interannual changes that had been previously undetected (see, for instance, Gribbin 1986). In fact, many papers were written about the large-scale changes in climate before the global circulation models were forecasting generalized warming (Hansen et al. 1981).

On the other hand, long before the actual recognition of climatic change, some authors pointed to large-scale shifts in the distribution of several species and related them to regional warming or cooling periods. Noticeably, Hubbs (1948) discussed the warm period occurring during the 1880s to 1890s, mostly as related to shifts in the distribution of several marine organisms, including the California sardine.

Periods of interannual thermal variation may be classified in terms of duration: the century-long time trend (secular), the interdecadal variation, and the high-frequency interannual changes, including the El Niño Southern Oscillation events. Regime changes are associated with the second component.

To identify the existence of such regimes along the west coast of North America, we compared local temperatures indices with a global index of change. As a first approach, we selected San Diego (related to the main spawning area of sardine) and San Francisco (the northernmost spawning center) SST and SAT series, and compared them with the selected global index (GSAT).

In figure 2, we plotted the GSAT series in the upper panel, with original data represented by circles, and the simple linear trend of the series (i.e., least squares fitted line). In the middle panel, we plotted the annual SAT anomalies for San Francisco and San Diego, with the simple linear trends for each data series. Finally, the lower panel shows the annual SST anomalies for both ports, with their linear trends.

Taking the maximum variation (the largest minus the smallest value in each series) as 100%, to standardize the values, the mean annual increase in temperature for the GSAT series is 0.3%, quite the same

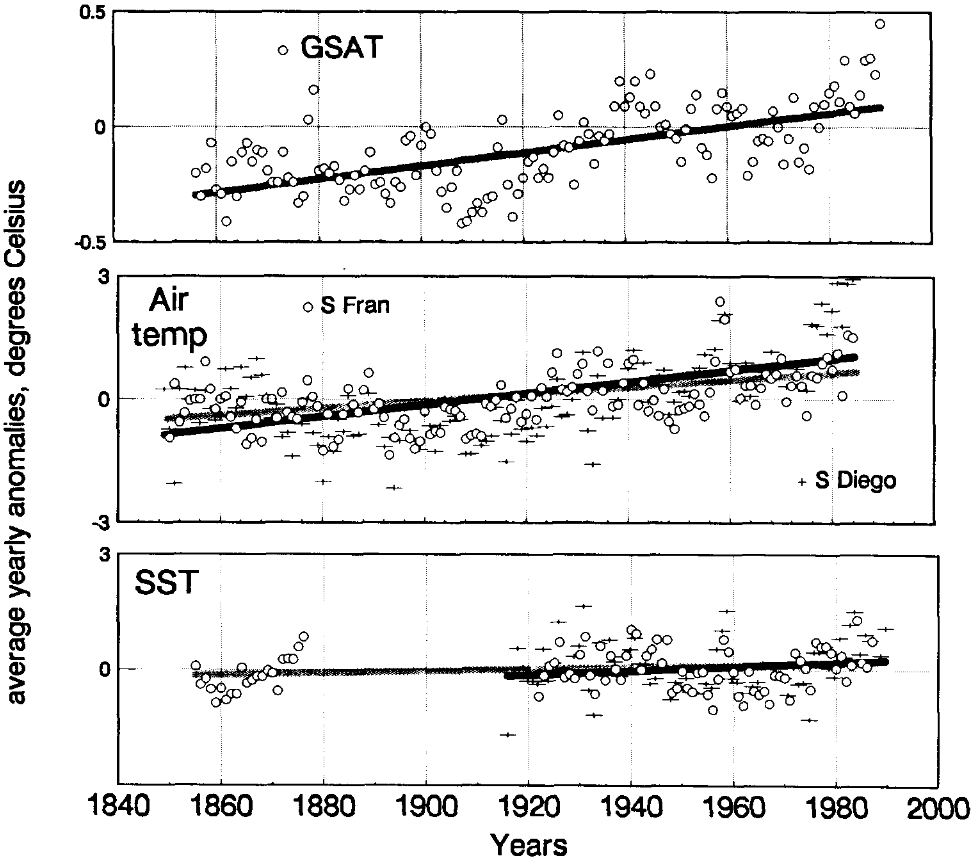

Figure 2. Temperature indices (data and linear trends). *Top panel*: GSAT, after Jones and Wigley (1990). *Middle panel*: San Francisco and San Diego SAT. *Bottom panel*: San Francisco and San Diego SST.

as the average for the two SAT series. However, the mean annual increase is only 0.1% for the SST series, or roughly one-third of the GSAT and SAT series. Leaving aside the fact that the GSAT series trend is as high as that of the air temperatures of fast-growing (and thus fast-warming) cities (which is indeed surprising, since only a tiny amount of the earth's surface is covered by fast-growing cities), it is evident that the ocean is warming at a slower rate.

It is unlikely that sardine abundance would be affected by this secular trend in SST. But it is evident from figure 2 that major changes occur in periods of about a decade; these changes are present both in the sea and in the air, as well as in the global index.

Once the secular trend is eliminated by detrending, and the high-frequency interannual variation is eliminated by smoothing, the resulting series basically show interdecadal variation. The annual average detrended and smoothed anomalies are shown in figure 3 (SAT) and figure 4 (SST). Besides the already mentioned variability, both figures show spatial coherence between the locations along the North American west coast, in both sea and air temperatures, for most times and most places. For the purposes of this presentation, and since we are interested only in major changes (i.e., persistent spatial and temporal changes), SST and SAT series may be pooled and combined in two series—one for SST and another for SAT.

The combined SST and SAT series from the beginning of the century are shown in figure 5, together with the detrended and smoothed GSAT

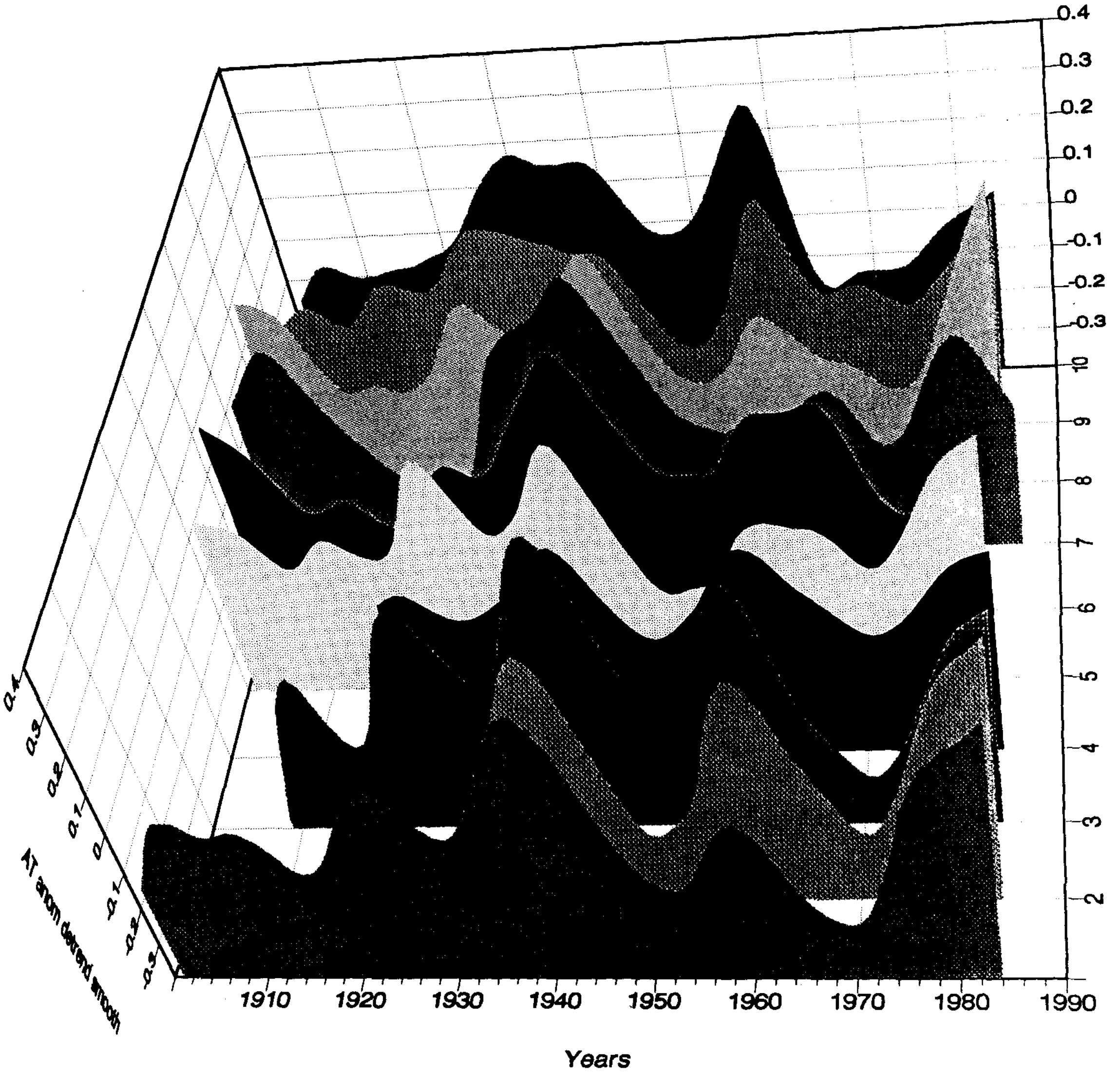

Figure 3. Detrended and smoothed SAT series (expressed as anomalies) of the following stations (from front to back): Juneau AK (1), Langara Island CAN (2), Prince Rupert CAN (3), Bull Harbour CAN (4), Olga WA (5), Seattle WA (6), Newport OR (7), Eureka CA (8), San Francisco CA (9) and San Diego CA (10). Anomalies in degrees Celsius.

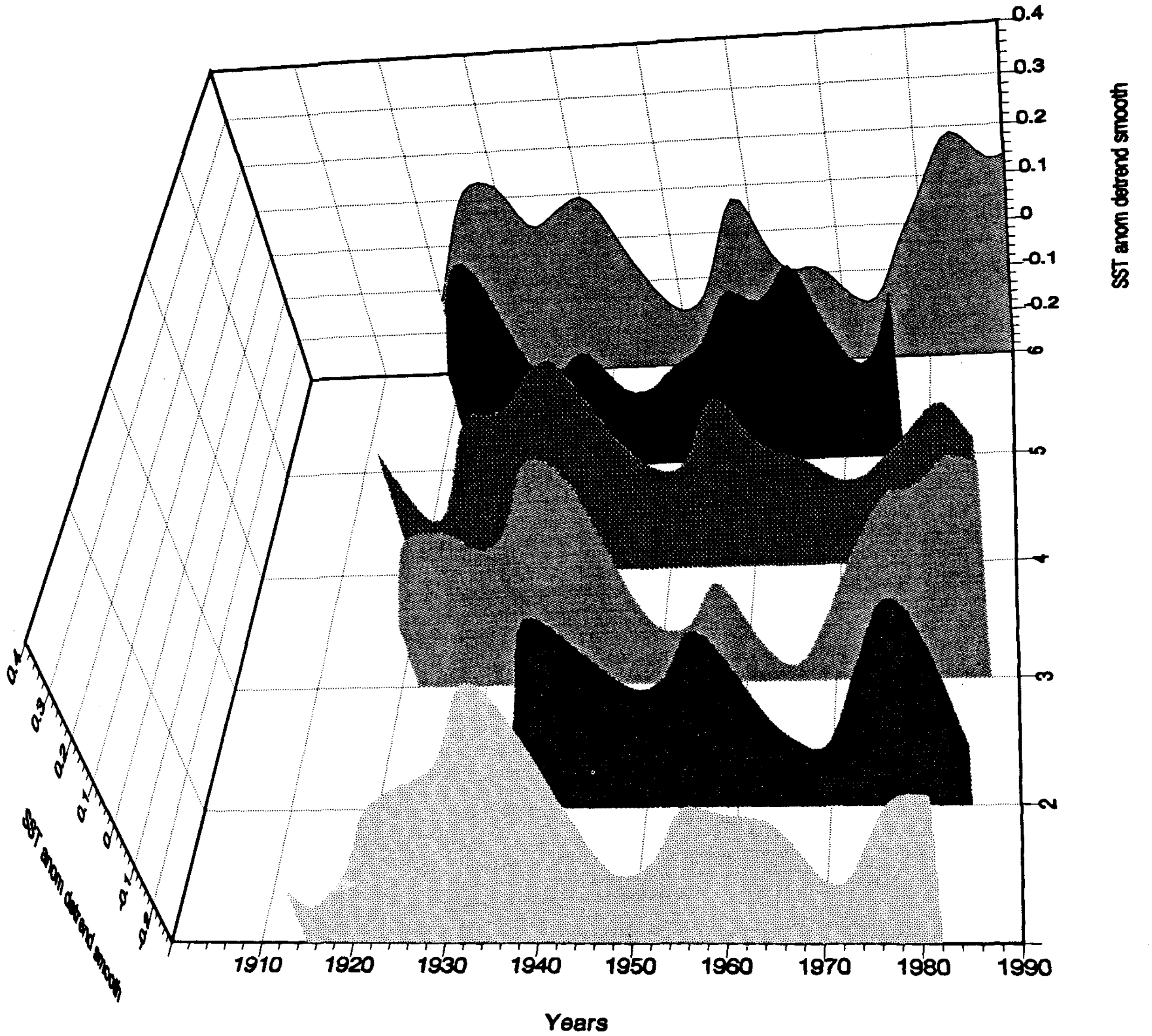

Figure 4. Detrended and smoothed SST series (expressed as anomalies) of the following stations (from front to back): Departure Bay CA (1), Crescent City CA (2), San Francisco CA (3), Pacific Grove CA (4), Balboa CA (5) and La Jolla CA (6). Anomalies in degrees Celsius.

series. Despite minor deviations, there is a coherent pattern between the three series with respect to parallel cooling-warming trends. However, a main difference between series is evident: a cooling trend is clear in the SAT since the early 1980s, while the SST continued to rise, although with a much lower rate than in the previous period. On the other hand, there is no change in the GSAT series, which shows a sustained warming trend since the late 1970s.

We suggest that regimes would be sustained periods (longer than one decade) of warm or cold average temperatures, as compared to the long-term means, which are coherent between time and geographic area. From figure 5, and in very rough terms, we can identify coherence between the global and the local levels. There was a cold regime from the beginning of the century up to around 1930; a warm regime between 1930 and about 1950, which peaked around 1940; a subsequent cold regime from 1950 until the mid 1970s (although a brief but intense warming was present during the late 1950s and the early 1960s, and was particularly evident at the local level); and a warm regime beginning in the mid 1970s and peaking during the early 1980s. Since then, local and global regimes do not agree: while global warming is persistent, local SAT has undergone a new cooling, and the local SST rate of change has decreased.

CALIFORNIA SARDINE ABUNDANCE REGIMES

In order to identify coherence between thermal and abundance regimes, we plotted the three se-

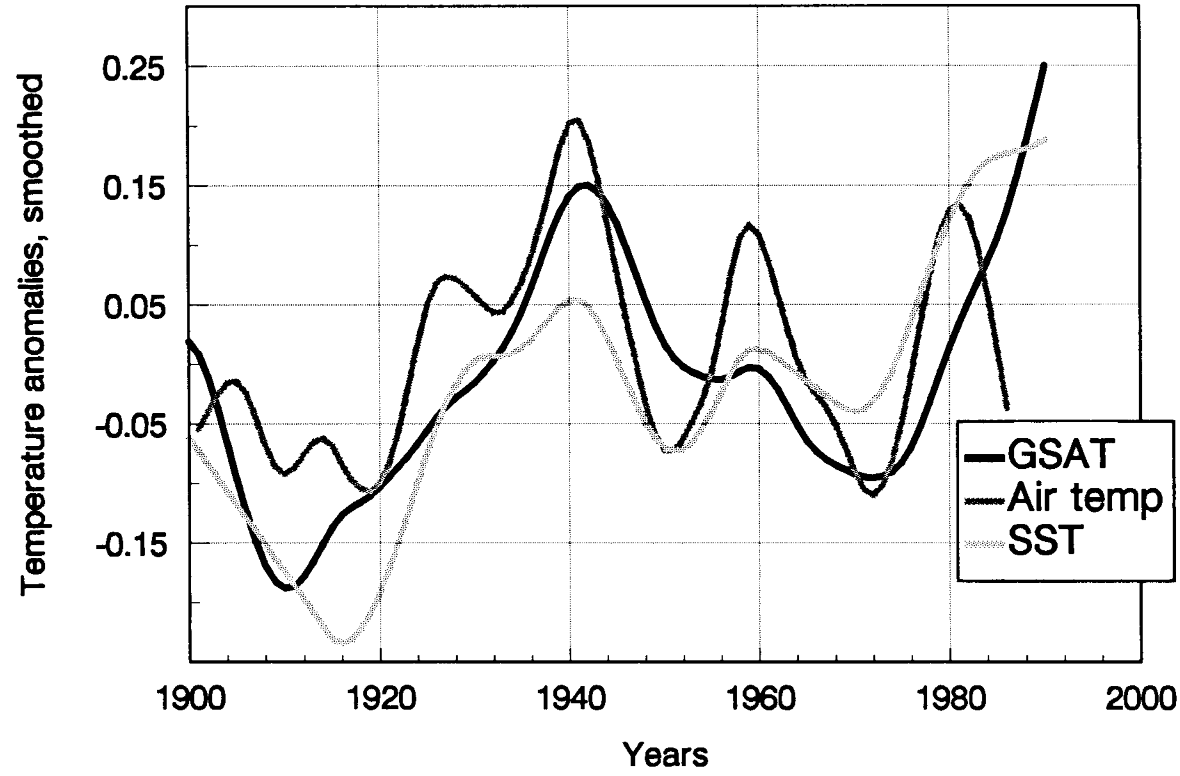

Figure 5. Averaged anomalies of the series presented in figures 3 (SAT) and 4 (SST), corresponding to the North American coastal stations showed in figure 1, together with the GSAT from Jones and Wigley (1990).

lected indices of sardine abundance together with the detrended-smoothed GSAT series (figure 6). Some considerations about these abundance indices may be useful. The first fact that we face when dealing with any abundance index is that, up to now, all of them have some limitations.

The validity of catch data as an index of abundance has been repeatedly questioned, since no variations in effort are taken into account. Radovich (1982) objected to the use of catch-per-effort data. Even though the analysis of minor variations in abundance might be rejected on the basis of these limitations, there should be no doubt that catch data do reflect gross trends in abundance. Except in the case of a regulated fishery (either by moratorium or some sort of effort limitation), landings are indeed roughly proportional to abundance. Thus we used available data from U.S. and Mexico fisheries until 1967, when a moratorium was declared for California.

Scale-abundance data from marine sediments of the Santa Barbara Basin are an independent estimate of population abundance. They have the limitation of being available for only one location; however, this location is near the center of the spawning area for the California sardine. Although the indices of abundance are limited, conclusions based on a simultaneous analysis (if the indices are in agreement) can be more reliable than indices that are analyzed individually.

There is a correspondence between the different sardine abundance regimes (figure 6). Sardine populations were abundant before the 1950s, scarce from then until the late 1970s, and growing since then to the mid 1980s. These abundance regimes are parallel to the global thermal regimes indicated by the detrended and smoothed GSAT series in the lower panel of figure 6. Warm global thermal regimes correspond to high abundance regimes of the California sardine, and vice versa. Thus, and from the aforementioned correspondence between local and global temperature regimes, it may be concluded that local temperature, global surface-air temperature, and California sardine abundance regimes are all similar.

PROPOSED MECHANISMS OF CHANGE AND POSSIBLE RELATIONS TO OTHER APPROACHES

A number of hypotheses for possible mechanisms have been proposed concerning the effect of environmental change on sardine abundance. Kondo (1980) suggested that the rapid increase in the Japanese sardine stock after 1970 resulted from a very strong year class, which was caused by a gradual

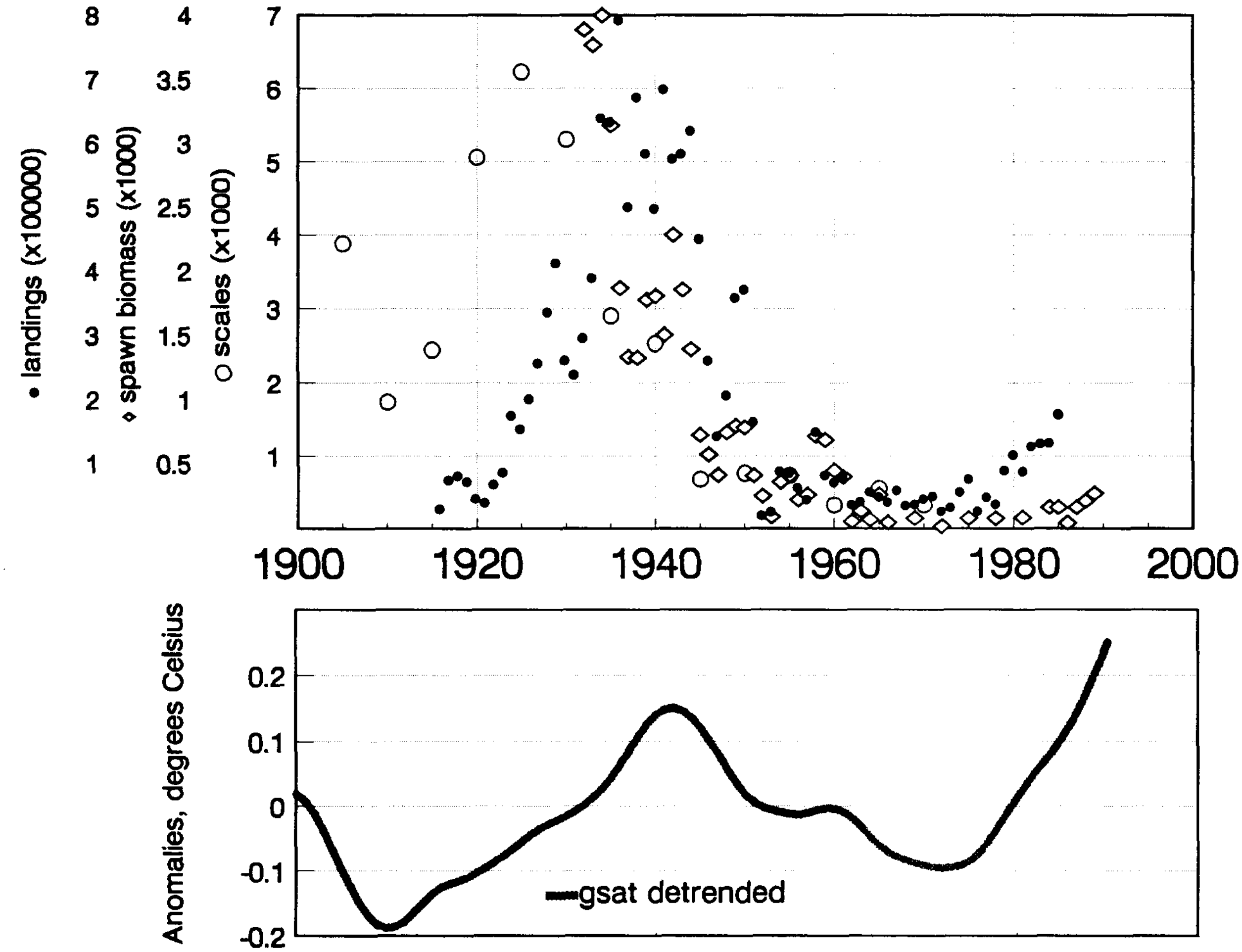

Figure 6. Indices of sardine abundance (landings, spawning biomass, and scales in varved sediments) as compared with the GSAT from Jones and Wigley (1990).

expansion of the spawning area, greater egg abundance, and more favorable conditions for the postlarval stage as a result of a shift of the Kuroshio Current. This current changed from meandering to straight when it was affected by an anomalous southern intrusion of the cold Oyashio Current. This shift in the oceanic circulation created a broad area suitable for copepod nauplii, thus allowing sardine postlarvae to survive the critical period after yolk absorption.

The effect of temperature in this mechanism may be generalized with respect to climatic regimes, since shifts in oceanic circulation are expected from one thermal regime to another. Lange et al. (1990) analyzed SST and sea-surface pressure series for the 1950–86 period, and pointed out that during recent years a weakening of the California Current and a reduction in upwelling activity have occurred.

This shift may lead to increased spawning area and egg abundance. It is not clear, however, if it may also lead to favorable conditions for the sardine larvae. On one hand, Lange et al. (1990) proposed low levels of productivity as a result of this change; thus a reduction in food supply for the larvae is to be expected. On the other hand, larval survival may be favored through thermal stratification (Lasker 1981) and reduction in turbulence and upwelling-derived offshore advection (Parrish et al. 1981).

Kawasaki and Omori (1988) proposed that increased solar input not only results in higher SST, but encourages expansion of the Japanese sardine population by increasing phytoplankton production. They noted that since this species depends strongly on phytoplankton it is also closely related to solar radiation.

If this mechanism applies to the California sardine, certain relationships must also be true. Abundance, temperature, and productivity must change rather simultaneously with each other if they are directly related to solar radiation. However, a direct

SST-productivity relationship does not seem consistent with the idea that upwelling activity determines productivity.

Regarding the effect of global warming on upwelling, Bakun (1990) suggested a mechanism in which enhancement of daytime heating by solar radiation, combined with nighttime inhibition of cooling, should lead to an increase in wind-stress-derived upwelling activity and thus to relative cooling of the surface coastal waters. He stated that upwelling activity has been decreasing in California since 1975, in agreement with the observed warming trend in SST. With this concept, there would be an inverse relation between SST and productivity, in both the secular and the interdecadal time scales.

Lange et al. (1990) obtained a data series of coastal primary production as indicated by the flux of diatoms to the marine sediments in the Santa Barbara Basin, for the period from 1950 through 1986. Unfortunately, this series covers only a period of low sardine abundance. However, Lange et al. found that during the 1954–72 period (cold SST), productivity was higher than in the period of warm SST during 1973–86, by a factor of five. They suggested that this difference was associated with the reduction in upwelling, and thus were in agreement with Bakun (1990). From these papers, it seems that sardine abundance is not directly governed by primary production in California, but the evidence must be considered inconclusive because no indications of primary productivity during a high-abundance mode are discussed.

We proposed a mechanism based on the spawning temperatures and some upwelling-related factor (Lluch-Belda, Hernández-Vázquez et al. 1991; Lluch-Belda, Lluch-Cota et al. 1991). The idea is that the California sardine population expands its habitat wherever proper SST and moderate upwelling activity exist. High productivity areas such as the Southern California Bight are in the cold limits of the sardine distribution, and can be occupied by resident populations only when SST is relatively high for sustained periods, allowing abundance to increase.

When cooling occurs, sardine spawning is restricted to Punta Eugenia, a less-productive area where spawning occurs year-round because of the higher temperatures and convenient upwelling activity. Besides temperature, there is a level of upwelling that is optimal for sardine spawning; when the levels are too high or too low, spawning decreases. In this mechanism, the association with thermal regimes is based on the direct effort of temperature on spawning activity.

From the above-discussed mechanisms, it is evident that some aspects of the recruitment problem and the regime problem are related. MacCall (1986) stated that sardine population growth and intraspecific competition are the main factors that force the expansion of the sardine population. Indeed, a growing population during a warm period should go through this process. Parrish et al. (1981) proposed that offshore advection during intensified upwelling may result in the loss of eggs and larvae to areas unsuitable for growth. Ahlstrom (1965) noted that high productivity (resulting from intensified upwelling) results in poor sardine year classes. Lasker (1981) proposed that a nonstratified ocean may result in poor survival. Indeed, many of these mechanisms may also operate within the regime problem.

However, the earlier idea — that is, the survival rate from the egg stage to the late larvae — demands special attention. If sardine abundance is determined this way, and is also related to temperature regimes, then some temperature-related factor should affect the egg-to-larvae process in a way that is reflected in abundance. Thus the egg-to-larvae proportion should be quite different between warm and cold regimes; a constant proportion would be, at least, difficult to explain.

Another possibility is that spawning itself may be related to temperature, and thus variable. Even with a constant ratio between eggs and larvae (i.e., a constant survival rate), abundance may be temperature-determined. Regarding the California sardine, Ahlstrom (1965) identified a rather constant rate between eggs and larvae through different years. In figure 7 we show the average proportion of positive stations for both eggs and larvae of sardine for the area between lines 80 and 100 and from the coast to station 100 of the CalCOFI grid, covering the Southern California Bight. In the same figure, we have placed the detrended GSAT regime index. Despite minor deviations, it is clear that there are more sardine eggs (and thus increased spawning) during the warm regime, and the relative abundance of both eggs and larvae is essentially similar.

If a rather constant egg-survival ratio is found to be a general phenomenon for sardine, as it seems to be for the area and period analyzed here, it would mean that spawning itself is variable, and depends on environmental conditions, as previously proposed (Lluch-Belda, Lluch-Cota et al. 1991). However, it should be stressed that the approaches are not mutually exclusive, since climate variations may directly determine spawning, and also modify the egg-survival rate. Many of the proposed mechanisms could be reconciled through this point of

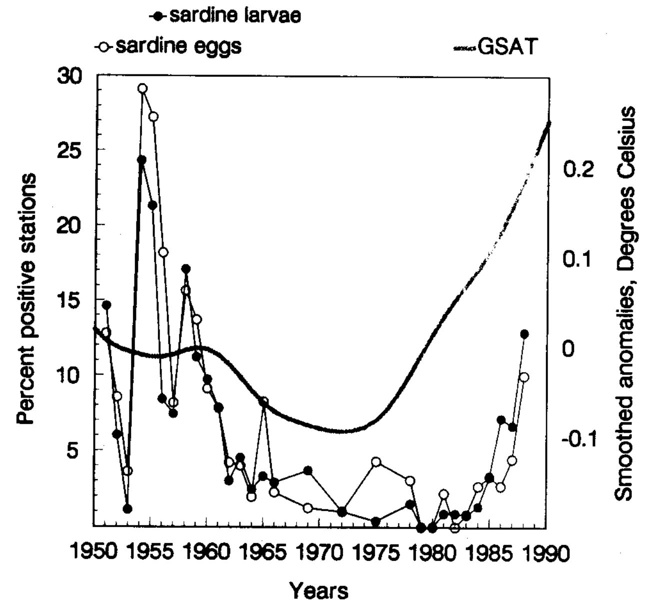

Figure 7. Average proportion of positive stations for sardine eggs and larvae for the area between lines 80 and 100 and from the coast to station 100 of the CalCOFI grid, together with the detrended GSAT from Jones and Wigley (1990).

view, although the relative contributions of both processes to the final abundance level remain a topic for future discussion.

Finally, the relation between the regime problem and the fishery problem may be more evident at the time the populations are being depleted. Diminished spawning due to environmental changes may result in poor recruitment. If a fishery is at the same time harvesting the nonspawning population, its total abundance would diminish much faster than as the result of natural mortality alone (which makes fishery regulation particularly important under these conditions). It would also seem reasonable that a smaller population resulting from intensive exploitation would take longer to grow, even under favorable climatic conditions. However, the events in the Japanese fishery, with a population growing explosively even under intense exploitation (Kawasaki 1983), seem to show otherwise and give insights into the high potential of population growth.

Up to now, there has been no agreement between the different authors, although some factors such as food supply; oceanic circulation patterns; changing winds and resulting upwelling patterns; and larval food access as related to turbulence, temperature, and habitat selection have been considered important. The difficulty in discriminating among these factors is that they are closely related and mostly change simultaneously. Despite the specific mechanism through which climatic regimes and abundance regimes may be related, no doubt should remain as to the existence of more than one "problem" at the root of the sardine population's fluctuations. However, the relative importance of these problems may be quite different, and a great deal of research must be done to reach more definitive conclusions.

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RECENT POPULATION TRENDS AND ABUNDANCE ESTIMATES FOR THE PACIFIC SARDINE (*SARDINOPS SAGAX*)

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ABSTRACT

Five different analytical approaches and several sources of data were used to investigate current sardine abundance and recent changes in population size. Each analysis and all available information show an increasing trend in sardine abundance since the late 1970s. Current estimates indicate that the 1990 spawning biomass fell within the range of 60,000 to 210,000 metric tons (MT). Greater precision may be required for population estimates as a commercial fishery develops. We suggest that an integrated method of stock assessment that combines fishery-dependent and fishery-independent data will best meet future stock assessment and management needs.

RESUMEN

Se investigó la abundancia y cambios recientes en el tamaño de la población de la sardina utilizando cinco enfoques analíticos y varias fuentes de datos. Tanto la información disponible como cada uno de los análisis revelaron que desde finales de los 70 la abundancia mostró una tendencia al alza. Estimaciones recientes indican que en 1990 la biomasa de los reproductores que desovaron fué de entre 60,000 a 210,000 toneladas métricas; las estimaciones podrían requerir mayor precisión al desarrollarse la pesquería comercial. Sugerimos que para satisfacer necesidades futuras de evaluación de stock y manejo se considere un método de evaluación de stock integrado, que combine datos dependientes e independientes de la pesquería.

INTRODUCTION

One characteristic of sardine resources (genera *Sardinops* and *Sardina*) is that the populations can fluctuate widely. Scale-deposition rates for Pacific sardines (*Sardinops sagax*) in California Bight anerobic sediment indicate such fluctuations (Soutar and Isaacs 1974). Depth-related variations in the numbers of sardine scales in sediment suggest periodic changes of significant magnitude in relative abundance, extending back over the past 200 years (Smith and Moser 1988). The study of Pacific sardine population dynamics has also indicated large changes in abundance during this century (Murphy 1966; MacCall 1979). Adjacent year classes have been shown to vary in numbers by more than an order of magnitude (Murphy 1966), presenting the potential for rapid increases or decreases in overall population size, should trends in recruitment develop.

The Pacific sardine resource off the west coast of North America currently extends from the northern part of California to central Baja California. A large fishery was supported by the Pacific sardine many decades ago, when the population ranged from Canada to Mexico. However, abundance declined dramatically from 1945 through 1965 (with some short-lived reversals), and the fishery collapsed (Radovich 1982). In 1967 a moratorium was placed on the taking of sardines along the California coast because of the depressed condition of the stock. Annual landings were negligible from then until recent years, when sardines were once again regularly encountered by California and northern Baja California fishermen.

In 1985 the sardine spawning biomass was estimated to have increased to at least 18,140 MT (Wolf and Smith 1986), and a catch quota of 907 MT was established, allowing a small directed fishery in the United States. At the same time, bait fisheries were allocated a separate quota of 544 MT per year. Total directed and bait fishery quotas were increased to 8,165 MT for the 1991 season in recognition of the continued expansion of the resource. In addition to the directed and bait fisheries, current management regulations allow a 35% maximum incidental take of sardines (by weight) in the California fishery for Pacific mackerel (*Scomber japonicus*) and jack mackerel (*Trachurus symmetricus*). Sardine by-catch in the mackerel fishery usually amounts to about 1,000–3,000 MT per year.

A fishery outside the control of United States authorities operates in Ensenada, Mexico, and probably harvests the same sardine stock as the southern California fishery. Ensenada sardine landings dominated the fishery in 1990, but were roughly similar in volume to those in the United States during most other recent years (table 1).

In response to apparent increases in sardine abundance and associated public interest in expanding the commercial fishery, a workshop was convened in September 1990 by the California Department of Fish and Game (CDFG) to develop recommendations for assessing and managing the resource. An objective of the workshop was to examine various sources of data concerning the status of sardines. In this paper, we review five independent and complementary analyses used by workshop participants to evaluate the current state of the population. The data, methods, and analyses reported here incorporate some improvements introduced as a result of work done since the workshop. Data employed in the analyses are described in the next section, followed by an explanation of methods and results for each approach. We compare results in the final section and suggest an approach for future assessment of the stock.

DATA

Several sources of information were available. Some were relatively long time series extending back over decades; others were more recent in scope, or fragmentary. Direct estimates of sardine biomass from virtual population analyses (VPA) were available for 1932–59 in Murphy 1966 and for 1945–65 in MacCall 1979. Biomass estimates from MacCall 1979 were used for years when estimates from both sources were available (table 2). No direct VPA biomass estimates were available for years after 1965.

The two general categories of information about sardine biomass during recent years are described in detail below. The first category consisted of data types similar to catch-per-unit-effort (egg density, larval density, and tons of sardine sighted per block by fish spotters); the second category consisted of indices that measured sardine biomass by means of presence-absence data (proportion of sea-survey stations positive for eggs and larvae, counts of blocks where sardines were seen by fish spotters, and counts of positive tows from CDFG sea-survey data).

TABLE 1
Annual Sardine Landings (MT) for Ensenada (Mexico) and California (U.S.), 1983–1990

Year	Ensenada	California			Grand total
		Directed	Incidental	Total	
1983	274	192	353	545	819
1984	0	61	238	299	299
1985	3722	14	593	607	4329
1986	243	421	762	1183	1426
1987	2432	600	1711	2311	4743
1988	2035	1034	2801	3835	5870
1989	6224	1400	4409	5809	12033
1990	11375	2035	1329	3364	14739

Data sources were the Instituto Nacional de Pesca for Ensenada; LMR Fisheries Research, Inc. for the 1989 incidental landings; and the California Department of Fish and Game for all other California landings.

Catch-per-unit-effort (CPUE) indices have lately received much criticism as tools for measuring relative abundance of pelagic fish like sardines because CPUE tends to decline more slowly than abundance (i.e., relationships between CPUE and biomass tend to be nonlinear: see Bannerot and Austin 1983 and references therein). Theory underlying the use of indices of abundance based on presence-absence data is described by Smith (1990), Mangel and Smith (1990), and Wolf and Smith (1985). As with CPUE data, it is possible that indices derived from presence-absence data do not change proportionally with abundance. This is a concern, particularly when data were collected from a geographic area smaller than the range of the stock.

California Cooperative Oceanic Fisheries Investigations

MacCall and Prager (1988) used an analysis of variance approach (ANOVA) to derive an index of abundance for Pacific sardine larvae sampled by California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys from 1951 to 1985. Their ANOVA model consisted of independent additive month, region, and year factors combined to estimate the log of the mean density of larvae in each month, region, and year. MacCall and Prager used antilogs of year factors from the ANOVA to obtain index values of relative annual larval abundance (table 2). This time series is especially valuable because it spans the decline of the 1950s and 1960s, the unfished low period of the 1970s, and the early recovery of the 1980s.

For this study, we used four additional types of CalCOFI data: estimates of sardine egg density (eggs/0.05 m^2); estimates of larval sardine density (larvae/0.05 m^2); the fraction of sampling stations at which eggs were found ("proportion positive for eggs"); and the fraction of stations at which larvae were found ("proportion positive for larvae"). These data were for winter and spring cruises (one cruise per year during January to March and one cruise per year during April to June) and probably covered the period of peak spawning for sardines. The data were

TABLE 2
Data Used in Analyses for Sardine

Year	Number stations	E	L	PE	PL	VPA	SQUIRE	LO	CDFG	ANOVA	WTS	SPT
1916	—	—	—	—	—	—	—	—	—	—	—	16.56
1917	—	—	—	—	—	—	—	—	—	—	—	16.68
1918	—	—	—	—	—	—	—	—	—	—	—	17.35
1919	—	—	—	—	—	—	—	—	—	—	—	16.85
1920	—	—	—	—	—	—	—	—	—	—	—	16.51
1921	—	—	—	—	—	—	—	—	—	—	—	16.50
1922	—	—	—	—	—	—	—	—	—	—	—	16.43
1923	—	—	—	—	—	—	—	—	—	—	—	17.33
1924	—	—	—	—	—	—	—	—	—	—	—	16.52
1925	—	—	—	—	—	—	—	—	—	—	—	16.96
1926	—	—	—	—	—	—	—	—	—	—	—	18.03
1927	—	—	—	—	—	—	—	—	—	—	—	16.84
1928	—	—	—	—	—	—	—	—	—	—	—	16.69
1929	—	—	—	—	—	—	—	—	—	—	—	17.14
1930	—	—	—	—	—	—	—	—	—	—	—	17.40
1931	—	—	—	—	—	—	—	—	—	—	—	18.45
1932	—	—	—	—	—	3,524	—	—	—	—	—	16.27
1933	—	—	—	—	—	3,415	—	—	—	—	—	15.62
1934	—	—	—	—	—	3,625	—	—	—	—	—	17.49
1935	—	—	—	—	—	2,845	—	—	—	—	—	16.67
1936	—	—	—	—	—	1,688	—	—	—	—	—	17.57
1937	—	—	—	—	—	1,207	—	—	—	—	—	17.00
1938	—	—	—	—	—	1,201	—	—	—	—	—	16.64
1939	—	—	—	—	—	1,608	—	—	—	—	—	17.13
1940	240	699.10	49.13	0.75	0.81	1,760	—	—	—	—	—	17.32
1941	210	336.90	36.88	0.63	0.75	2,457	—	—	—	—	—	17.62
1942	—	—	—	—	—	2,065	—	—	—	—	—	16.96
1943	—	—	—	—	—	1,677	—	—	—	—	—	16.95
1944	—	—	—	—	—	1,260	—	—	—	—	—	16.45
1945	—	—	—	—	—	720	—	—	—	—	—	16.57
1946	—	—	—	—	—	566	—	—	—	—	—	16.79
1947	—	—	—	—	—	405	—	—	—	—	—	16.85
1948	—	—	—	—	—	740	—	—	—	—	—	16.03
1949	—	—	—	—	—	793	—	—	—	—	—	16.48
1950	—	—	—	—	—	780	—	—	—	—	—	16.36
1951	96	33.33	2.06	0.17	0.15	277	—	—	—	16.75	1.00	16.59
1952	152	6.85	3.49	0.10	0.11	136	—	—	—	4.66	1.00	16.23
1953	226	0.21	0.07	0.03	0.01	202	—	—	—	0.48	1.00	16.20

(*continued on next page*)

"Number stations" is the total number of stations (tows) for CalCOFI data. E is mean number of eggs per 0.05 sq. m. L is mean number of larvae per 0.05 sq. m. PE is proportion of CalCOFI stations positive for sardine eggs. PL is proportion of stations positive for sardine larvae. VPA is biomass (thousand MT) of sardines age two and older from a virtual population analysis. SQUIRE is a catch-per-unit-effort-like index (short tons sighted per block) from fish spotters for nighttime flights over a core area where sardines are normally abundant. LO is the number of blocks in which sardines were spotted by fish spotters during each year. CDFG is California Department of Fish and Game sea-survey data (n.mi.^{2}). ANOVA is analysis-of-variance data from MacCall and Prager 1988; the original ANOVA data were logarithms but are given here in arithmetic units. WTS is for weights from MacCall and Prager (1988, table 2) used to scale the ANOVA data. SPT is for mean annual sea-surface temperatures (centigrade) at Scripps Pier. The symbol — indicates no data available.

from an area of the California Bight much smaller than the historical range of sardines; the boundaries were chosen to coincide with the boundaries of the ichthyoplankton survey conducted during 1941 (figure 3 in Smith 1990). Data for 1940–89 were obtained from table 1 in Smith 1990 and augmented to include data for 1990 (Paul Smith, NMFS, Southwest Fisheries Science Center, pers. comm.). There were 30 observations for each type of CalCOFI data, and a total of 120 CalCOFI observations (table 2).

CalCOFI cruises and sampling procedures are explained in Hewitt 1988. No cruises were conducted in some years, and the number of sampling stations in the study area varied from one survey year to the next. Distance between sampling stations was too great to precisely measure the density of sardine eggs and larvae at low biomass levels. Fortunately, indices of relative abundance based on presence/absence of eggs and larvae are expected to be more robust than density estimates at low biomass and sampling levels (Smith 1990; Mangel and Smith 1990).

Fish-Spotter Data

Fish spotters are pilots employed by commercial fishermen to locate, identify, direct the harvest of,

TABLE 2 *continued*
Data Used in Analyses for Sardine

Year	Number stations	E	L	PE	PL	VPA	SQUIRE	LO	CDFG	ANOVA	WTS	SPT
1954	219	39.67	11.98	0.15	0.11	239	—	—	—	104.79	1.00	16.81
1955	142	26.87	7.29	0.17	0.09	170	—	—	—	19.77	1.00	16.50
1956	156	47.88	6.90	0.09	0.05	108	—	—	—	3.50	1.00	16.37
1957	145	23.00	12.09	0.10	0.10	90	—	—	—	6.62	1.00	17.36
1958	171	86.38	8.86	0.30	0.31	177	—	—	—	7.79	1.00	17.84
1959	188	182.00	7.88	0.29	0.25	122	—	—	—	6.85	1.00	18.35
1960	197	117.14	4.47	0.18	0.17	88	—	—	—	2.25	1.00	16.61
1961	73	17.08	1.40	0.16	0.08	54	—	—	—	0.39	0.66	16.52
1962	64	1.77	0.95	0.02	0.05	27	—	6	—	1.04	0.48	16.24
1963	77	14.22	1.94	0.05	0.04	21	1.38	51	—	0.95	0.65	16.96
1964	183	0.43	0.00	0.02	0.01	11	1.31	36	—	0.06	0.57	16.42
1965	112	4.57	0.79	0.11	0.10	3	0.02	10	—	0.93	0.66	16.52
1966	169	2.01	0.29	0.01	0.05	—	0.03	9	—	0.25	1.00	17.00
1967	—	—	—	—	—	—	0.00	0	—	0.12	0.28	16.92
1968	—	—	—	—	—	—	0.01	2	—	—	—	16.93
1969	147	0.33	0.26	0.03	0.04	—	0.00	0	—	0.90	0.86	16.64
1970	—	—	—	—	—	—	0.00	4	—	—	—	16.62
1971	—	—	—	—	—	—	0.00	6	—	—	—	16.18
1972	118	0.00	0.03	0.00	0.01	—	0.00	1	—	0.07	0.54	16.87
1973	—	—	—	—	—	—	0.00	2	—	—	—	16.45
1974	—	—	—	—	—	—	0.00	0	—	—	—	16.47
1975	267	2.54	0.07	0.03	0.01	—	0.00	0	—	0.03	0.71	15.53
1976	—	—	—	—	—	—	0.00	0	—	—	—	17.26
1977	—	—	—	—	—	—	0.00	0	—	—	—	17.25
1978	189	0.38	0.18	0.03	0.02	—	0.00	0	—	0.11	0.87	17.42
1979	—	—	—	—	—	—	0.00	0	—	—	—	16.85
1980	—	—	—	—	—	—	0.00	0	—	—	—	16.62
1981	139	0.99	0.23	0.03	0.01	—	0.00	2	—	0.52	0.89	17.62
1982	—	—	—	—	—	—	0.24	8	—	0.09	0.19	17.12
1983	—	—	—	—	—	—	0.33	15	—	2.34	0.10	17.97
1984	141	3.40	6.50	0.06	0.04	—	2.77	20	—	0.62	0.89	18.31
1985	99	10.96	8.80	0.06	0.05	—	97.36	61	670	21.07	0.30	17.21
1986	183	3.45	3.62	0.01	0.04	—	32.35	58	970	—	—	17.72
1987	81	18.73	23.00	0.06	0.11	—	20.12	85	1,850	—	—	17.56
1988	85	40.75	2.25	0.08	0.05	—	145.75	109	2,508	—	—	16.99
1989	72	61.00	4.96	0.11	0.17	—	34.84	78	3,680	—	—	17.18
1990	66	77.89	5.71	0.03	0.08	—	39.03	80	1,480	—	—	17.88
1991	—	—	—	—	—	—	—	—	3,840	—	—	16.97

and estimate the size of fish schools (Squire 1961, 1972). Analogous to CalCOFI data, two indices of relative abundance based on fish spotter data were available: densities of sardines observed by fish spotters, and the proportion of total blocks searched by fish spotters in which sardines were observed (table 2).

An index of relative density (biomass per block sighted by fish spotters in each year) was calculated from flights conducted at night over a "core" area where sardines were relatively abundant (Squire 1972). There were 28 annual records for the period 1963–90 (table 2). Unpublished sardine density data from fish spotters used in this analysis were developed and provided by Jim Squire (NMFS, Southwest Fisheries Science Center, pers. comm.).

N. C. H. Lo (NMFS, Southwest Fisheries Science Center, pers. comm.) developed the proportion-positive-blocks index of relative abundance. Lo's index was calculated by counting "positive blocks" for sardines from 1962 to 1990 (29 annual records) where positive blocks were unique blocks in which sardines were seen by fish spotters (e.g., sardines were seen in six blocks by fish spotters during 1962; table 2). The proportion-positive index from fish-spotter data was calculated annually from all flights. Fish spotters covered a broader geographic area than the sardine stock in each year (N. C. H. Lo, unpublished data) so that counts of positive blocks were measures of the areal extent and size of the sardine stock.

Landings

Sardines commonly occur both in "pure" schools (sardines only) and in "mixed" schools with Pacific or jack mackerel. In recent years, incidental sardine catches in the mackerel fishery were a primary source of sardines in the southern California landings (table 1).

In 1988, LMR Fisheries Research, Inc. instituted a program to collect fishery-based data other than tons landed. Each year from 1988 through 1990, data were collected from the San Pedro fresh fish market and a Terminal Island cannery. Samples were collected at both locations during the directed sardine fishery in January, and during the year-round mackerel fishery. Species composition data were collected from about 30.5% of all wetfish fleet landings during the study period. When sardines were present, biological samples consisting of 25 randomly selected fish were collected from individual deliveries. These fish were measured (standard length to the nearest mm, appendix table A), weighed (round weight to the nearest 0.1 g, appendix table B), and examined for sex and maturity. Otoliths were removed for age determination (appendix table C). Ages were estimated by examining otoliths with reflected light under 18 × magnification (Sunada, undated; Mosher 1954).

The fishery data included information about the volume and age composition of landings during 1988–90, but were not suitable for standard VPA-based population estimates because the time series of catch-at-age data were short, and cumulative fishing mortalities during recent years may have been low (Pope 1972).

Sardine Egg Survey

From 1985 to 1991, CDFG conducted annual sea surveys to collect sardine eggs (Wolf and Smith 1986; Wolf et al. 1987). The extent of spawning area, defined by the number of sampling stations at which sardine eggs were found, was used to measure the areal extent and relative size of the spawning biomass. This approach allowed managers to track trends in biomass levels while the sardine population was relatively small and difficult to measure with conventional techniques (Wolf and Smith 1985). Smith's (1990) results and other analyses described in this paper indicate that spawning area is a useful index of biomass for sardines. Spawning area estimates for 1985–91 are given in table 2.

CDFG sea-survey design and sampling techniques are discussed in Wolf and Smith 1985 and 1986. Surveys were designed to take place during peak spawning and to cover waters in which spawning was likely to occur. The geographic extent of the surveys varied somewhat each year to accommodate new information about the range of sardine spawning. After the 1986 survey, which used a dense station plan over a relatively small area (Wolf et al. 1987), surveys encompassed the Southern California Bight and adjacent waters. Because the survey area increased slightly each year, a minor portion of the increase in observed spawning area may be due to eggs detected in areas not surveyed the year before. Also, spawning was observed at the edge of the survey grid in some years, indicating that some fish may have spawned outside the survey area. However, annual CalCOFI surveys (which cover a larger area) found few sardine eggs outside the areas identified by CDFG surveys during each year for 1985–91 (unpublished data), indicating that the actual spawning area was probably identified by the CDFG surveys each year.

Sea-Surface Temperatures (SST)

Scripps Pier SST data, which are the longest time series of uninterrupted oceanographic data for Pacific sardine habitat, were used in this analysis (table 2). MacCall and Prager (1988) identified three major regimes in the data for 1916 to the late 1980s: warm water from 1916 to the early 1940s, followed by cool water until the mid-1970s, and then warm water until the late 1980s. Additional data through 1991 indicate that warm conditions have continued.

METHODS AND RESULTS

Indices used in our analyses to measure sardine biomass (table 2) were generally consistent with one another and indicated similar trends in abundance. Correlation coefficients were positive except in two cases where the sample size was small (table 3). Correlations among CalCOFI indices and between VPA biomass estimates and CalCOFI indices were particularly high (correlation coefficients >0.8). Correlation coefficients between other pairs of indices were also high but not reliable because sample sizes were small.

Historical CalCOFI Larval Abundance

MacCall's (1979) VPA estimates of sardine biomass were used to calibrate MacCall and Prager's (1988) CalCOFI larval index to units of sardine biomass (age 2 and older). The two data sets overlap from 1951 to 1965, but with incomplete monthly and regional coverage by the 1961–65 CalCOFI surveys. Index values from MacCall and Prager's 1988 ANOVA model were scaled by a multiplicative constant (25,072 MT) so that the index had the same weighted geometric mean and units of measurement as VPA biomasses over the period of overlap. Weights were taken from table 2 of MacCall and Prager 1988; data for 1951–60 were given unit weight, and weights for 1961–65 ranged from 0.482 to 0.659 (table 2).

VPA spawning biomass estimates and scaled CalCOFI index values are shown in figure 1. Index

TABLE 3
Correlation Coefficients for Indices Used to Measure Sardine Biomass in a General Linear Model

	E	L	PE	PL	VPA	SQUIRE	LO
L	0.88						
	(30)						
PE	0.92	0.87					
	(30)	(30)					
PL	0.93	0.89	0.98				
	(30)	(30)	(30)				
VPA	0.81	0.91	0.89	0.93			
	(17)	(17)	(17)	(17)			
SQUIRE	0.47	0.22	0.36	0.20	0.86		
	(16)	(16)	(16)	(16)	(3)		
LO	0.74	0.57	0.44	0.54	0.091	0.78	
	(16)	(16)	(16)	(16)	(3)	(28)	
CDFG	0.56	−0.13	0.82	0.79	*	−0.006	0.56
	(6)	(6)	(6)	(6)		(6)	(6)

Column and row headings are defined in table 2. Sample sizes are given in parentheses. The asterisk is used where there was insufficient data to calculate a correlation.

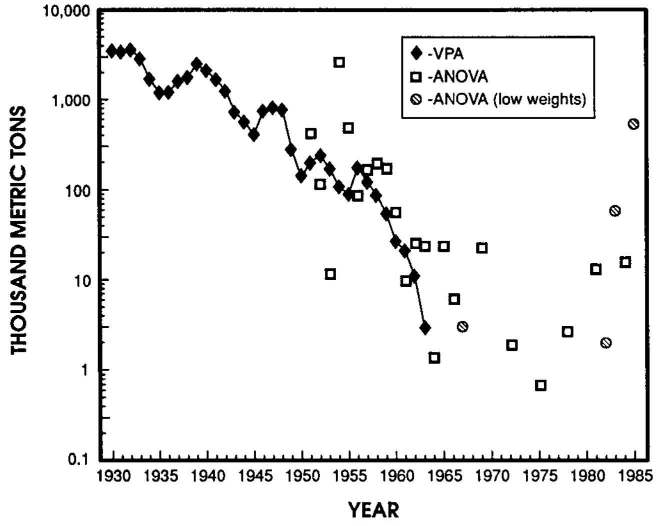

Figure 1. Sardine biomass (age 2 and older) estimated by VPA and ANOVA. ANOVA estimates are based on CalCOFI data and have been rescaled to the same units as VPA estimates. *Circles* indicate ANOVA estimates that are unreliable because of inadequate sampling (low-weight years).

values based on less than 30% coverage of the spawning months and regions (i.e., with weights <0.30) should be assumed unreliable. The remaining larval index values are still very imprecise, since errors appear as large as tenfold in some years. Nonetheless, long-term trends are clearly apparent in the time series of index values. The sardine population reached bottom during the mid-1970s. The recovery seems to have started in the late 1970s, but is not clearly apparent until the early 1980s.

General Linear Model Analysis

All of the data types in table 2 (with the exceptions of "Number Stations," "ANOVA," "WTS," and "SPT") were used in a statistical model to estimate recent levels of sardine biomass. The model was:

$$B_{t,y} = T_t Y_y z_{t,y} \qquad (1)$$

where $B_{t,y}$ was biomass (in absolute or relative units) of sardines in year y as measured by data type t; T_t was the effect for data type t; Y_y was the effect for year y; and $z_{t,y}$ was a statistical error. Taking logs gave the linear form:

$$\ln(B_{t,y}) = \ln(T_t) + \ln(Y_y) + \ln(z_{t,y}) \qquad (2)$$

which was the same as would be assumed in a two-way analysis of variance on log-transformed sardine biomass data with data types and years as factors. Statistical interactions between years and data types were not considered when equation 2 was fitted because of the scarcity of data for some years and to avoid complications in interpreting the results. Interactions are, however, biologically plausible and have been demonstrated elsewhere (MacCall and Prager 1988).

Models like equation 2 are known as general linear models or log-linear models. They are often used by fishery scientists and managers to derive a single index of relative abundance for a fish population from two or more types of data (e.g., catch rates from two types of fishing vessels) or data that were similar but collected from two or more temporal or spatial strata (Gulland 1956; Robson 1966; Kimura 1981, 1988; MacCall and Prager 1988). The general linear model (2) was fitted by standard linear regression techniques (Weisberg 1980) including residual plots, outlier analyses, and Cook's (1977, 1979) distance.

Statistical errors ($z_{t,y}$) in the general linear model (2) were assumed to be independent and lognormally distributed with variance constant over years

(y) and data types (t). The assumptions of normality and constant variance were required primarily for interpretation of statistical tests, which were not an important part of the analysis. The assumption of independence was more important (see below).

Abundance estimates for each year from model 2 were expressed in the same units as VPA biomass estimates (weight of sardines age 2 and older). The expected value for log-scale biomass was computed as:

$$\beta_{\mathrm{VPA},y} = \tau_{\mathrm{VPA}} + \Omega_y, \qquad (3)$$

where $\beta_{\mathrm{VPA},y}$ was the estimate of log-scale VPA biomass for sardines $[\ln(B_{\mathrm{VPA},y})]$ from model 2 for year y; τ_{VPA} was the estimate of the log-scale effect for VPA data $[\ln(T_{\mathrm{VPA}})]$; and Ω_y was the estimate of the log-scale effect for year y $[\ln(\mathrm{Y}_y)]$. Estimates of the expected value for sardine biomass on an arithmetic scale were obtained by taking exponents:

$$\Phi_{\mathrm{VPA},y} = \exp(\beta_{\mathrm{VPA},y} + \sigma^2/2) \qquad (4)$$

where $\Phi_{\mathrm{VPA},y}$ (which estimates $B_{\mathrm{VPA},y}$) is the index for year y (units MT of fish age 2 and older), and σ^2 is the variance of residuals from the fit of model 2. The factor $\sigma^2/2$ corrects for bias due to log transformation (Beauchamp and Olson 1973). An unbiased estimate of median biomass can be obtained from equation 4 by neglecting the correction factor.

Variances for log-scale indices of sardine biomass were calculated from sums of variances and covariances for estimates of parameters on the right-hand side of equation 3, which were obtained from the regression output. Arithmetic-scale confidence intervals for estimates of sardine biomass in each year were calculated from the log-scale confidence intervals by taking exponents and correcting for bias as in equation 4.

The CalCOFI and fish-spotter data used to fit the general linear model (2) were probably not completely independent, since all of the CalCOFI indices were based on data collected during the same ichthyoplankton surveys, and both fish-spotter indices were derived from data collected during the same flights. The practical consequence of this problem would be biased estimates of biomass for sardines, because the statistical errors for CalCOFI or fish-spotter indices in a particular year ($z_{t,y}$) would tend to be either all positive or all negative and would not "cancel each other out." The magnitude of this problem could not be determined from the available data, but it is necessary to consider potential bias when interpreting results.

We used weights for CalCOFI data when fitting model 2 in an effort to avoid potential problems with lack of independence. Weights used were 0.5 for CalCOFI data and 1.0 for all other data types, so that each CalCOFI observation would receive half the weight used for VPA, fish-spotter, or CDFG sea-survey data during parameter estimation. We considered it unnecessary to use weights to account for lack of independence among the two types of fish-spotter indices, because differences in their geographic and temporal scope should result in some degree of independence.

Model 2 was initially fit to data for all available years, but residual plots indicated nonlinear relationships between sardine biomass and most of the indices. The initial estimate of sardine biomass during 1990 was 200,000 MT. In order to limit bias from the linear model due to nonlinear relationships in the data, we omitted years for which the initial sardine biomass estimate was much smaller (<50,000 MT during 1964–83) or much larger (>500,000 MT during 1940–41) than the 1990 level, and fitted the model again. This approach confined the analysis to a range of sardine biomass levels within which the linear model was approximately valid. An additional advantage in excluding years with very low biomass is that "zeroes" (e.g., egg density data for 1972) were not used to estimate parameters. When zeroes are present, a positive constant must be added to all observations before the data are log-transformed (e.g., MacCall and Prager 1988). Approaches to choosing additive constants are well developed when log-linear models are used for hypothesis testing (Berry 1987) but not for estimation or measurement.

Model 2 was fitted to the data for 1951–63 and 1984–90 after data for high and low biomass years were omitted, and one anomalous observation (VPA biomass in 1953) was identified as an outlier (t test $= 4.43$, Bonferroni probability value for mistakenly rejecting the null hypothesis of no outlier <0.05; see Weisberg 1980). The model was fitted again after the outlier was omitted. There were 114 observations in the data set finally used.

Effects of years and data types were statistically significant (probability of no differences among years or data types <0.00). There were seven observations with large standardized residuals (absolute magnitude greater than 2.0), but none could be rejected as an outlier on statistical grounds. No observations had an unusually large influence on predicted values as indicated by Cook's distance. Standard deviations for residuals from the seven data types were similar.

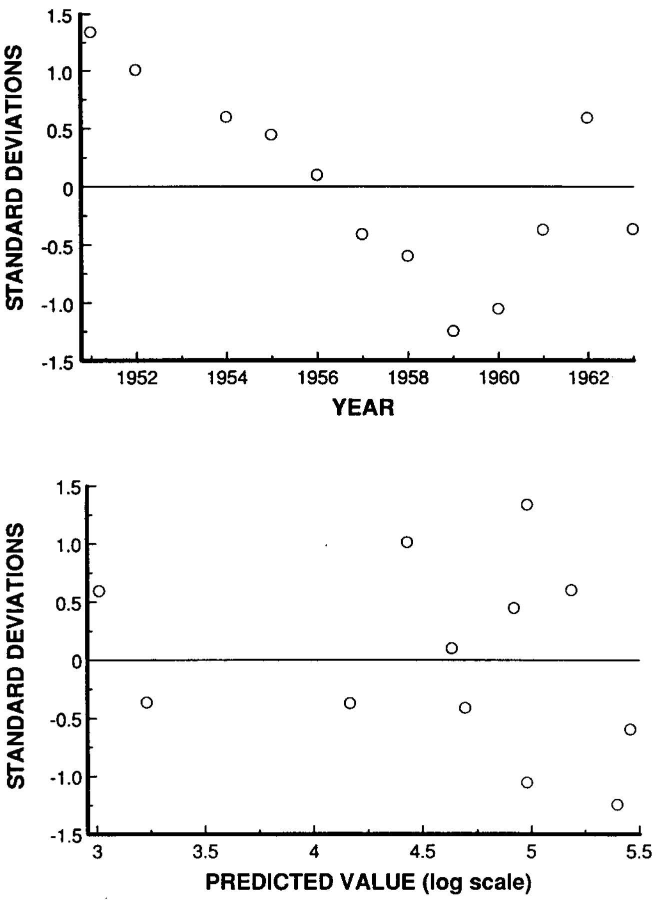

Figure 2. Studentized residuals from a general linear model. Residuals for sardine VPA data are plotted against year (*top*) and predicted log sardine biomass (*bottom*). Positive residuals occur where predicted values are too small; negative residuals occur where predicted values are too large.

Residual plots indicated that the linear model (2) was adequate for the reduced data set, although there was a trend in the plot of residual values for the VPA data versus time with predicted values being smaller than observed values (positive residuals) for 1940–55 (figure 2). This result indicates that estimates of VPA biomass for sardines from the model were generally too small (biased low) for 1951–55 and too high (biased high) for 1957–65.

Estimates of sardine biomass ($\Phi_{VPA,y}$) from the general linear model (table 4 and figure 3) indicated that sardine biomass increased after 1984, although the trend was somewhat erratic. Sardine biomass increased from about 30,000 MT in 1984 to about 160,000 MT in 1988–89 and then fell to 115,000 MT in 1990. These results were similar to trends reported by MacCall (1979), MacCall and Prager (1988), and Smith (1990), although similarity would be expected since the same data were used. Confidence intervals for the estimates of sardine biomass were quite broad, particularly for years in which sardine biomass was estimated to be large (figure 3). The 95% confidence interval for sardine biomass during 1990 was 62,000–214,000 MT.

TABLE 4

Sardine Biomass Estimates from GLM Analysis (Thousand MT of Fish Age Two and Older), with Upper and Lower Bounds for 95% Confidence Intervals

Year	Lo 95%	Biomass	Hi 95%
1951	84	176	371
1952	48	101	213
1953	2	6	14
1954	103	216	455
1955	79	166	349
1956	59	124	261
1957	63	132	278
1958	135	284	597
1959	127	267	561
1960	83	176	370
1961	37	78	164
1962	12	24	52
1963	16	30	58
1984	14	30	65
1985	49	99	202
1986	28	57	117
1987	58	119	243
1988	78	160	326
1989	78	160	326
1990	62	115	214

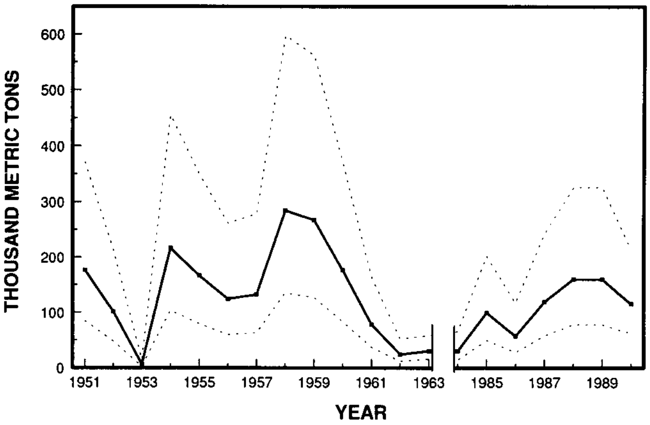

Figure 3. Sardine biomass estimates (age 2 and older) with 95% confidence intervals from a general linear model.

Egg Production Area Method

Since 1985, CDFG has used an egg production area method (Wolf and Smith 1985) and sea-survey data (table 2) to determine if sardine spawning biomass exceeded the 18,156-MT level necessary to allow a directed fishery. The area over which a specified or "threshold" spawning biomass would be expected to occur was:

$$A = \frac{B\,R\,F\,S\,m}{P_o\,k\,W}, \qquad (5)$$

where A is the spawning area occupied by the sardine population at biomass B, in nautical miles^2 (n.mi.^{2}); B is the spawning biomass (MT); P_o is the daily egg production, number eggs/0.05 m^2/day; W is the average weight of mature females (g); R is the sex ratio (fraction female, by weight); F is the batch fecundity (number eggs spawned/mature female/batch); S is the fraction mature females spawning per day; k is the conversion factor from g to MT; and m is the conversion factor from 0.05 m^2 to n.mi.^{2}. Equation 5 is derived from the original egg production method formula (equation 4 in Parker 1985) that expresses spawning biomass as a function of spawning area and other variables (Wolf and Smith 1986).

If the observed spawning area was equal to or greater than the threshold spawning area, then a quota was allotted for directed fishing. Using estimates for the parameters in equation 5, and assuming a sex ratio of 50% females by weight (table 5), the spawning area corresponding to 18,156 MT is 2,300 n.mi.^{2} (7,900 km^2). This may be an underestimate of threshold spawning area, since females may constitute slightly more than 50% of the population by weight. The estimate of 62% for sex ratio was based on a small number of samples and is assumed to be high. The observed spawning area exceeded the 2,300-n.mi.^{2} threshold in 1988, 1989, and 1991.

Sardine spawning area increased in each year after 1986, except in 1990 when it dropped below the level observed in 1987 (figure 4). The spawning biomass for sardines during 1990 (estimated by inverting equation 5) that corresponds to the observed spawning area of 1,480 n.mi.^{2} (5,083 km^2) is 12,000 MT. This estimate seems low relative to total sardine landings during 1990 (14,739 MT) as well as to biomass estimates from other sources for 1989 and 1990. Apparently the current best estimates for the parameters in equation 5 are imprecise, or the parameter values have changed over time. Additional research will be required if this approach is used in the future.

TABLE 5

Best Estimates for Parameters Used to Estimate Area Occupied by Spawning Sardines at the Threshold Level of Spawning Biomass (18,156 MT or 20,000 Short Tons)

Parameter	Symbol	Best estimate and units
Sex ratio	R	
Measured		62% females, by weight
Assumed		50%
Batch fecundity	F	62,500 eggs/batch/ mature female/day
Spawning fraction	S	11.5% spawning females/mature females/day
Conversion factor (0.05 m^2 to n.mi.^{2})	m	1.458×10^{-8} n.mi.^{2}/ 0.05 m^2
Conversion factor (0.05 m^2 to km^2)	m_1	5×10^{-8} km^2/0.05 m^2
Egg production	P_0	2.4 eggs/0.05 m^2/day
Conversion factor (g to MT)	k	1×10^{-6} MT/g
Female weight	W	172 g

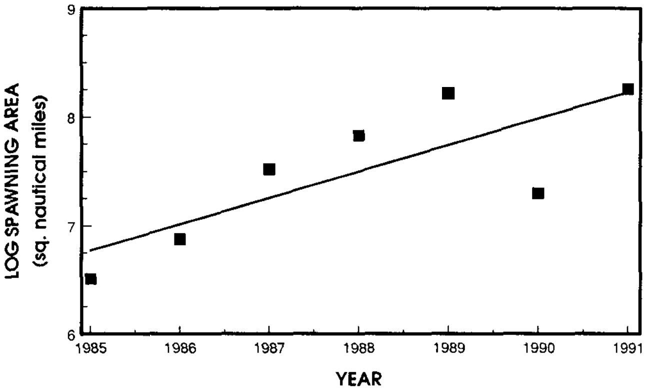

Figure 4. Sardine spawning area from CDFG sea surveys, 1985–91. Line was fitted by linear regression.

Linear regression was used to fit a line to the CDFG sea-survey data, with years as the independent variable, and the natural logarithm of relative spawning areas as the dependent variable (figure 4). Log-transformed spawning-area data increased in an approximately linear fashion during 1986–91, indicating that sardine spawning biomass increased exponentially. If the slope of the log-scale linear regression is b, then $\exp(b) - 1$ gives the average percent annual increase in spawning area from 1986 to 1991. The estimate of b obtained from the regression (0.242) corresponds to an average annual increase of 27% in sardine spawning area and biomass. The 95% confidence interval for the average annual increase was 8%–50%.

Life-Table Estimates

Sardine abundance during 1989 was estimated by simulation in a life table using three types of data: age composition of landings, tons landed, and CDFG estimates of spawning area. The most important assumptions in the simulation were that recruitment increased at a constant rate for the 1981–87 year classes and that total mortality rates for sardine did not change from 1983 to 1989.

Age-composition data for 1988–90 were combined because data and catch curves for individual years were similar, as would be expected under conditions such as those assumed for the simulation

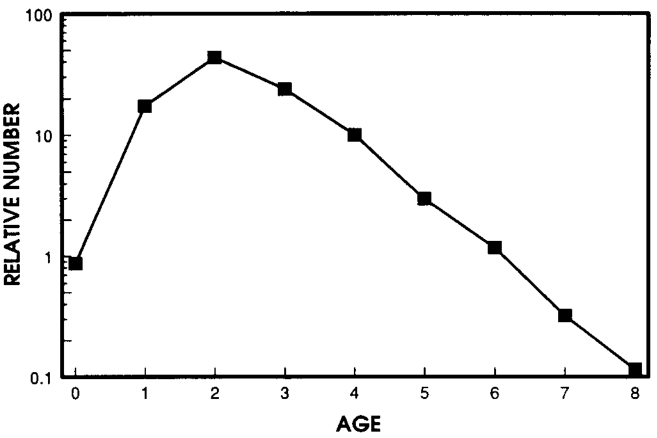

Figure 5. Sardine catch curve from commercial landings in southern California, 1988–90.

(Ricker 1975). Sardines age 3 and older were fully recruited to the fishery (figure 5 and appendix table C). The slope of the catch curve for fully recruited sardines during 1988–90 estimated by Heinke's method (Ricker 1975) from the combined data set was $Z_a = 1.13 \text{ yr}^{-1}$. If the number of sardine recruits had been constant in recent years, then 1.13 yr^{-1} would be a reasonable estimate of the actual instantaneous mortality rate (Z) experienced by fully recruited individuals in the stock. The assumption of constant recruitment was not plausible, however, because CDFG sea-survey data indicate that sardine spawning area and biomass increased by about 549% from 1986 to 1989. Density-dependent effects on recruits per unit of spawning biomass are thought to be minimal at low biomass levels, so it is likely that recruitment increased in proportion to spawning biomass and spawning area. Consequently, the slope of the catch curve (Z_a) was greater than the actual mortality experienced by the fully recruited ages (Z).

A simulated life table was constructed to account for the effect of increasing recruitment on age composition of landings and the slope of the catch curve. Recruitment in the life table was assumed to increase at a constant but unknown rate for the 1981–87 year classes, which were present as age-2 and older fish during 1983–89. The number of age-2 sardines in the simulation during 1989 (the 1987 year class) was assigned the arbitrary value of 100, and the number of recruits in previous years was calculated assuming a constant proportional rate of increase (α). Once the number of recruits in each year was specified, and assuming constant mortality (Z), the number of sardines in each year class from 1983 to 1989 could be calculated by standard methods:

$$N_{a,t} = N_{a-1,t-1}\, e^{-Z} \text{ and} \tag{6}$$

$$R_t = N_{2,t} = 100/\alpha^{1989-t} \tag{7}$$

where $N_{a,t}$ is the number of fish age a ($a > 2$) in year t (e.g., 1987); R_t is the number of recruits (2-year-old sardines) in year t; Z is the total mortality rate; and α is the proportional annual increase for recruitment.

We converted relative numbers of fish in each age during each year to relative biomass for each age group using mean weight-at-age data for sardines taken by the commercial fishery from 1988 to 1990:

$$B_{a,t} = N_{a,t} w_a \tag{8}$$

where w_a is the weight of fish age a. We derived weight at age from data in appendix B by using the mean of the monthly values for each year, then using the mean of the three annual estimates to obtain w_a.

	Age						
	2	3	4	5	6	7	8
w_a (Average weight [g] per fish)	139.1	161.8	173.5	181.5	193.3	191.6	192.8

Relative total biomass in each year was obtained by summing $B_{a,t}$ for each age. Relative spawning biomass in each year was calculated from relative biomass at age, assuming that one-half of sardines age 2 spawn and that all sardines age 3 and older spawn (Clark 1934; MacGregor 1957). We calculated the slope of the catch curve (Z_a) for sardines in the simulation by applying Heinke's method to the simulated age-composition data for 1988 to 1989.

We used an iterative approach to systematically vary the annual increase in recruitment (α) in the simulation until the ratio of spawning biomass in 1985 and in 1989 agreed with that actually observed. For each iteration we specified a new value of α, and adjusted the mortality rate in the model until the slope of the actual and simulated catch curves matched exactly. The simple ratio of beginning/ending year biomasses was suitable for solving the iteration because annual spawning area increased at a nearly constant rate from 1985 to 1989, making it unnecessary to match biomass estimates for each year in between. Intermediate years were fit by the simulation because of the assumption that recruitment also increased at a constant rate during those years. The closest match between the observed and simulated data was for α = 160% and $Z = 0.65 \text{ yr}^{-1}$.

	Observed	Life-table simulation
Ratio 1985/1989 spawning biomass	549%	535%
Slope from catch curves	1.13	1.13

An estimate of the fishing mortality rate (F) for sardines during 1983–89 was obtained from the estimate of total mortality:

$$F = Z - M \tag{9}$$

where M is the rate of natural mortality. The rate of natural mortality (M) for sardines is uncertain. Murphy (1966) and MacCall (1979) used $M = 0.4\ \text{yr}^{-1}$ for VPA analyses, although Murphy used $M = 0.8\ \text{yr}^{-1}$ for 1951 and later year classes. In this analysis we used a range of 0.3–0.6 yr^{-1} for M. Biomass in 1989 was calculated from the ratio of fishing mortality rate (annualized) and landings:

$$B_a = C/F \tag{10}$$

where B_a is the average biomass (MT) and C is total landings during 1989. Sardine landings during 1989 (C), assuming that the southern California and Ensenada fisheries exploit the same stock, amounted to 12,033 MT, and biomass estimates for 1989 ranged from 41,000 to 247,000 MT.

Z	M	F	Biomass (landings/F)
0.65	0.3	0.35	40,747
0.65	0.4	0.25	54,399
0.65	0.5	0.15	86,387
0.65	0.6	0.05	246,727

No particular value of M within the indicated range is thought to be the best estimate under current conditions. However, for the specific purpose of comparison with the historical biomass estimates given in table 2, the current biomass estimate associated with $M = 0.4$ (54,399 MT) is probably the most appropriate, because it is based on the same estimate of M that was adopted for the earlier VPA analyses.

The precision of life-table estimates for sardine biomass was not calculated, because the number of observations used to fit the model (spawning area in 1985 and 1989) were too few to obtain meaningful results from approaches based on asymptotic theory or bootstrap methods.

Factors Affecting Sardine Biomass

There has been a long and colorful debate (Radovich 1982) about the relative importance of environment, ecology, and fishing on short- and long-term changes in sardine abundance (Smith and Moser 1988). Water temperatures are believed to affect abundance (Radovich 1982), although a variety of other environmental factors have also been identified (Kondo 1980). The transition from warm to cold water in the early 1940s corresponds approximately to the decline in abundance at that time.

Data and results from our analyses, and new Scripps Pier temperature data extend the historical record for sardines (figure 6). Like the historical data, our new data indicate that water temperatures and fishing both affect abundance. The historical record (pre-1965) indicates that sardine biomass decreased in the late 1930s and early 1940s, when exploitation increased beyond 20% annually and sea-surface temperatures declined to or below the historical average (16.9°C). Exploitation rates during 1941–65, when sardine biomass declined consistently, were generally higher than 30% and, in 1958, as high as 68%. Temperatures during the same period were generally well below the historical average except during the 1957–59 El Niño.

Data and results for recent years (1965 and after) indicate that sardine biomass remained low during 1965–74, when recorded landings were nil and temperatures were generally below average. Biomass began to increase in about the late 1970s, when water temperatures increased beyond the historical average and exploitation rates remained near zero. Sardine biomass continued to increase from the late 1970s to 1990 as warm-water conditions continued and exploitation rates remained less than 10% per year. Thus, since the early 1930s, sardine biomass increased with warm water and low exploitation rates, and decreased with cold water and higher exploitation rates (>20% per year).

DISCUSSION

Sardine analyses prepared for the September 1990 workshop provided a foundation for discussions about the status and management of sardines. The workshop approach offered an effective format for assembling current data from diverse sources and developing timely population estimates needed for management during the initial stages of recovery. Concerns about weaknesses in individual analyses were alleviated by general agreement among the independent lines of evidence.

All of the analyses presented at the workshop indicated a generally increasing trend in sardine bio-

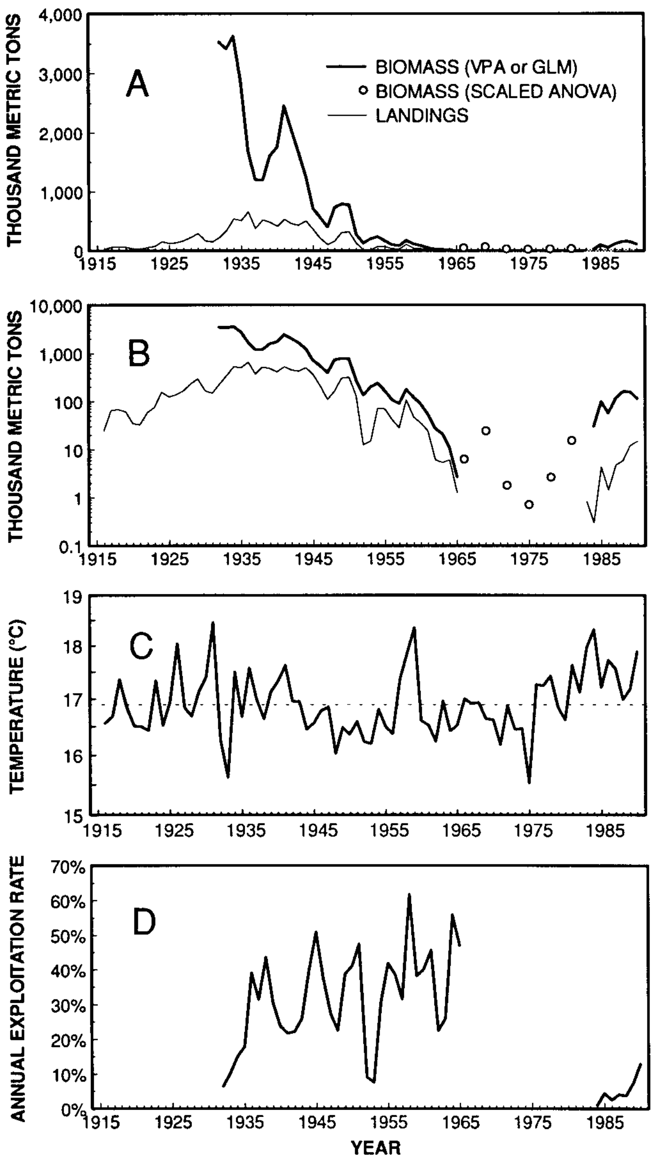

Figure 6. (*A,B*) Biomass estimates and landings data for Pacific sardines; (*C*) mean annual sea-surface temperature data from Scripps Pier; and (*D*) annual exploitation rates for sardines. Biomass estimates for 1932–44 are from VPA analysis by Murphy (1966); estimates for 1945–65 are from VPA analysis by MacCall (1979); estimates for 1966, 1969, 1972, 1975, 1978, and 1983 are scaled ANOVA values from figure 1 and MacCall and Prager (1988), with low-weight years omitted; estimates for 1984–90 are from a general linear model (table 4). Landings data for 1916–49 are from Murphy (1966); data for 1950–65 are from MacCall (1979); and data for 1983–90 are from table 1. Landings data for 1916–65 are for fishing seasons (e.g., the data for 1916 are for landings from June 1916 to May 1917); landings data for 1983–90 are for calendar years. The effects of mixing landings data from calendar years and fishing seasons are insignificant. A crude measure of annual exploitation for sardines in each year was obtained by dividing annual sardine landings (California plus Ensenada) by sardine biomass.

mass from the late 1970s to 1989. The rate of recovery slowed during 1990–91, but there was no indication of year-class failure.

The range of biomass estimates from our analyses was broad, illustrating the uncertainty about current sardine abundance levels. A subjective conclusion based upon a majority of the data and findings at the workshop was that the 1990 spawning biomass probably fell within the 95% confidence limits of the general linear model analysis, i.e., 60,000–210,000 MT.

The analyses described in this paper were designed to make simultaneous use of a variety of data, although no single assessment used all of the available data. The results we obtained indicate that more completely integrated models (Deriso et al. 1985; Gavaris 1988; Methot 1989) based on fishery-dependent and fishery-independent data will be useful for sardine assessments. We expect that one facet of sardine research will be to develop better population models of this type.

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APPENDIX

TABLE A

Sardine Length-Frequency Data (SL, mm) from Landings at Terminal Island and San Pedro, 1988–1990

Length	1988							1989						
(mm)	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
<151	1	—	—	—	—	—	—	4	—	—	—	—	—	—
151–155	—	—	—	1	—	—	—	6	—	3	2	—	—	—
156–160	—	—	—	—	—	1	—	1	—	3	6	—	2	1
161–165	—	—	—	1	—	1	—	2	—	22	12	—	8	3
166–170	—	—	—	3	—	—	1	—	1	17	19	—	7	8
171–175	—	—	—	3	—	3	—	2	—	12	20	—	10	7
176–180	1	2	—	9	—	9	—	4	—	7	16	—	4	3
181–185	3	5	1	5	—	7	—	1	—	11	9	—	7	17
186–190	7	—	1	9	—	10	—	7	—	5	8	—	13	43
191–195	11	—	4	4	—	4	1	17	5	9	4	—	9	63
196–200	29	—	3	14	—	3	—	21	4	16	13	—	7	45
201–205	23	1	16	23	2	5	—	13	5	8	14	1	12	39
206–210	20	—	29	36	5	9	1	26	11	19	12	—	24	28
211–215	19	3	51	46	10	13	3	27	20	25	23	2	20	39
216–220	7	9	39	71	8	21	7	58	33	36	37	—	32	43
221–225	4	16	29	36	5	8	6	39	47	39	46	3	40	28
226–230	—	12	11	31	3	17	5	33	28	29	41	8	17	12
231–235	—	7	3	9	2	14	4	18	27	13	32	5	13	5
236–240	—	7	5	6	—	7	4	11	7	5	26	1	7	4
241–245	—	1	—	1	—	1	1	2	4	1	10	3	3	—
246–250	—	1	2	2	—	—	1	2	3	1	12	2	—	—
251–255	—	—	1	—	—	—	—	1	1	—	3	—	—	—
256–260	—	—	—	—	—	—	—	—	—	—	4	—	—	—
261–265	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	125	64	195	310	35	133	34	295	196	281	369	25	235	388

Length	1989					1990								Total*
(mm)	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	
<151	—	—	—	—	—	5	—	—	—	—	—	—	—	10
151–155	—	—	—	—	—	—	—	—	—	—	—	—	—	12
156–160	—	—	—	—	—	1	—	—	—	—	—	—	—	15
161–165	1	—	—	—	—	—	—	—	—	—	—	—	1	51
166–170	2	—	2	—	—	—	—	—	—	—	—	—	2	62
171–175	8	—	6	—	—	—	—	—	—	—	—	—	1	72
176–180	27	14	21	1	5	2	—	1	—	—	—	—	2	128
181–185	46	25	55	3	9	14	2	—	—	—	—	—	4	224
186–190	85	23	118	15	35	39	4	5	6	—	—	—	3	436
191–195	149	47	190	20	46	93	6	21	7	—	—	—	2	712
196–200	177	50	223	30	64	115	19	49	4	—	—	—	—	886
201–205	127	51	101	15	51	108	41	77	13	1	2	2	—	751
206–210	134	37	37	7	17	132	39	131	16	1	5	4	5	785
211–215	173	39	23	4	7	93	40	103	12	2	23	24	12	856
216–220	148	43	23	2	8	85	48	155	14	8	32	42	14	1,023
221–225	104	36	11	2	4	56	52	118	8	5	57	41	36	876
226–230	47	25	4	—	2	36	26	91	10	6	63	47	40	644
231–235	14	15	—	—	—	14	22	32	1	4	48	30	22	354
236–240	6	12	—	—	—	7	9	15	1	6	34	23	17	220
241–245	2	5	—	—	—	1	4	6	2	1	18	10	3	79
246–250	—	1	1	—	—	—	3	2	1	1	6	13	4	58
251–255	—	—	—	—	—	—	—	3	—	—	4	7	1	21
256–260	—	1	—	—	—	—	—	—	—	—	—	—	2	7
261–265	—	—	—	—	—	—	1	—	—	—	—	—	—	1
Total	1,250	424	815	99	248	801	316	809	95	35	292	243	171	8,283

*June 1988–August 1990

TABLE B

Average Round Weight (g) by Age of Sardines from Landings at Terminal Island and San Pedro, 1988–1990

	Year class											Weighted average*
	1990	1989	1988	1987	1986	1985	1984	1983	1982	1981	1980	
1988												
Jun			—	96.0	137.2	163.8	146.0	—	—	—	—	136.6
Jul			—	133.0	194.0	197.7	202.1	175.0	230.0	—	—	194.5
Aug			—	117.3	152.0	166.4	185.9	205.0	218.0	—	—	155.5
Sep			—	105.1	155.4	175.1	188.0	—	—	—	—	157.6
Oct			—	—	146.4	162.2	—	168.0	—	—	—	151.5
Nov			55.0	90.2	153.6	180.3	196.8	201.0	183.0	184.5	—	152.7
Dec			—	—	136.3	146.7	152.0	—	—	—	—	173.9
1989												
Jan		—	110.4	116.2	141.7	161.5	184.4	199.0	—	—	—	154.9
Feb		—	80.5	116.8	173.2	197.7	200.7	203.0	213.0	167.5	—	176.6
Mar		—	69.2	108.0	163.6	170.2	185.1	—	—	—	—	139.9
Apr		—	75.5	104.5	164.5	204.2	217.1	230.8	195.4	197.0	182.0	150.9
May		—	—	149.0	186.5	164.5	192.3	—	—	—	—	181.2
Jun		64.3	98.3	133.6	162.2	164.6	186.6	201.2	—	—	—	149.5
Jul		83.9	106.2	119.8	150.3	158.5	169.2	192.8	—	—	—	132.6
Aug		111.1	111.8	127.9	148.5	156.4	166.0	—	—	—	—	134.5
Sep		—	108.3	133.2	153.4	180.1	185.1	175.4	—	—	—	132.9
Oct		84.8	101.3	116.0	138.4	160.8	138.2	148.1	—	—	—	104.9
Nov		—	108.6	122.3	125.2	—	159.3	—	—	—	—	112.2
Dec		—	103.8	117.9	120.0	153.3	131.4	—	—	—	—	108.1
1990												
Jan	—	89.4	123.4	147.8	158.3	170.2	160.5	147.9	—	—	—	134.2
Feb	—	121.9	130.1	157.8	170.0	168.2	160.2	—	—	—	—	148.1
Mar	—	116.0	134.2	157.4	162.9	165.3	170.4	185.7	192.4	—	—	151.7
Apr	—	110.4	134.8	156.5	167.4	185.8	—	—	—	—	—	148.3
May	—	—	128.4	168.9	183.2	197.9	—	—	—	—	—	171.7
Jun	—	—	163.0	177.7	184.5	197.8	190.5	210.4	—	—	—	180.9
Jul	—	—	156.3	171.6	176.1	185.6	189.3	200.9	214.3	—	—	173.0
Aug	60.5	—	162.1	163.7	172.7	176.4	189.3	—	—	—	—	166.5

*All ages combined

TABLE C
Age Composition (Number of Fish) of Sardines from Landings at Terminal Island and San Pedro, 1988–1990

	Year class											Sample size
	1990	1989	1988	1987	1986	1985	1984	1983	1982	1981	1980	
1988												
Jun			1	2	99	6	2	—	—	—	—	110
Jul			—	6	9	24	17	4	1	—	—	61
Aug			—	6	142	12	10	2	1	—	—	173
Sep			3	30	206	34	20	—	—	—	—	293
Oct			—	—	28	5	—	1	—	—	—	34
Nov			1	29	64	16	15	3	1	2	—	131
Dec			—	—	4	3	1	—	—	—	—	8
1989												
Jan		—	15	25	73	15	8	3	—	—	—	139
Feb		—	2	4	142	22	11	6	1	2	—	190
Mar		—	63	38	140	16	15	—	—	—	—	272
Apr		—	41	13	58	17	24	9	5	1	1	169
May		—	—	3	16	2	4	—	—	—	—	25
Jun		7	18	55	62	7	8	1	1	—	—	159
Jul		7	56	178	117	20	7	2	—	—	—	387
Aug		5	51	184	197	45	10	—	—	—	—	492
Sep		—	143	112	75	19	5	2	—	—	—	356
Oct		7	670	81	30	4	1	1	—	—	—	794
Nov		—	75	19	3	—	1	—	—	—	—	98
Dec		—	173	60	6	1	1	—	—	—	—	241
1990												
Jan	—	48	386	218	78	13	15	1	—	—	—	759
Feb	—	1	132	120	43	10	5	—	—	—	—	311
Mar	—	5	298	285	127	47	23	5	1	—	—	791
Apr	—	7	44	25	11	8	—	—	—	—	—	95
May	—	—	4	16	12	3	—	—	—	—	—	35
Jun	—	—	56	84	105	27	14	5	—	—	—	291
Jul	—	—	48	79	76	22	12	5	1	—	—	243
Aug	5	7	56	45	40	10	6	—	—	—	—	169
Total	5	94	2,336	1,717	1,963	408	235	50	12	5	1	6,826

RECOVERY OF THE PACIFIC SARDINE AND THE CALIFORNIA SARDINE FISHERY

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ABSTRACT

The Pacific sardine (*Sardinops sagax*) supported the largest fishery in North America in the 1930s and 1940s, but was severely depleted by the 1970s. A moratorium on fishing sardines was enacted in 1974 and remained in effect until 1986, when a small directed fishery was allowed. As the population increased, small quotas for live and dead bait were established, and the directed quota was increased in 1991 and 1992. Management efforts were designed to ensure the continued recovery of the sardine while providing a small catch and minimizing the impact of the incidental catch of sardines in the mackerel fishery. A series of management workshops in recent years generated estimates of sardine abundance, and strategies for managing the recovering resource. With the traditional fleet in economic difficulty and offshore fishing by factory trawlers a possibility, the future of the sardine fishery is uncertain.

RESUMEN

La sardina del Pacífico, (*Sardinops sagax*), sostuvo la pesquería mas grande de Norteamérica durante los 30 y los 40; sin embargo, durante los 70 el stock se encontraba sumamente diezmado. En 1974 se estableció una moratoria a la pesca, permaneciendo en efecto hasta 1986, año en que se autorizó una pequeña captura. A medida que la población incrementó, se permitieron pequeñas capturas de sardina a usarse como carnada. Los tamaños de captura directa permitida aumentaron en 1991 y 1992. La administración de esta especie fué diseñada con el objetivo de asegurar su recuperación continua, permitiéndose a la vez una captura pequeña, y para minimizar las capturas incidentales del recurso en la pesquería de la macarela. Una serie de talleres sobre la administración de la sardina produjeron estimaciones de la abundancia del recurso y, por otro lado, estrategias para la recuperación del mismo. Debido a las dificultades económicas que enfrenta la flota tradicional y a la posibilidad de una pesca de altura por buques-factoría de arrastre, el futuro de la pesquería de la sardina es incierto.

INTRODUCTION

The Pacific sardine (*Sardinops sagax*) fishery began in central California in the late 1800s and developed in response to a demand for food during World War I (Schaefer et al. 1951). From the mid 1930s to the mid 1940s the fishery was the largest in the Western Hemisphere (Frey 1971a; Ahlstrom and Radovich 1970), with peak landings of over 790,000 short tons[1] in the 1936–37 season, and average landings over 600,000 tons per season (figure 1). The fishery began to collapse a few years later, and catches declined over the next two decades, with short-term reversals, to less than 100 tons per year in the 1970s. Sardine biomass (figure 2) declined from nearly 4 million tons in the mid 1930s to levels thought to be as low as 5,000 tons by the 1970s (Murphy 1966; Smith 1972; MacCall 1979).

Most sardine landings during the historical fishery were made in California (figure 1). The fishery collapsed first in the north, with landings ceasing in the Pacific Northwest in 1949–50 and in northern California in 1952–53. The catch was insignificant by the early 1960s, and most subsequent landings have occurred in southern California and Baja California, Mexico (Radovich 1982).

Sardines harvested in the historical fishery were primarily canned or reduced to fish meal and oil, although small amounts were used for live and dead bait. Reduction of sardines began as a means to utilize offal from the canning process, but whole sardines were soon used because the production of meal and oil was often more profitable than canning. The state of California favored human consumption over reduction, and most regulations were designed to limit the excess reduction of edible fish (Schaefer et al. 1951).

Before 1967, management of the sardine fishery consisted almost exclusively of controls on tonnage of whole fish used for reduction under permits issued to noncanning processors; case pack requirements to limit the amount of reduction by canners; and restriction of the fishing season to ensure that fish were in prime canning condition and that markets were not saturated (Schaefer et al. 1951; Frey 1971a). Reduction ships operated in waters beyond the jurisdiction of the state from about 1930 to 1938, until a voter-approved initiative restricted vessels

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[1] Commercial landings, biomass estimates, tonnages specified in legislation, and quotas are reported in short tons throughout this paper.

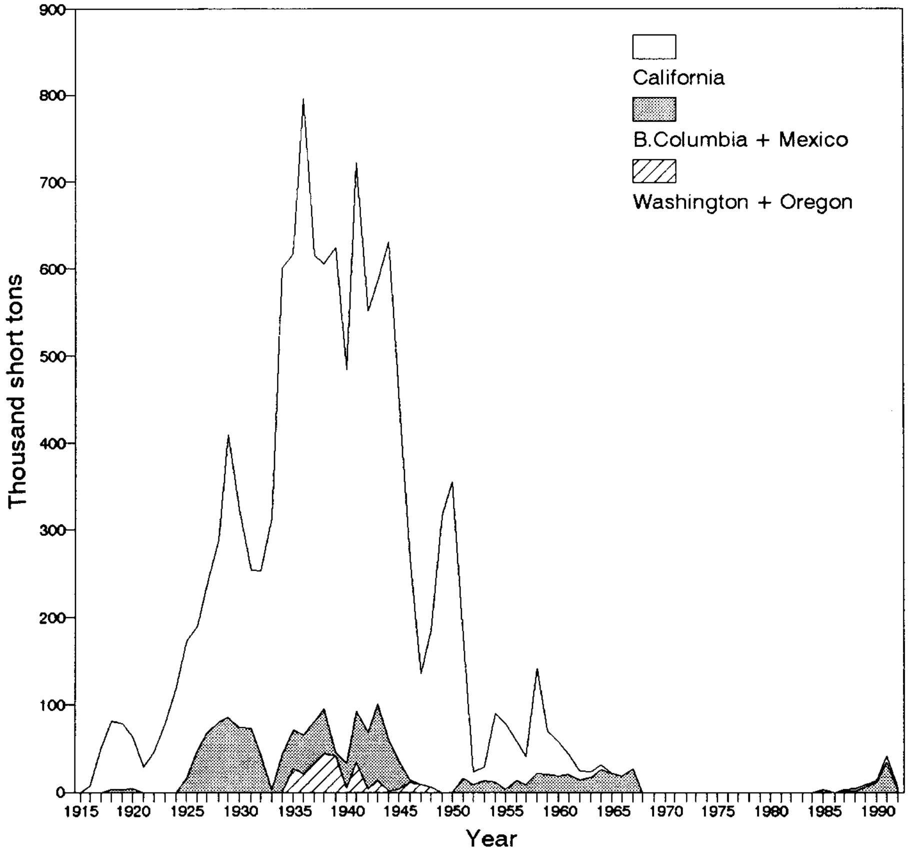
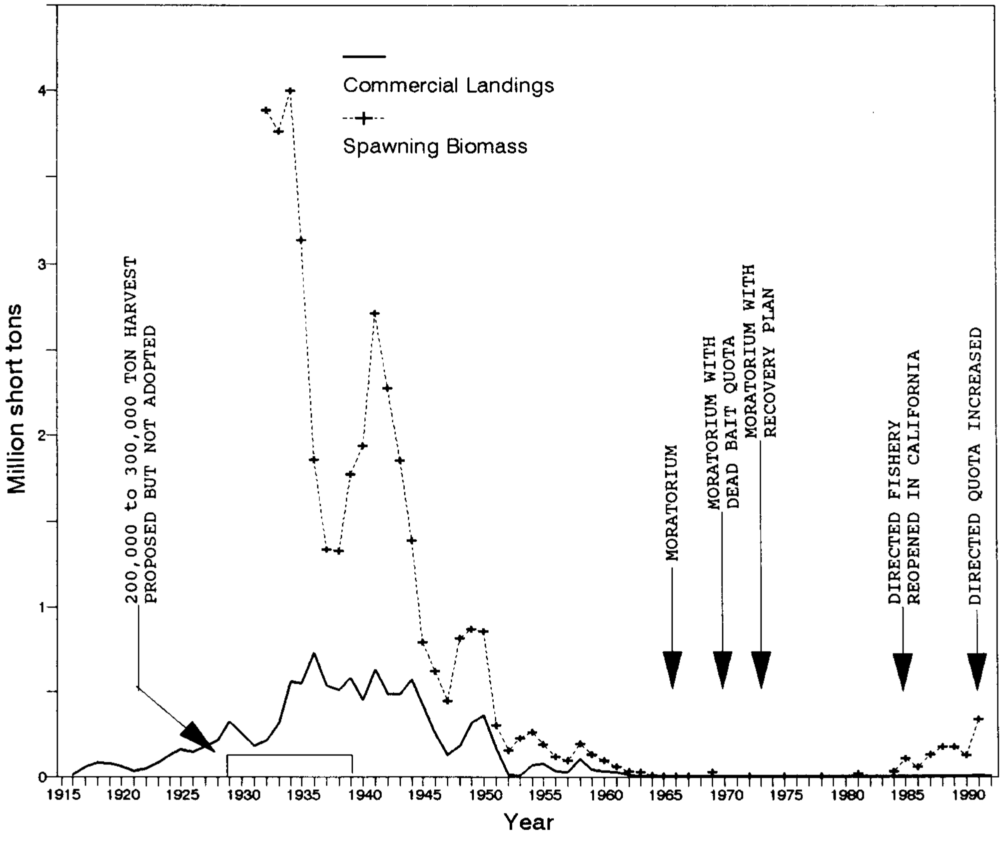


Figure 1. Sardine landings in short tons from 1916 through June 1992. The gray portion of the curve shows British Columbia landings before 1949, and Ensenada, Mexico, landings after 1950. California landings from Frey 1971a for years 1916–69 and from CDFG records for years 1970–June 1992. British Columbia, Washington, and Oregon landings from Radovich 1982 (seasonal landings were assigned to calendar year of the first half of season). Ensenada landings from MacCall 1979 for seasons 1951–52 to 1965–66; Barnes et al. 1992 for years 1983–91; and Walterio Garcia, Instituto Nacional de Pesca, pers. comm., through June 1992.

Figure 2. Sardine landings (California and Ensenada, Mexico) and spawning biomass (fish age 2+) in short tons. California landings from Frey 1971a for years 1916–69 and from CDFG records for years 1970–June 1992. Ensenada landings from MacCall 1979 for seasons 1951–52 to 1965–66 (seasonal landings were assigned to calendar year of the first half of season); Barnes et al. 1992 for years 1983–91; and Walterio Garcia, Instituto Nacional de Pesca, pers. comm., through June 1992. Before 1951, and from 1966 to 1982, Ensenada landings are not available. Biomass is from Murphy 1966 for years 1932–44, MacCall 1979 for years 1945–65, and Barnes et al. 1992 for years 1966, 1967, 1969, 1972, 1975, 1978, 1981, 1984–91.



that fished in state waters from delivering to the reduction ships, and market conditions also declined.

The regulatory history of the sardine fishery might best be described as "too little too late." Regulatory authority for the sardine fishery in California rested with the legislature, which delegated only limited authority to the Fish and Game Commission. State biologists expressed concern about the size of the sardine fishery and the threat of resource depletion as early as 1930 and suggested that authority to regulate the total catch be given to the state fisheries division (Schaefer et al. 1951). Recommendations to limit total catch of sardines to levels ranging from 200,000 to 300,000 tons were made as early as 1929, and by various researchers over the next several years (Scofield 1932, 1934; Clark 1939), but no such action was taken (figure 2). Industry opposed any regulation of total catch, and a long and intense debate ensued over whether the decline of the sardine fishery and population was due to overfishing or environmental factors (Clark and Marr 1955). Although the sardine crisis gave rise to extensive and innovative research (Scheiber 1990), the debate also clouded the issue and deferred measures that were necessary for effective control of the fishery (Radovich 1982).

In 1967, well after the fishery had collapsed, the California legislature passed an "emergency" bill (Assembly Bill [AB] 743) declaring a two-year moratorium on fishing sardines (figure 2). Ahlstrom and Radovich (1970) characterized this as the most decisive management action in the 50-year history of the fishery, and as an acknowledgment that the fishery had ceased to exist. The law eliminated direct harvest of sardines for reduction and canning, but allowed an incidental catch of 15% by weight mixed with other fish in a load. Most of the incidentally landed sardines were supplied as dead bait to a lucrative market in central California and sold for $200 to $400 per ton, which was considerably higher than the $70–$75 price for sardines landed at the canneries (Hardwick 1968).

In 1969, AB 564 was enacted to permit 250 tons of sardines to be landed annually for dead bait, with the provision that boats could possess and land no more than 3 tons per day. The price had increased to $300–$500 per ton (Frey 1971b). The value of sardines as dead bait and the new quota resulted in an increase in the harvest during 1970–72 (Crooke 1972). Sardines landed incidentally after the quota was reached could be used for canning, preserving, and reduction only. After the passage of AB 564, this bait market remained the most significant economic factor in the sardine fishery (Haugen 1973).

In 1974, Senate Bill (SB) 192 established a complete moratorium on directed fishing for sardines. The incidental catch provision continued, except that use was restricted to canning or reduction to eliminate the dead bait market. This measure also required the California Department of Fish and Game (CDFG) to monitor the status of the resource annually, and provided for a 1,000-ton directed fishery when the spawning biomass reached or exceeded 20,000 tons. In addition, this legislation established the intent of the legislature to rehabilitate the sardine resource and authorized CDFG to regulate total catch: as the spawning population increased above 20,000 tons, the seasonal quota could be increased, but only to the extent that the population could continue to increase, and with the long-term objective of maximizing the sustained harvest. The moratorium appears to have been successful, because sardine biomass has apparently increased (Barnes et al. 1992). Following the moratorium, and in accordance with SB 192, a small directed fishery was first allowed in 1986, and has recently been increased.

The purpose of this paper is to describe management and monitoring efforts during the moratorium, and to review management and fishery developments in California during the early recovery of the Pacific sardine resource following the moratorium.

THE MORATORIUM, 1974–1985

Monitoring and Management

From 1974 through 1978, sardines occurred rarely as incidental catch in the mackerel fishery (consisting of jack mackerel, *Trachurus symmetricus*, and Pacific mackerel, *Scomber japonicus*); rarely or not at all in CDFG night-light surveys and midwater trawl surveys for young-of-the-year pelagic fish; and rarely in California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton surveys (Klingbeil 1975, 1976, 1977, and 1978). Beginning in 1979 and continuing through 1981, live bait fishermen in southern California reported more frequent encounters with juvenile sardines; sardines increasingly appeared in young fish surveys; and sardines appeared more frequently in mackerel landings, although still in small amounts (Klingbeil 1979, 1980, 1981). Incidental landings of sardines in the mackerel fishery increased steadily to 145 tons in 1982, and to 388 tons in 1983 (table 1). This was the largest take since 1966, before moratorium regulations were established. Mackerel and live bait fishermen reported increased sightings of sardine schools, and sardines

TABLE 1
Landings (Short Tons) in Sardine Fisheries, 1974–1991

	Incidental				Directed			Dead bait				Live	
Year	North	South	Total	Percentage*	North	South	Total	North	Central	South	Total	bait	Total
1974		7	7										7
1975		3	3										3
1976		27	27										27
1977		6	6										6
1978		5	5										5
1979		18	18										18
1980		38	38									14	52
1981		31	31									9	40
1982		145	145									41	186
1983		388	388									213	601
1984	70	188	258									68	326
1985	37	615	652	1.3								16	668
1986	45	797	842	1.4	79	363	442					21	1,305
1987	20	1,863	1,885	3.1	22	401	423					238	2,546
1988	11	3,075	3,087	5.0	0	1,085	1,085					55	4,227
1989	4	2,871	2,875	4.4	258	924	1,182				250	111	4,418
1990	69	1,395	1,464	3.9	269	1,369	1,638	0	188	50	238	599	3,939
1991	0	1,295	1,295	3.4	1,075	5,747	6,822	0	424	70	494	300	8,911

*Percentage by weight of sardines in total mackerel (Pacific mackerel, jack mackerel, and sardine) landings. Before 1985, sardines were less than 1% of total.

in the live bait fishery and CDFG sea surveys increased as well (Klingbeil and Wolf 1984).

Concern about the increasing availability and incidental take of sardines resulted in two pieces of legislation in 1983. AB 394, passed as an urgency measure in April, required CDFG to monitor incidental catch of sardines, and allowed the percentage of sardines that could be taken incidentally to increase or decrease. Specifically, the tolerance would increase from 15% to 25% if the overall percentage of sardines in the mackerel fishery (consisting of Pacific mackerel, jack mackerel, and sardines) exceeded 5% in the preceding month. Subsequent increases in 10% increments (up to 45%) would result if the percentage of sardines exceeded one-third of the previously established tolerance. Similarly, the tolerance level would decrease by 10% increments (down to 15%) if the percentage of sardines in the mackerel catch was less than one-fourth the tolerance limit of the preceding three months. This legislation was designed to lessen the impact of the recovering sardine resource on other fisheries, particularly the mackerel fishery.

AB 457, which took effect in January 1984, allowed the first 250 tons of sardines taken incidentally during the year to be used for any purpose (table 2). This measure once again made sardines available for the dead bait market, but since the market was then primarily supplied by imported sardines, it was expected that demand for local fish landed in California would be moderate. After the first 250 incidental tons were landed, incidentally landed sardines could be used for live bait, reduction, and canning, but not for dead bait. As a result, fresh fish markets without canning or reduction facilities could sell sardines as fresh fish during part of the year (before the 250-ton quota was filled), and incidentally caught sardines could be used for live bait.

In 1984 incidental landings of sardines declined in comparison to 1983 landings, but the frequency of sardines in CDFG midwater trawls remained high, and sardines occurred incidentally with the mackerel catch in Monterey. The incidental catch in the live bait fishery also increased.

AB 3403, which was passed in September 1984, extended the statutes regulating incidental take of sardines until July 1, 1986. In addition, this bill established a 75-ton annual live bait quota (table 2) for sardines under a revocable permit, and required fishermen who took live bait to submit logbooks. Both of these provisions were again intended to minimize the impact of the increasing sardine population on fishermen and dealers.

The 1985 incidental catch totaled 652 tons (table 1), the largest annual take in 20 years. For the first time, landings in the Monterey mackerel fishery accounted for a sizable fraction (6%) of the statewide catch, and fishermen in the area reported sighting "pure" sardine schools on several occasions (Klingbeil 1986). A decline in sardine landings for live bait during 1985 was attributed to decreased demand, since live bait haulers often targeted on squid that had recently become available (Klingbeil 1986). The

TABLE 2
Quotas and Incidental Tolerance Limits for Sardine Fisheries, 1974–1991

Year	Incidental tolerance (by weight)	Quotas (short tons)			
		Live bait	Directed	Dead bait	Total
1974–82	15%	—	—	—	
1983	15%	—	—	(250)[a]	
1984	15%	75	—	(250)	75+[b]
1985	15%	150	—	(250)	150+
1986	15%	150	1,000	(250)	1,150+
1987	25%	350	1,000	(250)	1,350+
1988	35%	350	1,000[c]	(250)	1,350+
1989	35%	350	1,000	250[d]	1,600+
1990	35%	350	1,000	250[e]	1,600+
1991	35%	350	6,150	500	10,000[f]
1992	35%	1,000	20,500	500	25,000

[a] Dead bait landings were included in incidental catch: the first 250 tons of incidental catch could be used for any purpose, including dead bait.
[b] Total incidental catch was unrestricted and variable.
[c] Directed quota was allocated 20% for north, 80% for south.
[d] Separate 250-ton dead bait quota was established (500 tons if directed quota is 2,500 tons or more).
[e] Directed quota allocation was changed to ⅓ for north, ⅔ for south.
[f] Incidental catch (3,000-ton reserve) was included in total harvest.

sardine live bait quota was increased from 75 to 150 tons by AB 426, which became effective on January 1, 1986.

Population Assessment

From 1974 through 1985, annual assessments of the sardine population were limited to a qualitative examination of various sources of information, including incidental and live bait fishery data, CDFG sea-survey catches of young sardines, the occurrence of sardine eggs and larvae in CalCOFI ichthyoplankton surveys, observations by aerial fish spotters employed by industry, and anecdotal information. The data were sufficient to indicate trends in sardine biomass, but no direct estimates of the biomass were attempted. The annual assessment requirement established by SB 192 was met by a statement that the sardine resource appeared to remain below 20,000 tons, and the moratorium continued (Klingbeil 1975, 1976, 1977, 1978, 1979, 1980, 1981, 1982, 1983a; Klingbeil and Wolf 1984; Wolf 1985).

The indirect information available in 1985 indicated that sardine biomass might be approaching 20,000 tons, so attempts were made to estimate the biomass directly. Wolf and Smith (1985) used the extent of spawning area, defined by the number of sampling stations in which sardine eggs were present, to determine if the sardine spawning biomass was greater than 20,000 tons. The first spawning area survey was conducted in 1985, and the spawning area (670 n.mi.^{2}; table 3) indicated that the spawning biomass was at least 20,000 tons (Wolf and Smith 1986). As a result, CDFG announced a 1,000-ton fishery for the 1986 season, thus ending the 12-year moratorium (Wolf and Smith 1986).

THE EARLY RECOVERY, 1986–1991

Fishery Management

1986. The 1986 directed sardine fishery opened on January 1, 1986, with a quota of 1,000 tons (table 2). Landings were steady, but averaged only about 150 tons per month, since fishermen continued to fish for mackerel during this period. The fishery was closed on July 11, when the quota was reached. All landings of sardines made during the open fishing period, including "pure" loads and sardines caught incidentally with other species, were counted against the quota. Directed landings totaled 79 tons in northern California and 363 tons in southern California, and were used primarily as dead bait for the central California striped bass fishery. Incidental landings continued after the close of the quota season, with a total of 842 tons taken incidentally with mackerel during the year (table 1), and canned with mackerel as pet food. Sardines contributed 1.4% of the total mackerel catch, and occurred in about 60% of the landings.

Sardine live bait catch totaled 21 tons, and was well below the 150-ton quota. The availability of squid, often a preferred bait for big game fish, again resulted in a decreased demand for sardines. Landings from all sources totaled 1,305 tons in 1986 (table 1).

1987. The 1987 directed sardine fishery opened on January 1 with a quota of 1,000 tons. Landings averaged 325 tons per month until the quota fishery was closed on April 17. The 1987 fishery lasted a little more than half as long as the 1986 fishery. Directed landings totaled 423 tons (401 tons in northern California and 22 tons in southern California) and accounted for 32% of the 1,000-ton quota. Following the closure of the directed fishery, the incidental tolerance limit was increased from 15% to 25% by weight (table 2) because sardines constituted 5% of the total mackerel landings in March. Incidental landings for 1987 totaled 1,885 tons. Sardines composed 3.1% of total mackerel landings during the year.

Sardines were an important component of the live bait fishery in the first half of 1987, primarily because schools of northern anchovy (*Engraulis mordax*) were unavailable. To alleviate the effects of poor bait availability on the sportfishing industry, AB 1093 was enacted to increase the live bait quota from 150 to 350 tons (table 2). The live bait catch totaled 238 tons for the year. Landings from all sources totaled 2,546 tons in 1987 (table 1).

1988. The 1988 directed sardine fishery opened on January 1 with a quota of 1,000 tons, and differed considerably from the directed fisheries of the previous two years. The quota was landed in only two weeks, and the fishery was closed on January 15. The increasingly shorter duration of the directed fishery, and the large proportion (81%) of pure loads suggested that sardines were more available to fishermen and that pure schools were more common. About 59% of landings in 1986 and 65% of landings in 1987 in the directed fishery were incidental and mixed with mackerel. Most of the landings in 1986 were made by a single vessel, but in 1988 several purse seine boats were fishing for sardines. In 1988, for the first time since the late 1960s, sardines were canned for human consumption, and the product was test-marketed. Some of the catch was still canned for pet food, but considerably less was used for dead bait.

Directed landings totaled 1,085 tons, and were made entirely in southern California. Incidental landings for the year totaled 3,087 tons, of which only 11 tons were landed in Monterey. The tolerance limit for sardines landed incidentally with mackerel was increased from 25% to 35% in April (table 2), because sardines constituted 11% of total mackerel landings during March. Fishermen in southern California complained that sardines were so abundant they interfered with fishing on traditional mackerel grounds, particularly around the northern Santa Barbara Channel Islands. Even though incidental landings of sardines dropped below 8.75% during subsequent three-month periods, CDFG did not reduce the 35% tolerance limit. The catch of sardines in live bait totaled 55 tons. Landings from all sources in 1988 totaled 4,227 tons (table 1).

Fishermen reported that they were setting on schools with a high percentage of sardines but not landing the fish because of low tolerance limits and because the canneries generally would not buy such loads, since the fish were marketed as mackerel. Legislation (AB 4064) was passed in 1988 allowing the tolerance limit to be increased based on fish taken or wrapped in a net rather than only landed. This was largely a symbolic gesture, however; higher tolerance limits were rarely exceeded because of the cannery restrictions. Provisions of AB 4064 also allocated the directed fishery quota between northern and southern California (20% of the quota was reserved for fishermen landing their catches north of Point Buchon, San Luis Obispo County, and 80% for fishermen landing their catches south of Point Buchon). This allocation assured Monterey fishermen and processors access to sardines. Monterey boats usually participated in the Pacific herring (*Clupea harengus*) fishery in January, and local fishermen and processors complained that sardines were generally not available in central California until later in the year when the sardine quota had been taken by fishermen in the south. AB 4064 also established a 250-ton quota (500 tons if the directed quota was increased to 2,500 tons or more) specifically for dead bait purposes; this quota was available beginning on March 1 of each year.

1989. The 1989 directed fishery opened on January 1 with a 1,000-ton quota (200 tons allocated to landings in northern/central California and 800 tons allocated to southern California). Directed landings in southern California totaled 924 tons, and the fishery closed on January 12, three days earlier than the previous year. No landings were made in northern/central California until February, and the fishery remained open until early April. Directed landings in the north totaled 258 tons, and consisted almost entirely of pure loads of sardines. Most of the catch in both areas was canned for human consumption. Incidental landings totaled 2,875 tons, and almost all were made in southern California. Sardines contributed 4.4% of total mackerel landings.

The 250-ton dead bait fishery for 1989 was closed on March 20, when it was estimated that the quota had been filled. This quota was difficult to monitor because processors were not required to specify the use of purchased sardines on landing receipts. Unless a landing exceeded the tolerance limit (35% sardines by weight), sardines in the load were generally not declared as dead bait. Landings of sardines in live bait totaled 111 tons. Landings from all sources totaled 4,418 tons in 1989 (table 1).

Legislation (AB 2351) was enacted in March 1989 and went into effect on January 1, 1990, allocating the dead bait quota so that 125 tons were reserved for landings south of Point Buchon, 50 tons between Point Buchon and Pescadero Point (San Mateo County), and 75 tons north of Pescadero Point. This bill also specified that all sardine fishing for dead bait required a written order from a processor; all fish had to be landed in a whole condition; and landing receipts had to specify use. These measures were intended to ensure that dead bait allocations were used for that purpose, and to facilitate monitoring of the quota.

1990. The 1990 directed fishery opened on January 1 with a 1,000-ton quota allocated in the same manner as the previous year. The fishery in southern California was closed on January 6 after only six days of fishing, with a total catch of 1,369 tons. Sardines were abundant and available near the Los Angeles Harbor. Fishing in northern California began in late January and was closed on April 25, with a total take of 269 tons. Most of the directed catch was used for human consumption, the remainder for dead bait and pet food. Incidental landings totaled 1,464 tons and represented 3.9% of the total mackerel catch. This represented a 49% decline in incidental landings, and was the third year the proportion of sardines in the incidental catch declined. However, the decline in incidental landings was largely attributable to a decline in the mackerel catch.

The dead bait fishery opened coastwide on March 1, 1990. The southern California fishery was closed on March 2, after 188 tons were landed (125-ton allocation) in only two days of fishing. The central California allocation (50 tons) was met on April 10. No landings were made against the northern allocation (50 tons). The sardine live bait catch totaled 599 tons; landings exceeded the 350-ton quota because of an error in tallying the logbook catch. Landings from all sources totaled 3,939 tons in 1990 (table 1).

AB 3861, passed in March 1990, modified the allocation formula for the directed fishery by reserving one-third of the quota for fishermen landing their catches north of San Simeon Point (San Luis Obispo County) and two-thirds for fishermen landing their catches south of that point. An opening date of August 1 was established for the northern area directed fishery. In addition, the allocation formula for the dead bait quota was changed to reserve 62 tons for fishermen landing their catches north of Pescadero Point, 62 tons for fishermen landing their catches between Pescadero Point and San Simeon Point, and the remainder for fishermen landing their catches south of San Simeon Point. Such quota allocations were of a political rather than management nature, and in general CDFG maintained a neutral position in such decisions. The boundary between northern and southern California was changed to discourage southern California boats that fished in southern California from landing their catches in a port north of the boundary and thus against the northern quota allocation; landings were made in Morro Bay (north of Point Buchon and south of San Simeon Point) during 1990 and trucked south.

AB 3211, enacted in September 1990 and effective immediately, allowed sardines taken incidentally to be used for any purpose. Use restrictions on incidentally taken sardines were eliminated because sardine abundance was increasing, because there was now a separate dead bait quota, because dead bait demand had apparently decreased as a result of a decline in the central California striped bass fishery, and so that incidentally harvested sardines could be used for human consumption.

1991. Initial quotas in 1991 were based on a total harvest target of 5% of the estimated spawning biomass of 100,000 tons. In addition to the 350-ton live bait quota and the 250-ton dead bait quota (which were fixed by statute), 3,000 tons were reserved for expected incidental landings. The initial directed quota was set at 2,499 tons, with one-third (833 tons) reserved for the northern allocation and two-thirds (1,667 tons) for the southern allocation. The directed quota was 79% higher than a strict 5% harvest would dictate (1,400 tons, given the incidental reserve and fixed quotas), but less than 2,500 tons, which was the level of directed quota that would trigger an increase in the dead bait quota from 250 to 500 tons. The low incidental catch in 1990 and the reduced allocation percentage of the directed quota for southern California were also considered in setting the initial directed quota for 1991. This was the first time the directed fishery quota was higher than the 1,000-ton level, and represented a change in management to control the total harvest, including consideration of the incidental catch.

The 1991 directed fishery opened in southern California on January 6. In an effort to minimize landings over the quota, the southern directed fishery was opened for one day (24-hour period) per week until the quota was reached. This strategy was designed to provide adequate time for mailing notices of fishery closures to sardine fishermen as required by law, and helped prevent overharvests (such as occurred in 1990) resulting from the large daily landing capacity of the fleet and the relatively small quota. A total of 1,879 tons was landed against the 1,667-ton quota during two 24-hour fishing periods, and the fishery was closed on January 14, 1991.

Following a reexamination of information about the status of the sardine resource, the 1991 total harvest level was increased to 10%, or 10,000 tons. This resulted in a 6,150-ton directed fishery quota, with 4,100 tons allocated to southern California and 2,050 tons to northern California. The dead bait quota was increased to 500 tons as required; the live bait quota remained at 350 tons; and the incidental catch reserve remained at 3,000 tons (table 2). The southern California directed fishery opened again on March 4, with a 2,434-ton quota. The fishery was closed on March 25 with 2,636 tons landed during four 24-hour fishing periods; the catch was canned for human consumption.

The northern California directed fishery opened on August 1 with a 2,050-ton allocation. The fishery remained open for the rest of the calendar year, and 1,075 tons were landed against the quota. The fishery was closed after only five months because the legislation that changed the opening date of the northern fishery did not provide for a year-round fishery, but rather prohibited fishing north of San Simeon Point before August 1 of each year.

The dead bait fishery opened in all areas on March 1. The southern area fishery was closed on April 8, with 424 tons landed during one 24-hour fishing period. The central area fishery closed on May 24, with 70 tons landed. No landings were made against the northern area quota. The sardine live bait catch in 1991 totaled 300 tons.

In October, CDFG estimated that only 1,000 tons of the 3,000-ton incidental reserve would be landed by the end of the year, and made the remaining 2,000 tons available as a directed quota. The southern California allocation (1,333 tons) opened on October 27, and 1,232 tons were landed in two 24-hour fishing periods. The fishery closed on November 4. There were no additional landings made against the northern allocation. Incidental landings for 1991 totaled 1,295 tons, and represented 3.4% of the total mackerel catch. The incidental catch was low, primarily because of a decrease in mackerel landings. Landings from all sources during 1991 totaled 8,911 tons (table 1).

AB 173, enacted in July 1991 and effective immediately, reestablished the procedures for setting tolerance limits for incidentally taken sardines. The original legislation eliminated this section of the Fish and Game Code in January, but the 35% tolerance limit was enforced during the interim. AB 173 also extended the 350-ton live bait quota, and allowed CDFG to increase the live bait quota beyond the 350-ton level, provided such increases do not impede the recovery of the sardine resource. This bill allowed sardines taken as dead bait to be sold to commercial fishermen; previously, sardines so caught could be sold only for use by sport anglers.

Summary. With the exception of 1990, total sardine landings increased steadily between 1986 and 1991 (table 1). The largest increase was between 1990 and 1991, mainly because of the increase in the directed quota, and to a lesser degree because of an increase in the dead bait quota. Directed landings increased fourfold between 1986 and 1990, and fourfold between 1990 and 1991. The live bait catch varied between 1986 and 1991, but increased overall. The incidental catch increased between 1986 and 1988, but declined each year thereafter, partly because of the decline in mackerel landings (Wolf 1992). The proportion of sardines in the mackerel fishery peaked in 1988 at 5%, and declined steadily through 1991. Although the occurrence of sardines in the mackerel fishery was believed to indicate sardine abundance, there does not appear to be a relationship. The average ex-vessel value of sardines in all fisheries between 1986 and 1990 was $183 per ton (Thomson et al. 1992). In general, fishermen have received less for sardines ($80 to $105 per ton) than for mackerel ($120 to $130 per ton) at the canneries since 1986.

Population Assessments

Spawning area surveys (Wolf and Smith 1985, 1986; Wolf et al. 1987; Wolf 1988a,b, 1989; Barnes et al. 1992) were used exclusively from 1986 through 1989 to evaluate the size of the sardine population relative to 20,000 tons, and were the basis for allowing the 1,000-ton directed fishery each year. Briefly, the area over which a 20,000-ton spawning biomass would be expected to produce eggs was calculated from estimates of the egg production rate per unit area and rates at which adults produce eggs. If the survey detected a spawning area as large as or larger than the predicted spawning area, then the spawning biomass was presumed to be 20,000 tons, and a 1,000-ton directed quota was allowed.

From 1986 through 1988, the sardine spawning area detected by CDFG surveys increased steadily, and in each year indicated a spawning biomass of at least 20,000 tons (table 3). For 1990 and 1991, spawning area surveys conducted by CDFG (Wolf and Larson 1991) were used in conjunction with other information to assess the status of the sardine population. Spawning area decreased in 1990, and increased substantially in 1991 (table 3).

In September 1989, CDFG convened the first of three annual workshops to review the status of the sardine resource and to develop management recommendations. State, federal, and fishing industry biologists presented data and analyses and discussed management options. Although the group did not develop an estimate of the size of the sardine population during the first meeting, participants agreed that an increase in the directed quota above 1,000 tons was not warranted at that time.

The second sardine assessment and management workshop was held on September 27 and 28, 1990, and involved state, federal, fishing industry, and Mexican federal biologists. To facilitate in-depth discussions, all participants were invited to submit a synopsis of data and analyses concerning the status of the Pacific sardine resource. These synopses were distributed to all participants for review before the workshop. Discussion centered on data sources, options for assessment and analysis, and alternatives for short-term and long-term management of sardines. The goals of the workshop were to identify assessment techniques and set harvest levels to ensure rehabilitation of the resource, and to develop a management plan for a fully rehabilitated stock.

Several sources of data and information were presented, including CalCOFI egg and larval surveys, observations of sardines by aerial fish spotters, CDFG spawning area surveys, catch and age data from current fisheries collected by CDFG and industry biologists, and data from historical fisheries. Barnes et al. (1992) review five analytical approaches used in the workshop and recent trends in sardine abundance. A rehabilitated sardine resource was defined by workshop participants as one that has a spawning biomass (age 2 and older) of at least 1 million tons, and that occupies an area and has an age structure similar to those during previous periods of high abundance. Once the population reaches 1 million tons, management would shift from the goal of rehabilitation to management of a fully rehabilitated stock. Sardines generally increase during periods of warm water (Barnes et al. 1992), and it was recommended that rehabilitation be achieved within the next decade to take advantage of current favorable environmental conditions. Also, management should be based on total harvests, and during periods of poor recruitment total harvests should be reduced. The participants recommended that during rehabilitation, U.S. harvest levels should not exceed 5% of the spawning biomass. In one scenario, the long-term exploitation that could be sustained by sardines was estimated to be about 20%: 10% was subtracted to allow for rehabilitation, and the remaining 10% was split — 5% for sardine harvest in Mexico and 5% for the United States. Another scenario was based on the current estimated rate of increase of the population (about 30% per year) and the conclusion that a 5% harvest would allow the population to continue to increase at a rate (about 25% per year) that would achieve rehabilitation within 10 years; the Mexican catch was not explicitly addressed. The group reached a consensus that the spawning biomass in 1990 was about 100,000 tons, and recommended a 5,000-ton harvest.

TABLE 3
Sardine Spawning Area from CDFG Surveys

Year	Predicted spawning area (n.mi.^{2})	Observed spawning area (n.mi.^{2})
1985	500	670
1986	500	970
1987	500	1,850
1988	500	2,508
1989	2,300[a]	3,680
1990	2,300	1,480
1991	2,300	3,840

[a] Predicted spawning area was recalculated in 1989.

Following the workshop, CDFG reexamined the recommendations and considered comments received at an industry meeting. It was suggested that current estimates of sardine productivity obtained at the workshop (30% to 40% per year) were too low, because the observed rates of increase occurred at the same time as annual harvest levels of at least 5%. Better estimates of current productivity might have been 35% to 45%. As a result, CDFG increased the 1991 harvest level to 10%, since it appeared that this harvest would still allow the population to grow at the desired rate.

The third sardine assessment and management workshop was held by CDFG on October 1, 1991, and was attended by state, federal, and fishing industry biologists. As in the previous year, summaries of data and analysis were submitted and reviewed before the workshop. Data sources and analytical methods were similar to the 1990 workshop. The group estimated the adult sardine population to range between 275,000 and 495,000 tons. This estimate was based on incomplete data for 1991. Participants again recommended a 10% total harvest for the U.S. fishery, but also recommended that expected landings of sardines by Mexico be considered as part of the total harvest. Using the range of population estimates, the 10% harvest guideline, and an expected Mexican catch of 13,500 tons (based on preliminary 1991 landings), the participants recommended a U.S. harvest limit between 14,000 and 36,000 tons. Since the higher biomass estimate was based on preliminary 1991 data, a preliminary 1992 quota between 14,000 and 25,000 tons was recommended. CDFG opted for the higher quota, and set the total U.S. harvest for 1992 at 25,000 tons. Specific fishery quotas included a 3,000-ton incidental reserve, a 1,000-ton live bait quota, a 500-ton dead bait quota, and 20,500 tons for the directed quota (with 6,833 tons allocated to the north and 13,667 tons to the south). In mid 1992, once 1991 data are complete, the biomass estimate and Mexican catch data will be updated, and the quota will be revised as appropriate.

CURRENT FISHERY CONDITIONS

Directed sardine landings during the first half of 1992 were low, and through June totaled only 5,000 tons, or 37% of the southern California quota. The major cannery in southern California is on indefinite furlough while the owners, a local fishermen's cooperative, face possible bankruptcy proceedings. Mackerel have been the mainstay of the southern California purse seine fleet for many years (Klingbeil 1983b), but the value (price per ton) of mackerel has declined over the last decade (Thomson et al. 1992) and, in the last two years, the catch and biomass have decreased. Canneries have been unable to develop a market for canned sardines (at least the current one-pound tall pack), and processors have reportedly been unable to attract the investment capital they require to develop new sardine products and establish new markets without a guaranteed, substantial increase in the quota. The traditional southern California purse seine fleet, which survived the demise of the sardine by fishing anchovies and then mackerel, has been in slow decline for several decades. It is ironic that the California purse seine fleet may cease to exist just as the sardine resource is making its recovery, an event these fishermen have long awaited.

The Pacific Fishery Management Council (PFMC), which includes state and federal authority, began developing a new Coastal Pelagic Species Fishery Management Plan in 1991. Responsibility for management of Pacific sardines, Pacific mackerel, and jack mackerel will shift from the state of California to PFMC when the plan is implemented in 1993. PFMC already manages the northern anchovy resource and fisheries. The development of a coastal pelagic species plan was undertaken because fisheries based on a rehabilitated sardine population may operate outside the jurisdiction of California in federal waters, Mexican waters, and state waters off Oregon and Washington, as well as on the high seas. Another factor contributing to the decision was the possibility that factory trawlers may fish for jack mackerel in waters beyond state jurisdiction, and thus not be subject to any management controls. Effective management of coastal pelagic species will be enhanced by a cooperative state and federal effort, particularly in light of the current shortage of resources for management and assessment at both state and federal levels.

A bilateral management agreement with Mexico to facilitate the cooperative management of coastal pelagic species is a high priority for the plan. Coastal pelagic species, including anchovy, jack and Pacific mackerel, and sardines, are transboundary stocks that reside off the coasts of both Mexico and the United States, and are exploited by both countries. Recent combined catches of sardines by the United States and Mexico have been high, exceeding 40,000 tons in 1991; landings during the first half of 1992 have been lower (figure 1). Continued high landings and the absence of cooperative management could retard or suppress the recovery of the Pacific sardine.

DISCUSSION

Management of a resource like the Pacific sardine in the early part of recovery requires that the resource be protected, but also that adverse impacts on other fisheries be minimized as much as possible without jeopardizing the recovery process. Management efforts are further complicated by limited information about the status of the population when fisheries are minor or nonexistent, and precise, direct estimates of a relatively small biomass are difficult to obtain because they are too expensive, particularly in the absence of a fishery.

The workshop approach was an effective means of collating available information, and developing useful and timely management recommendations. Consultation with various experts enhanced managers' credibility, particularly with industry, and the inclusion of industry biologists in the process fostered a cooperative, rather than adversarial, approach to solving management and allocation problems. This approach can serve as a model for future management.

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Part III

SCIENTIFIC CONTRIBUTIONS

DISTRIBUTION OF LARVAL PACIFIC SARDINE, *SARDINOPS SAGAX*, IN SHALLOW COASTAL WATERS BETWEEN OCEANSIDE AND SAN ONOFRE, CALIFORNIA: 1978–1986

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ABSTRACT

Spatial and temporal distributions of larval Pacific sardine, *Sardinops sagax*, were investigated at two nearshore sites between San Onofre and Oceanside, California. Neuston, midwater, and epibenthic samples were collected at night with plankton nets towed at a randomly selected isobath within each of five sampling blocks between the 6-m and 75-m isobaths at each site. The San Onofre site was sampled from January 1978 through September 1986; the site near Oceanside was sampled from July 1979 through September 1986. Sampling frequency varied from weekly to quarterly, depending on other requirements of the study.

The average cross-shelf distribution of larvae differed little from year to year: abundance usually was highest between the 12-m and 45-m isobaths, particularly for yolk-sac and preflexion larvae. Densities were typically highest in midwater. Vertical and cross-shelf distributions were similar at both study sites.

Larvae were found nearly year-round, but were most abundant in summer and fall. Seasonal abundance patterns differed relatively little between sites or from year to year. Abundance was quite low from 1978 to 1980, then increased dramatically to a peak in 1984.

The results of this study, together with other published reports, suggest that the resurgence of the Pacific sardine off southern California in the early 1980s began in 1981 in shallow waters along the central southern California coast.

RESUMEN

Se investigó la distribución espacio-temporal de las larvas de *Sardinops sagax*, la sardina del Pacífico, en dos estaciones costeras entre San Onofre y Oceanside, California. Se colectaron muestras durante la noche en el neuston, a media agua y en el epi-bentos; en cada localidad se hicieron arrastres en curvas isobatas elegidos aleatoriamente en cada uno de cinco bloques de muestreo (entre las curvas isobatas de 6 y 75 m). El sitio en San Onofre fué muestreado de Enero de 1978 a Septiembre de 1986, y el cercano a Oceanside de Julio de 1979 a Septiembre de 1986. La frecuencia de muestreo fué variada, de semanal a trimestral, dependiendo de otros requerimentos del estudio.

La distribución promedio de las larvas en sentido perpendicular a la costa varió poco de año a año, encontrandose la máxima abundancia entre las curvas isobatas de 12 y 45 m; esto fué particularmente cierto para los estadios de saco vitelino y pre-flexión. Las densidades más altas se encontraron a media agua. Las distribuciones vertical y en sentido perpendicular a la costa fueron similares en ambos sitios de estudio.

Se encontraron larvas durante todo el año, con máximos en verano y otoño. Los patrones de abundancia estacional difirieron relativamente poco entre los distintos sitios o de año a año. La abundancia larval fué relativamente baja en 1978–80 y subsecuentemente se incrementó de manera substancial hasta alcanzar un máximo en 1984.

Los resultados de este estudio, aunados a otros reportes ya publicados, sugieren que el repunte a principio de los 80 de la sardina del Pacífico en el Sur de California empezó en 1981 en aguas someras de la costa central del Sur de California.

INTRODUCTION

The rise and fall of the Pacific sardine fishery along the west coast of the United States between about 1915 and the mid 1960s has been extensively documented and discussed (e.g., Murphy 1966; Ahlstrom and Radovich 1970; MacCall 1979; Radovich 1982). A minor fishery continued after the mid 1960s until 1974, when a moratorium was declared. In the early 1980s Pacific sardine again began to increase in California waters (e.g., Bedford et al. 1982; Wolf and Smith 1985), and in 1986 a small directed fishery once again was permitted (e.g., Wolf and Smith 1986; Wolf et al. 1987).

Lavenberg et al. (1986), reporting on nearshore ichthyoplankton surveys along the southern California coast, suggested that this resurgence may have begun in shallow coastal waters, as would be

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predicted by MacCall's (1983) model of habitat selection by declining fish populations. The purpose of this report is to further document the spatial and temporal distributions of larval Pacific sardine in shallow coastal waters of southern California in the years just before, and during, the resurgence of the early 1980s. This report is based on a longer time series (1978–86) and more complete water-column coverage than have been documented before from the shallow coastal zone.

METHODS

Ichthyoplankton samples were collected from January 1978 through September 1986 along an onshore-offshore transect approximately 1 km south of the San Onofre Nuclear Generating Station (SONGS), and from July 1979 through September 1986 along a similar transect off Stuart Mesa, approximately 17 km south of the SONGS transect (figure 1). The sampling methodology, which was the same at both sites, was described by Barnett et al. (1984), Walker et al. (1987), and Moser and Watson (1990). Briefly, a stratified random design (Snedecor and Cochran 1967) was used to sample the neustonic (top 16 cm), epibenthic (bottom 67 cm), and remaining midwater layers of the water column along a randomly selected isobath within each of five blocks at each site on each survey date. These blocks were defined by bottom depth: (A) 6–9 m, (B) 9–12 m, (C) 12–22 m, (D) 22–45 m, and (E) 45–75 m.

Three different nets, equipped with 0.333-mm-mesh Nitex and flowmeters, were used to sample the entire water column. A Manta net, 88 cm wide by 16 cm deep, was used to sample the neuston; a 71-cm bongo net was used for a stepped-oblique tow through the midwater column; and an Auriga net (MBC Applied Environmental Sciences, 947 Newhall Street, Costa Mesa, CA 92627) 2 m wide by 0.5 m high was used in the epibenthic stratum. All tows were taken at night along the chosen isobaths, at about 1 m/s for a fixed time selected to filter a target volume of 400 m^3. Samples were not collected in block E on two dates in 1985 because of equipment problems. All samples were preserved in the field in 10% Formalin in seawater.

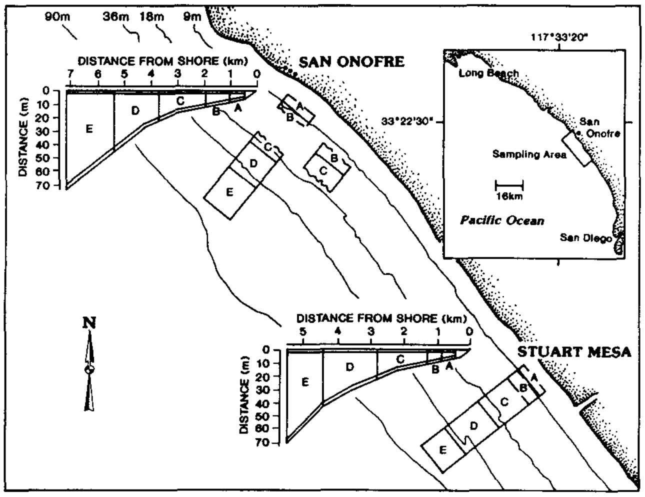

Figure 1. Locations of the study sites along the southern California coast, with schematic profiles of the bathymetry at each site. On each survey date, a sample was taken at a randomly selected isobath within each of the five blocks (A–E) at each site.

Although this study yielded information on the temporal and spatial distributions of larval Pacific sardine, acquiring such information was not its specific intent. Instead, the study was designed to predict, and subsequently measure, how two new SONGS units would affect the plankton. Consequently, sampling frequency varied considerably, according to the changing requirements of the power plant study. Sampling frequency ranged from approximately weekly toward the end of the predictive phase of the study (1980) to quarterly during the 3-year interim between the plant's preoperational and operational phases (1981–83). Most sampling was done in spring and summer (March–September).

In the laboratory, most samples were subsampled with a Folsom plankton splitter before being sorted for fish larvae (average for all samples = 25% sorted, range = 3.1%–100%). After sorting, each subsample was checked to ensure that at least 90% of the larvae were removed. Larval Pacific sardine were counted in four developmental stages (yolk-sac, preflexion, notochord flexion, postflexion) for a subset of the 1978–79 samples (one transect per survey) and for all subsequent samples. A small proportion of the larvae were too damaged to allow unequivocal identification of developmental stage; since most of those were small, all were arbitrarily assigned to the preflexion class. The count data were converted to number per 100 m^3, and these density data were used to calculate abundance (number under 10 m^2 in each block and number in a 1-m-wide strip between the 6–75-m isobaths at each site). No corrections were made for the missing block E values on the two 1985 surveys; for those dates cross-shelf abundance values may be somewhat underestimated.

The density data and abundance-per-block data were transformed by log $(x + 0.1)$ and analyzed using ANOVA and Student-Neuman-Keuls (SNK) multiple range tests to examine spatial patterns (results evaluated at $\alpha = 0.05$). The surveys lacking block E samples were deleted from the statistical analyses in order to maintain a balanced design, and surveys during which sardine larvae were not collected were deleted because they contained no information about location. Incidence was calculated as the percentage of total tows that contained Pacific sardine larvae.

Seasonal patterns and interannual changes in abundance were examined qualitatively with the cross-shelf abundance values (number/m between the 6–75-m isobaths); these patterns are presented in figures.

RESULTS

Spatial Distribution

Overall, larval Pacific sardine at both study sites were most abundant in block D, between the 22-m and 45-m isobaths; abundance decreased at the shoreward and seaward stations. The most shoreward station (6–9-m depth) had the lowest abundance. Cross-shelf patterns varied somewhat from year to year, but in general they were similar at both sites throughout the study (figure 2).

There was slight evidence of a possible ontogenetic seaward shift in a cross-shelf distribution at both sites, with yolk-sac larvae most abundant in block C, preflexion and flexion larvae most abundant in block D, and postflexion larvae slightly more abundant in block E (figure 3). However, most of these patterns were not statistically detectable (table 1). At San Onofre, only the high abundance of preflexion larvae in block D could be distinguished from their low abundance in block A. At Stuart Mesa, higher abundances of preflexion larvae in blocks C, D, and E were distinguishable from lower abundance in blocks A and B, whereas for flexion larvae the higher abundance in block D was distinguishable from the lower abundance in block A (table 1).

Larvae occurred most frequently in midwater (incidence overall 20% at San Onofre and 28% at Stuart Mesa), secondarily in the neuston (15% at San Onofre, 22% at Stuart Mesa), and least in the epibenthos (8% at San Onofre, 11% at Stuart Mesa). All stages appeared more frequently in midwater than in the other strata. Yolk-sac and preflexion larvae were somewhat less common in the neuston and relatively uncommon in the epibenthos, while flexion and postflexion larvae appeared almost equally frequently in neustonic and epibenthic samples.

Mean larval density values largely reflected the incidence values, and apparently differed little between study sites. Yolk-sac and preflexion larvae typically were most numerous in midwater and neuston samples (figures 4 and 5). Yolk-sac larvae were rare in epibenthic samples, but preflexion larvae were moderately dense in the epibenthic stratum of the more shoreward blocks (figures 4 and 5). Flexion and postflexion larvae were distributed more uniformly through the water column, although somewhat lower near shore and higher farther from shore (figures 4 and 5).

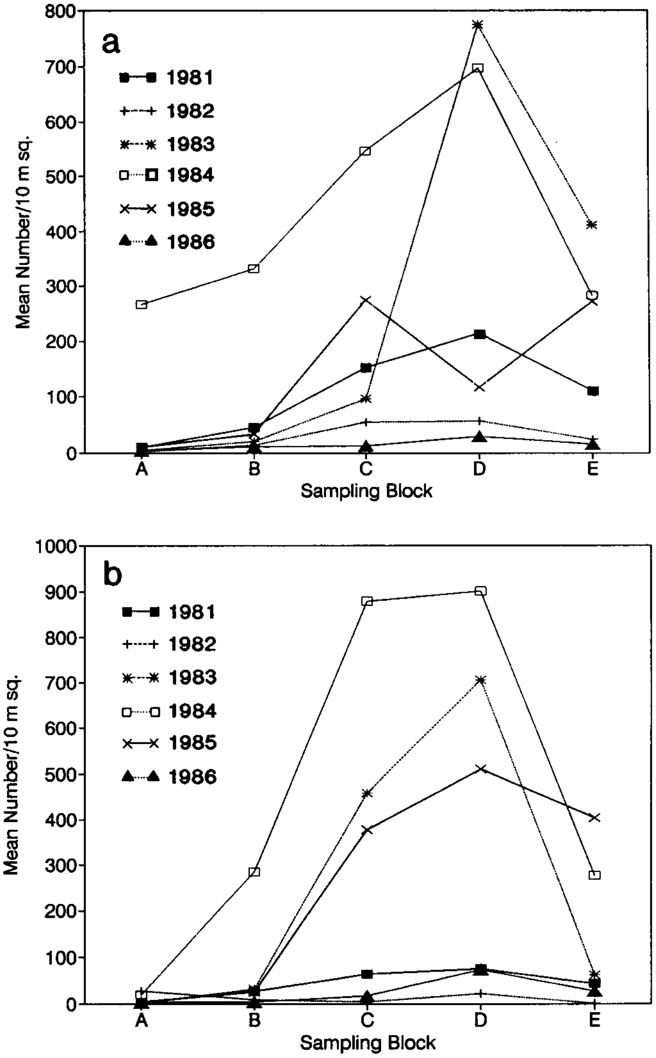

Figure 2. Mean number of larval Pacific sardine under 10 m² of sea surface in each sampling block. The very low abundances in 1978–80 are not shown. All larval stages are pooled. *a* = San Onofre; *b* = Stuart Mesa.

Analysis of variance demonstrated significant differences in density among vertical strata for yolk-sac and preflexion larvae at both sites, but failed to indicate significant differences among strata for the older larvae at San Onofre (table 2). There were no statistically significant differences between blocks (block main effects) at San Onofre, and only one significant block X stratum interaction at either site

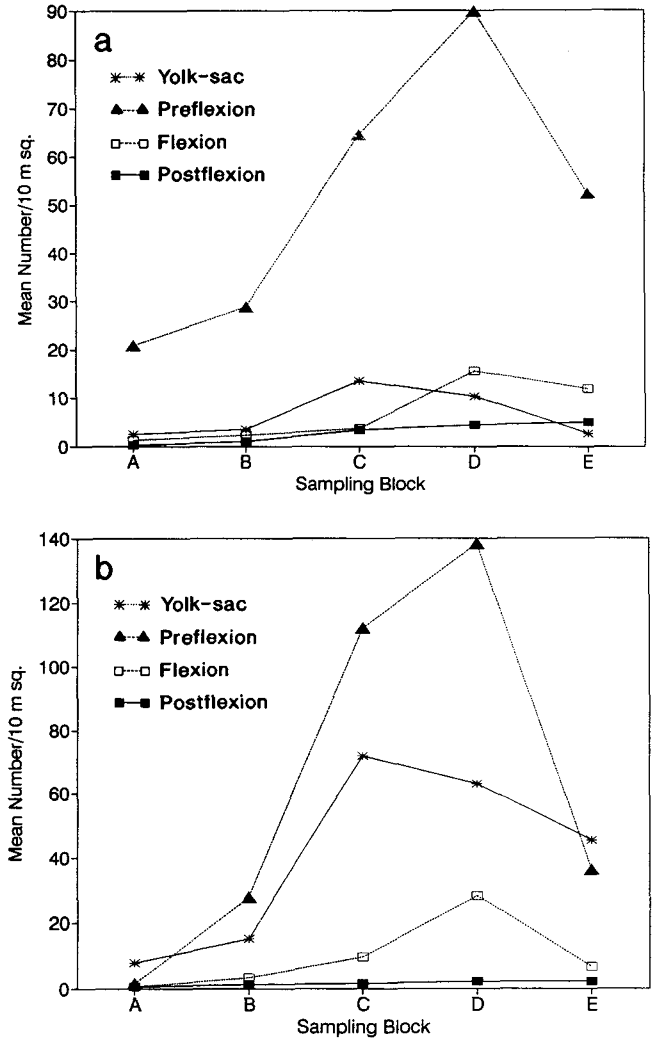

Figure 3. Mean number of larval Pacific sardine under 10 m^2 of sea surface in each sampling block. Each developmental stage is plotted separately; all years are pooled. *a* = San Onofre; *b* = Stuart Mesa.

(postflexion larvae at Stuart Mesa), although some block main effects and interactions approached significance (0.10 > *p* > 0.05; table 2).

Temporal Distribution

Seasonal pattern. Larval sardines were collected in every month except January and February, with a distinct maximum in summer and fall (figure 6). Incidence (percent positive collections, all years at both sites pooled) increased from 7%–27% between March and May to 60%–79% during June–September, then declined to the winter nadir, except during December, when six of seven transects yielded sardines. Although incidence varied somewhat from year to year and increased substantially beginning in 1981, there were no consistent changes to suggest a shift in the seasonal pattern over the nine years of the study (figure 7). Incidence at the Stuart Mesa site tended to be a little lower than at San Onofre in spring (typically 50%–90% of San Onofre values), but a little higher in summer (usually 110%–140% of San Onofre values).

Abundance largely mirrored incidence, with none to few larvae in winter and spring, rapidly increasing abundance to a maximum in September and October, then a rapid decline to the winter nadir (figure 6b). Apart from a substantial increase in abundance that began in 1981, there were no consistent year-to-year changes that would suggest a shift in seasonal pattern (appendix). Patterns were similar at both study sites, except that the summer-fall peak was smaller and earlier at San Onofre than at Stuart Mesa (figure 6b). The high larval incidence in December surveys noted above was attributable to consistent collection of small numbers of larvae.

Incidence and abundance of yolk-sac larvae were examined in order to better estimate the spawning season. Almost all yolk-sac larvae were collected between May and October (one transect occupancy each in March 1980 and December 1983 also yielded yolk-sac larvae). Incidence increased steadily from 16% in May to 50% in August, then declined steadily to the winter minimum, indicating that spawning takes place principally in summer (figure 8a). There were no consistent differences in seasonal incidence over the years to suggest a shift in spawning season. Incidence was higher at Stuart Mesa than at San Onofre (typically 130%–200% of San Onofre values) in summer and fall.

Abundance of yolk-sac larvae differed somewhat from incidence (figure 8). Abundance did generally

TABLE 1
Results of ANOVA and SNK Analyses on Cross-Shelf Distributions of Larval Pacific Sardine

	ANOVA result			SNK result				
Stage	*N*	*F*	*P*					
San Onofre								
Yolk-sac	17	0.67	>.05	E	A	B	D	C
Preflexion	32	2.44	<.05	A	E	B	C	D
Flexion	21	1.83	>.05	A	B	D	C	E
Postflexion	22	0.61	>.05	A	B	D	E	C
Stuart Mesa								
Yolk-sac	21	1.96	>.05	E	A	B	D	C
Preflexion	30	8.19	<.05	A	B	C	E	D
Flexion	22	2.25	>.05; <.10	A	B	E	C	D
Postflexion	19	0.49	>.05	E	C	D	B	A

Only positive survey dates (*N*) were included in the analyses. SNK results are shown with sampling blocks (A–E) ordered from lowest geometric mean abundance (left) to highest geometric mean abundance (right). Sampling blocks joined by underlines are statistically indistinguishable (evaluated at α = 0.05).

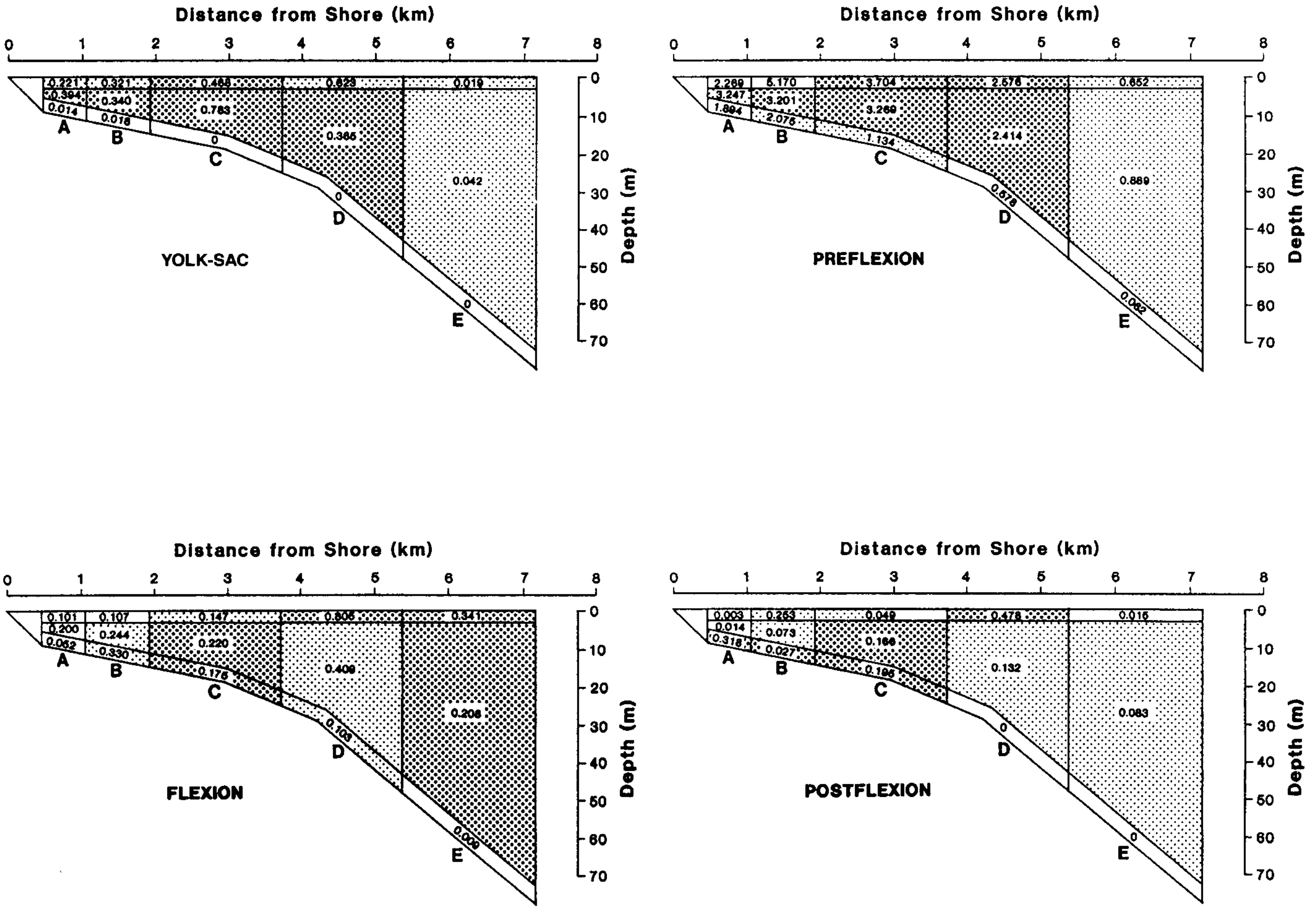

Figure 4. Mean number of larval Pacific sardine per 100 m^3 of water in each stratum (neuston, midwater, epibenthos) in each sampling block at San Onofre. Each developmental stage is plotted separately; all years are pooled. Neustonic and epibenthic strata are vertically exaggerated in these schematic representations. Shading indicates rankings of the geometric mean densities from the ANOVA on density: dark = the five highest-ranked means; light = the five middle-ranked means; white = the five lowest-ranked means.

increase from spring to a fall maximum, but with two or three smaller peaks at about 2-month intervals during the spring and summer. The minor peaks were about one month earlier at San Onofre than at Stuart Mesa, but the major peak was in October at both sites (figure 8b). The abundance of yolk-sac larvae varied considerably from year to year, but there were no consistent changes to suggest a shift in spawning season.

Interannual change. Larval Pacific sardine were collected in relatively few of the 1978–80 samples (figures 7, 9, 10): incidence in those years ranged from a low of 2% in 1979 to 6% in 1980. Incidence increased dramatically in 1981 (to 39%), reached a maximum of 44% in 1984, and remained above 20% through 1986.

Larval abundance likewise was quite low in 1978–80, especially in 1979, then increased substantially, peaking in 1984 (figures 9a, 10a; appendix). The initial increase was somewhat larger at San Onofre, but subsequently tended to be higher at the Stuart Mesa site.

These initial increases of larval Pacific sardine in 1981 were largely attributable to preflexion and older stages. The incidence of yolk-sac larvae did not begin to increase until 1982 (figures 9a, 10a); yolk-sac abundance did not increase markedly until 1984 (figures 9b, 10b). Yolk-sac larval incidence peaked near 20% at both sites in 1984, then by 1986 returned to the low levels (<5%) typical of the early years of the study. Yolk-sac larval abundance also peaked at San Onofre in 1984, but at Stuart Mesa it continued to increase to a much higher peak in 1985. At both sites, 1986 abundances were quite low, comparable to the levels characteristic of the first years of the study.

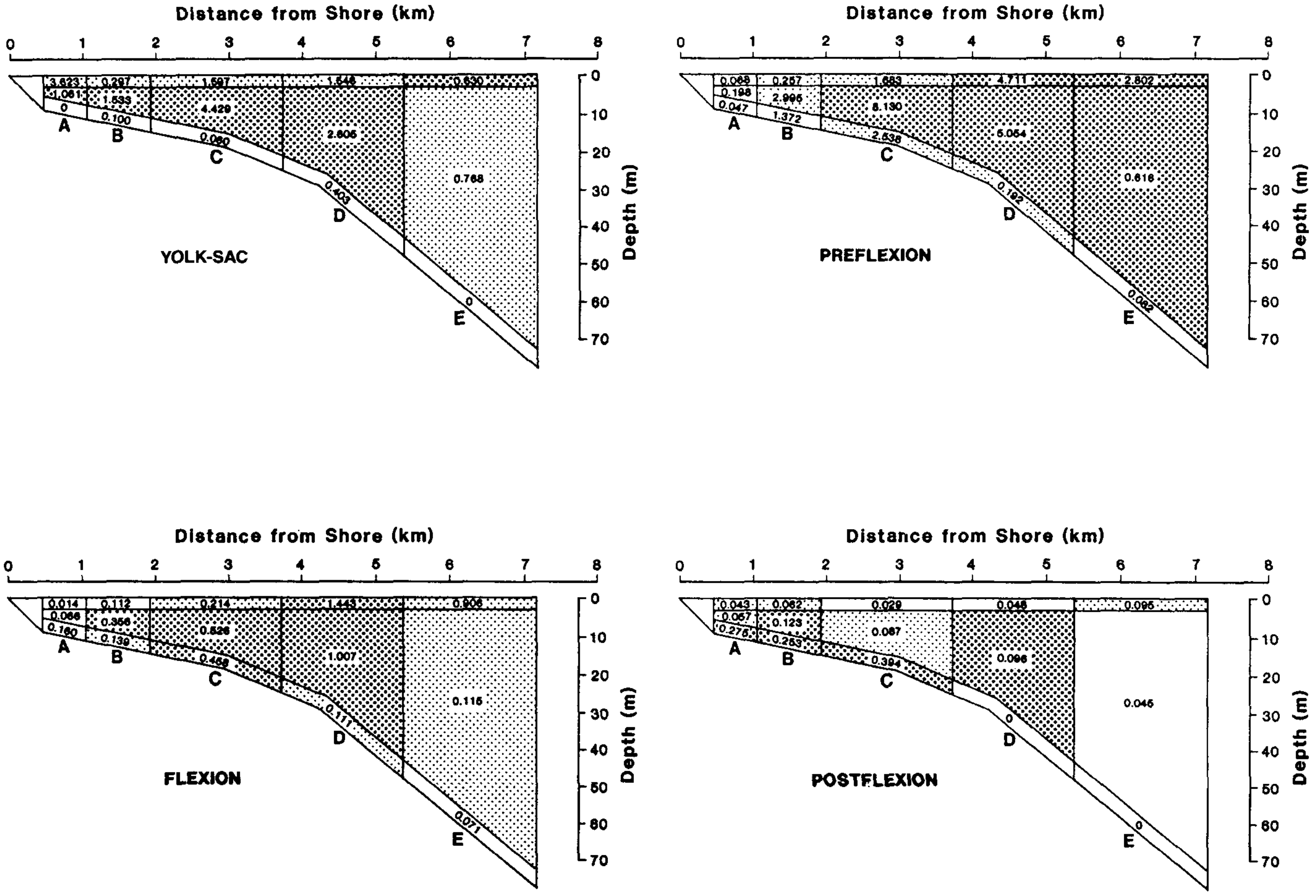

Figure 5. Mean number of larval Pacific sardine per 100 m^3 of water in each stratum (neuston, midwater, epibenthos) in each sampling block at Stuart Mesa. Each developmental stage is plotted separately; all years are pooled. Neustonic and epibenthic strata are vertically exaggerated in these schematic representations. Shading indicates rankings of the geometric mean densities from the ANOVA on density: dark = the five highest-ranked means; light = the five middle-ranked means; white = the five lowest-ranked means.

DISCUSSION

Spatial Distribution

Lavenberg et al. (1986, 1987) showed that over the southern California continental shelf, Pacific sardine eggs were more abundant shoreward from the 36-m isobath than at the 75-m isobath during 1978–86, suggesting that the shallow coastal zone was an important spawning area in those years. In both the Lavenberg et al. 1986 study and this one, Pacific sardine larvae were most abundant in this same zone. This was particularly true for younger larvae in this study: yolk-sac and preflexion larvae were usually most abundant in samples collected between the 12-m and 45-m isobaths, and least abundant in samples collected shoreward and seaward of those depths.

Cross-shelf patterns were much less consistent for the older larvae, suggesting that they were more patchily distributed and that the patches were more widely dispersed across the inner half of the continental shelf. There was no evidence that larvae attempted to remain in the shallow zone, and only a slight suggestion that the older larvae made any directed movement away from it. CalCOFI ichthyoplankton surveys in 1978, 1981, and 1984 yielded few larval Pacific sardines along the transect lines (80–97) off southern California (Ambrose et al. 1988; Sandknop et al. 1988; Stevens et al. 1990), except in March, June, and July 1984, when a few relatively large catches were made, mainly at nearshore stations (Stevens et al. 1990). Together, these studies suggest that between 1978 and 1984–86 sardines spawned chiefly in the zone bounded by the 12-m and 45-m isobaths, and that larvae slowly dispersed from this spawning center, but remained primarily over the continental shelf.

Phytoplankton and microzooplankton biomass usually display onshore-offshore gradients along the southern California coast, with higher values nearer

TABLE 2
Summary of ANOVA on Density (Number per 100 m³) in the 15 Strata (3 Vertical Strata × 5 Cross-Shelf Blocks) Sampled at Each Location

Larval stage	Source	d.f.	M.S.	*F*	*P*
San Onofre					
Yolk-sac	Blocks	4	0.66	1.72	>0.10
	Strata	2	6.01	15.77	<0.01
	Interaction	8	0.25	0.67	>0.10
	Error	225	0.38		
Preflexion	Blocks	4	1.32	2.26	>0.05; <0.10
	Strata	2	4.68	8.02	<0.01
	Interaction	8	0.33	0.56	>0.10
	Error	480	0.58		
Flexion	Blocks	4	0.85	2.31	>0.05; <0.10
	Strata	2	0.72	1.95	>0.10
	Interaction	8	0.39	1.06	>0.10
	Error	300	0.37		
Postflexion	Blocks	4	0.43	1.97	>0.05; <0.10
	Strata	2	0.14	0.64	>0.10
	Interaction	8	0.37	1.72	>0.05; <0.10
	Error	315	0.22		
Stuart Mesa					
Yolk-sac	Blocks	4	0.88	1.79	>0.10
	Strata	2	7.67	15.56	<0.01
	Interaction	8	0.56	1.13	>0.10
	Error	300	0.49		
Preflexion	Blocks	4	4.63	8.73	<0.01
	Strata	2	7.81	14.73	<0.01
	Interaction	8	0.70	1.33	>0.10
	Error	435	0.53		
Flexion	Blocks	4	2.24	5.86	<0.01
	Strata	2	0.30	0.78	>0.10
	Interaction	8	0.48	1.26	>0.10
	Error	315	0.38		
Postflexion	Blocks	4	0.53	2.47	<0.05
	Strata	2	0.25	1.16	>0.10
	Interaction	8	0.44	2.03	<0.05
	Error	270	0.22		

Only positive dates were included in the analyses.

shore (e.g., Mullin 1986). The high rates of phytoplankton production, and the high concentrations of microzooplankton and macrozooplankton near shore (e.g., Beers and Stewart 1967; Lasker 1978; Petersen et al. 1986; Barnett and Jahn 1987) should provide a good feeding environment for Pacific sardine, and might have enhanced egg quality or production as well as larval survival during the study period. MacCall (1983, 1990) predicted that just such a productive nearshore zone would support the remnants of a depleted population such as the Pacific sardine, and that any subsequent resurgence of the population would originate from this core area. This may partially explain the observed increase.

In the shallow nearshore zone there was little evidence of strong vertical stratification, except that the younger larvae (yolk-sac and, to a lesser extent, preflexion) were rare in the lower 0.5 m of the water column. (These samples, however, were all collected at night, and the vertical distributions observed may not reflect daytime patterns; e.g., Silliman 1943).

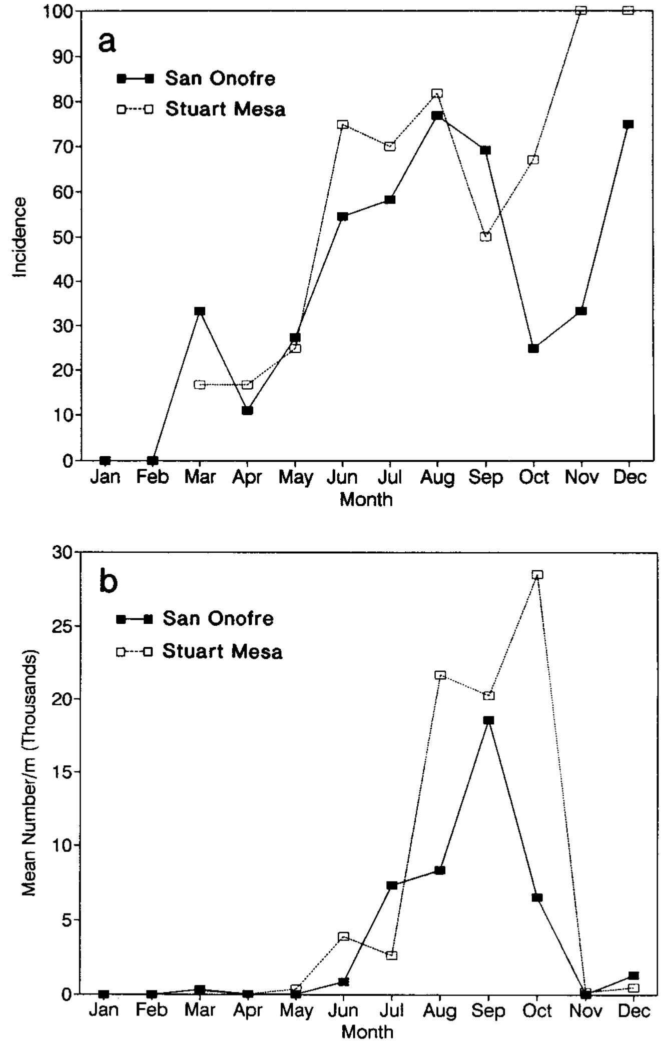

Figure 6. *a*, Monthly mean incidence (percent positive collections) and *b*, abundance (number under a 1-m-wide strip between the 6-m and 75-m isobaths) of larval Pacific sardine. All developmental stages and all years are pooled.

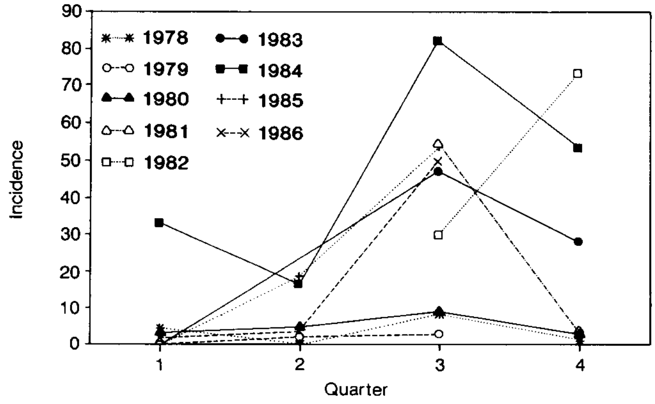

Figure 7. Incidence (percent positive collections) of larval Pacific sardine, 1978–86, plotted by quarter. All developmental stages, and data from both study sites are pooled.

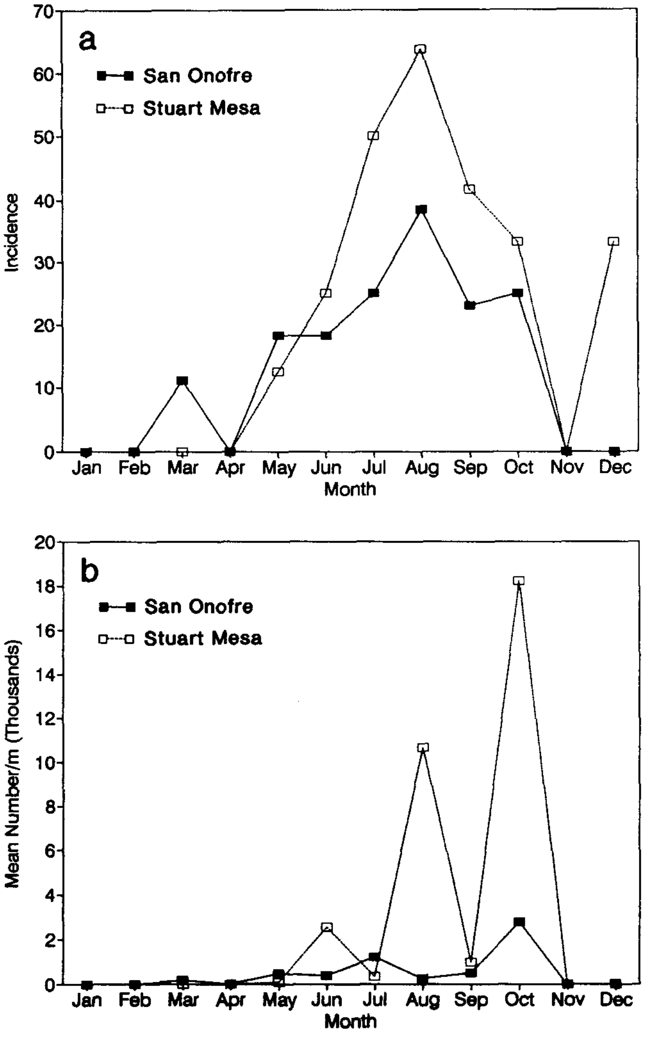

Figure 8. *a*, Monthly mean incidence (percent positive collections) and *b*, abundance (number under a 1-m-wide strip between the 6-m and 75-m isobaths) of yolk-sac larval Pacific sardine. All years are pooled.

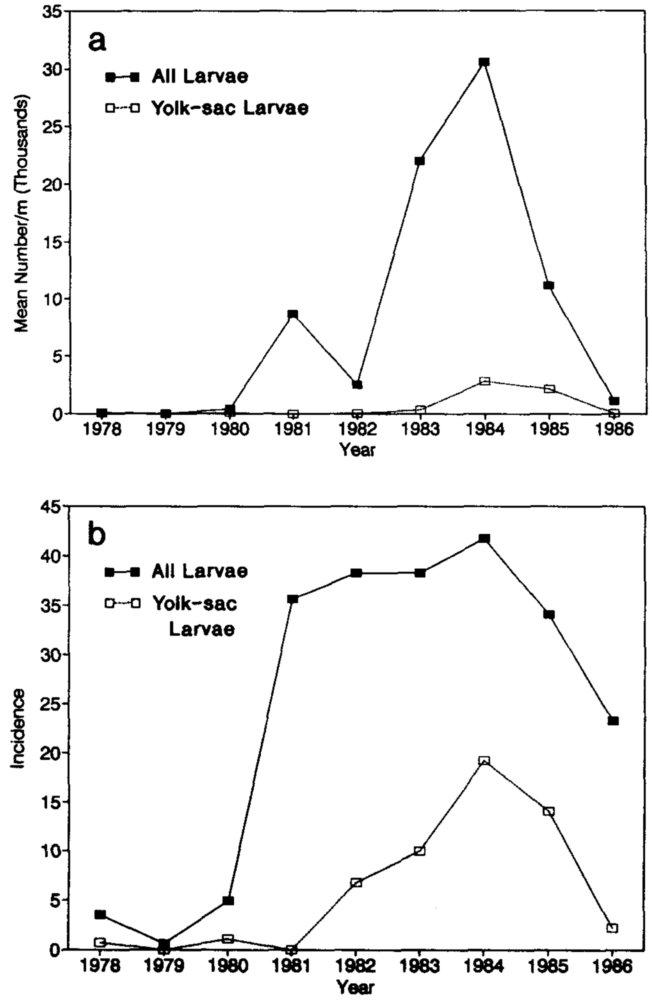

Figure 9. *a*, Annual mean abundance (number under a 1-m-wide strip between the 6-m and 75-m isobaths) and *b*, incidence (percent positive collections) of larval Pacific sardine off San Onofre.

Postflexion larvae, on the other hand, tended to appear in the lower 0.5 m, but usually only at shallower depths (≤22 m). By avoiding the epibenthic stratum, the small larvae may avoid being eaten by the many large larval and small juvenile fishes resident on the shallow shelf (e.g., croakers, gobies: Barnett et al. 1984; Brewer and Kleppel 1986; Jahn and Lavenberg 1986). The postflexion larvae may be large enough to avoid this danger. But whether predator avoidance does actually limit the vertical distribution of larval Pacific sardine in nearshore waters is purely speculative at this point.

Temporal Distribution

Ahlstrom (1960, 1967) showed that off southern California in the 1950s, Pacific sardines spawned largely in spring and summer, and occasionally at other seasons during warmer years. From 1978 to 1986, spawning was nearly year-round, but was almost always highest in summer or fall (Brewer and Smith 1982; Lavenberg et al. 1986, 1987; this study). It has been speculated that this shift in the principal spawning season represented a movement into southern California waters of a later-spawning southern stock (Brewer and Smith 1982; Lavenberg et al. 1986), perhaps facilitated by the somewhat warmer temperature regime during those years.[1] An alternative suggestion that the warmer temperature may have allowed more extended spawning by the local population (e.g., Lavenberg et al. 1986), as happened in the late 1950s (Ahlstrom 1960), seems

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[1] S. Hernández-Vázquez, D. Lluch-Belda, D. Lluch-Cota, and C. Salinas-Zavala. Interannual variability of sardine and anchovy eggs and larvae in the Southern California Bight related to sea surface temperature, upwelling index and small zooplankton biomass: 1951–1988. Calif. Coop. Oceanic Fish. Invest. Ann. Conf. 22–24 October 1991, Lake Arrowhead, Calif.

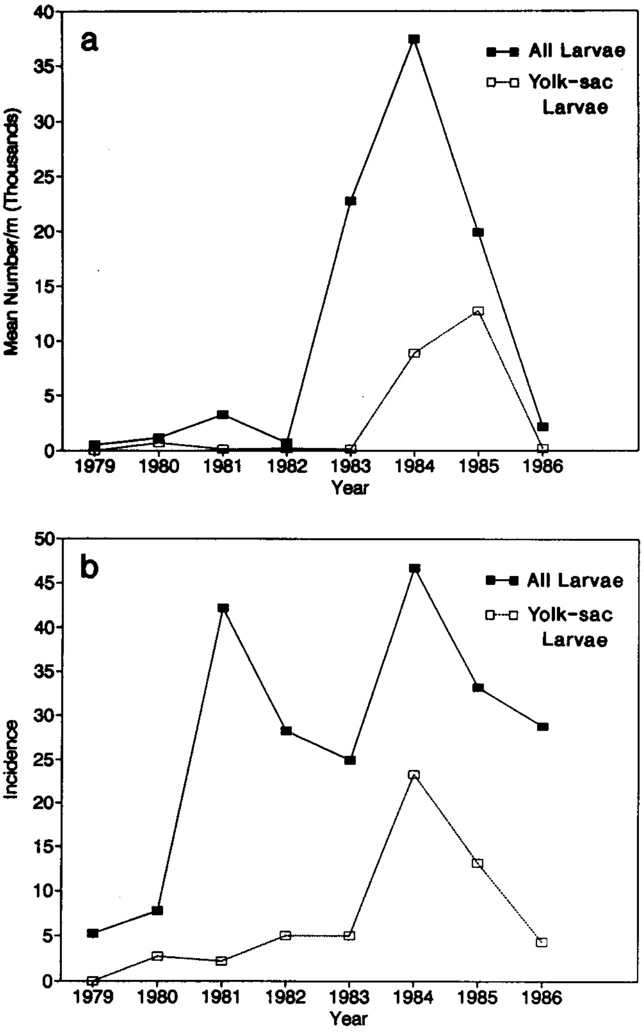

Figure 10. *a*, Annual mean abundance (number under a 1-m-wide strip between the 6-m and 75-m isobaths) and *b*, incidence (percent positive collections) of larval Pacific sardine off Stuart Mesa.

unlikely to solely account for the strong summer-fall spawning peak, but it may well have contributed to both the extended spawning season and the shift in timing. Lavenberg et al. (1987) noted a return to spring-summer spawning in 1986; no such shift was apparent in this study.

The resurgence of the Pacific sardine began in the early 1980s (Wolf and Smith 1985; Lavenberg et al. 1986, 1987); I suggest that it started in 1981. The initial increase near San Onofre apparently was not attributable to local spawning, since increases for yolk-sac larvae lagged total larvae by a considerable period. Lavenberg et al. (1986) reported that sardine larval abundance first increased north of San Onofre, primarily in the Seal Beach area in 1982, and subsequently spread north and south along the coast in 1983. Because nearshore currents along the southern California coast usually flow alongshore toward the south (Winant and Bratkovich 1981), it seems reasonable to speculate that the early increases in larval abundance in the San Onofre vicinity represented southward alongshore advection of larvae from some spawning site farther north (but probably not as far north as Seal Beach, since an egg spawned there would be a well-developed larva or juvenile 2 to 5 weeks old by the time it reached San Onofre). Alternatively, yolk-sac larvae may simply have not been collected, or not retained in the nets if they were collected, during the early years of this study. Although it seems likely that yolk-sac sardine larvae were not quantitatively sampled by the 0.333-mm-mesh nets used (because of extrusion), no systematic change during the course of the study would have caused the yolk-sac larvae to be undersampled more in some years than in others. The precipitous decline in larval abundance in 1986 is consistent with the report by Lavenberg et al. (1987) that no Pacific sardine eggs were collected off San Onofre in 1986 (although they were abundant at the Santa Monica Bay and San Pedro Bay sites).

In summary, on the basis of this and other studies, it appears that the resurgence of the Pacific sardine off southern California began in 1981 in shallow waters off the central coast.

ACKNOWLEDGMENTS

This study was based on a larger study of ichthyoplankton in the vicinity of San Onofre, California, conducted by MEC Analytical Systems, Inc. for the Marine Review Committee of the California Coastal Commission. The Marine Review Committee does not necessarily accept the results, findings, or conclusions stated herein.

I thank the many technicians at MEC Analytical Systems, Inc. who spent long hours collecting and processing the samples that provided the basis for this study. I thank H. G. Moser for reviewing an earlier draft of the manuscript, and D. Foster for typing it.

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APPENDIX

Number of Larval Pacific Sardine under a 1-m-Wide Strip between the 6-m and 75-m Isobaths off San Onofre and Stuart Mesa on Each Survey Date: 1978–86

	Number of larvae (thousands)	
Starting date	San Onofre	Stuart Mesa*
1978		
24 Jan.	0	
16 Feb.	0	
6 Mar.	0.231	
21 Mar.	0	
3 Apr.	0	
26 Apr.	0	
8 May	0	
22 May	0	
5 June	0	
21 June	0	
7 July	0.355	
17 July	0.002	
2 Aug.	0.002	
16 Aug.	0	
7 Sept.	0.851	
3 Oct.	0	
8 Nov.	0.001	
28 Nov.	0	
27 Dec.	0	
1979		
3 Feb.	0	
26 Feb.	0	
26 Mar.	0	
25 Apr.	0	
23 May	0.002	
25 June	0	
24 July	0	0
22 Aug.	0	2.527
23 Aug.	0	0
20 Sept.	0	0
21 Sept.	0	0
1980		
10 Mar.	1.783	0
17 Mar.	0	0
24 Mar.	0	0
4 Apr.	0	0
14 Apr.	0	0
23 Apr.	0	0
5 May	0	0
12 May	0	0
19 May	0	0
26 May	0	0
2 June	1.389	1.384
9 June	0	0
17 June	1.350	0
24 June	0	0
30 June	0.002	21.332
7 July	0	2.421
14 July	0	0
21 July	0	0.001
28 July	0	0
1980, cont'd.		
4 Aug.	4.156	4.482
11 Aug.	0.793	0
18 Aug.	1.367	3.256
25 Aug.	0.059	1.103
1 Sept.	0	0.320
8 Sept.	0.022	0
22 Sept.	0.002	0
26 Sept.	0	0
29 Sept.	0.002	0
6 Oct.	0	0
13 Oct.	0	0.003
1981		
7 July	24.831	9.080
15 Sept.	1.194	0.432
17 Nov.	0	0.185
1982		
9 Mar.	0	0
13 July	5.127	1.965
26 Aug.	0.099	0.373
10 Dec.	4.677	0.314
1983		
12 May	0	0
19 July	1.018	0.954
23 Aug.	86.468	89.389
14 Dec.	0.423	0.587
1984		
13 Mar.	0.886	1.411
7 May	0	0
30 May	6.104	2.805
19 June	0.903	0.987
23 Aug.	13.770	11.067
13 Sept.	196.829	197.311
4 Oct.	26.251	85.524
21 Dec.	0.025	0.473
1985		
21 Jan.	0	0
22 Apr.	0	0
13 May	0.056	0.051
4 June	4.624	7.667
25 June	0.920	0.001
18 July	54.868	3.971
6 Aug.	0.028	0.327
26 Aug.	2.108	126.126
12 Sept.	38.030	40.550
1986		
5 Mar.	0	0
1 Apr.	0	0.001
30 Apr.	0.055	0
21 July	1.687	7.748
2 Sept.	4.283	4.355
25 Sept.	0.518	0.516

*Sampling began at the Stuart Mesa site in July 1979.

SPATIAL AND TEMPORAL DISTRIBUTIONS OF PACIFIC HAKE, *MERLUCCIUS PRODUCTUS*, LARVAE AND ESTIMATES OF SURVIVAL DURING EARLY LIFE STAGES

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ABSTRACT

Information on the distribution and abundance of Pacific hake larvae was examined for evidence of strong or weak year classes and larval drift. Estimates of larval mortality rates were derived and applied to a life-table simulation to examine hypotheses about factors that produce strong or weak year classes. Indices of late-stage larval abundance indicated that strong year classes were established during the egg or larval stage of development. Estimates of larval mortality applied to a life-table simulation also indicated that strong year classes were established during the early or late larval period. Analysis of the spatial distribution of larvae indicated that inshore regions and regions west of Point Conception are favorable to survival of hake larvae.

RESUMEN

Se examinaron datos de distribución y abundancia de larvas de merluza del Pacífico para examinar la deriva larvaria y descubrir la presencia de clases anuales fuertes o débiles. A fin de investigar hipótesis sobre los factores que producen clases anuales fuertes o débiles se utilizaron tablas de vida con datos simulados, a las que se les aplicó datos estimados de mortalidad larvaria. Indices de abundancia de estadios larvarios tardíos indicaron que las clases anuales fuertes se determinaron durante las fases de huevo o larvarios. Asimismo, las estimaciones de mortalidad larvaria aplicadas a las tablas de vida con datos simulados indicaron que las clases anuales fuertes se determinaron durante las fases larvarias tempranas o tardías. Análisis de la distribución de larvas revelaron que tanto la zona costeras como la región al oeste de Point Conception son favorables para la sobrevivencia de las larvas de merluza.

INTRODUCTION

Numerous studies of environmental influences on recruitment of commercially exploited fish stocks in the northeast Pacific Ocean have been conducted. These investigations suggest that environmental factors affect survival through four primary mechanisms: larval transport, concentration of prey, changes in the location of spawning, and physiological influences on embryonic or larval development (table 1). Secondary mechanisms such as predation can be inferred from these initial factors. Many of these conclusions were based on correlative models. Walters and Collie (1988) described some of the problems associated with using correlative models to study recruitment processes of marine fish. Drinkwater and Myers (1987) showed that correlative models seldom have continuing predictive power.

The potential for spurious correlation in recruitment studies can be minimized by identifying plausible mechanisms through examination of egg, larval, and juvenile distribution and abundance. Subsequent investigations of processes underlying recruitment can proceed in three stages. First, key events in the life history that influence survival should be identified. Such identification would limit the number of environmental variables and the time of year to be considered in an investigation. Identification of key events can also be useful in developing hypotheses about recruitment processes. Second, the distribution of individuals within the selected time frame should be analyzed for spatial features that may influence recruitment and define the area for environmental-recruitment comparisons. Finally, the time series of key indicators of temporal and spatial processes that potentially influence survival should be compared with the time series of recruitment. This three-stage research approach was applied in an evaluation of factors underlying recruitment of Pacific hake (Hollowed 1990). This paper presents the results of the temporal and spatial analyses found in the first two stages of this approach.

The coastal stock of Pacific hake (*Merluccius productus*), also known as Pacific whiting, varies widely in year-class strength. Early in their lives, Pacific hake are found in waters off the coast of California, an upwelling region with a dynamic oceanic environment. In this region, the interannual oceanic variability causes a strong biological response (Chelton et al. 1982). The strong signals in recruitment of

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[Manuscript received February 14, 1992.]

TABLE 1
Summary of Oceanic Influences on Recruitment of Commercially Exploited Fish and Shellfish in the Northeast Pacific

Species	Reference	Proposed mechanism	Variable
Bluefin tuna	Mysak 1986	Alteration of migration routes	El Niño–Southern Oscillation (ENSO)
Coho salmon	Nickelson 1986	Reduced predation offshore, increased prey availability and thus faster growth	Upwelling during spring and summer
Dover sole	Hayman and Tyler 1980	Prey concentrations, location of settling	Upwelling
Dungeness crab	Johnson et al. 1986	Transport of zoea	Wind stress
	Jamieson et al. 1989	Transport	Current patterns
English sole	Kruse and Tyler 1983	Alteration of spawning period, rates of gonadal development	Temperature
	Hayman and Tyler 1980	Prey concentrations	High storm frequency, low mean wind speed
	Botsford et al. 1989	Prey concentrations	Productivity
	Forrester 1977	Egg viability	Temperature
	Ketchen 1956	Pelagic stage duration and transport	Temperature
Jack mackerel	Zwiefel and Lasker 1976	Incubation period, larval growth	Temperature
	Theilacker 1986	Starvation, predation	Productivity
	Hewitt et al. 1985	Starvation, predation	Productivity
Northern anchovy	Lasker 1975, 1981	Prey concentration	Wind-driven turbulence
	Peterman and Bradford 1987	Prey concentration	Wind-driven turbulence
	Husby and Nelson 1982	Transport and prey concentrations	Turbulence, upwelling, strength of thermocline
	Power 1986	Larval transport	Upwelling
	Fiedler 1984	Extension of spawning range	ENSO
	Zweifel and Lasker 1976	Incubation period, larval growth	Temperature
	Methot 1986	Maturity schedule	Temperature
Pacific cod	Tyler and Westrheim 1986	Larval transport, survival of eggs and larvae	Transport and temperature
Pacific hake	Bailey 1981	Larval transport	Upwelling, temperature
	Zwiefel and Lasker 1976	Incubation period, larval growth	Temperature
	Bailey and Francis 1985	Larval transport, growth, spawning location	Upwelling, temperature
	Hollowed and Bailey 1989	Larval transport, growth, prey concentration	Upwelling, spring transition
Pacific halibut	Parker 1989	Larval transport	Wind
Pacific herring	Pearcy 1983, Mysak 1986	Wide range of factors	ENSO
	Alderdice and Hourston 1985	Embryonic and larval survival	Temperature, salinity
	Stocker et al. 1985	Physiological effect, prey production	Temperature, river discharge
	Schweigert and Noakes 1991	Transport	Ekman transport, upwelling
	Tanasichuk and Ware 1987	Ovary weight and fecundity	Temperature
Pacific mackerel	Sinclair et al. 1985	Reduced southward transport	ENSO, temperature
	Parrish and MacCall 1978	Prey concentrations, vulnerability to predation, change in distribution	Temperature, upwelling, wind stress
Pacific sardine	Zweifel and Lasker 1976	Incubation period	Temperature
	Bakun and Parrish 1980	Prey concentrations and circulation	Annual upwelling 39°N Feb.–June upwelling and wind-stress curl
Petrale sole	Alderdice and Forrester 1971	Incubation, hatching success	Temperature and salinity
	Forrester 1977	Pelagic stage duration, settling time, prey concentrations	Temperature
Rock sole	Fargo and McKinnell 1989	No proposed mechanism	Temperature
	Forrester 1977	Egg development, larval retention	Temperature (Feb.–Apr.), transport
Sablefish	McFarlane and Beamish 1986	Prey concentrations	Transport and temperature
Sockeye salmon	Mysak 1986	Alteration of migration routes	ENSO
	Thomson et al. 1992	Alteration of migration routes	Wind-driven current
Walleye pollock	Ingraham et al. 1991	Egg transport, spawning location	Large-scale atmospheric forcing
	Kim 1989	Depth distribution of eggs and larvae	Density
	Hinckley et al. 1991	Larval transport	Advection
	Schumacher and Kendall 1991	Larval transport, larval retention	Advection, storm frequency
Widow rockfish	Norton 1987	Larval transport	Advection, atmospheric circulation

Pacific hake and in the region's oceanic conditions provide an opportunity to study the relationship between recruitment success and interannual variations in ocean conditions.

Bailey et al. (1986) showed that strong year classes of Pacific hake could be clearly identified from indices of juvenile abundance (2 months–1 year old). From this observation, the authors concluded that the magnitude of a hake year class was determined by processes occurring during the first year of life.

For this analysis, I examined interannual variability in both the larval and juvenile phases to identify

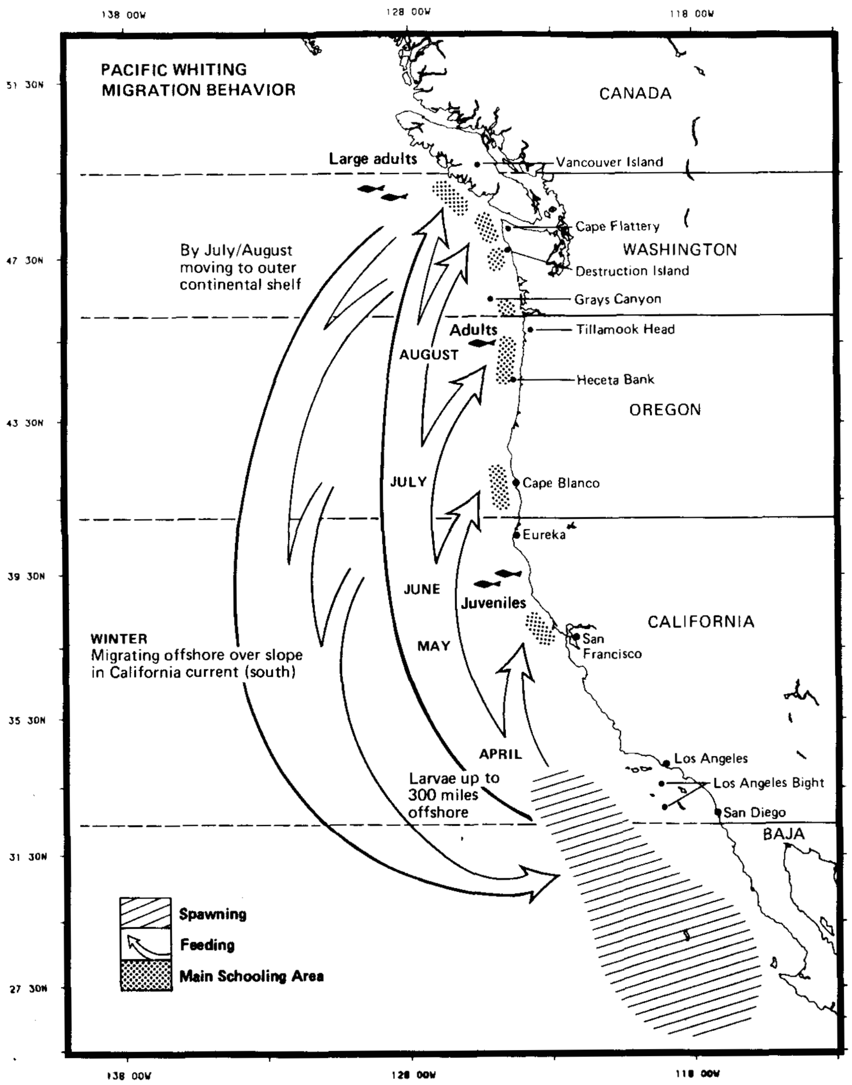

Figure 1. Migratory pattern of Pacific hake.

the point in the life history when a strong relationship between early abundance (larval or juvenile) and observed recruitment to the fishery was established. Next I analyzed the spatial distribution of larval hake, using an extended time series of larval and juvenile abundance from California Cooperative Oceanic and Fisheries Investigation (CalCOFI) surveys and California Department of Fish and Game (CDFG) anchovy (*Engraulis mordax*) surveys.

Pacific hake are most abundant over the continental shelf and slope within the California Current system from roughly 25°N to 50°N (figure 1). In summer, adult hake migrate to the northern end of their distribution to feed. In autumn the adults migrate southward to spawn off the coasts of central and southern California and the Baja California peninsula.

Indices of larval abundance show that most of the spawning occurs between January and March. The fish spawn in midwater depths (130–500 m) over the continental slope; after hatching, larvae are distributed within or just below the mixed layer (Bailey et al. 1982). Early-stage hake (eggs, larvae, and juveniles less than 2 years old) are found in waters off the coast of California. Hake larvae eat a broad size-range of prey, predominantly copepod eggs, nauplii, copepodites, and adults (Sumida and Moser 1980).

DATA SOURCES

Larval Data

CalCOFI survey data formed the basis for my examination of the distribution and abundance of larval hake. From 1950 to 1960, monthly surveys were conducted along a fixed sampling grid. From 1961 to 1969, annual surveys were conducted every third month (January, April, July, and October), and from 1969 to 1984, the grid was completely sampled every third year (i.e., 1972, 1975, 1978, 1981, and 1984; Hewitt 1988). From 1969 to 1984, stations were not consistently sampled in any particular month, but always in the first and second quarters of the year (Hewitt 1988). Since 1985, quarterly surveys have been conducted over a reduced portion of the sampling grid.

Larval hake were sampled by oblique tows with a 1-m ring net from 1951 to 1976 and with bongo nets after 1976. The depth of the tows was 150 m from 1951 to 1965, and 210 m thereafter. The number of fish larvae captured was standardized to the number per 10 m^2 of sea-surface area on the basis of the depth and duration of each tow as described in Smith and Richardson (1977). Estimates of the number of larval hake observed were available for most years from 1951 to 1986, except for 1970, 1971, 1973, 1974, and 1976. Information on the size distribution of larval hake was available for 1961, 1963–69, 1972, 1975, and 1977–85.

Juvenile Survey Data

Data on juvenile abundance were obtained from CDFG pelagic fish surveys (Bailey et al. 1986). Data for juvenile hake were available from 1965 to the present. Indices of juvenile abundance were updated to include more recent years, 1984–85. In general, hydroacoustic surveys were conducted during the day, and midwater trawl samples were collected at night along the same track lines. A midwater trawl with a 50- or 60-ft^2 opening and 1.27-cm mesh at the cod end was deployed for 20 minutes in the upper 15 fathoms of the water column. Data from hauls taken between 30° and 35°N were used in this study. Two indices of juvenile abundance based on the percent occurrence and catch per unit effort (CPUE) of juvenile hake observed between April and March of the next year are presented. Percent occurrence was calculated as the percent of all autumn or winter hauls that recorded catches of 0-age hake (Bailey et al. 1986). Catch per unit effort was calculated as

$$\text{CPUE} = \ln[(\text{number hake/hours trawled}) + 1)]/n, \qquad (1)$$

where n is the number of tows (Bailey et al. 1986).

The number of months available for the Bailey et al. study varied between years. For example, in 1984 the year-class index was based on a single cruise made in November. I used only data collected during autumn-winter cruises (September–March) for this study.

Recruitment Estimates

Estimates of the number of fish recruited to the fishery at age 2 were derived from the recruitment estimates of Dorn and Methot (1989). These recruitment estimates were produced using the stock synthesis model (Methot 1986, 1989) and are dependent on age-composition data from the fishery and adult surveys.

METHODS

Larval Abundance and Distribution

Early-stage hake larvae have been observed off central and southern California and Baja California. The sampling area used for CalCOFI surveys was divided into 23 regions covering 1.7556×10^{11} m^2 (Lo 1986). The southern regions (12–20) were not sampled from 1980 to 1988; regions 1–3 were sampled only in 1969 and 1972. Therefore, for time-series comparisons, I used a consistently sampled subset including regions 4, 5, 7, 8, 9, and 11 (figure 2).

The regional subset was further broken down into four areas representing nearshore locations, areas west of Point Conception, and offshore areas north or south of Point Conception. The boundaries of these subareas are illustrated in figure 3.

Indices of larval abundance were based on the mean number of larvae per 10 m^2 over the sampling area. I divided the indices of abundance and the size distribution of larvae (standard length) into three categories corresponding to early (1.75–4.25 mm)[1], middle (4.25–11.25 mm), and late (11.25–15.5 mm) stages of development.

For early and late-stage larvae, I used observations from the subset of consistently sampled regions to estimate abundance. For early-stage larvae, I calculated a weighted mean number of larvae per unit area (y) for the regional subset using samples collected between January and March.

$$y = \Sigma_{r = 4,5,7,8,9,11} (W_r y_r) \qquad (2)$$

where W_r was the regional weight based on the surface area within each of the six regions in the subset (table 2, following Lo 1985), and y_r was the sample mean count per station for the region. I used a similar weighted mean for late-stage larvae collected between March and May.

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[1] Observations showed yolk-sac larvae of hake were never smaller than 2 mm.

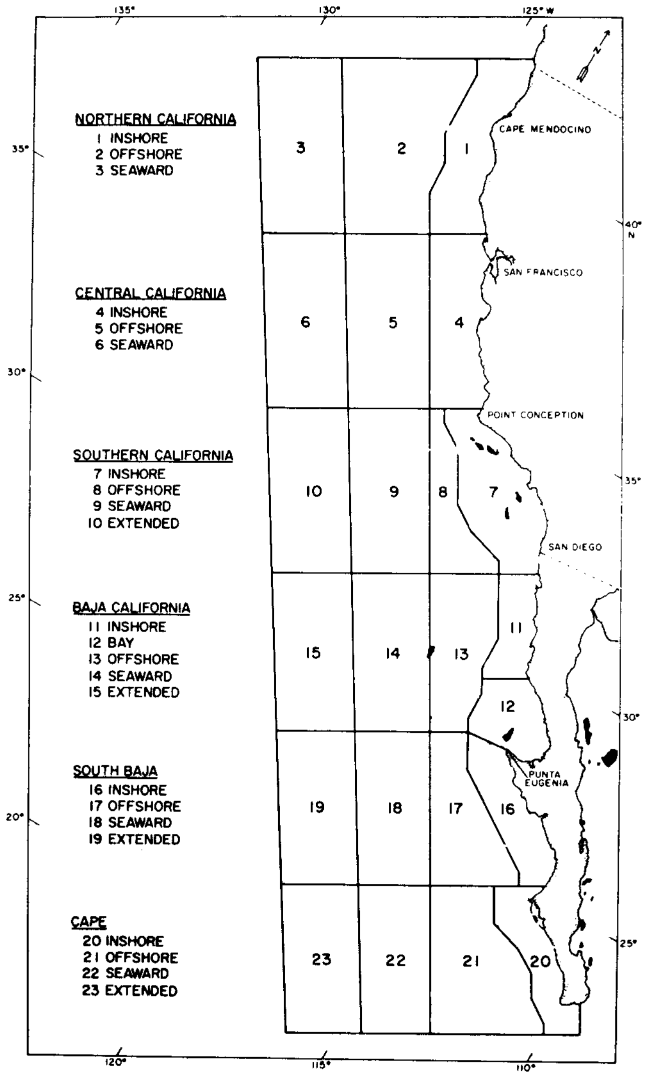


Figure 2. Sampling regions for CalCOFI larval fish surveys.

TABLE 2
Surface Areas and Weights for CalCOFI Regions 4–11

CalCOFI region	Area (million m^2)	Regional weight
4	61.05	0.152
5	98.78	0.247
7	68.96	0.172
8	41.16	0.103
9	98.78	0.247
11	31.71	0.079
Total	400.44	1.000

To identify relationships between the larval abundance indices and adult hake populations, I compared the time series of larval data to recruitment indices and egg production estimates. I divided the time series of larval abundance indices into two intervals corresponding to periods when the meter net

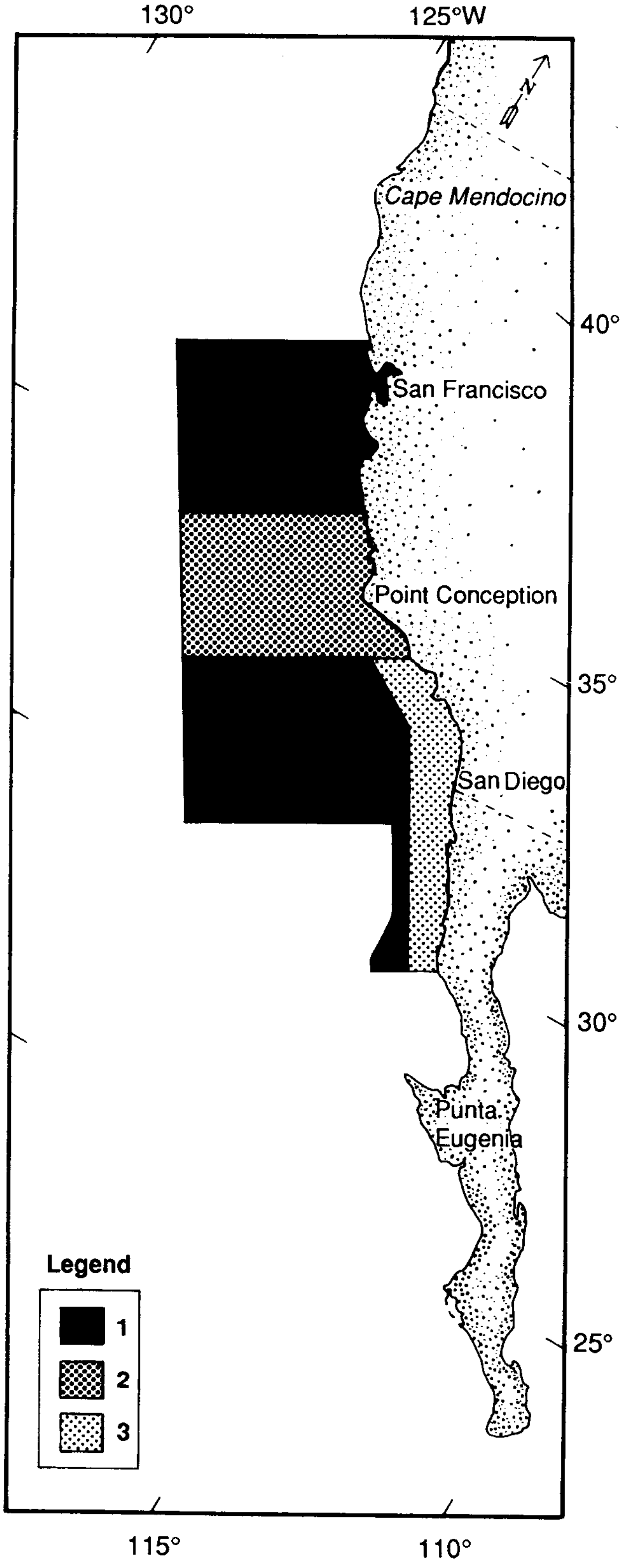


Figure 3. Subareas within the regional subset representing areas north or south of Point Conception (1), west of Point Conception (2), and near shore (3).

(1961–75) and bongo nets (1977–84) were used. This division is necessary because the catchability of the two configurations cannot be considered equivalent (Lo 1985, 1986). Data after 1985 were not included in this analysis because the sampling area was reduced to include only regions 7, 8, and 9.

To summarize the spatial distributions of early and late-stage larvae, I used the distributional centroid and the variance of the spatial distribution (Koslow et al. 1985; Heath and MacLachlan 1987; Kim 1987; Kendall and Picquelle 1990). I also plotted the observed distribution of larvae to examine the relative fit of the centroid to the observed data. The centroids were estimated in terms of the mean latitude and longitude weighted by the number of larvae at each station. The centroid equals the weighted mean position. An ellipse representing the standard deviation of the first two principal axes of the bivariate normal distribution was plotted to illustrate the central location of the larvae (Kendall and Picquelle 1990).

I compared distributions of early and late-stage larvae using years with a well-defined temporal peak in abundance in both larval stages. This criterion was imposed to limit the comparisons to years when a cohort of larvae could be identified in both the early and late-stage data sets. I also compared the distributions of late-stage larvae in years of strong recruitment into the fishery.

Construction of Life Table

Using the format of Smith (1985), I constructed a life table for hake. Independent estimates of natural mortality rates were obtained for embryonic and early-stage larvae based on estimates of egg production and larval abundance. For juveniles less than 135 mm, I assumed mortality to be a function of size. I also assumed that the estimated mortality rates within a size range for juvenile northern anchovy (*Engraulis mordax*) were generally applicable to Pacific hake. For juveniles greater than 135 mm (1 year +) daily mortality rates were based on an estimate of adult annual instantaneous mortality (0.2) for hake (Hollowed et al. 1988).

Estimate of Daily Mortality for Embryonic Stage

I estimated the abundance of hake larvae for the embryonic stage as follows. I calculated the total number of eggs spawned in a given year from the most recent estimates of numbers-at-age, percent mature-at-age provided by Dorn and Methot (1989), and an estimate of the fecundity-at-age. I calculated fecundity-at-age from the relationship between fork length (FL) and fecundity (E) for the Georgia Strait Pacific hake stock (equation 3; Mason 1986) and the population mean length-at-age:

$$E = 0.5501 \star \mathrm{FL}^{3.3896} \qquad (3)$$

Where E is number of yolked oocytes >200 μm, and FL is the fork length in centimeters.

An estimate of the total abundance of early-stage larvae (1.75–4.25 mm) was derived from CalCOFI data. I estimated the total number of early-stage larvae by multiplying the mean number of early-stage larvae per m^2 in a given region by the area of that region and summing over all regions. The total number of early-stage larvae was calculated from areas 4–13 (figure 2).

Daily instantaneous natural mortality (M) was estimated from the following equation:

$$N_t = N_o \star \exp(-M \star d) \qquad (4)$$

where N_t was the total abundance of early-stage larvae in a given year; N_o was the egg production for that year; M was the estimate of daily natural mortality; and d was the duration in days between the egg and early larval stages.

In an analysis of growth rates derived from daily increments on otoliths, Bailey (1982) found that hake grew linearly during the first 20 days after hatching. He concluded that larval growth could be described with the following equation:

$$\mathrm{SL} = 2.75 + 0.16 \star d \qquad (5)$$

where SL is the standard length of the preserved larvae in millimeters. I used equation 5 to estimate that early-stage larvae were 0–10 days old.

Bailey (1982) noted that growth increments begin 1 to 2 days before complete yolk-sac absorption. He found that the time from hatching to complete absorption of the yolk sac was temperature-dependent. Fifty percent of laboratory-reared larvae had completely absorbed their yolks after 6.4 days at 12°C and 4.2 days at 15°C. Hake larvae tend to aggregate at the bottom of the thermocline. Barilotti et al. (1984) found that the thermocline depth generally corresponded with the depth of the 14°C isotherm. Assuming temperatures of 14°C, I estimated the time to complete absorption of the yolk sac as 5 days, and assumed that daily rings began to be added after 3 days.

I estimated the incubation time for hake eggs as a function of average water temperature at 100 m. The mean temperature at 100 m for the first quarter (1954–87) was 9.97°C within a 3° square including the California Bight (30°–33°N; J. Norton, Pacific Fisheries Environmental Group, Monterey, pers. comm.). Bailey (1982) found the time for 50% hatching of eggs reared at 12°C was 4.5 days, and at 8°C, 6.5 days. Using a Gompertz-type growth relationship, Zwiefel and Lasker (1976) estimated that the incubation time of hake eggs reared at 9°C was 5 days; at 10°C the time was 6 days. Using these estimated incubation times and the mean temperature at 100 m, I assumed that eggs hatch after approximately 5 days. Growth ring deposition began after 3 days, so I assumed that early larvae were 8 to 18 days old, and I estimated mortality assuming that early larvae were 13 days old.

Estimate of Daily Mortality for Early to Late Larvae

Daily mortality rate for the period between early and late stages of development was estimated as follows. I used growth rates derived from daily increments on hake otoliths (Bailey 1982) to calculate the age of late larvae:

$$\mathrm{SL} = 1.72 \star \exp(3.15 \star (1 - \exp(-0.02624 \star d))) \qquad (6)$$

For larvae from 11.25 to 15.25 mm, approximately 40 days would have elapsed since deposition of the first daily growth ring.

I further adjusted the average age of late-stage larvae estimated from equation 6 to include 5 days for the egg stage and 3 days until the beginning of daily growth ring deposition. Thus I assumed the late-stage larvae to be roughly 48 days old.

I calculated natural mortality by comparing the early and late-stage larval abundance indices discussed above for years when abundance peaked in the early and late-stage indices. I calculated mortality from equation 4, where N_0 was the abundance of early-stage larvae, N_t was the abundance of late-stage larvae, and the duration was 35 days — i.e., 48 days (the mean age of late-stage larvae) minus 13 days (the mean age of early-stage larvae).

Estimate of Stage Duration for Juveniles

Juvenile-stage durations were based on observed length at age from CDFG surveys. Figure 4 shows the length range of 0-age juvenile hake from the CDFG surveys. I estimated juvenile-stage durations by assuming a growth rate of 0.39 mm per day, derived from the linear relationship between the midpoint of the length range and Julian date for juveniles from spring, summer, and autumn cruises (figure 4).

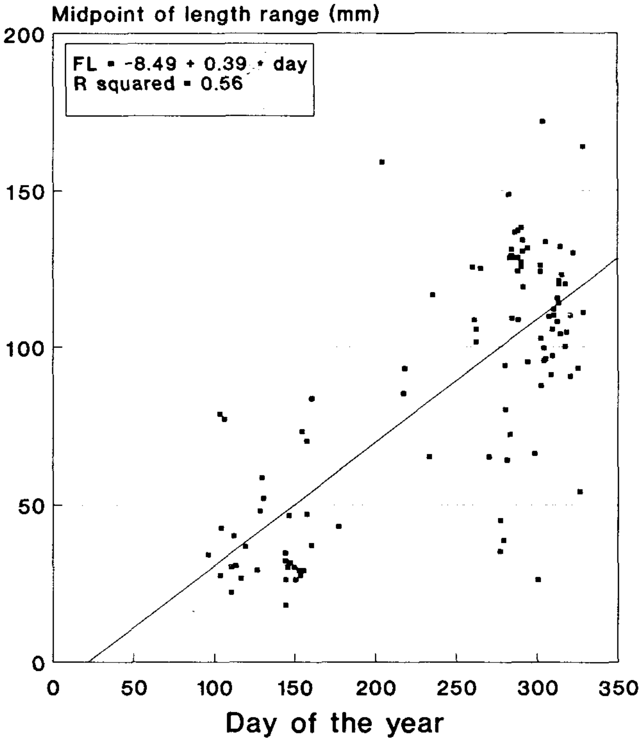


Figure 4. Midpoint of length ranges of 0-age Pacific hake in individual hauls by day. The regression of length versus day was used to estimate daily growth rates of juvenile hake.

$$\mathrm{FL} = -8.4897 + 0.3911 \star \mathrm{DAY}\ R^2 = 0.56. \qquad (7)$$

If early-stage larval growth followed this regression, the hatch date would be in late January. Such a date would be consistent with temporal distributions of early-stage larvae.

Life-Table Simulation Model

Mortality through each life stage was followed, beginning with an estimate of egg production. The number of eggs used to initiate the model was the average of estimated numbers based on population from Dorn and Methot (1989). I used the initial estimate of eggs as the starting point for the hypothetical cohort. Then I varied each duration and mortality rate for each life stage to produce a twenty-fold increase or decrease in recruitment.

RESULTS

Larval Spatial and Temporal Distribution

When stations were sampled over a wide geographic area (1963–75), an average of 84% of the early-stage larvae and 96% of the late-stage larvae were taken in regions 4, 5, 7, 8, 9, and 11 (table 3;

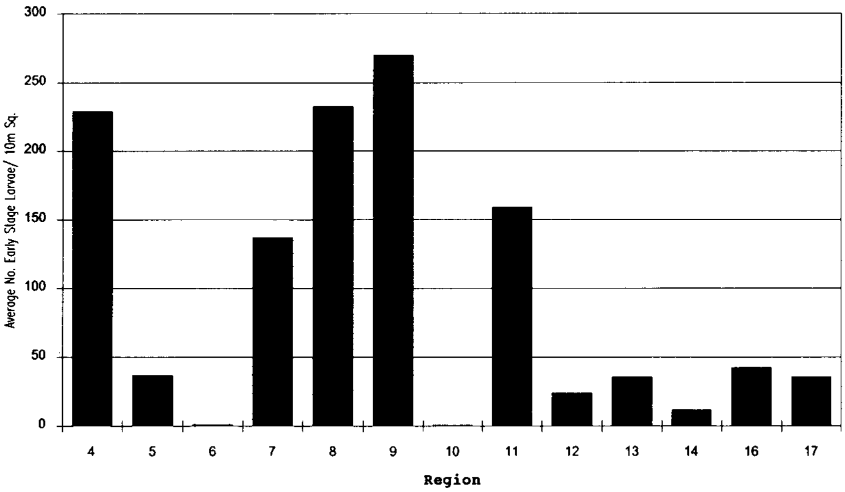


Figure 5. Summary of the average abundance of early-stage hake larvae (1.75–4.25 mm) by region, collected between January and March in CalCOFI surveys from 1963–1975. No early stage hake larvae were collected in regions that are not represented.

TABLE 3
Percentage of Total Early and Late Larvae Observed within the Subset (CalCOFI Regions 4, 5, 7, 8, 9, and 11)

Year	Percentage early larvae (1.75–4.25 mm)	Percentage late larvae (11.25–15.25 mm)
1961	–	98.30
1962	–	–
1963	88.20	97.84
1964	65.32	94.48
1965	47.77	79.07
1966	88.94	94.57
1967	–	–
1968	99.87	–
1969	91.30	100.00
1970	–	–
1971	–	–
1972	96.88	100.00
1973	–	–
1974	–	–
1975	90.94	100.00
1977	100.00	100.00
1978	96.22	100.00
1979	99.89	100.00
Average	87.76	96.75

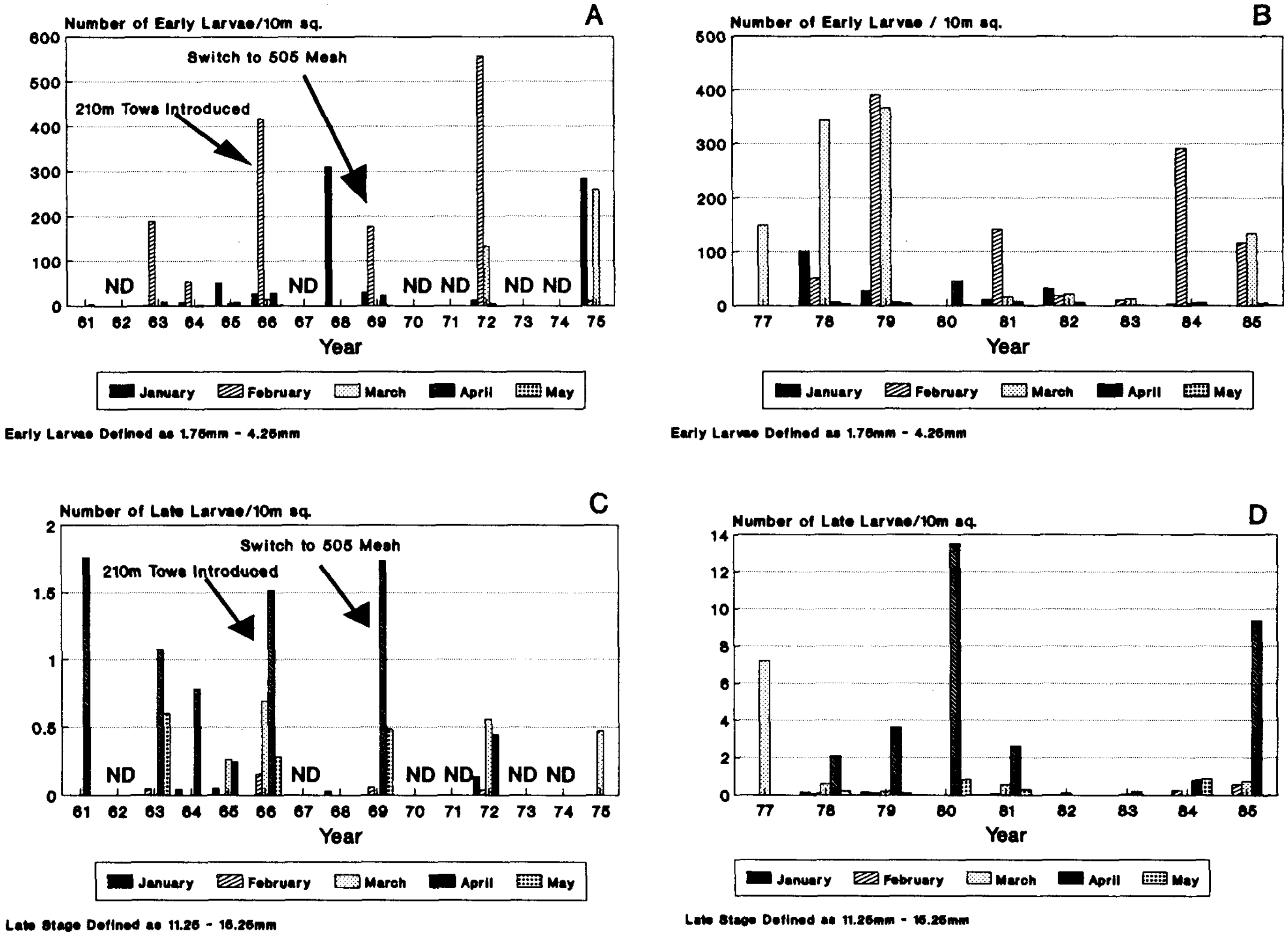
figure 5). These regions were well sampled in most years. Based on these observations, I defined the regional subset as the area encompassing regions 4, 5, 7, 8, 9, and 11 (figure 2).

The temporal distribution of larvae over the entire time period (1961–85) revealed peak periods of early and late-stage abundance. Within the regional subset, most early-stage larvae were taken in the first three months of the year, with a peak in February (figures 6a, b). Most late-stage larvae were taken between March and May (figure 6c, d). In years when sampling was distributed across all three months, late-stage abundance was generally highest in April (figures 6c, d).

Mortality Estimates

Comparisons of egg production to early-stage larval abundance were made for eight years when sampling occurred in January, February, and March (1966, 1972, 1975, 1978, 1979, 1981, 1982, and 1984; figure 6). Estimates of instantaneous natural mortality during the embryonic stage for these eight years ranged from 0.23 to 0.41 d^{-1} (table 4). The differences in mortality estimates may be due in part to incomplete sampling of the spawning range of coastal hake. The average daily mortality (M = 0.31) for embryonic hake fell between the mortality estimates for anchovy calculated by Smith (1985; M = 0.25) and Peterman et al. (1988; M = 0.41). Peterman et al. gave annual estimates of daily natural mortality for northern anchovy between the time of spawning and the mean of the yolk-sac larvae. The annual estimates of hake and anchovy embryonic mortality were not correlated (table 4).

Larval abundance clearly peaked for the early and late-stage indices in nine years (1963, 1964, 1966, 1969, 1972, 1978, 1979, 1981, and 1985; figure 6). Estimates of daily mortality rates between early and late stages of larval development for these nine years ranged from 0.11 to 0.20 (table 5). The average daily mortality rate for early-stage hake larvae (0.15) was similar to estimates for larval anchovy between approximately 4 and 10 mm long (Smith 1985; 0.160), and for yolk-sac-to-19-day-old anchovy larvae (Peterman et al. 1988; 0.186). The estimates indicate that roughly 14% of the hake larvae are lost per day in the early-to-late larval period.



Early Larvae Defined as 1.75mm - 4.25mm

Early Larvae Defined as 1.75mm - 4.25mm

Late Stage Defined as 11.25 - 15.25mm

Late Stage Defined as 11.25mm - 15.25mm

Figure 6. Summary of the monthly average number of early or late larvae per 10 m².

TABLE 4

Estimated Abundance and Corresponding Daily Natural Mortality Rates for Embryonic Hake (1.75–4.25 mm) Compared with Daily Mortality for Embryonic Northern Anchovy

Year	Eggs (trillion)	Larvae (trillion)	Estimate of hake mortality (d^{-1})	Estimate[a] of anchovy mortality (d^{-1})
1966	731.2	8.46	0.34	0.42
1972	437.8	11.01	0.28	0.25
1975	476.3	18.55	0.25	0.44
1978	378.1	12.42	0.26	0.59
1979	326.1	17.20	0.23	0.48
1981	298.6	2.35	0.37	0.38
1982	275.8	1.41	0.41	0.36
1984	344.6	3.32	0.36	0.36
Average			0.31	0.41

[a] Peterman et al. 1988

TABLE 5

Estimated Daily Mortality Rates for Intermediate Hake Larvae Compared with Daily Mortality for Northern Anchovy Larvae

Year	Early larval[a] abundance no./10 m²	Late larval[b] abundance no./10 m²	Estimate of hake mortality[c]	Estimate of anchovy mortality[d]
1963	69.921	0.992	0.12	—
1964	32.261	0.827	0.10	—
1966	203.551	1.105	0.15	0.17
1969	132.426	0.761	0.15	0.21
1972	270.932	0.797	0.17	0.18
1975	407.620	0.358	0.20	0.18
1978	310.222	0.642	0.18	0.17
1979	428.142	0.884	0.18	0.22
1981	58.240	1.362	0.11	0.18
1985	273.755	1.984	0.14	0.19
Average			0.15	0.19

[a] 1.75–4.25 mm

[b] 11.25–15.25 mm

[c] Based on differences in the abundance indices of early and late larvae assuming a 35-day period of growth

[d] Peterman et al. 1988

Life-Table Simulations

The estimate of recruitment (0.060 billion) produced from the life-table simulation was similar to the observed estimates of poor recruitment at age 2 (0.063 billion; table 6). Strong recruitment at age 2 was estimated to be 3.180 billion. Estimates of strong and poor recruitment were calculated as the mean of the upper and lower quartiles of the recruitment time series presented in Dorn and Methot (1989). Approximately 99% of the cohort is lost by the time the young reach 10 mm. Estimates of early-stage abundance showed no significant relationship with egg abundance (figure 7). This may indicate that significant embryonic mortality already occurred, and that the rate of embryonic mortality must vary interannually.

Recruitment levels at age 2 on the order of 1.2 billion hake (a twenty-fold increase, a level similar to the lowest of the strong year classes) could only be produced by shortening the larval stage or the natural mortality rate during the egg or larval stages (table 7). In contrast, recruitment levels at age 2 of .012 billion hake (a twenty-fold decrease, a level similar to the lowest of the weak year classes) could result from variations in the mortality rate or duration of any life stage (table 7).

Juvenile and Larval Indices of Abundance

Figure 8 illustrates the updated time series of indices of age-0 juvenile hake abundance (based on autumn and winter cruises) and recruitment to the fishery at age 2 (Dorn and Methot 1989). Although the pattern of year-class strength was not exactly mirrored in the juvenile indices, juvenile percent occurrence or CPUE was usually elevated when there were strong year classes (figure 8). The notable ex-

TABLE 6

Estimated and Postulated Life Table for the Coastal Stock of Pacific Hake

Category	Length (mm)	Mortality (daily)	Duration (days)	Initial number
Embryo[a]	Egg–4	0.313	16	4.48×10^{14}
Early larva[b]	4–10	0.150	23	2.99×10^{12}
Late larva[c]	10–35	0.050	89	9.51×10^{10}
Juvenile II	35–60	0.020	64	1.11×10^{9}
Juvenile III	60–110	0.010	128	3.09×10^{8}
Juvenile IV	110–135	0.0027	64	8.58×10^{7}
Juvenile V	135+	0.00056	346	7.22×10^{7}
Recruits @ age 2	—	—	—	5.95×10^{7}

[a] Duration of the embryonic stage was estimated by assuming a 5-day incubation period, 3 days before daily ring deposition, and 8 days of growth to reach 4 mm (derived from equation 5).

[b] Duration of stage estimated from equation 6 (31 days) and assuming a 5-day incubation period and 3 days before daily ring deposition. The duration represents the estimated age (39 days) minus the embryonic stage (16 days).

[c] Duration of stage estimated from equation 6 (120 days) and assuming a 5-day incubation period and 3 days before daily ring deposition. The duration represents the estimated age (128 days) minus the embryonic and early larval stages.

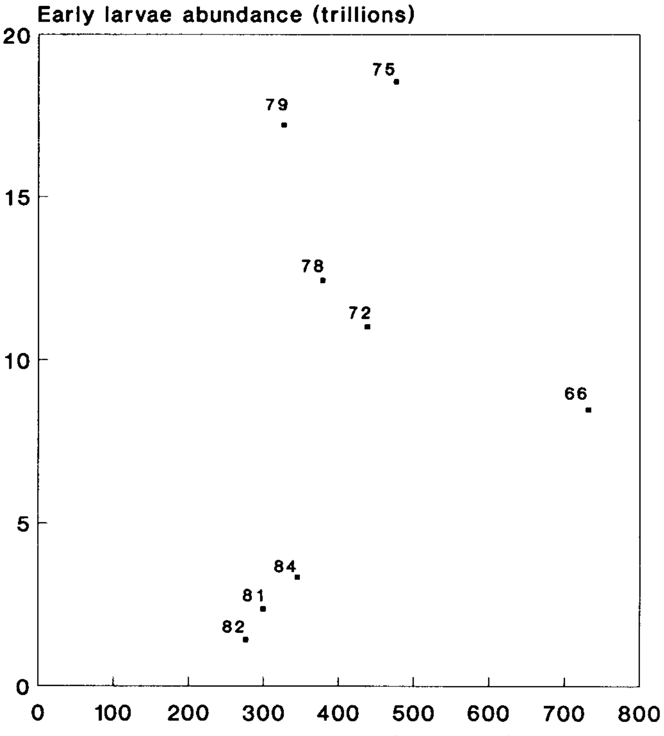


Figure 7. Relationship between estimated levels of egg production and observed abundance of early larvae.

TABLE 7

Parameter Changes Leading to a Twenty-Fold Increase or Decrease in Recruitment for Coastal Pacific Hake

Stage	Instantaneous daily mortality	Duration of stage (days)
Embryo (egg to 4 mm)		
Starting	0.313	16.00
1/20×	0.414	21.14
20×	0.126	6.43
Early larva (4–10 mm)		
Starting	0.150	23.00
1/20×	0.220	33.74
20×	0.020	3.03
Late larva (10–35 mm)		
Starting	0.050	89.00
1/20×	0.068	121.20
20×	0.016	29.08
Early juvenile (35–60 mm)		
Starting	0.020	64.00
1/20×	0.045	144.50
20×	unr	unr
Juvenile II (60–110 mm)		
Starting	0.010	128.00
1/20×	0.022	289.00
20×	unr	unr

unr = unreasonable value

ception was a low juvenile index in 1984, a year that produced a strong year class.

The time series of late-stage larval abundance also seems to be related to year-class strength. Again, with the notable exception of the 1984 year class, the index of late-stage larval abundance was high when there were strong year classes (1961, 1977, and 1980; figure 9). This relationship is most apparent from samples taken with a bongo net (figure 9), possibly because that net more efficiently samples large larvae. A strong relationship is not readily apparent in the pre-bongo data because there were no data for three of the four strong year classes (1967, 1970, and 1973).

The indices of mean larval abundance could have been influenced by rare encounters with larval patches of high abundance. Large concentrations of larvae were observed in a few stations. The influence of these patchy concentrations can be minimized by using trimmed means in which the upper and lower 5% of the distribution is ignored. Comparison of the trimmed mean catch-per-tow values with the mean catch-per-tow values shows that the large concentrations of larvae increased the mean substantially. But the trend showing high late-stage larval abundance in years that produced strong year classes was still apparent in the trimmed means (table 8).

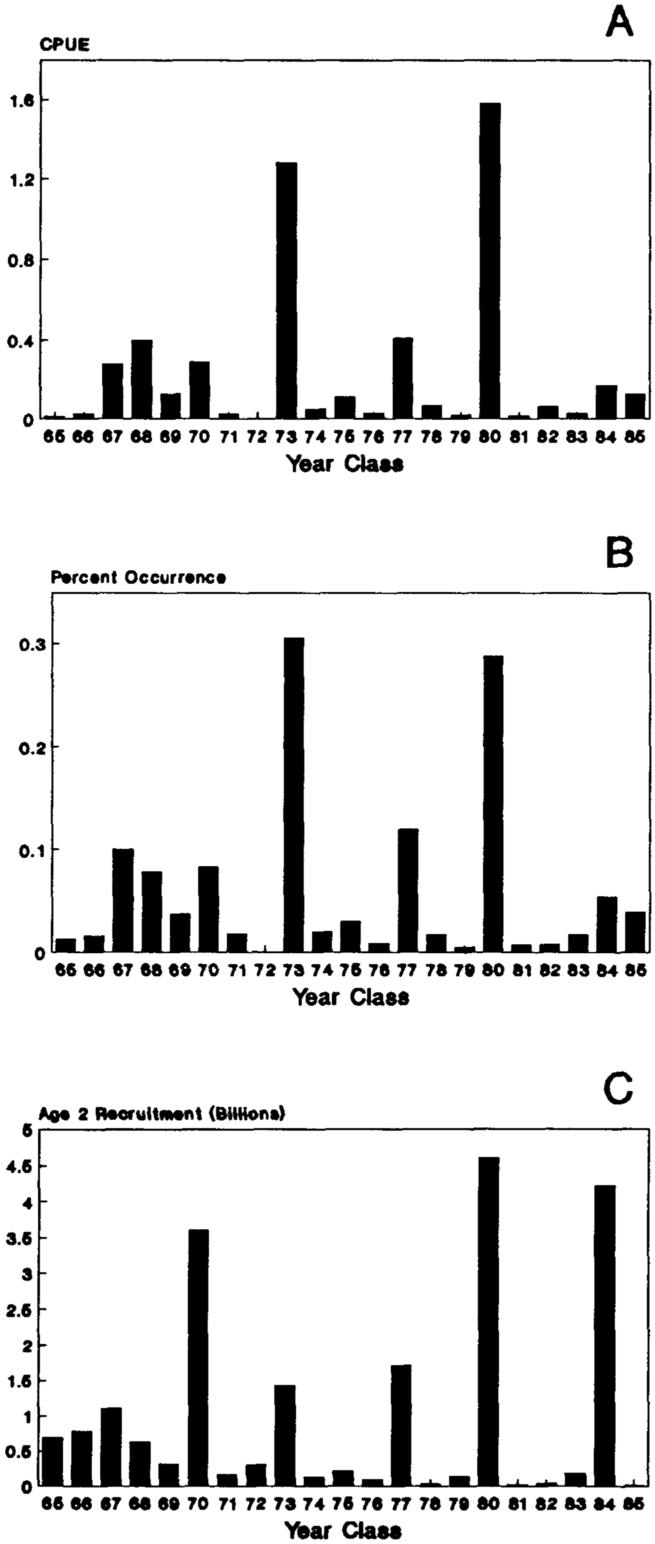


Figure 8. Catch per unit of effort (CPUE, *top*) and percent occurrence (*middle*) of 0-age hake in midwater trawl surveys compared with year-class strength determined by catch-at-age analysis (*bottom*).

Larval Distribution

Clearly defined peaks of abundance for both early and late-stage larvae were identified in nine years (1964, 1966, 1969, 1972, 1975, 1978, 1979, 1981, and 1985; figure 6). The early-stage larvae were widely distributed throughout the region, whereas the late-stage larvae were more concentrated (appendix). On average, early-stage larvae were observed in 47% of the stations; late-stage larvae in only 11% of the stations (table 8). Comparison of the mean catch-per-tow values with the trimmed mean-per-tow values shows that there were also localized patches where early-stage larvae were abundant (table 8).

The distributions of late-stage larvae that produced strong year classes are shown in figure 10. Most late-stage larvae were found south of Point Conception in 1961 and 1977; most were found north of Point Conception in 1980 and 1984, perhaps because spawning locations differed. Average temperatures at stations in region 7 (south of Point Conception) during January and February were 14.6°C in 1961, 16.0° in 1980, and 15.3° in 1984. Hollowed (1990) estimated the 1977 temperature in region 7 as 14.4°C. So the fish may have spawned farther south in 1961 and 1977 because temperatures were lower. The early-stage larval distributions

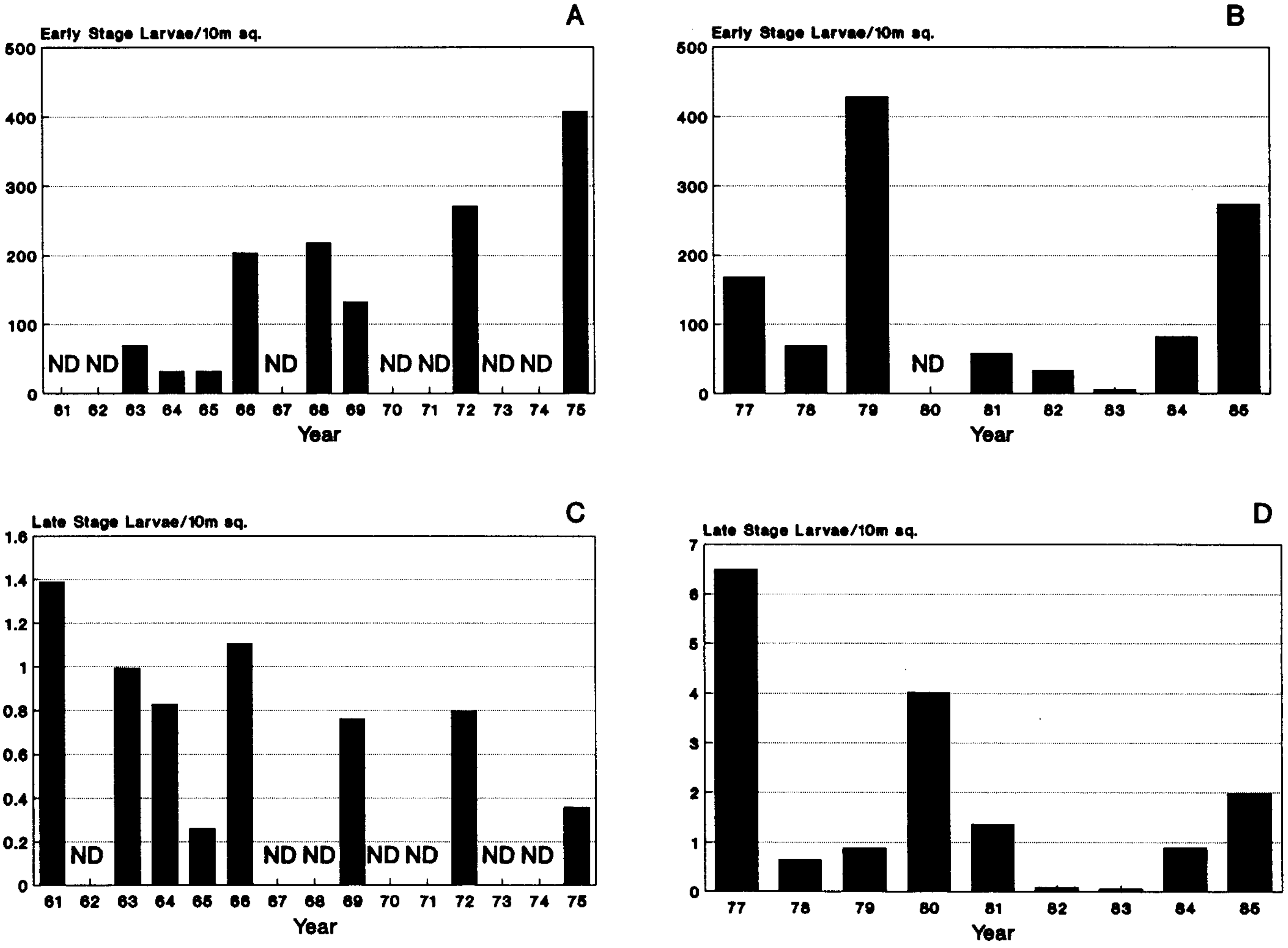


Figure 9. Time series of larval abundance indices for early and late Pacific hake larvae. The early-stage index is based on the average number of larvae (1.75–4.25 mm) per 10 m^2 in surveys conducted from January to March. The late-stage index represents the average number of larvae (11.25–15.25 mm) in surveys from March to May.

observed in 1984 (appendix) indicated northward spawning. Early-stage larval distributions were not available for 1961, 1977, or 1980.

Larvae that survived to the late stage were concentrated near shore or directly west of Point Conception (appendix). Mean catch per station for nearshore areas and areas west of Point Conception combined was generally higher than for other areas (table 9). Mean catch per station was higher in offshore regions in 1961 and 1985 (table 9). In 1961, the late-stage larvae were concentrated in offshore areas south of Point Conception (figure 10). In 1985, late-stage larvae were concentrated in offshore areas north of Point Conception (appendix).

DISCUSSION

This study produced three major findings. Processes controlling the production of strong year classes of Pacific hake seem to occur during the early or late or larval period. Estimates of larval mortality rates were similar in magnitude to estimates for northern anchovy but did not show similar interannual variations. Finally, transport to nearshore nursery grounds in the California Bight or areas within the offshore plume near Point Conception seems to play an important role in producing strong year classes.

The estimates of larval distribution, abundance, and mortality must be considered rough because of several sampling problems associated with the data sets used in this analysis. Crecco et al. (1983) noted that accurate estimates of larval abundance and daily mortality rates depend on the assumption that larvae of all size groups are equally vulnerable to capture. This assumption may not have been met because the data were not corrected for gear selectivity, extrusion, or avoidance by hake larvae. Differences in gear selectivity were indirectly addressed, however,

TABLE 8
Comparison of Abundance Indices for Early and Late-Stage Hake Larvae

Year	Percent occurrence	Weighted mean	Mean	SD	Trimmed mean	Maximum no./10m^2
Early-stage larvae						
1963	–	69.9	–	–	–	–
1964	58	32.3	26.5	112.6	10.5	1,463.1
1965	–	32.4	–	–	–	–
1966	65	203.6	221.0	836.3	65.8	7,238.4
1968	–	218.0	–	–	–	–
1969	51	132.4	112.5	556.4	41.8	8,485.1
1972	66	270.9	251.8	1340.6	70.0	19,444.7
1975	50	407.6	255.0	1222.2	62.4	14,269.1
1977	–	168.6	–	–	–	–
1978	38	310.2	211.6	1701.5	25.9	28,272.0
1979	54	428.1	305.0	1493.0	67.0	14,994.0
1981	28	58.2	52.9	518.5	8.0	7,352.0
1982	–	34.2	–	–	–	–
1983	31	6.3	11.3	518.5	4.3	459.0
1984	21	83.0	103.7	964.2	3.9	14,143.3
1985	58	273.8	129.4	738.7	18.6	7,721.1
Average	47	170.6	152.8		34.4	11,258.3
Late-stage larvae						
1961	25	1.390	1.667	4.071	0.961	25.9
1963	–	0.992	–	–	–	–
1964	16	0.827	0.784	2.322	0.361	16.7
1965	–	0.262	–	–	–	–
1966	17	1.105	0.848	2.595	0.389	19.6
1969	14	0.761	1.055	3.835	0.333	28.6
1972	8	0.797	0.629	2.761	0.104	21.1
1975	2	0.358	0.289	2.252	0.000	27.5
1977	15	6.495	7.200	21.620	3.600	154.3
1978	6	0.642	0.924	5.681	0.064	91.0
1979	8	0.884	1.119	4.492	0.349	46.2
1980	11	4.071	7.120	48.400	0.640	503.2
1981	10	1.362	1.663	9.078	0.474	124.7
1982	–	0.094	–	–	–	–
1983	–	0.061	–	–	–	–
1984	6	0.893	0.653	2.853	0.049	20.2
1985	7	1.984	1.376	6.022	0.183	46.0
Average	11	1.352	1.948		0.577	86.5

by dividing the larval time series into periods when the 1-meter ring nets and the bongo nets were used.

Extrusion of small larvae may have been significant for early-stage hake. Lo (1983) found that within the size range for early-stage larvae (1.75–4.25 mm), high percentages of anchovy larvae (93% of 1.75-mm larvae and 47% of 4.25-mm larvae) would have been extruded through the 505-μm–555-μm-mesh netting frequently used in CalCOFI surveys. Lo showed only minor differences between larval extrusion rates with the 550-μm ring net and 505-μm bongo nets. Because hake larvae have larger heads than anchovy larvae, fewer of them may be extruded (Smith and Richardson 1977); however, the heads are soft because they are not fully ossified, so extrusion could bias the estimates of early-stage mortality.

If extrusion rates for hake larvae were similar to those estimated for anchovy larvae by Lo (1983), the estimates of early-stage larval abundance would exceed the estimates of annual egg production. In such a case, the estimates of egg production would be erroneous. My estimates of the maturity schedules and fecundity of hake were approximations based on early examinations of hake maturity (Best 1963) and fecundity schedules for Georgia Strait Pacific hake (Mason 1986).

The mortality estimates for early-stage larvae also could have been biased by larger larvae's avoidance of the net. Hewitt and Methot (1982) noted that more large anchovy larvae were captured at night than during the day. Therefore, I estimated the ratio of mean catch during the day (0830–1630 h) to mean catch during the night (2030–0230 h) for the early and late-stage size classes. In 11 out of 15 years the mean catch of early-stage larvae was higher during the day than during the night (table 10). In all years sampled, the mean catch of late-stage larvae was

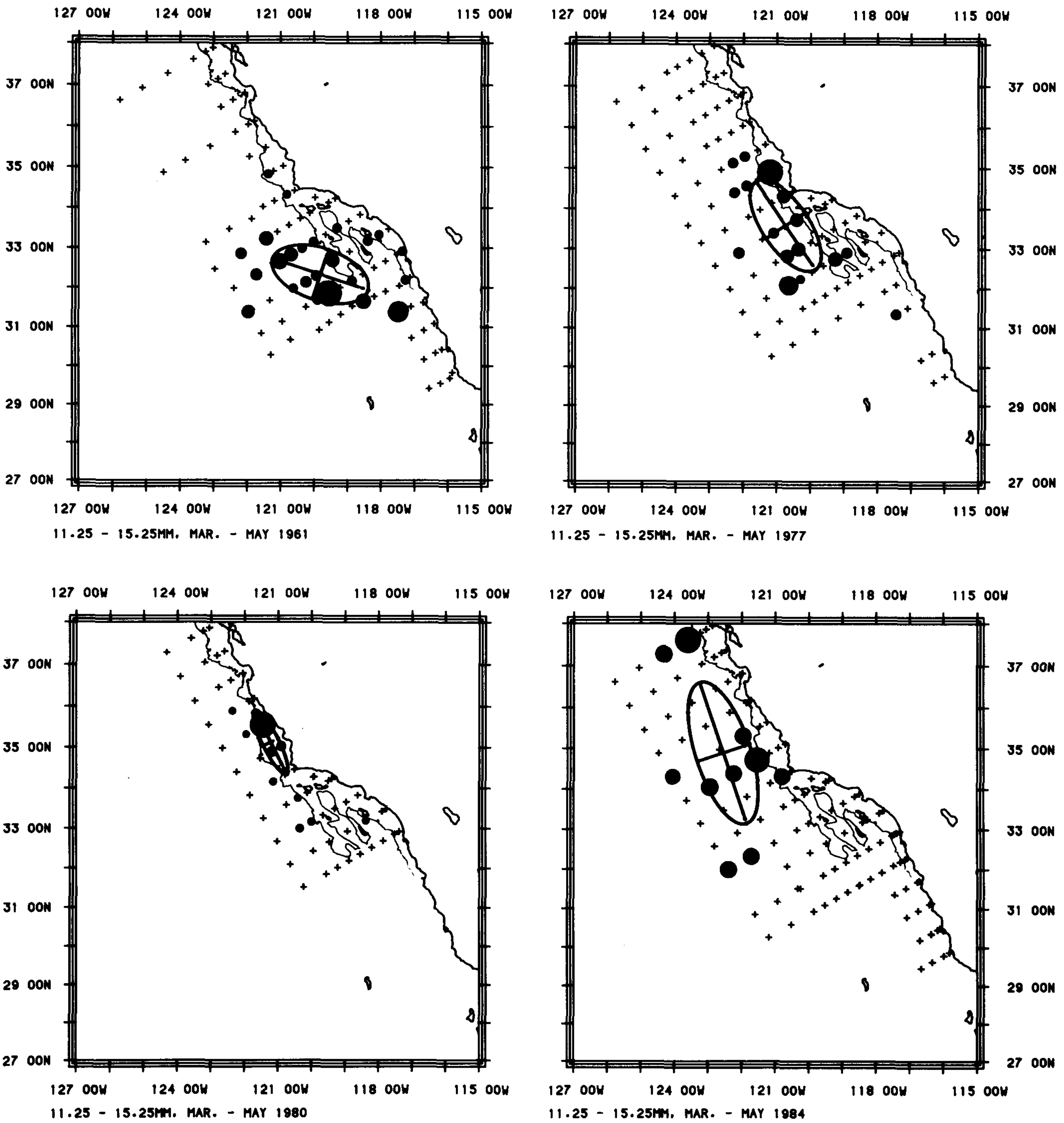


Figure 10. Comparison of late-stage larval distributions observed in years that produced strong year classes: 1961, 1977, 1980, and 1984. Dot size indicates the abundance of larvae relative to the maximum value observed in that year (1961 = 26, 1977 = 154, 1980 = 503, and 1984 = 20). The relationship between the abundance at each station and the size of the dot is linear. *Crosses* indicate stations where hake larvae were not observed.

lower during the day than during the night (table 10). This may indicate that late-stage hake larvae migrate vertically in a diurnal pattern.

Alternatively, the lower mean catch of late-stage larvae observed during the day may be attributed to net avoidance. The higher mean catch of early-stage larvae during the day may result from larval behavior. If early-stage larvae are more active during the

TABLE 9

Mean Density of Late-Stage Hake Larvae That Were Near Shore or West of Point Conception[a] in Regions 4, 5, 7, 8, 9, and 11

Year	Density (no./10 m²)			
	Inshore*	Point Conception	Other areas	Combined areas[b]
1961	1.308	0.909	2.245	1.125
1964	0.447	1.152	0.797	0.775
1966	0.221	2.060	0.660	1.000
1969	0.771	2.000	0.646	1.396
1972	0.381	1.568	0.000	0.988
1975	0.206	0.611	0.125	0.321
1977	1.000	13.806	5.333	9.630
1978	1.099	1.757	0.252	1.473
1979	0.396	1.696	1.103	1.131
1980	0.379	24.929	0.875	12.439
1981	2.702	1.902	0.606	2.400
1984	0.000	2.167	0.565	0.729
1985	0.000	1.189	2.479	0.494

[a] See figure 3 for definition of subareas.

[b] Combined areas refers to the mean number of hake larvae per station found in nearshore areas and areas west of Point Conception.

day, they may be concentrated higher in the water column. If extrusion rate is a significant factor for early-stage larvae, then larvae captured at deeper depths would spend more time in the net and would probably have greater extrusion rates than those captured at shallower depths. Because the day:night mean catch ratios varied considerably between years (table 10), a more rigorous method of examining net avoidance must be undertaken before a correction factor is applied to the larval data set.

Finally, the CalCOFI larval surveys were not designed to sample Pacific hake larvae. The depth of the tows (standard at 210 m to surface) may not have adequately sampled the entire vertical distribution of hake larvae, which may extend deeper. In addition, the distribution of hake larvae can be patchy in both space and time, and sampling at a few selected locations each month cannot precisely reflect the true dynamics of larval birth and death rates.

Problems also exist in interpreting the results from the midwater trawl juvenile surveys. The mesh size of the net, depth of tow, and geographic distribution of the midwater surveys were not optimal for sampling hake juveniles, which are only captured incidentally. The midwater sampling data, however, generally reflect relative year-class strength, further indicating that the signal of variations in abundance of young-of-the-year hake is strong.

This study shows that relative year-class strength can be determined in the larval and early juvenile stages of Pacific hake. Strong year classes are characterized by high abundances of large larvae and young-of-the-year juveniles; weak year classes occurred when the indices of large larvae or young-of-the-year juvenile abundance were low. Given the sampling problems described above, the observation that relative abundance of larvae usually reflects year-class strength indicates that the larval signal of hake must be very great, particularly in years of high abundance.

An exception to this relationship was observed in 1984, when relatively few late-stage larvae and juveniles were observed but recruitment was high. One explanation is that the traditional spawning locations of hake shifted north in 1984. Several pieces of evidence support this explanation.

Evidence of spawning in the north in 1983 and 1984 is substantiated by hake eggs in National Marine Fisheries Service ichthyoplankton surveys off the coasts of Oregon and Washington (Art Kendall, Alaska Fisheries Science Center, Seattle, WA, pers. comm.). Ichthyoplankton surveys were conducted

TABLE 10

Ratio of Mean Catch during Day (0830–1630 h) to Mean Catch during Night (2030–0230 h) for Early and Late-Stage Larvae

MP* Size (mm)	1-Meter ring net									Bongo net							
	1961	1963	1964	1965	1966	1968	1969	1972	1975	1978	1979	1980	1981	1982	1983	1984	1985
2.0	—	7.15	2.69	0.59	0.94	2.00	0.68	11.88	18.63	0.33	0.25	—	1.25	—	—	—	0.00
2.5	—	5.57	0.38	1.43	1.21	1.93	1.28	17.57	5.48	1.58	0.52	—	3.17	47.25	2.15	417.20	0.92
3.0	—	4.53	0.16	1.14	3.10	11.91	0.42	1.50	3.23	0.35	0.24	—	1.35	22.05	0.85	16.54	0.82
3.5	—	3.28	0.41	1.38	1.49	8.63	0.49	0.28	3.67	0.19	0.44	—	0.49	14.06	1.45	2.86	5.33
4.0	—	1.10	0.36	3.96	1.20	3.25	0.33	0.48	1.95	0.29	1.43	—	0.40	—	0.77	1.92	4.69
Average	—	4.33	0.80	1.70	1.59	5.54	0.64	6.34	6.59	0.55	0.58	—	1.33	27.79	1.31	109.63	2.35
11.75	0.31	0.30	0.16	0.38	0.17	—	0.00	0.00	0.00	0.00	0.00	0.66	0.13	—	0.00	0.00	2.21
12.75	0.08	0.00	1.58	0.00	0.12	—	0.38	0.00	0.62	0.27	0.18	0.00	0.00	—	—	0.00	0.37
13.75	0.00	1.33	0.20	0.00	0.42	—	0.09	0.00	—	0.80	0.92	0.33	0.50	—	—	0.00	0
14.75	0.31	0.44	0.79	0.00	0.00	—	0.31	0.00	—	0.00	0.00	1.33	0.00	—	—	1.31	—
Average	0.18	0.52	0.68	0.10	0.18	—	0.20	0.00	—	0.27	0.28	0.58	0.16	—	—	0.33	—

*Midpoint of size range

in the springs of 1980–84 and 1987, and covered an area from 40°N to 48°N. Except for 1983 and 1984, no hake eggs or larvae were observed in these surveys. The percent occurrence of hake eggs in spring (March–April) surveys was 10.48 in 1983 and 14.52 in 1984. In those years most eggs were found between 40° and 44°N.

The 1982–83 El Niño may have influenced the 1983–84 spawning distribution of Pacific hake in several additional ways. Pearcy and Schoener (1987) speculated that the northern extension of hake egg and larval distribution correlated with oceanic conditions associated with the strong 1983–84 El Niño, including reduced southerly flow of the California Current, weak upwelling, onshore transport of oceanic and Columbia River plume waters, and anomalous poleward currents.

Fiedler (1984) noted that anchovy spawning distributions also extended north of Point Conception in 1983. He suggested that under normal ocean conditions, anchovy spawning is excluded from regions north of Point Conception by the plume of cold California Current water. There was no evidence of the cold-water plume south of Point Conception during CalCOFI survey 8302 (Feb. 9–Mar. 29). The absence of the cold-water plume in the spring of 1983 may also explain the northward spawning of Pacific hake in that year.

Chelton et al. (1988) describe a strong poleward flow along the central California shelf between Point Conception and Point Sur throughout February–July 1984. This observation was based on current measurements taken from eleven locations off the central California coast as part of the Central California Coastal Circulation Study. The enhanced poleward surface flow may partly explain the spawning off Oregon and the northerly distribution of hake larvae in 1984.

The observation that events during larval life may be important in determining year-class strength differs from Peterman et al. (1988), who made a similar study of northern anchovy and concluded that year-class strength was established in the juvenile stage. The conclusions of Peterman et al. (1988) may not reflect the importance of mortality during the early developmental stages of northern anchovy. The poor relationship between anchovy pre-recruits and recruitment indices may have resulted from data gaps in the CalCOFI sampling program. There appears to be a correspondence between anchovy pre-recruits and recruitment indices in 1965–75, when the sampling was best, whereas the relationship erodes from 1978 to 1985, when the sampling area and frequency were reduced (Peterman et al. 1988).

An alternative explanation for the different conclusions drawn from the analysis of northern anchovy and Pacific hake lies in the different growth and behavior of the two species. Northern anchovy tend to spawn closer to shore than Pacific hake. The growth characteristics of northern anchovy also differ from those of Pacific hake. And because anchovy is an important prey to many other animals throughout its life, predation may have a greater effect on recruitment than it does for postlarval Pacific hake.

The life-table simulation showed that decreases in recruitment could originate at any stage, but substantial increases could only originate from lower mortality rates or shorter egg or larval stages. This result corroborates the analysis of late-stage abundance data, which indicated that strong year classes could be detected early in the life history.

The results of this study are consistent with those of Smith (1985), who constructed a life table for northern anchovy and conducted simulations to identify critical life stages. He also concluded that strong year classes of northern anchovy could only be produced by accelerating the growth through early and late larval stages, or diminishing mortality during the early or late larval period.

Evidence that strong year classes are established early in development has been noted in other fish stocks. The magnitude of American shad (*Alosa sapidissima*) year classes appears to coincide with years of high juvenile abundance, and can be attributed to mortality in the larval period (Crecco et al. 1983; Crecco and Savoy 1987; Savoy and Crecco 1988). Sundby et al. (1988) concluded that year-class strength of Arcto-Norwegian cod (*Gadus morhua* L.) is established during the larval stage. Houde (1987) analyzed the impact of variations in life-stage duration or mortality during the egg, yolk-sac, larval, and juvenile stages in five different fish species. He concluded that for most species the larval stage holds the greatest potential for regulating year-class size.

The observation that weak year classes could be manifested by changes in growth or natural mortality in the egg, larval, or juvenile stages was addressed by Houde (1987). He noted that although codlike species exhibited moderate potential for regulating recruitment in the juvenile stage, the major processes controlling year-class strength probably occurred in the larval phase. He based this conclusion on the assumption that the initial number of juveniles upon which variable mortality or growth can operate depends on survival during the larval stage. A similar conclusion could be applied in the case of Pacific hake.

Analysis of the distribution of hake larvae showed that animals surviving to late stages were usually concentrated in nearshore areas or regions west or southwest of Point Conception. The latter regions correspond closely with the large offshore plume which is a prominent feature off the California coast in most years (Fiedler 1984; Davis 1985; Poulain and Niiler 1989). One explanation for the survival of larvae located nearshore in the California Bight or west of Point Conception is that these regions are highly productive.

Survival of larval hake may also depend on the relative availability of prey. A principal prey of Pacific hake, *Calanus pacificus*, produces eggs after exposure to increased phytoplankton production. These eggs and nauplii serve as prey for larval hake. Thus factors influencing the phytoplankton bloom may also influence hake survival.

Runge (1981) found that zooplankton production was generally higher in regions rich with phytoplankton. Therefore, high phytoplankton concentration may be associated with higher concentrations of larval prey. Hakanson (1987) found that *C. pacificus* volumes off Point Conception generally corresponded with areas of high chlorophyll. In 1984 high volumes of *C. pacificus* were located between Monterey Bay and Point Conception.

Sumida and Moser (1980) found that hake larvae ingested a broad size range (70–200 μm) of copepods. Willason et al. (1986) found that two euphausiids (*Euphausia pacifica* and *Nematoscelis difficils*) and a copepod (*C. pacificus*) collected in April 1981 were most abundant in waters off Point Conception. They also found that *E. pacifica* and *C. pacificus* found near Point Conception and south of San Francisco had higher lipid content and more active digestive enzymes than animals collected from other areas of the California Current. These findings led the authors to conclude that zooplankton in regions off Point Conception and south of San Francisco undergo prolonged periods of better nutritional conditions.

Reduced offshore advection may favor survival of hake larvae. In the nearshore regions, offshore transport is minimized. Power (1986) simulated drift patterns for northern anchovy larvae in the California Bight. The model included long-term mean geostrophic, wind-driven current velocities to 50 m, and turbulent diffusion. Power's simulations indicated that offshore-directed Ekman transport did not strongly affect anchovy larvae in the nearshore region. There was significant seaward transport of larvae out of the California Bight when spawning extended into offshore regions or when Ekman transport increased considerably.

More complicated processes may reduce offshore advection of larvae in the plume west of Point Conception. Entrainment in eddies, or vertical migrations of late-stage larvae may retard offshore transport and may be important in keeping hake larvae west of Point Conception, where prey is most abundant. Fiedler (1986) used satellite imagery to show a general correspondence between the distribution of larval anchovy and a displaced eddy in 1985.

Bakun (in press) noted that areas influenced by Ekman transport exhibit a layered structure, with surface waters directed offshore and subsurface waters directed onshore. He speculated that pelagic organisms migrating vertically in an area influenced by Ekman transport could maintain their relative position. Myers and Drinkwater (1988/1989) showed that diurnal vertical migration of fish larvae in the northwest Atlantic could reduce horizontal advection by Ekman transport. Evidence presented earlier in this paper suggests that late-stage hake larvae migrate diurnally (table 10). This mechanism may explain how hake larvae remain in the region west of Point Conception.

In conclusion, the results of this study indicated that production of strong year classes of Pacific hake was regulated by factors influencing survival during the early and late larval periods. Estimates showed that mortality was very high at young ages. The life table simulation also indicated that strong year classes were established during the early or late larval periods. Analysis of the spatial distribution of hake larvae revealed that inshore areas and regions west of Point Conception seem favorable for survival of hake larvae. Zooplankton abundance is high in these areas, and transport offshore is minimized near shore. These findings establish the temporal and spatial setting for future analyses of factors underlying the recruitment of Pacific hake.

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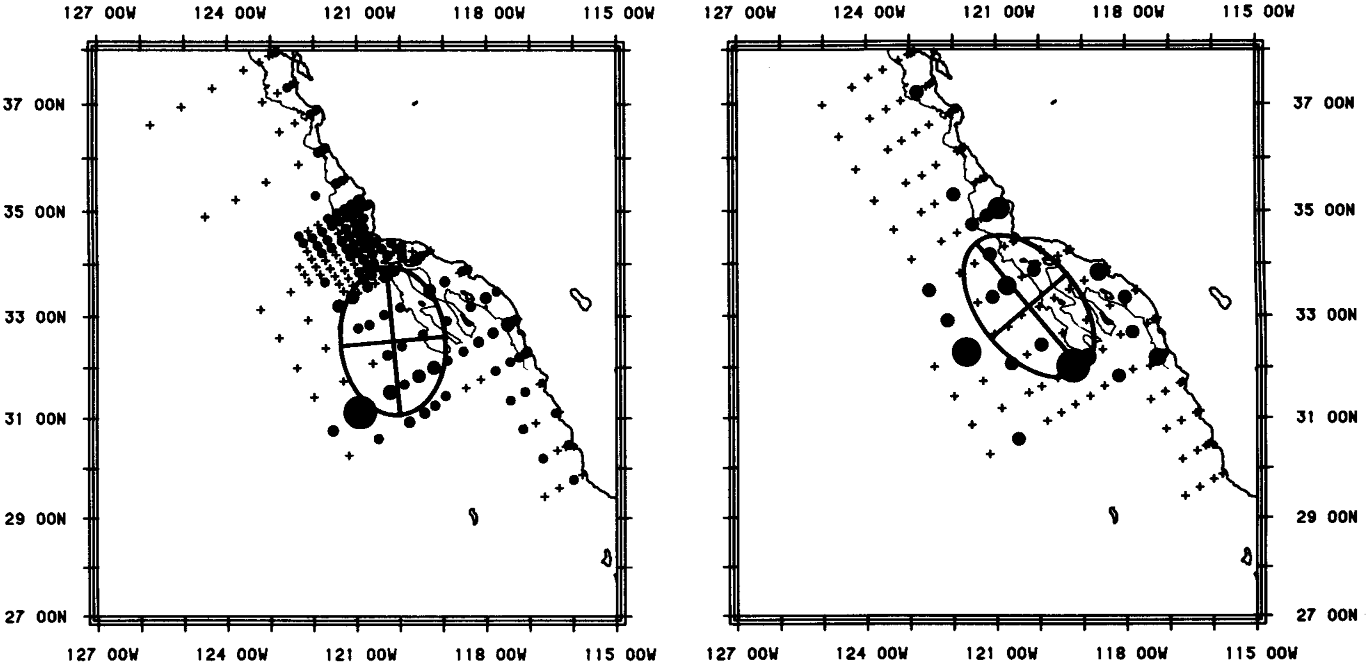
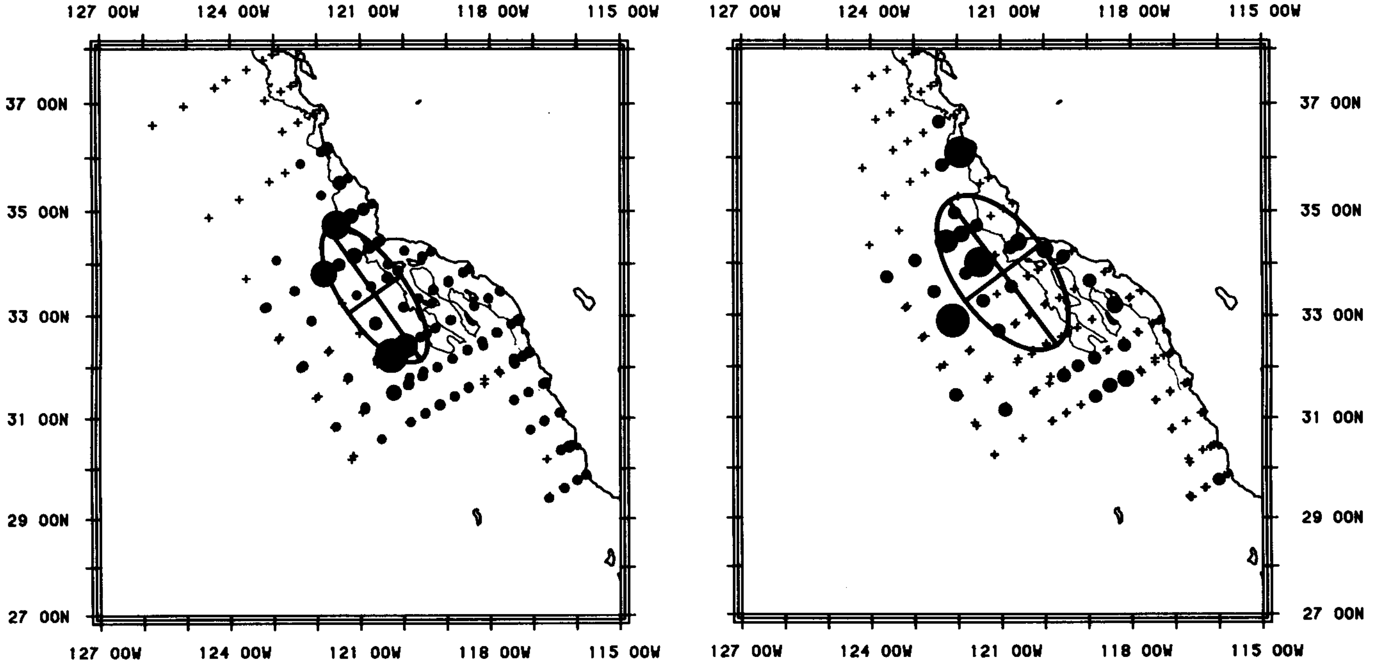
APPENDIX



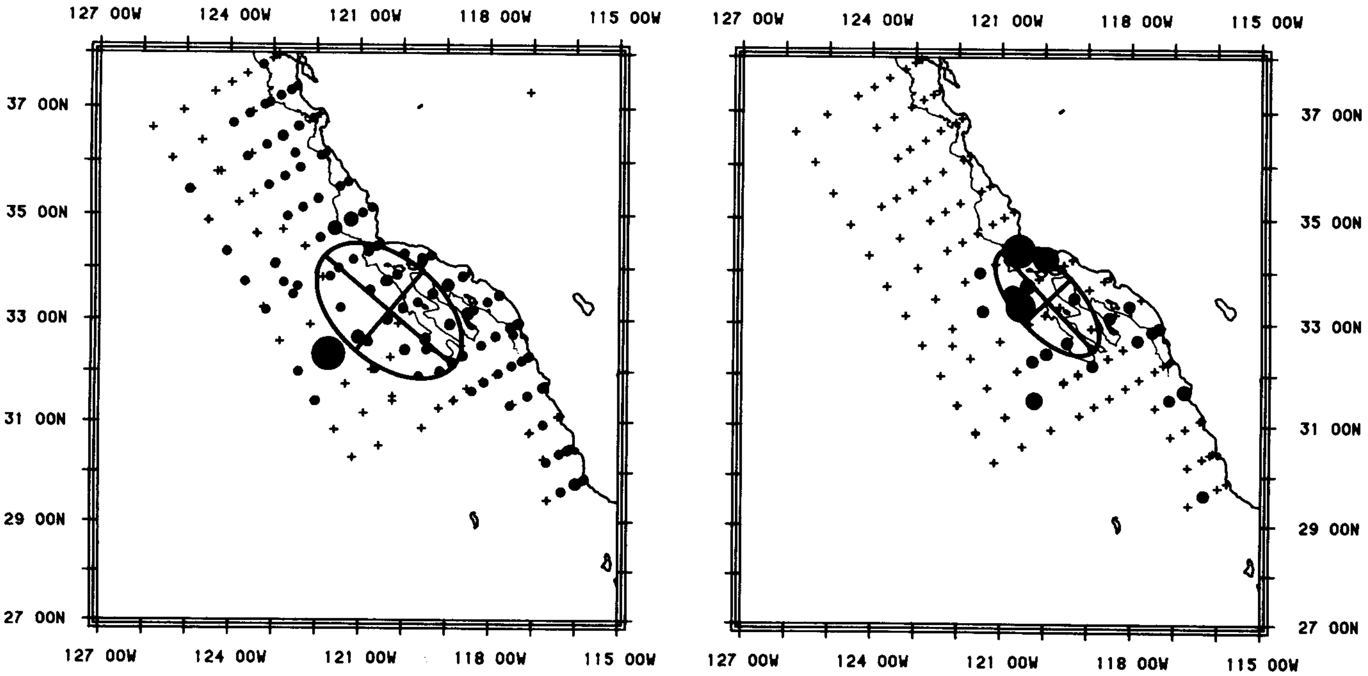
1.75 - 4.25MM. JAN. - MAR. 1964
11.25 - 15.25MM. MAR. - MAY 1964

Figure A-1. Early and late-stage larval distributions observed in 1964. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 7,352, late stage = 17). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.



1.75 - 4.25MM. JAN. - MAR. 1966
11.25 - 15.25MM. MAR. - MAY 1966

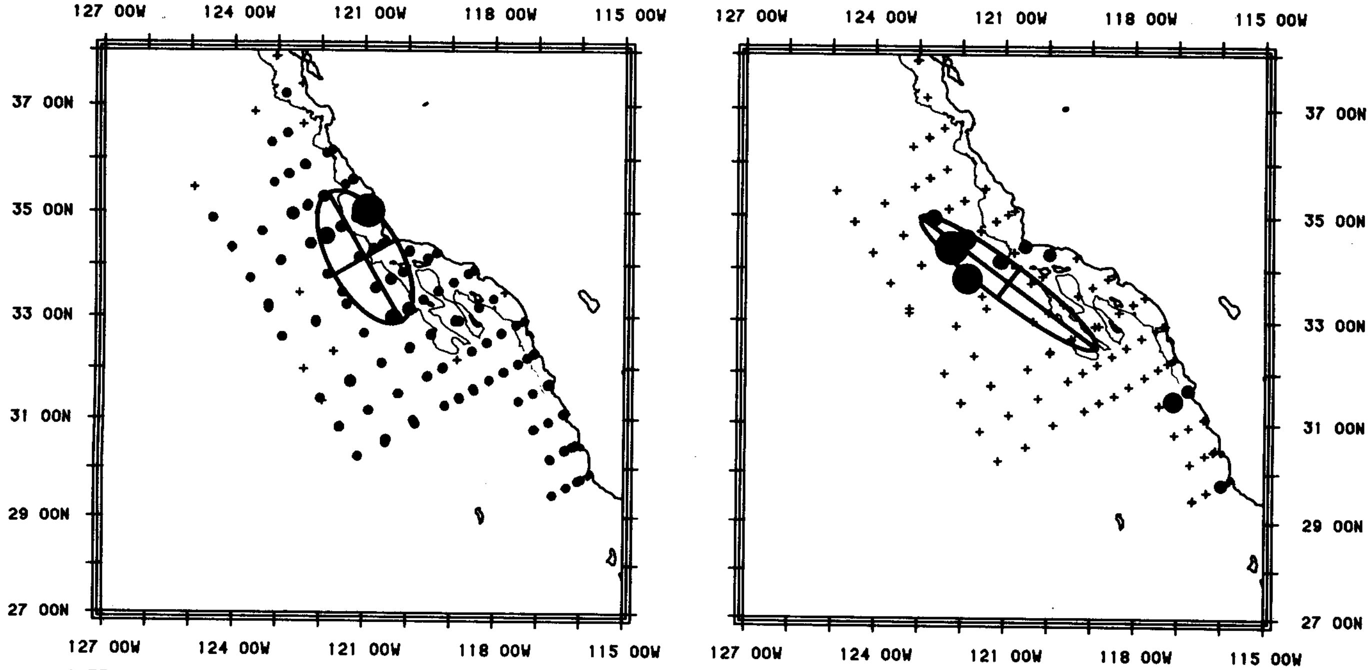
Figure A-2. Early and late-stage larval distributions observed in 1966. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 7,238, late stage = 20). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.



1.75 - 4.25MM. JAN. - MAR. 1969

11.25 - 15.25MM. MAR. - MAY 1969

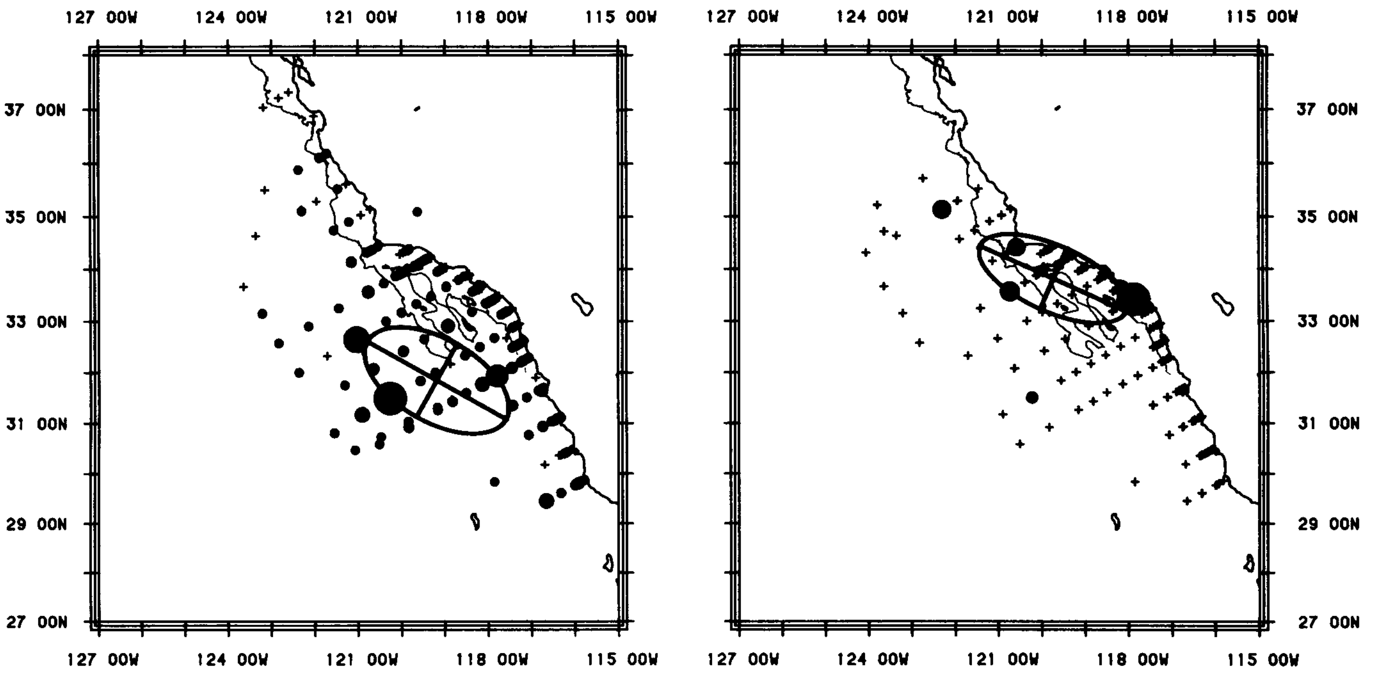
Figure A-3. Early and late-stage larval distributions observed in 1969. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 8,485, late stage = 29). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.



1.75 - 4.25MM. JAN. - MAR. 1972

11.25 - 15.25MM. MAR. - MAY 1972

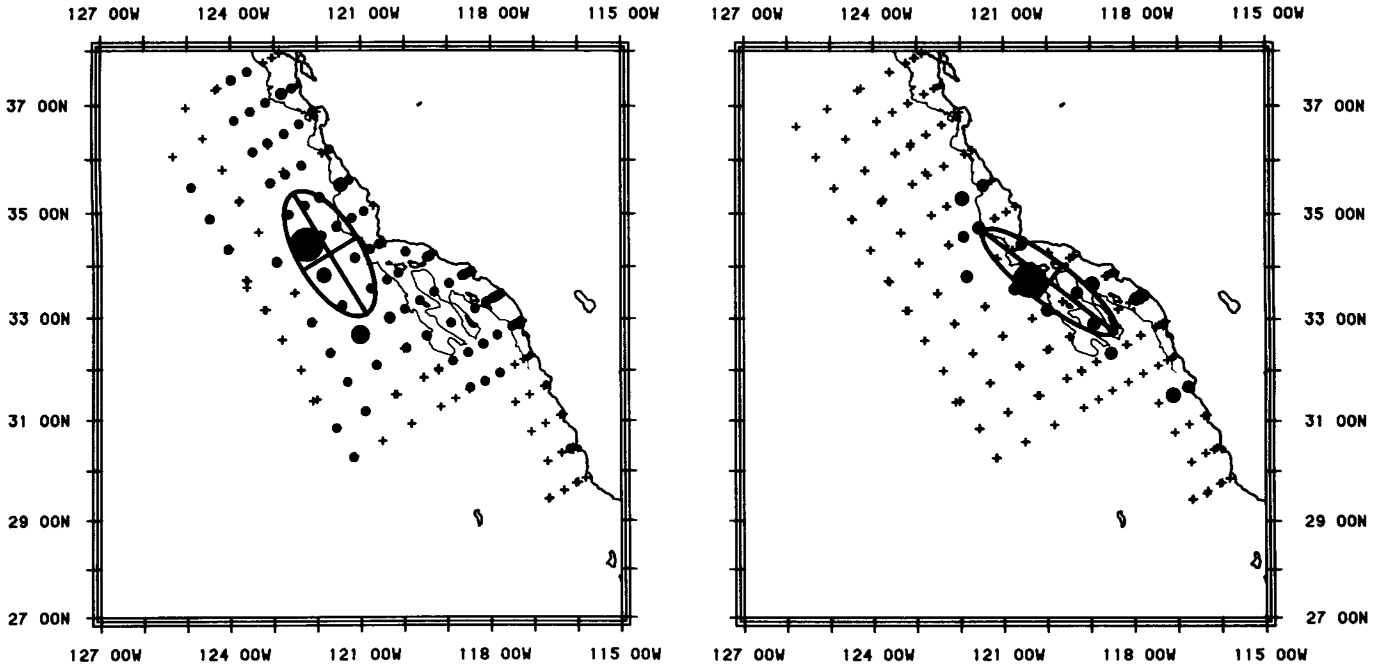
Figure A-4. Early and late-stage larval distributions observed in 1972. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 19,445, late stage = 21). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.



1.75 - 4.25MM. JAN. - MAR. 1975

11.25 - 15.25MM. MAR. - MAY 1975

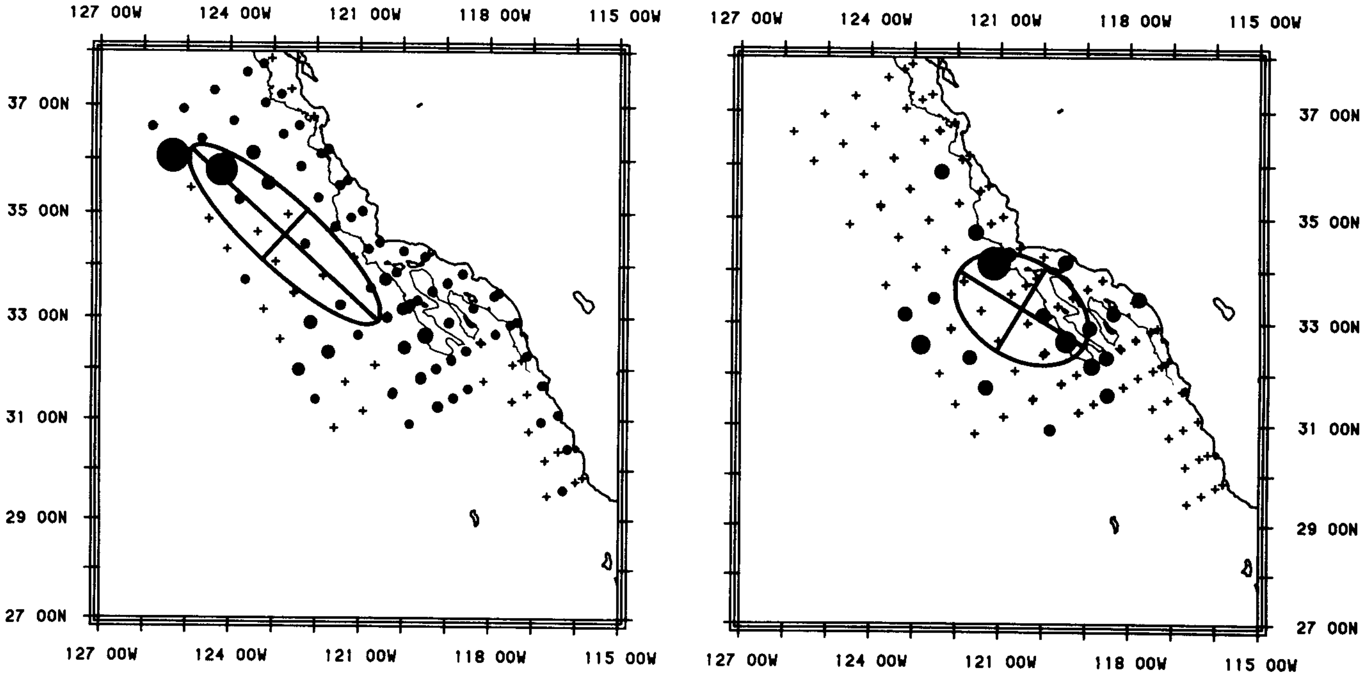
Figure A-5. Early and late-stage larval distributions observed in 1975. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 14,269, late stage = 27). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.



1.75 - 4.25MM. JAN. - MAR. 1978

11.25 - 15.25MM. MAR. - MAY 1978

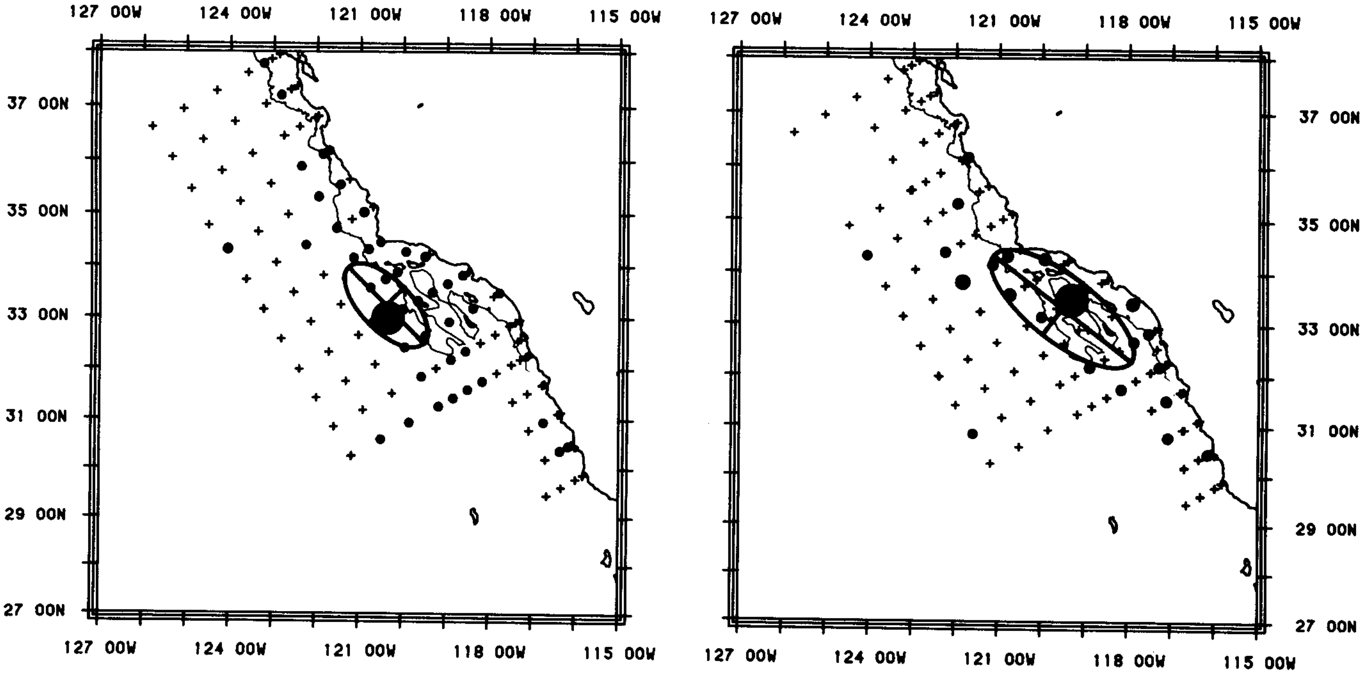
Figure A-6. Early and late-stage larval distributions observed in 1978. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 5,871, late stage = 91). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.



1.75 - 4.25MM. JAN. - MAR. 1979

11.25 - 15.25MM. MAR. - MAY 1979

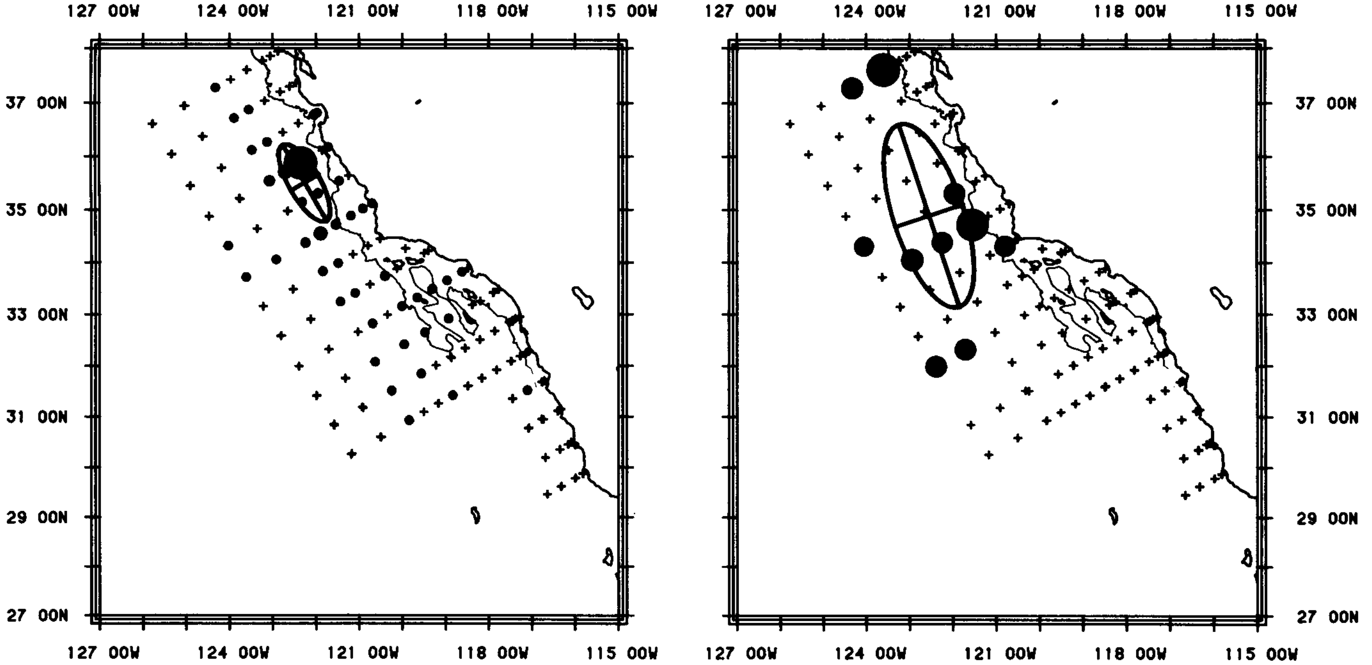
Figure A-7. Early and late-stage larval distributions observed in 1979. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 14,994, late stage = 46). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.



1.75 - 4.25MM. JAN. - MAR. 1981

11.25 - 15.25MM. MAR. - MAY 1981

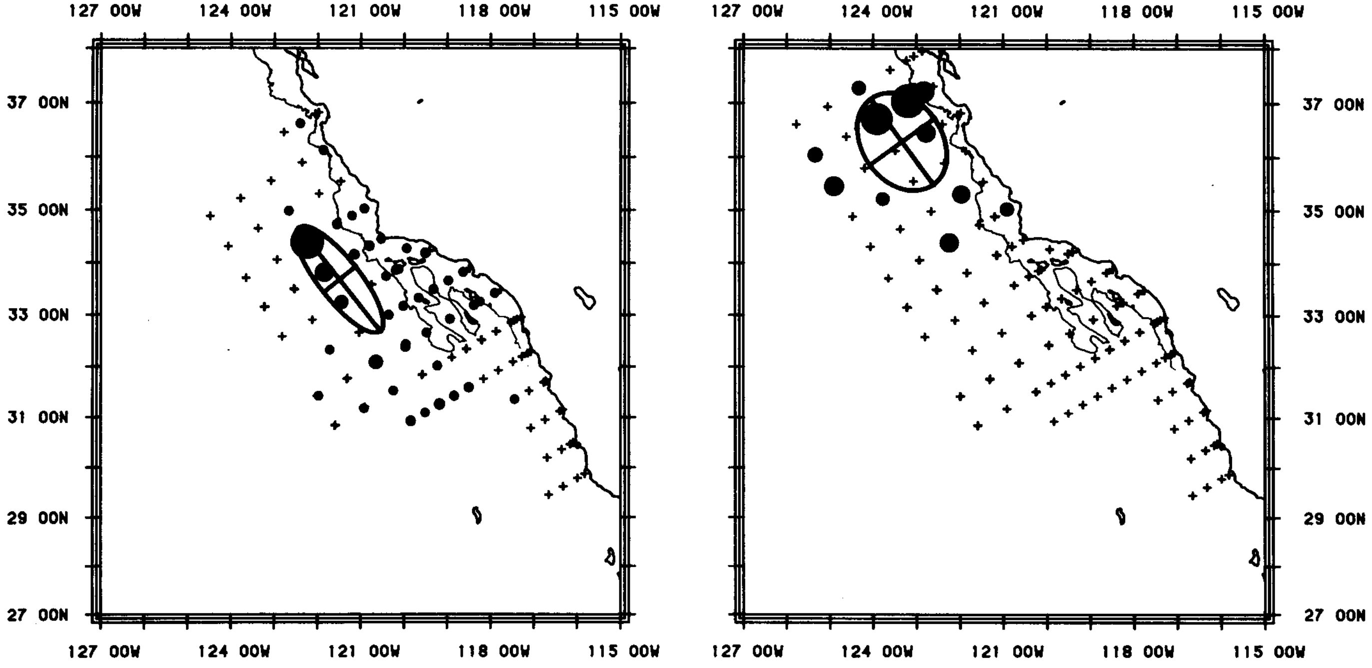
Figure A-8. Early and late-stage larval distributions observed in 1981. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 7,352, late stage = 125). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.



1.75 - 4.25MM. JAN. - MAR. 1984

11.25 - 15.25MM. MAR. - MAY 1984

Figure A-9. Early and late-stage larval distributions observed in 1984. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 14,143, late stage = 20). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.



1.75 - 4.25MM. JAN. - MAR. 1985

11.25 - 15.25MM. MAR. - MAY 1985

Figure A-10. Early and late-stage larval distributions observed in 1985. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 7,721, late stage = 46). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.

FLUCTUACIONES PERIODICAS DE LA CAPTURA DE SARDINA CRINUDA (*OPISTHONEMA* SPP.) EN EL GOLFO DE CALIFORNIA, 1972–1990

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ABSTRACT

Catch and catch-by-effort data from thread herring (*Opisthonema* spp.) landings at Mazatlán (1972–90) are analyzed. The periodicity of the fluctuations of both variables was successfully estimated using periodical regression methods. The maximum residual errors were detected after El Niño events. According to our results a decline in the catch is expected. This decline could be detected as an increase in school density and a decrease in school number, and it would be a response to environmental changes. This would result in a possible increase of the catch per unit of effort whenever fishing is successful.

RESUMEN

Se analizan las variaciones de la captura y captura por esfuerzo de la sardina crinuda (*Opisthonema* spp.) desembarcada en Mazatlán (1972–90). Aplicando métodos de regresión periódica se estimó la periodicidad de las fluctuaciones de ambas variables, obteniéndose así un elevado ajuste. El máximo error residual en los modelos generados se obtuvo en años que sucedieron a eventos cálidos de tipo "El Niño". Tomando como base los resultados se pronostica un descenso en las capturas del recurso. Esta disminución podría manifestarse con un aumento en la densidad y reducción en el número de los cardúmenes y sería una respuesta a cambios ambientales; esto daría como resultado probable elevadas capturas por unidad de esfuerzo en lances exitosos.

INTRODUCCION

La sardina crinuda *Opisthonema* spp. en el Golfo de California es actualmente el segundo recurso más importante para la industria reductora mexicana (con la sardina Monterrey *Sardinops sagax caerulea* en primer término), desplazando a la anchoveta norteña *Engraulis mordax* cuya producción se redujo durante 1990 a menos del 1% del total de desembarcos de pelágicos menores en Baja California, principal entidad productora de anchoveta en México (García et al. 1990).

La captura de sardina crinuda dentro de esta región incluye a las especies simpátricas *Opisthonema libertate*, *O. bulleri* y *O. medirrastre*; aunque la distribución del recurso es más amplia, la captura se concentra en aguas de los estados de Sonora y Sinaloa, donde también se agrupa la flota pesquera (Anónimo 1985).

La pesquería de estas especies se ha estudiado prácticamente desde su inicio (Sokolov y Wong 1973; Páez 1976), y al aumentar su importancia dentro de la producción pesquera nacional se ha incrementado el número de trabajos de investigación relacionados con este recurso. En particular, la identificación de las tres especies que incluyen esta pesquería ha sido el objetivo principal de una serie de estudios (López 1986; Rodríguez 1987; Hedgecock et al. 1988).

Desde el punto de vista pesquero se han aplicado distintos métodos de evaluación del recurso (Cisneros et al. 1988; Lyle et al. 1989; Acal 1990). Los resultados obtenidos, en particular los derivados de modelos de producción excedente, no han tenido éxito debido a su limitado carácter predictivo, y en los últimos años se han superado las estimaciones más optimistas del rendimiento máximo sostenible, sin que se haya observado una reducción real en la captura obtenida por unidad de esfuerzo.

Esta pesquería, que se inició a principios de la década 1970–80, ha venido incrementando de forma sostenida el volumen global de captura, pasando de casi 4,000 a más de 25,000 toneladas métricas (TM), en un periodo menor de 20 años sin una correspondencia proporcional del esfuerzo nominal (Lyle et al. 1989).

Dicho aumento en la producción ha manifestado oscilaciones anuales, aparentemente cíclicas, de distinta magnitud. Fluctuaciones como las mencionadas han sido descritas para pesquerías de otras latitudes (Caddy 1979; Van Winkle et al. 1979; Astudillo y Caddy 1986; Lluch-Belda et al. 1986) habiéndose asociado a variaciones climáticas, cambios en el poder de pesca de la flota y a distintos aspectos

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[Manuscript received January 15, 1992.]

relacionados con el reclutamiento de las poblaciones sujetas a explotación.

En el presente trabajo se analizan las fluctuaciones observadas en la captura de la sardina crinuda a fin de determinar la posible existencia de periodicidad y validar, dentro de las limitaciones que impone la información disponible, su aplicación en métodos de evaluación del recurso.

METODOS

Las especies del género *Opisthonema* tienen diferente distribución espacio-temporal en el Pacífico, por lo que la composición específica de la captura varía a lo largo de la temporada; el máximo aporte proviene de la especie *O. libertate.* Debido a este grado de mezcla, a la sobreposición de carácteres merísticos que dificultan su inmediata identificación específica (Rodríguez 1987; Hedgecock et al. 1988) y por falta de datos sobre las proporciones relativas obtenidas en las distintas temporadas, se agruparon las tres especies en una categoría única.

En este trabajo se utilizó únicamente la información procedente de los desembarcos de la flota sinaloense cuyos límites de operación coincidían originalmente con los del estado, dividido en cuatro zonas administrativas, habiéndose agregado en años recientes una quinta zona que amplía el área de pesca hasta Puerto Vallarta, Jalisco (figura 1).

Los datos de captura (TM) y esfuerzo (días de viaje) corresponden a las temporadas de pesca (Oct.–Sep.) de 1972–73 a 1989–90, habiéndose obtenido de los archivos del Centro Regional de Investigación Pesquera (CRIP), de la Delegación de Pesca y de las empresas sardineras ubicadas en Mazatlán. Debido a la diversidad de las fuentes y a que la base de datos diarios se encuentra en una fase de depuración, los resultados se consideran preliminares.

En primer término se analizaron los datos originales de captura C y esfuerzo f por temporada. Posteriormente se efectuó una normalización del esfuerzo (fn) en función de la capacidad de bodega. Estos valores se obtuvieron al multiplicar el esfuerzo f por un factor de corrección, que es el cociente de la media anual de la capacidad de bodega entre el promedio de la serie de datos.

Para cada serie (C, f y fn) se aplicó un análisis de regresión lineal con respecto al tiempo (t), con el objeto de identificar tendencias y para determinar, en su caso, la existencia de periodicidad. Una tendencia se consideró válida cuando el análisis de la varianza (ANOVA_{reg}) indicó un coeficiente de la regresión significativamente distinto de cero.

Las fluctuaciones en la captura y captura por unidad de esfuerzo (C/fn) se analizaron por medio de la regresión periódica (Batschelet 1981; Ruiz 1989), eliminando la tendencia al incluir elementos de la regresión lineal (Caddy 1979), de acuerdo al modelo siguiente:

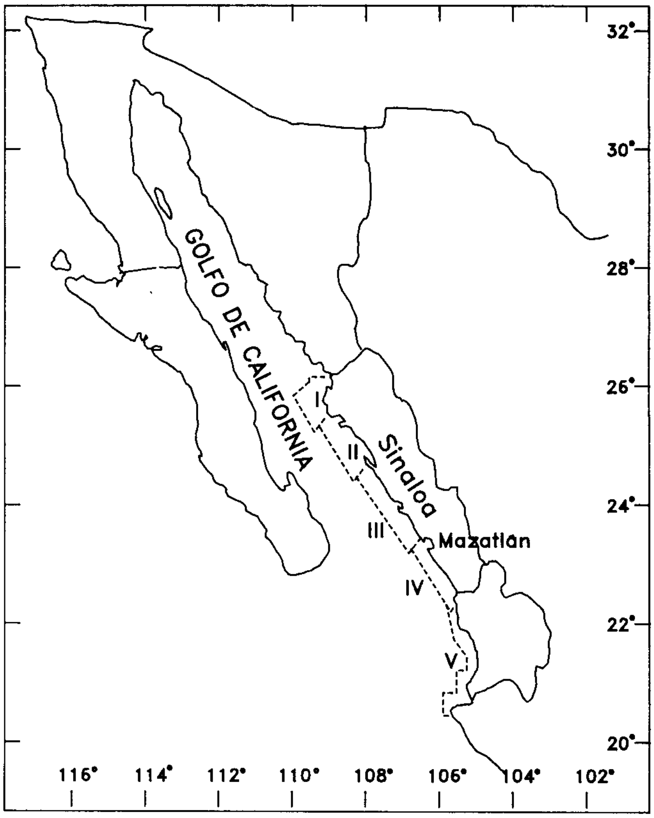

Figura 1. Area de captura de sardina crinuda *Opisthonema* spp. en el sur del Golfo de California y zonas administrativas de pesca (I–V).

*Thread herring (*Opisthonema *spp.) capture areas in the southern Gulf of California, and administrative fishery zones (I–V).*

$$C_t = \hat{C}_t - a\hat{C}_t \,\mathrm{Sin}(2\pi(t + \phi)/T)$$

donde C_t es la captura estimada; $\hat{C}_t$ es el valor obtenido para el mismo período por medio de la regresión lineal; a es un coeficiente que permite expresar el incremento en la amplitud de las oscilaciones y que equivale a la razón entre los valores anuales y el valor medio de la serie de capturas; t es el tiempo (año–1900); ϕ es una función de la fase de máxima amplitud t_0; y T es el período en años.

Un procedimiento similar se siguió al analizar la serie de capturas por unidad de esfuerzo (C/fn). Los valores de los parámetros fueron ajustados por métodos iterativos empleando el algoritmo de Marquardt (Draper y Smith 1981) hasta obtener la suma de los cuadrados mínima (MSC).

RESULTADOS

Durante el periodo estudiado se observó un aumento constante en la captura anual desembarcada con el tiempo t, aunque se manifestaron fluctuaciones de distinta magnitud con respecto al valor de C_t estimado por la regresión lineal. El coeficiente de dicha regresión indica un incremento anual de aproximadamente 770 TM/año, existiendo un alto nivel de colinearidad entre las variables consideradas ($r = 0.74$). Este coeficiente resultó significativamente distinto de cero ($\text{ANOVA}_{\text{reg}}$, $P = 95\%$), por lo que se consideró como una verdadera tendencia de la captura. El valor negativo de la ordenada al origen resultó de la aplicación del dato (año–1900) para la variable t en la regresión lineal (figura 2).

El esfuerzo bruto (f) presentó asimismo variaciones durante el mismo período, aunque no siguió ninguna tendencia aparente con respecto al tiempo (figura 3a). Una vez que el esfuerzo fue normalizado en función de la capacidad de bodega (fn), la tendencia que mostró esta variable fue similar a la que se presentó en la captura (figura 3b), estando altamente correlacionadas ambas variables ($r = 0.87$).

Esta colinearidad entre C y fn implica constancia en la C/f, pudiendo ser ésta una de las principales razones por la que los intentos para explicar la dinámica de la población de la sardina crinuda en función de modelos de producción (Molina et al. 1984; Zamudio 1986; De Anda y Lyle 1987) han resultado poco efectivos, ya que una de las premisas básicas de estos modelos (Schaefer 1954; Fox 1970), la proporcionalidad inversa entre C/f y f, no se cumple. Esta situación es característica de algunas poblaciones de pelágicos en los que aparentemente el coeficiente de capturabilidad q no es constante, sino que es una función dependiente de la biomasa de estas poblaciones altamente gregarias (MacCall 1976, 1979; Radovich 1976).

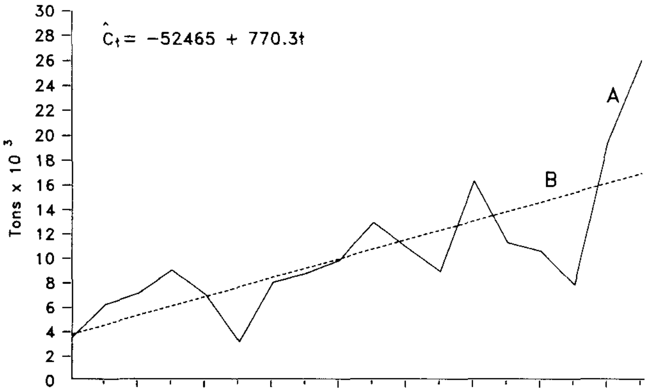

Figura 2. Desembarcos de sardina crinuda (*Opisthonema* spp.) en Mazatlán. A = Volumen de captura por temporada de pesca; B = ajuste lineal de la captura con respecto al tiempo.

*Thread herring (*Opisthonema *spp.) landings at Mazatlán. Line A = capture per fishing season; line B = linear fit of capture with respect to time.*

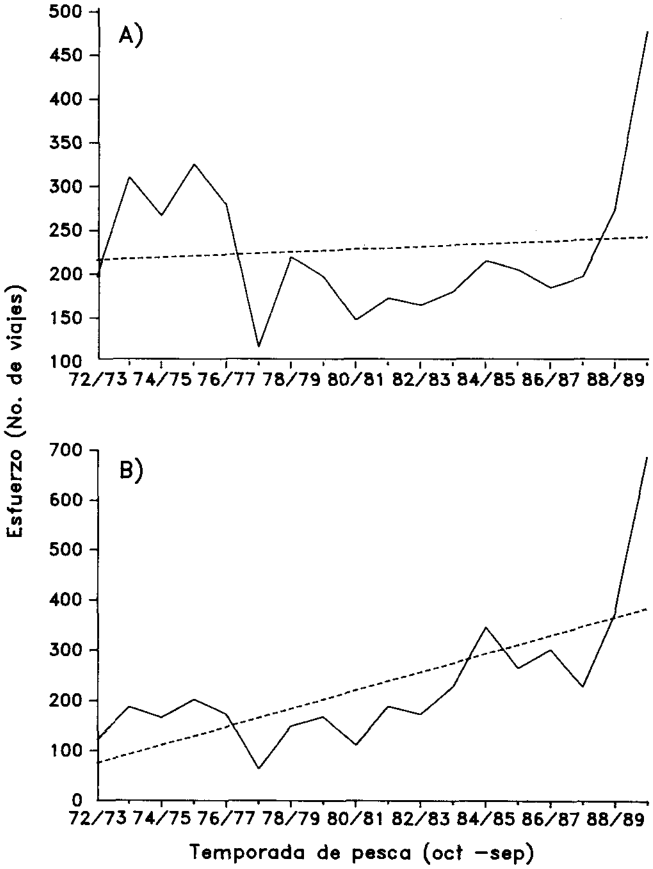

Figura 3. Serie temporal de esfuerzo pesquero aplicado a la pesquería de *Opisthonema* spp. en el sur del Golfo de California. *A*, Esfuerzo bruto *f*; *B*, esfuerzo normalizado *fn*. (–) datos por temporada de pesca; (---) ajuste lineal.

Opisthonema *spp. fishery effort time series in the southern Gulf of California.* A, *Gross effort* f; B, *normalized effort* fn. *(–) data per fishing season; (---) linear fit.*

Considerando los citados métodos de evaluación del stock, Molina et al. (1984), Zamudio (1986) y De Anda y Lyle (1987) han llegado a la conclusión de que la pesquería entraría en riesgo de extinción al rebasarse la captura máxima sostenible, estimada en aproximadamente 15,000 toneladas anuales. Con la aplicación de otros métodos de evaluación, a partir de huevos y larvas (Acal 1990) se ha estimado un rendimiento potencial de aproximadamente 19,000 TM, con un volumen de biomasa de la población adulta cercano a las 77,000 TM.

En los dos últimos años se ha superado ampliamente el rendimiento máximo estimado por los métodos de producción excedente y si bien se observó una reducción de la C/f para la temporada 1989–90 con respecto a la anterior, en general ésta se ha mantenido estable desde 1983 a la fecha. Si se considera a esta variable como un índice de la abundancia del stock, no existirían evidencias reales para asumir una situación de riesgo en la pesquería.

Esta relativa estabilidad de la C/f puede relacionarse con deficiencias en el registro del esfuerzo más que con cambios en el tamaño de la población, ya que sólo se cuenta con los datos de viajes con captura, lo que implica un sesgo de la información. Una mayor confiabilidad de los resultados de la aplicación de los métodos de evaluación antes citados requeriría de la cantidad real de lances del arte de pesca, y del número total de viajes con y sin captura de sardina crinuda.

Asimismo, la captura no se realiza de una forma completamente aleatoria sobre una población homogéneamente distribuida, sino que la operación se efectua cuando existe una alta probabilidad de éxito.

De igual manera, si se contase con una evaluación correcta del esfuerzo, podría estimarse su efecto sobre la amplitud de las oscilaciones de las capturas anuales, ya que niveles elevados de esfuerzo pueden actuar como agentes desestabilizadores del crecimiento de la población, propiciando la tendencia observada en las fluctuaciones (Caddy 1979).

Con objeto de disminuir el error asociado con dichas oscilaciones al aplicar el modelo de regresión periódica, se adecuó la función considerando la amplitud de las fluctuaciones anuales. Con un modelo simple de estas características, en él que únicamente se incluye una componente armónica, se estimaron ciclos de captura con periodo T de aproximadamente ocho años (7.6) cuya fase de máxima amplitud t_0 se situó cercana a los cuatro años (3.81). Por medio de este ajuste se obtuvo un valor del coeficiente de determinación (R^2) del 74% y una MSC de 1.36E + 08.

Un mejor ajuste de las observaciones se obtuvo con el modelo $C_t = \hat{C}_t - a\hat{C}_t \,\mathrm{Sin}(2\pi(t + \phi_1)/T_1) + b\hat{C}_t \,\mathrm{Cos}(2\pi(t + \phi_2)/T_2)$, que incluye dos componentes armónicas y por medio del cual se determinaron dos ciclos superpuestos, con periodos aproximados de ocho (7.6) y cinco (4.9) años. Las t_0 correspondientes alcanzaron valores de 5.9 y 2.8 años, respectivamente, mientras que la mínima suma del error cuadrado se redujo a 5.18E + 07, con un coeficiente $R^2 = 90.0\%$.

El máximo error en el ajuste se presentó en aquellas temporadas que siguieron a los años con anomalías térmicas observadas en la región (McLain 1983), por lo que cabría esperarse que integrando el componente ambiental al modelo se obtendría un mejor ajuste, a la vez que daría un carácter más predictivo al modelo.

Basándose en los resultados obtenidos al aplicar ambos modelos de regresión periódica a los datos de captura de sardina crinuda, la producción pesquera entraría en una fase de descenso a partir de la temporada 1990–91. De seguir la tendencia señalada se obtendría la producción más baja en las temporada 1992–93 y 1993–94, con aproximadamente 11,000 TM para el modelo de regresión con dos componentes armónicas y 14,000 para el de una, similares a los que se obtuvieron entre las temporadas 1984–85 a 1986–87 (figura 4).

Este resultado no ha sido corroborado en la práctica dado que la información disponible para las últimas temporadas, a partir de 1989–90, incluye numerosas fuentes de error que están siendo analizadas.

Otros estudios en los que se han determinado ciclos de periodicidad similar a los que se observan para sardina crinuda han sido señalados para sistemas pesqueros del Atlántico (Caddy 1979; Van Winkle et al. 1979) y del Mediterráneo (Astudillo y Caddy 1986); estos resultados también están limitados, en cuanto a su validez estadística, por el tamaño de las series de datos.

Por lo que respecta a la variable C/f se observó asimismo un comportamiento cíclico, que en este caso se ajustó a un período único de 13.3 años con t_0 situada en 4.9 años. En función de este modelo que incluye un parámetro de ajuste del sesgo (Batschelet 1981), la C/f estaría en una fase ascendente (figura 5). Al igual que con la captura, para esta variable existe alguna asociación con las anomalías térmicas ya señaladas, disminuyendo el rendimiento, con respecto a los valores esperados, al año siguiente de presentarse los eventos cálidos.

Este efecto es más evidente para la temporada 1982–83, cuando las condiciones provocadas por El

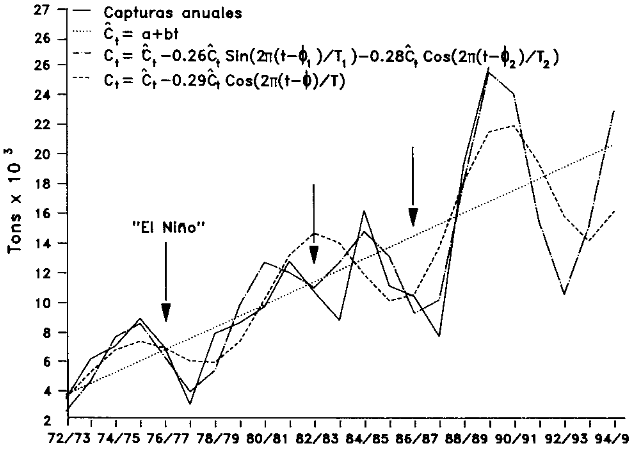

Figura 4. Desembarcos de sardina crinuda en Mazatlán y ajustes con modelos de regresión lineal y periódica.

Thread herring landings at Mazatlán, and linear and periodic fits.

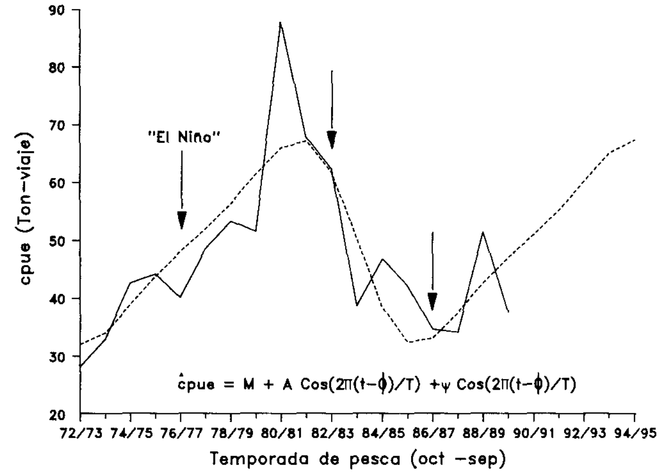

Figura 5. Captura por esfuerzo normalizado para la sardina crinuda (*Opisthonema* spp.) desembarcada en Mazatlán. (–) datos por temporada de pesca; (---) ajuste periódico con sesgo positivo.

*Normalized catch-by-effort for thread herring (*Opisthonema *spp.) landed at Mazatlán. (–) data per fishing season; (---) periodic fit with positive bias.*

Niño fueron extremas, elevándose la temperatura de forma anómala desde la superficie hasta aproximadamente 200 m de profundidad. Para las otras temporadas el efecto causado por este fenómeno fue más débil (McLain 1983; Cole and McLain 1989).

Las condiciones oceanográficas tendrían su efecto más acusado sobre la estructura del cardumen al limitar la producción de alimento. La variabilidad de estas condiciones influiría en las predicciones generadas por los modelos de regresión periódica; las predicciones serían mas probables al aumentar la estabilidad de las fluctuaciones ambientales.

El pronóstico de aumento en la *C/f*, considerando a esta variable como un índice de abundancia, conduciría a la idea de incremento en la biomasa; sin embargo, esta situación es incompatible con los resultados señalados para la captura (reducción del volumen global) a menos que se consideren las dos situaciones siguientes:

1. La biomasa de la población de sardina crinuda se incrementa pero la accesibilidad al recurso se modifica reduciendo la posibilidad de captura.
2. Solamente se manifiestan cambios a nivel de la estructura de los cardúmenes, incrementando su tamaño pero disminuyendo en número.

La primera hipótesis es poco probable teniendo en cuenta la autonomía de la flota y los actuales sistemas de detección del recurso. La segunda hipótesis implica una disminución efectiva del stock, con cardúmenes densos pero escasos; esto resultaría en elevadas capturas por esfuerzo en los lances exitosos, aunque la disponibilidad de los mismos resultaría reducida, generando una baja producción; ésta sería, por lo tanto, la hipótesis más viable.

La asociación entre una reducción de la biomasa de especies pelágicas y un incremento en la capturabilidad ha sido discutida por MacCall (1976), Radovich (1976) y Csirke (1989) entre otros, quienes plantean similares características de explotación en stocks que han llegado al abatimiento total de la producción pesquera.

Estos autores, particularmente Radovich (1976), señalan que para pesquerías en donde se emplean redes de cerco no es notable la reducción en la *C/f*, aún cuando la población decline. Esto se debe a la dificultad que existe para evaluar el esfuerzo en las etapas de máxima abundancia, a la distribución contagiosa del recurso, al conocimiento de las zonas de pesca por parte de los pescadores y a la comunicación que existe entre la flota; estos últimos factores reducen la incertidumbre del proceso de pesca en las etapas de disminución del stock.

Por lo anterior no puede asumirse un carácter predictivo para los modelos aquí propuestos debido a que el carácter cíclico que se observa en las capturas de sardina crinuda puede estar determinado por dos factores principales sujetos a alteración.

En primer término, la aparente periodicidad en la producción del recurso está siendo alterada por la magnitud del esfuerzo pesquero. Esta variable modifica la amplitud de las oscilaciones tal como sucede en las dos últimas temporadas en estudio, donde el incremento del esfuerzo introdujo la máxima diferencia con respecto a la tendencia seguida por esta variable.

En segundo lugar, aunque las condiciones oceanográficas han seguido un patrón de fluctuaciones más o menos regulares durante el periodo estudiado, también tienen un carácter altamente incierto de difícil introducción en modelos de evaluación pesquera. Estas condiciones influyen directamente sobre la abundancia del recurso incidiendo sobre la producción de alimento y otros procesos biológicos.

En suma, aunque se carece del carácter predictivo que se asume para otros modelos de evaluación pesquera, dadas las limitantes impuestas por el tamaño de las series temporales, se considera que el uso de regresiones periódicas es adecuado para describir la evolución de la pesquería de la sardina crinuda en el Golfo de California.

Asimismo los resultados obtenidos en el presente trabajo permiten señalar el riesgo en que se encuentra el recurso, ya que si bien la biomasa adulta de sardina crinuda se valora en aproximadamente 80,000 TM (Acal 1990) esta estimación es puntual y no permite realizar un seguimiento temporal. Situaciones similares a las que aquí se discuten han sido observadas en pesquerías que se han colapsado.

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SPAWNING FREQUENCY AND BATCH FECUNDITY OF CHUB MACKEREL, *SCOMBER JAPONICUS*, DURING 1985

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ABSTRACT

The average female *Scomber japonicus* collected from April through July of 1985 spawned 8.8 times during the 101-day sampling period. The average interval between spawns was 1.3 days in 32 females with more than one spawning stage in their ovary. The average batch fecundity was 68,400 oocytes, or 168 oocytes per gram female wet weight (without ovary).

RESUMEN

Hembras de *Scomber japonicus* colectadas de Abril a Julio de 1985 desovaron en el periodo de muestreo de 101 días un promedio de 8.8 veces. Treinta y dos hembras tuvieron un intervalo promedio entre los desoves de 1.3 días; los ejemplares poseían más de un estadio de desove en sus ovarios. La fecundidad por cada puesta del grupo promedió 68,400 ovocitos, equivalentes a 168 ovocitos por gramo de hembra (peso húmedo; excluyendo el ovario).

INTRODUCTION

Scomber japonicus, chub mackerel, spawn more than once per season (Knaggs and Parrish 1973; Peña et al. 1986; Asano and Tanaka 1989), but the frequency is unknown. The objective of this study was to determine the frequency of spawning and estimate batch fecundity (number of oocytes per spawn) of *S. japonicus*.

MacGregor (1976) believed that the standing stock of yolked oocytes in the ovary of *S. japonicus* before spawning equalled the potential fecundity for the year, a condition called determinate fecundity (Hunter and Macewicz 1985a). But recent studies of other scombroid fishes indicate that fecundity is not fixed at the beginning of year for black skipjack, *Euthynnus lineatus* (Schaefer 1987); skipjack tuna, *Katsuwonus pelamis* (Hunter et al. 1986); or yellowfin tuna, *Thunnus albacares* (Schaefer 1988; McPherson 1991). These fishes spawn many times, yielding annual fecundities far greater than the standing stock of yolked oocytes at the beginning of the spawning season. This latter condition is called indeterminate annual fecundity (Hunter et al. 1985). It seems certain that the Atlantic mackerel, *Scomber scombrus* L., spawns more than once per season (Bara 1960; Maridueña 1984), but debate continues about whether the fecundity of *S. scombrus* is determinate or indeterminate (Macer 1976; Johnson 1977; Alheit et al. 1987; Anon 1987; Greer Walker et al. 1987; Watson et al. 1992; Priede and Watson, in press).

To determine whether fecundity of *S. japonicus* is determinate or indeterminate, we compare the production of spawn over our survey period (batch fecundity × daily spawning frequency × survey duration in days) to MacGregor's (1976) estimates of annual fecundity. If *S. japonicus* is determinate, the production of spawn should be lower for our survey period, since we sampled only the peak months of spawning and not the whole season (March to October; Schaefer 1980).

In addition to clarifying the issue of fixed annual fecundity, our estimates of spawning and fecundity rates for *S. japonicus* are of general interest. As a preliminary measure of reproductive effort of the species, they are the baseline data essential for estimating *S. japonicus* biomass from the abundance of eggs or larvae.

METHODS

From April 2 to July 11, 1985, we collected 329 female *S. japonicus* in a series of 30 opportunistic collections taken in the Southern California Bight with hook-and-line or purse seine gear (table 1). All but two of the collections were made during the day, between 0700 and 1510; the two night collections were made between 1955 and 2045 (collection 29) and between 2330 and 0015 (collection 6).

The fish were sexed and measured (fork length), and the females were assigned a maturity stage from the California Department of Fish and Game's (CDFG) standard maturity guide for wetfish (table 2). The guide, based on gross anatomical criteria, is a modified version of the Hjort index (Hjort 1910). Ovaries were removed and preserved in 10% neutral buffered Formalin. The otoliths were removed, and annual growth rings were counted to determine age (year class). Sampling was continued until 20 ran-

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TABLE 1

Number of Female *S. japonicus* per Collection, with Histological Identification

Coll. number	Date Mo.	Date Day	Location °N	Location °W	Number of females[1] Immature	Mature A[2]	Mature P[3]	Total
1	4	02	33.25	117.38	1	0	0	1
2	4	04	33.43	118.16	2	0	1	3
3	4	05	33.48	118.25	8	3	9	20
4	4	11	33.45	118.09	8	1	11	20
5	4	19	33.44	118.06	3	0	0	3
6	4	21	34.24	119.45	4	0	16	20
7	4	26	33.22	117.36	3	4	3	10
8	5	01	33.45	118.09	3	3	13	19
9	5	05	33.36	117.58	0	5	3	8
10	5	07	33.45	118.09	1	1	3	5
11	5	08	33.24	117.37	0	6	5	11
12	5	09	33.45	118.09	4	0	1	5
13	5	15	33.43	118.16	0	3	17	20
14	5	16	34.27	120.32	0	1	0	1
15	5	17	33.43	118.16	1	5	14	20
16	5	21	33.45	118.09	5	2	7	14
17	5	23	33.43	118.16	0	2	8	10
18	5	30	33.43	118.16	0	0	5	5
19	5	31	33.45	118.09	1	0	7	8
20	6	04	33.45	118.09	1	3	7	11
21	6	05	33.27	117.43	0	7	0	7
22	6	07	33.45	118.09	4	6	10	20
23	6	12	33.27	117.40	0	19	1	20
24	6	21	33.45	118.09	2	3	11	16
25	6	21	33.43	118.14	0	9	1	10
26	6	26	33.27	117.43	5	5	0	10
27	6	30	33.33	117.49	0	8	0	8
28	7	02	33.45	118.09	2	7	11	20
29	7	04	32.47	117.17	0	1	2	3
30	7	11	33.43	118.16	0	1	0	1
All					58	105	166	329

[1] All females were collected off southern California in 1985. Collection 6 was taken by purse seine, the rest by hook and line.

[2] Active: ovaries contain yolked oocytes; if α atresia of yolked oocytes was present, less than 50% of the oocytes were affected.

[3] Postspawning: ovaries with 50% or more of the yolked oocytes in α-stage atresia, or ovaries without yolked oocytes in which β-stage atresia was present.

TABLE 2

Anatomical Classification Used by California Department of Fish and Game to Identify Mature *S. japonicus*

Stage	Description
[*Immature*]*	
1	Virgin individuals. Very small sexual organs close under vertebral column. Females: often wine-colored, with torpedo-shaped ovaries. Eggs invisible to naked eye. Males: testes very small, knife-shaped, and quite thin. In chub mackerel, testes can be longer than half the ventral cavity.
[*Mature*]*	
2	Maturing virgins or recovering spents. Females: ovaries longer than half the ventral cavity. Eggs may or may not be visible to naked eye. Males: testes easily identifiable, but still thin and knife-shaped.
3	Sexual organs swelling. Eggs definitely visible to naked eye. Ovaries and testes occupying about half the ventral cavity.
4	Ovaries and testes filling nearly ⅔ of ventral cavity. Eggs still opaque. Testes swollen, milt whitish.
5	Ovaries and testes filling ventral cavity. Ovaries often with some large transparent eggs.
6	Roe and milt running. Slight pressure on belly of fish exudes roe or milt.

*Heading not a part of CDFG classification system.

dom females had been obtained or until no more fish were available in a particular catch.

Ovaries were prepared according to histological techniques described by Hunter and Goldberg (1980) and Hunter and Macewicz (1985a), and the resulting histological slides were analyzed and classified. Rates of absorption of postovulatory follicles were verified from ovaries of 73 females spawned in the laboratory using procedures of Leong (1971). We also used the histological classifications to evaluate the gross anatomical grading scale routinely used by CDFG to assess the reproductive state of *S. japonicus*. Finally, we estimated batch fecundity, using the hydrated oocyte method of Hunter et al. (1985).

Histological Classification

The oocytes of *S. japonicus* ovaries develop asynchronously; that is, oocytes in many stages of development occur simultaneously in reproductively active ovaries (Wallace and Selman 1981). We used the simplified classification system described by Hunter and Macewicz (1985a,b) to describe the ovaries of *S. japonicus*, instead of the more detailed systems common in teleost literature (see, for example, Andrews[1] or Bara 1960). We categorized the most developed mode of oocytes for each ovary as either unyolked, partially yolked, yolked, or hydrated. We examined the nucleus of the yolked oocytes to see if it had begun to migrate to the animal pole; migration of the nucleus is the precursor to hydration and begins about 24 hours before spawning (Hunter and Macewicz 1985a). After ovulation, the follicles surrounding the hydrated oocytes remain in the ovarian tissue, where they degenerate and are resorbed. All postovulatory follicles were identified and subsequently aged.

The ovarian sections were graded for the presence of alpha (α) atresia of yolked oocytes and grouped into $\alpha < 50\%$ (0 to 49% of the yolked oocytes are in α-stage atresia) or $\alpha \geqslant 50\%$ (50% or more of the yolked oocytes are in α-stage atresia). Any presence

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[1] C. B. Andrews. 1931. Unpublished manuscript: The development of the ova of the California sardine (*Sardina caerulea*). Stanford University, Stanford, Calif. 88 pp.

of beta (β) atresia was also noted. In northern anchovy β atresia follows α-stage atresia of yolked oocytes (Hunter and Macewicz 1985b); we assumed the atretic process was the same in *S. japonicus*. We analysed ovarian atresia (resorption of oocytes) to determine if a female had finished spawning for the season (Hunter and Macewicz 1980, 1985b).

In order to evaluate our histological analyses, it is necessary to define terms for the reproductive status of female *S. japonicus*:

Immature: Females that have never spawned and cannot be expected to do so in the current reproductive season.

Mature: Females that have spawned in the current reproductive season or can be expected to do so.

Active: Mature females capable of spawning at the time of capture or by the end of our sampling period. The ovaries of these females contain yolked oocytes; if α atresia of yolked oocytes is present, less than 50% of the oocytes are affected. Postovulatory follicles may be present.

Postspawning: Mature females incapable of spawning at the time of capture or in the near future but that have spawned previously. Females are considered to be recent postspawning when in their ovaries 50% or more of the yolked oocytes are in the α stage of atresia, and to be late postspawning when there are no yolked oocytes, but β-stage atresia is present in the ovary.

Spawning Frequency

Laboratory calibration. To measure the rate of spawning using postovulatory follicles one must be able to stage the postovulatory follicles according to their age and know how long such stages last. Ovaries from *S. japonicus* induced to spawn in the laboratory were preserved at 0, 6, 12, 18, 24, 48, and 72 hours after spawning, and analyzed. The histological characteristics of *S. japonicus* ovaries are similar to those described for *Engraulis mordax* (Hunter and Goldberg 1980; Hunter and Macewicz 1980, 1985a,b) and *K. pelamis* (Hunter et al. 1986), except that red blood cells are occasionally observed in the lumen of postovulatory follicles. The degeneration and resorption of *S. japonicus* postovulatory follicles are described below as a function of elapsed time after spawning, when fish are held at 20°C.

0–3 hours: Within a few hours after spawning, no degeneration of the follicle is evident. Other characteristics at this time include a convoluted shape with many folds or loops; a lumen containing little granular or particulate material; a definite granulosa cell layer lining the lumen; linearly arranged, cuboidal granulosa cells with prominent healthy nuclei; and a clearly defined thecal connective tissue layer with blood capillaries (figure 1).

6 hours: Similar to a 0–3-hour-old postovulatory follicle, except that degeneration of the postovulatory follicle is evident because a few of the nuclei of the granulosa cells are dense or pycnotic.

12–18 hours: Additional signs of degeneration of the postovulatory follicle are evident. The postovulatory follicle is smaller than it was at 6 hours, and it has fewer convolutions. The granulosa layer still comprises numerous cells, although some cytoplasmic vacuoles or granules are present, and cell membranes are less distinct. More of the granulosa nuclei are pycnotic, and the nuclei are not always linearly arranged. The thecal layer appears slightly thicker than at 6 hours because the follicle has compacted.

24 hours: The postovulatory follicle is about half the size of one at 0–3 hours, and the shape is more angular, with fewer folds. The lumen is smaller and may contain red blood cells. The granulosa layer has degenerated further than at 18 hours; there are fewer cells, some pycnotic nuclei, few intact cell membranes, numerous vacuoles, and no alignment of nuclei. The thecal layer remains a distinct, thick band of cells (figure 1).

48 hours: Very few granulosa nuclei remain in the postovulatory follicle. Although the thecal layer appears thick, the follicle is small, about ⅓ the size at 24 hours, and can be confused with late-stage β atresia (Hunter and Goldberg 1980; Hunter and Macewicz 1985a).

72 hours: The postovulatory follicles are completely resorbed or are indistinguishable from late β atresia.

Analysis of field data. Postovulatory follicles in ovaries of field-caught *S. japonicus* were assigned an age (time after spawning) using the characteristics described above, the time of collection, and the estimated time of peak spawning (about 2200; Schaefer 1980). Twenty-eight collections were taken during the day, when females have oocytes with migratory nuclei, but no oocytes that are fully hydrated. We considered these fish to be capable of spawning on the evening following their capture because we believe that the migratory-nucleus stage persists in the ovary for less than 24 hours, as in Pacific sardine and northern anchovy. We are not able to verify this point because our field samples were taken during the day. But the absence of any fully hydrated oocytes during the day clearly indicates that hydration lasts less than 24 hours.

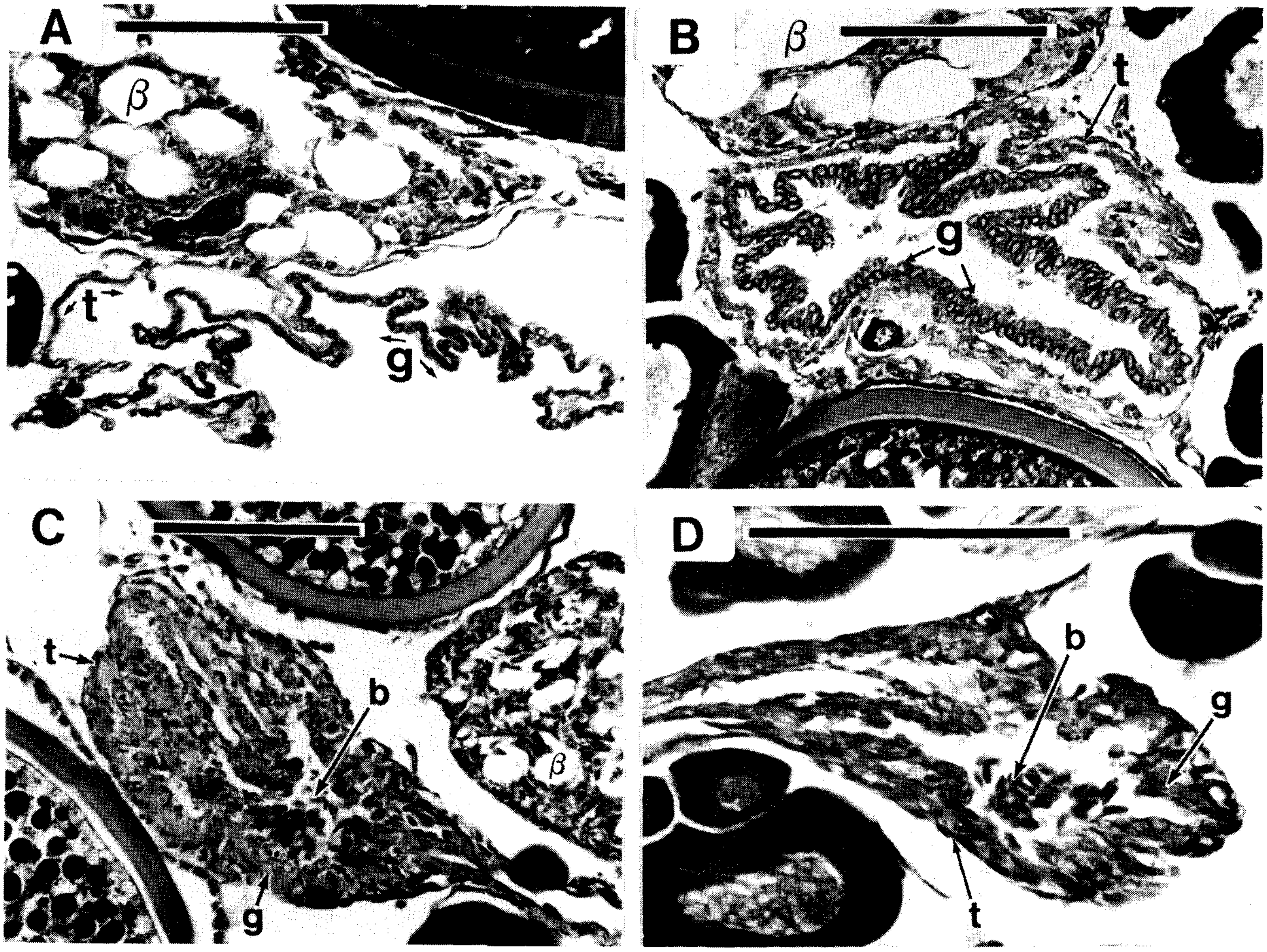

Figure 1. Postovulatory follicles from *S. japonicus* spawned in the laboratory (induced by hormones). No degeneration is evident in *A* (at ovulation) or in *B* (1 hour after spawning). By 24 hours after spawning (*C* and *D*), degeneration is considerable. Bars = 0.1 mm; b = red blood cells; g = granulosa cell layer; t = thecal connective cell layer; β = beta atresia.

To estimate spawning frequency, we identified in each spawning female the presence or absence of the following:

- oocytes with migratory nuclei
- hydrated oocytes within the follicles
- new postovulatory follicles (0–9 hours) and hydrated oocytes
- postovulatory follicles 10–33 hours old
- postovulatory follicles 34 or more hours old

Some of the ovaries contained more than one age of postovulatory follicles (figure 2); others contained oocytes with migratory nuclei as well as postovulatory follicles. All spawning stages were identified, and any combination of these five stages was recorded for each fish.

Batch Fecundity

We estimated the batch fecundity of 13 females. Batch fecundity for each female was the mean of three estimates. Each estimate was calculated by $(N/T_w)O_w$, where N is the number of oocytes in the late migratory-nucleus stage in a weighed tissue sample of the ovary (T_w), and O_w is the ovary weight (Hunter et al. 1985). Tissue could be taken from any location in the ovary, since Peña et al. (1986) showed that with the hydrated oocyte method, location does not affect the estimate of batch fecundity. The migratory-nucleus stage immediately precedes hydration (Hunter and Macewicz 1985a). Oocytes with migratory nuclei can be seen in Formalin-preserved ovaries because they are larger and less opaque than the other yolked but nonhydrated oocytes, and they

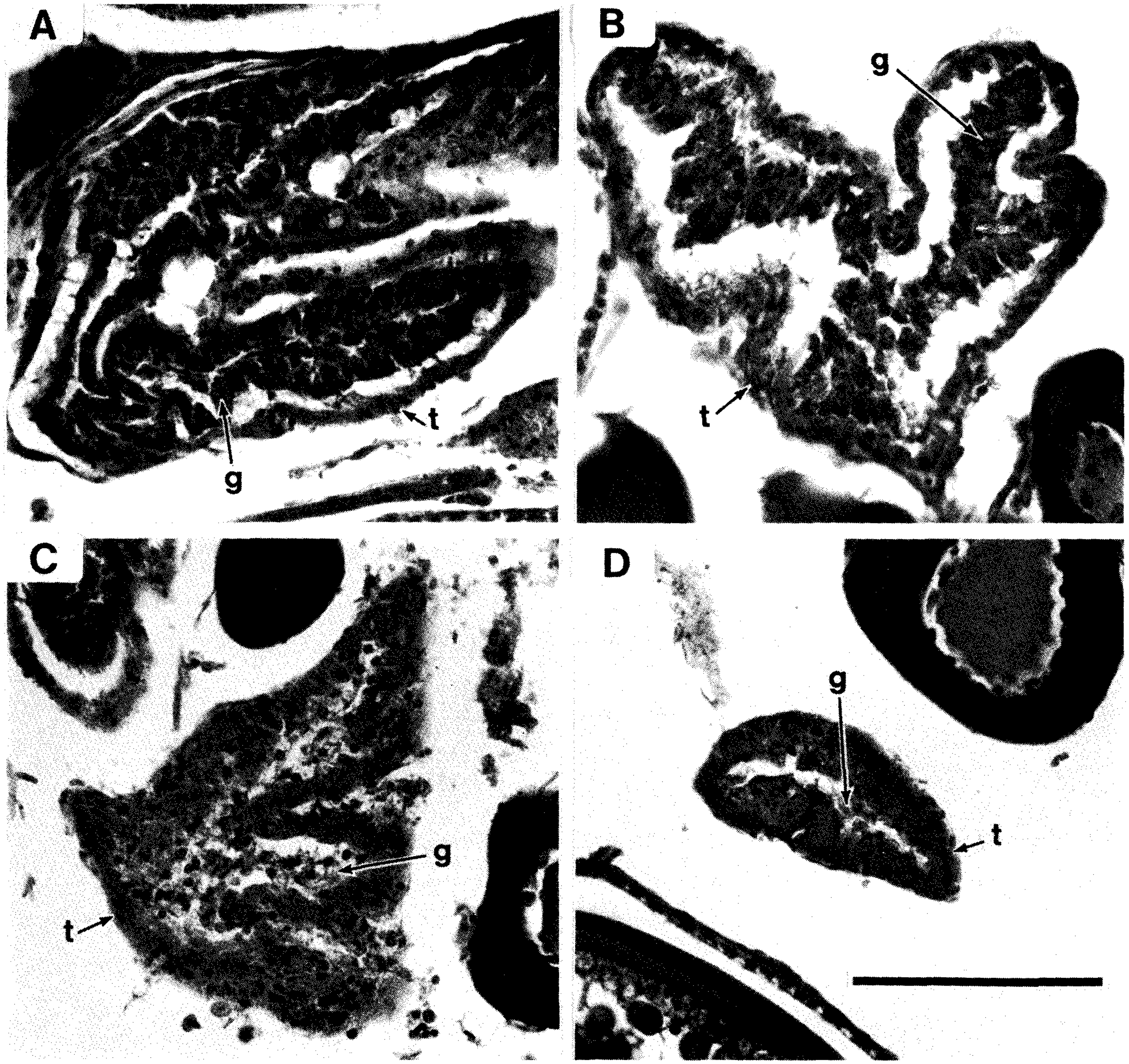

Figure 2. Multiple stages of postovulatory follicles from two *S. japonicus* females collected in the field. Female 9-03 contained postovulatory follicles aged 0–3 hours (*A*) and about 24 hours old (*C*) in her ovary. Female 26-06 contained postovulatory follicles about 12 hours old (*B*) and more than 33 hours old (*D*). Same magnification for *A* to *D*; bar = 0.1 mm; g = granulosa cell layer; t = thecal connective cell layer.

have a clear band on the periphery resulting from the initial fusing of the yolk globules. The more advanced oocytes have a single oil droplet.

RESULTS AND DISCUSSION

Spawning Frequency

Of the 329 female *S. japonicus* analyzed, 271 were mature. Of the mature females, 58 had spawned or would imminently spawn because their ovaries contained postovulatory follicles or oocytes with migratory nuclei (table 3).

The best measures of the percentage of females that spawned per day were the percentage of the mature females having oocytes with migratory nuclei (8.1%), and the percentage of the mature females with postovulatory follicles 10–33 hours old (9.2%). Females with postovulatory follicles older than 34 hours were not used because we were uncertain about their age. Since the oocytes with migratory nuclei and the postovulatory follicles 10–33 hours old indicate different spawning events (figure 3), they can be used as two independent estimates of spawning frequency. The mean of the two estimates

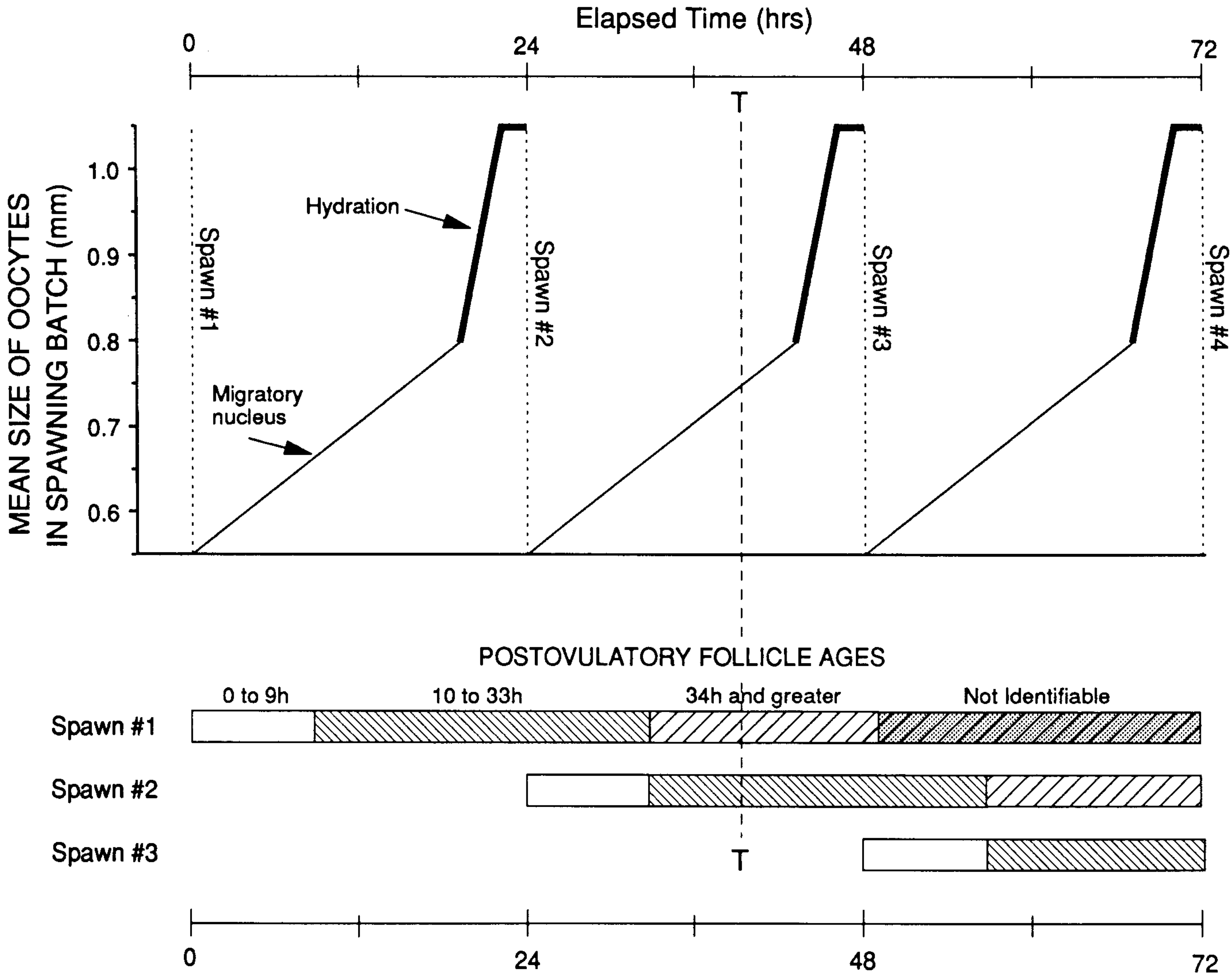

Figure 3. Conceptual diagram showing when various histological stages could be identified in an ovary of an *S. japonicus* female that spawned every day. Stages include migratory nucleus and hydration (0–24 hours before spawning), and postovulatory follicles 0–9 hours old, 10–33 hours old, and 34 hours and older. If a female is collected at time T in the cycle, three spawnings can be identified in the ovary: oocytes with migratory nuclei for spawn #3; 14-hour-old postovulatory follicles from spawn #2; and postovulatory follicles 38 hours old from spawn #1. Stippled area indicates period when postovulatory follicles may be confused with late β atresia.

was 8.7%, indicating that 8.7% of the females spawned per day, or that the average female *S. japonicus* spawned every 12 days. Because the sampling period was 101 days long, this estimate also indicates that the average female spawned 8.8 times during these 101 days.

Most (81%) of the spawning females (those with oocytes with migratory nuclei, or with postovulatory follicles) were collected in June, the month of peak spawning for *S. japonicus* according to the abundance of larvae in CalCOFI plankton collections (Kramer 1960). In June, 20.6% of the females spawned per day, indicating that the average mature female spawned about every five days in June, whereas 2.7% of the mature females spawned per day in May, and 6.8% in July (table 4).

The ovaries of 32 females contained multiple spawning stages. That is, a single ovary contained postovulatory follicles of two different ages, or postovulatory follicles and oocytes with migratory nuclei, or some other combination (table 3). Because we know the approximate age for each of these spawning stages, it is possible to calculate the interval between them. Thus we calculated that the average interval between spawnings for these 32 females was 1.3 days (table 5).

The frequency of spawning tended to increase with female age (table 6). Knaggs and Parrish (1973) concluded that older *S. japonicus* spawn for longer periods than younger ones. In our study none of the mature one-year-old fish were spawning, and only 3.9% of the mature two-year-olds were spawning,

TABLE 3
Spawning Female *S. japonicus* Taken in the Study ($N = 58$) with Ovaries Indicating Past Spawning (Postovulatory Follicles Present) or Imminent Spawning (Oocytes with Migratory Nuclei)

Coll. number	Fish number	Time PST	Year class	CDFG stage	Migratory nucleus	Postovulatory follicles 10–33 hours	Postovulatory follicles 33 < age < 72 hrs
7	05	0815	1981	5	+[1]	–	–
9	03[2]	1420	1980	6	+	+	+
13	18	1100	1980	3	+	–	–
13	19	1105	1983	2	+	–	–
15	02	1005	1980	4	+	–	+
15	06	1040	1982	3	–	–	+
15	12	1110	1981	4	–	–	+
16	03	0955	1981	3	+	–	–
21	01	1242	1981	3	–	+	–
21	02	1245	1981	3	+	+	+
21	03	1250	1981	3	+	+	+
21	04	1253	1981	3	+	–	+
21	05	1440	1981	2	–	+	+
21	06	1445	1981	3	–	+	+
21	07	1450	1980	4	+	–	+
22	07	0730	1981	2	+	–	–
23	01	1220	1981	3	–	–	+
23	02	1225	1982	2	–	+	+
23	03	1230	1981	3	–	+	+
23	04	1240	1981	4	+	–	+
23	05	1250	1981	3	–	+	+
23	06	1250	1981	3	–	–	+
23	07	1300	1981	3	+	+	+
23	08	1310	1980	4	–	–	+
23	09	1315	1981	4	–	+	–
23	10	1320	1981	3	–	+	+
23	11	1325	1981	3	–	+	+
23	12	1325	1982	3	–	+	+
23	13	1325	1981	4	+	–	+
23	14	1330	1981	3	+	–	+
23	15	1330	1981	3	–	–	+
23	16	1330	1982	3	–	+	–
23	17	1330	1981	3	+	+	+
23	18	1340	1980	4	+	–	+
23	19	1340	1981	3	+	–	+
23	20	1345	1980	2	–	+	–
24	02	0710	1981	3	–	–	+
25	03	0940	1981	3	–	–	+
25	04	1000	1981	3	–	–	+
25	06	1100	1981	4	–	–	+
25	07	1115	1981	3	–	–	+
25	09	1220	1980	4	–	–	+
26	05	1133	1981	3	–	–	+
26	06	1137	1981	4	–	+	+
26	07	1141	1982	3	+	–	+
26	08	1149	1981	4	+	+	+
26	10	1200	1981	4	–	–	+
27	01	1425	1982	2	–	+	+
27	02	1440	1982	3	–	–	+
27	03	1442	1981	3	–	+	+
27	04	1450	1981	3	–	+	+
27	05	1454	1983	3	–	–	+
27	06	1456	1981	2	–	+	+
27	07	1458	1981	2	–	+	+
27	08	1502	1983	2	–	–	+
28	03	0740	1981	3	+	–	+
28	18	1105	1982	3	+	–	+
29	02	2025	1981	4	–	+	+

[1] + indicates that the state was present.

[2] Ovary had a few hydrated oocytes in the lumen, and new postovulatory follicles, indicating that the female had spawned within the last 0–3 hours, an unusual time of day for *S. japonicus*.

TABLE 4

Percentage of Mature Female *S. japonicus* Classified as Active or Postspawning, and Percentage Spawning per Day

Month	Active[1] %	Postspawning Recent[2] %	 Late[3] %	Number mature females	Spawning per day MN[4] %	 PO[5] %	 Mean %
April	17	12	71	48	2	0	1.0
May	25	33	41	111	4	1	2.7
June	67	14	19	90	16	26	20.6
July	41	45	14	22	9	4	6.8
All	39	24	37	271	8.1	9.2	8.7

[1] Indicated histologically by presence of yolked oocytes, α atresia <50% of yolked oocytes, and, possibly, postovulatory follicles.
[2] α atresia is present in 50% or more of the yolked oocytes.
[3] There are no yolked oocytes in the ovary, but β atresia is present.
[4] Oocytes with migratory nuclei are present in the ovary; spawning is imminent.
[5] Postovulatory follicles are 10–33 hours old; female spawned the previous night.

TABLE 5

Computation of Mean Interval between Spawnings for *S. japonicus* Females with Combinations of the Following States in the Ovary: Oocytes with Migratory Nuclei (MN); 10–33-Hour-Old Postovulatory Follicles (PO_a); and >33-Hour-Old Postovulatory Follicles (PO_b)

Spawning states present in ovary	Minimal interval between spawnings[1] (*i* in days)	Number females *N*	Potential days *i* × *N*
MN + PO_b	2	11	22
PO_a + PO_b	1	15	15
MN + PO_a + PO_b	1	6	6
Total		32	43
Average interval between spawnings[2]:	43/32 = 1.34		

[1] The interval between spawnings for females with only a single spawning state in the ovary is ⩾3 days, since 72 hours is the maximum period during which postovulatory follicles can be detected.
[2] 25 females had a single spawning state. If these females were included, the average interval would be 118/57, or 2.07 days.

TABLE 6

Frequency of Spawning of Mature *S. japonicus* Females by Age and Year Class

Age (years)	Year class	Immature *N*	Mature *N*	Spawning per day mean percentage[1]
1	1984	11	3	0
2	1983	2	13	3.9
3	1982	10	44	6.8
4	1981	29	166	9.9
5	1980	5	43	8.1
6+	1978 & 1979	1	2	0

[1] Calculated from the number of mature females having oocytes with migratory nuclei in their ovaries, and from the number of mature females with postovulatory follicles 10–33 hours old in their ovaries; original data in table 3.

compared to 8.7% for the mature females as a whole. These data support the conclusion of Knaggs and Parrish, but more histological data, sampled over the whole spawning season, are needed to determine spawning by age.

The foregoing analysis indicated that the average female *S. japonicus* may spawn 8.8 times in 101 days, but it is clear that individual females do not spawn at regular intervals over this period. Rather, many of the spawnings must occur in rapid succession at daily or every-other-day intervals. It is interesting to speculate on the possible length of the spawning period for an individual female. If a female spawned 8.8 times at an interval of 1.3 days, the period would be 11.4 days long. If the average interval were 2 days, the period would be 18 days long. The latter period fits the data better because the percentage of spawning females with only one spawning stage (44%) would be too high if the spawning cycle were only 11 days long.

Fecundity

The average batch fecundity for the 13 females having oocytes with migratory nuclei was 68,400 oocytes, or 168 oocytes per gram of female wet weight, without ovary (table 7). By multiplying the mean batch fecundity by the number of spawns (8.8) we find that a female averaging 444 g would spawn about 602,000 oocytes during the 101-day survey period. This estimate is nearly five times higher than MacGregor's estimate of 126,000 oocytes for the annual fecundity of a 444-g female. Clearly, the standing stock of advanced oocytes does not indicate potential annual fecundity; consequently, we consider the annual fecundity of *S. japonicus* to be indeterminate.

The average Peruvian *S. japonicus* (281 g, without ovary) was estimated to have a mean relative batch fecundity of 278 oocytes per gram (Peña et al. 1986). This is somewhat higher than our estimate of 168 oocytes per gram for a 444-g female. Owing to high variability and few observations, it is uncertain if these differences reflect actual differences between stocks.

TABLE 7
Batch Fecundity (Number of Oocytes to Be Spawned in the Batch) of Thirteen *S. japonicus* Females with Oocytes in the Late Migratory-Nucleus Stage

Coll. & fish number	Time of day collected	Fork length (mm)	Body weight without ovary (g)	Ovary weight (g)	Batch fecundity	
					Per female	Per g body wt
7-05	0815	324	416.79	34.77	85,566	205.3
15-02	1005	319	382.64	46.56	120,537	315.0
26-08	1149	326	424.29	36.44	92,405	217.8
23-04	1240	310	355.32	35.59	69,930	196.8
21-03	1250	340	496.01	32.54	74,723	150.6
21-04	1253	315	380.92	30.95	57,247	150.3
23-07	1300	320	407.68	25.93	47,801	117.3
23-13	1325	301	320.83	34.22	72,338	225.5
23-14	1330	320	409.68	23.32	36,510	89.1
23-17	1330	300	328.45	22.76	35,807	109.0
23-18	1340	340	494.53	34.01	80,807	205.3
23-19	1340	326	438.70	22.03	23,280	53.1
21-07	1450	340	481.64	46.90	91,680	190.4
				Mean	68,356	168.0

Our batch fecundity of *S. japonicus* (168 oocytes per gram body weight, without ovary) is about three times that estimated for *S. scombrus*, which ranges from 28 to 55 oocytes/g body weight (Alheit et al. 1987; Watson et al. 1992). This difference between species may be partly due to differences in egg size. The *S. japonicus* egg is about 1.0 mm in diameter (Kramer 1960; Fritzsche 1978); the *S. scombrus* egg is about 1.2 mm (Russel 1976; Fritzsche 1978). The ratio of the diameter cubed for the two species is 1:1.7, indicating that the egg mass of *S. scombrus* may be nearly twice that of *S. japonicus*. Thus the differences in batch fecundity may be explainable in part by differences in egg size, assuming that the energy investment per batch was about the same in the two species. Although this is a plausible explanation, it is certainly speculative, because we have no true mean egg size for either population at present. Egg size of both species varies considerably between localities and seasons, making accurate comparisons difficult.

Atresia

Alpha atresia of the advanced yolked oocytes was common throughout the spawning season. Even early in the season (April) 12% of the females were classed as recent postspawning because of the high levels of α-stage atresia (table 4). Anchovy usually do not spawn when their ovaries are in this advanced state of atresia (Hunter and Macewicz 1985b), and we presume this is also the case for *S. japonicus*. In addition, the atretic condition that follows this state, late postspawning (table 4), was common in *S. japonicus* throughout the spawning season.

Hunter and Macewicz (1985b) believe that highly atretic ovaries are a normal occurrence in the annual reproductive cycle in fishes with indeterminate fecundity. They conclude that highly atretic ovaries indicate fish that have ended their reproductive season, and should be considered as synonymous with "spent," or postspawning, ovary classes. High levels of atresia might be induced by abnormal events such as an epidemic or environmental stress rather than by the normal cessation of spawning, but we believe that the normal cessation of spawning is much more likely. It is also possible that during a single spawning season *S. japonicus* may pass through more than one cycle of oocyte maturation, spawning, and atresia.

The most striking feature of our data on atresia was that females with highly atretic ovaries were common early in the spawning season. In anchovy, this condition is prevalent only near the end of the season, when spawning is declining for the stock as a whole. The prevalence of atresia indicates that the spawning cycles of *S. japonicus*, unlike those of the anchovy, are not synchronized for the stock as a whole but rather seem to vary from sample to sample. Spawning may be synchronized at some lower level of organization than the stock, such as the school or school group (Smith 1975). Alternately, schools may segregate according to behavioral traits, with spawning schools occupying different areas from postspawning schools.

Regardless of the mechanisms involved, the patchiness of spawning individuals indicates that obtaining representative samples of an *S. japonicus* stock may be very difficult. Considering the patchiness of spawning and postspawning females and the fact that our sampling was opportunistic, our samples may not accurately represent spawning rate of the stock over the 101 days. Since many females spawned at intervals of every 1.3 days, and in June the average female spawned every 5 days, we believe that our estimate of 8.8 spawns per year for the average female may be low.

Evaluation of Anatomical Classification of Ovaries

To determine the value of classifying ovaries by means of gross anatomical criteria, we used the Hjort maturity index modified by CDFG (table 2) as well as histological criteria to classify the *S. japonicus* ovaries (table 8). CDFG considered only stage 1, in table 2, as immature, and stages 2–6 as mature. Histological analysis indicated that the mature females occurred in all stages (table 8). On the basis of the histological evidence, the misclassified immature females in stage 1 were considered to be in postspawning condition, because they were resorbing their ovaries. Surprisingly, the percentage of all females classed as mature was similar regardless of the method used to classify them. When anatomical criteria were used, 90% of all females were estimated to be mature; when histological criteria were used, 82% were mature. The failure to detect postspawning females using anatomical criteria was counterbalanced by histological identification of immature females in CDFG stages 2 and 3.

Spawning females occurred in every anatomical stage except stage 1 (tables 3 and 8). But according to CDFG criteria, spawning females occur only in stages 5 and 6 (table 2). Clearly, the CDFG anatomical criteria do not identify all the spawning females.

Although anatomical staging is useful when studying a population (e.g., the duration of spawning seasons), it is inaccurate when considering individual fish. Our findings agree with those of Asano and Tanaka (1989), who studied reproduction of the Japanese stock of *S. japonicus*. They concluded that females with active ovaries, those actively spawning, and those in postspawning condition cannot be accurately separated if only anatomical criteria are used. Similarly, West (1990) states in his review that macroscopic staging may result in unacceptably high errors when used to examine the ovarian development of an individual fish.

Histological methods obviously provide more detailed and accurate assessments of fish maturity and reproduction. There will always be a need for gross anatomical methods because of the speed and ease that they offer. We believe that the six-stage anatomical grading system of CDFG needs revision. With the unaided eye, only three characteristics actually can be detected: (1) yolked oocytes not present, (2) yolked oocytes visible, and (3) hydrated oocytes visible. The rest of the characteristics used are unreliable or imply knowledge of maturity and spawning that the observer does not have; thus, we recommend a three-stage system.

CONCLUSIONS

Our estimate of spawning rate for the population of *S. japonicus* is lower than one would expect from information available about other scombroid fishes. We estimated that 8.7% of *S. japonicus* females spawned per day, whereas estimates for most other scombroid fishes indicate that they spawn at much higher rates. For example, 85% of female skipjack tuna spawn per day (Hunter et al. 1986); 18%–47% of black skipjack spawn per day (Schaefer 1987); 80% of yellowfin tuna spawn per day (Schaefer 1988); and 18%–62% of *S. scombrus* spawn per day (Priede and Watson, in press). We suspect that the actual rate of spawning of *S. japonicus* females may

TABLE 8

Comparison of California Department of Fish and Game Anatomical Maturity Classification and Histological Classification of the Ovaries of *S. japonicus* Collected in 1985

Number of females	Anatomical classification[1]		Histological classification			
	Stage number	Fish maturity	Immature %	Mature: Postspawn %	Mature: Nonspawn %	Mature: Spawn %
34	1	Immature	44	56	0	0
174	2	Mature	23	68	3	5
91	3	Mature	3	29	32	36
26	4	Mature		4	42	54
2	5	Mature		0	50	50
1	6	Mature		0	0	100
Fraction mature:	294/328 = .90			270/328 = .82		

[1] See table 2 for description of stages.

have been much higher for four reasons: (1) our opportunistic sampling may have biased our estimate; (2) females with multiple stages in the ovary spawned every 1.3 days; (3) our studies of atresia indicated that the distributions of postspawning and spawning females may have been highly contagious; and (4) our samples did not adequately cover the entire spawning season.

We believe that our estimates of a spawning rate of 8.7% of the female population per day and 8.8 spawnings per year for the average female are low. We hope this paper will encourage others to carry out a thorough study with a formal sampling design that takes into account age and size patterns in spawning rate, batch fecundity, and duration of the spawning season.

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NEUSTONIC ICHTHYOPLANKTON IN THE NORTHERN REGION OF THE CALIFORNIA CURRENT ECOSYSTEM

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ABSTRACT

Analysis of ichthyoplankton data collected off Washington, Oregon, and northern California during the 1980s indicates a neustonic assemblage of fish eggs, larvae, and juveniles. This assemblage is most diverse over the shelf and continental slope. Diel variation in the occurrence and abundance of certain species of fish larvae in the neuston samples is striking. Three categories are apparent among the neustonic ichthyoplankton. Obligate members include larvae and early juveniles of nine species that occurred permanently and almost exclusively in the neuston but were scarce or absent in subsurface samples. Other taxa of larvae and juveniles were abundant at the surface only at night and are identified as facultative members of the neuston. Several taxa of fish eggs were abundant in the neuston; they seem to accumulate at the surface because of positive buoyancy. They are considered strays in the neuston.

Fish larvae in the neuston were larger overall than those deeper in the water column; this is advantageous in terms of seeking prey and avoiding predators. Juveniles were also common in the neuston, but recently hatched larvae were largely absent.

Several factors may limit the successful habitation of the neuston by fish eggs and larvae: high levels of damaging UV radiation, intensive wave action, a reduced biota, enhanced visibility to predators, and larval dispersal. However, adaptations to these potentially adverse factors are apparent among the species. Advantages to a neustonic existence may include enhanced growth, reduced levels of predation, and suitable concentrations of food. The main reason that larvae and juveniles of certain species select the neuston as a suitable ecological niche is probably the unique trophic conditions that prevail in this biotope.

RESUMEN

Análisis de datos de ictioplancton colectados en las costas de Washington, Oregon y en el norte de California durante la década del 80 señala la existencia de un grupo neustónico de huevos de peces, larvas y juveniles. Este grupo tiene máxima diversidad sobre la plataforma y el talúd continental. La variación diurna en la ocurrencia de algunas especies de peces en el neuston es sorprendente. El ictioplancton neustónico puede dividirse en tres categorías. Miembros obligados, que incluyen larvas y juveniles tempranos de nueve especies que ocurren permanente y casi exclusivamente en el neuston, pero escasos o ausentes en las muestras sub-superficiales. Otro grupo de taxa de larvas y juveniles fué abundante en la superficie sólo de noche y se identifican como miembros facultativos del neuston. Varios taxa de huevos de peces fueron abundantes en el neuston donde aparentemente se acumulan debido a que poseen flotación positiva; se considera que este es un grupo "extraviado" en el neuston.

Las larvas de peces en el neuston fueron mas grandes que las encontradas a mayor profundidad en la columna de agua; se considera que esto es ventajoso al buscar presas y evitar depredadores. Los juveniles también se encontraron a menudo en el neuston, contrastando con larvas de reciente eclosión, quienes estuvieron ausentes.

Varios factores podrían limitar al neuston como un hábitat exitoso para el ictioplancton: altos niveles de radiación ultravioleta, oleaje intenso, una biota disminuída, mayor visibilidad para los depredadores y dispersión larval. Sin embargo, las especies muestran adaptaciones a esos factores adversos. Las ventajas de una existencia neustónica incluirían mayor crecimiento, menores niveles de depredación y concentraciones de alimento adecuadas. La razón principal por la cual larvas y juveniles de algunas especies eligen al neuston como un nicho ecológico conveniente estriba probablemente en las condiciones tróficas únicas que prevalecen en este biotopo.

INTRODUCTION

A diverse assemblage of planktonic organisms occurs in the uppermost surface layer (10–20 cm) of the oceans and is collectively referred to as the neuston (Zaitsev 1970; Peres 1982). The composition and abundance of neustonic organisms vary consider-

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ably, both geographically and temporally. In general, concentrations of neuston are higher in neritic areas than in the open ocean at the same latitudes (Hempel and Weikert 1972; Peres 1982). Holdway and Maddock (1983a) also showed that tropical and subtropical neritic and upwelling areas supported greater concentrations of neuston than oceanic and boreal zones. Diel variation in occurrence and abundance of organisms in the neuston is well documented. Although many members of the neuston are permanently present in the surface zone (obligate members), a diverse range of organisms concentrates at the surface only during certain hours (facultative members), mostly at night (Zaitsev 1970; Hempel and Weikert 1972; Peres 1982; Holdway and Maddock 1983a, b).

Fish eggs, larvae, and juveniles are abundant in the neuston, which is considered an important nursery ground for the early stages of many fish (Zaitsev 1970; Hempel and Weikert 1972; Moser 1981; Peres 1982). Although eggs of various fish species concentrate in the neuston, essentially because of their positive buoyancy, larvae and juveniles actively migrate to the surface zone and may be obligate or facultative members of the neuston. The importance of the neustonic realm in the ontogeny and ecology of larval fish populations varies with geographical area and local conditions. Factors such as latitude, surface water temperature, water depth, nutrient concentration, and upwelling all affect the diversity, age structure, and vertical migratory patterns of fish larvae in an area (Hempel and Weikert 1972; Tully and O'Ceidigh 1989a).

Several studies of planktonic neuston in the northeast Pacific were carried out during the 1970s and 1980s. Most were for the purpose of documenting fish larvae in the neuston. Richardson (1975) made a preliminary report on the occurrence and abundance of fish larvae and juveniles in the neuston along an east-west transect off the mid-Oregon coast. Ahlstrom and Stevens (1976) documented species composition and abundance of fish larvae in the neuston and in the water column over an extensive area of the northeast Pacific, including the coastal and oceanic zone from northern Washington to southern Baja California. In their account of the distribution of ichthyoplankton in the Southern California Bight, Gruber et al. (1982) compared the occurrence of larvae in neuston tows with their occurrence in oblique tows. These studies established that many species of fish larvae are abundant in the surface zone as well as deeper in the water column but that an additional group of species is almost exclusively neustonic. Brodeur et al. (1987) and Brodeur (1989) examined species composition and abundance of fish larvae and invertebrate components of the neuston in coastal waters of the northeast Pacific as part of a study of juvenile salmonids' feeding habits. Shenker (1985, 1988) was the first to carry out a biological and ecological investigation of neustonic larval and juvenile fishes in the northeast Pacific. That study, however, was restricted to a single transect of stations off the Oregon coast.

From 1980 to 1987, a series of cooperative U.S./U.S.S.R. ichthyoplankton surveys was conducted off the U.S. west coast from 48°N to 40°N (Dunn and Rugen 1989). These surveys were designed to determine spatial and temporal patterns in the ichthyoplankton. The neuston as well as the water column fauna was sampled, and hydrographic data were collected. Preliminary results from these surveys were given in Kendall and Clark 1982a, b; Clark 1984, 1986a, b; Bates 1984; Clark and Kendall 1985; Clark and Savage 1988; and Savage 1989a, b. These data made it possible to investigate the occurrence and ecology of fish eggs and larvae in the neuston over a large area and in comparison with their occurrence deeper in the water column.

In this investigation, species composition and relative abundance are documented, as are length-frequency distributions of larvae and diel variation in their occurrence and abundance in the neuston. Different categories of neustonic ichthyoplankton, such as obligate and facultative members, are identified. Horizontal patterns of distribution are described for the numerically dominant neustonic taxa. The ecological significance of a neustonic existence for early life stages of these fish is also discussed.

MATERIALS AND METHODS

The cooperative ichthyoplankton surveys conducted off the U.S. northwest coast during the 1980s involved the U.S. Northwest and Alaska Fisheries Center in Seattle, and the U.S.S.R. Pacific Research Institute in Vladivostok. Over a period of seven years, ten cruises were made. During each cruise, a maximum of 125 stations was occupied (table 1). Seasonal coverage was limited: six of the ten cruises were made in spring (March to early June); one cruise in summer (August 1980); one in winter (January 1987); and two in autumn (October–November 1981 and November–December 1983). The station grid covered an area of approximately 249,000 km^2 off Washington, Oregon, and northern California. Stations were more closely spaced over the shelf and slope than in deep water west of the 1,000-m isobath (figure 1).

TABLE 1
Sampling Schedule and Number of Stations Sampled for Ichthyoplankton

Cruise	Vessel	Cruise dates	Stations occupied: Neuston tows	Stations occupied: Bongo tows
TK80	*Tikhookeanski* U.S.S.R.	Apr. 20–May 15, 1980	125	125
PO80	*Poseydon* U.S.S.R.	Aug. 1–20, 1980	91	91
PO81	*Poseydon* U.S.S.R.	May 9–June 2, 1981	123	123
DA81	*Mys Dalniy* U.S.S.R.	Oct. 24–Nov. 19, 1981	125	125
PO82	*Poseydon* U.S.S.R.	May 3–June 1, 1982	124	49
EQ83	*Equator* U.S.S.R.	Apr. 23–May 15, 1983	124	124
MF83	*Miller Freeman* U.S.A.	Nov. 11–Dec. 2, 1983	113	113
PO84	*Poseydon* U.S.S.R.	Mar. 11–Apr. 4, 1984	124	124
BA85	*Mys Babyshkina* U.S.S.R.	Apr. 19–May 11, 1985	124	124
MF87	*Miller Freeman* U.S.A.	Jan. 7–31, 1987	88	88
Total number of stations occupied			1161	1086

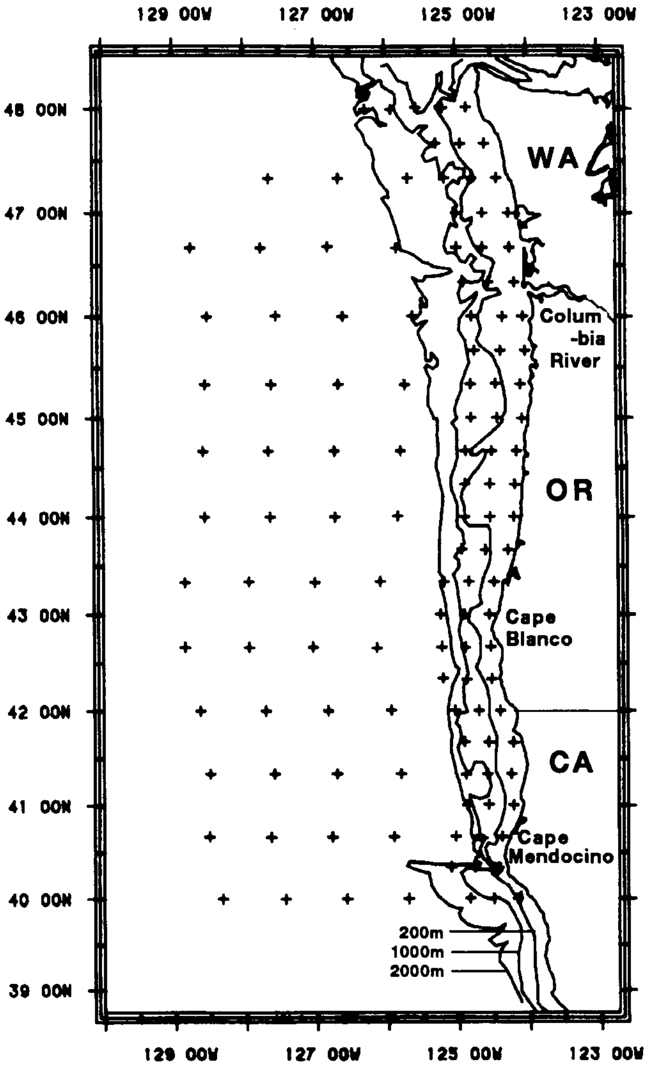


Figure 1. Survey area, sampling stations, and bathymetry off the U.S. west coast.

During each cruise, plankton was sampled for fish eggs and larvae, and hydrographic casts were made to determine temperature and salinity at all stations. Water samples were collected with Niskin bottles at nominal depths of 0, 5, 10, 15, 20, 25, 30, 35, 50, 75, 100, 200, 250, and 300 m, as depth permitted. For 10 minutes at each station, paired neuston tows were made with Sameoto samplers (Sameoto and Jaroszynski 1969) with 0.3-m-high-by-0.5-m-wide frames and 0.505-mm mesh netting. The samplers were towed at a speed of 2.0 knots and sampled approximately the upper 15 cm of the water column. Following standard procedures, oblique tows to 200-m depth, or 5 m from the bottom in water shallower than 200 m, were carried out at each station. For these tows, 60-cm-frame bongo samplers fitted with 0.505-mm-mesh nets were used (Smith and Richardson 1977). Flowmeters in the mouths of the samplers were used to determine the volume of water filtered by each net.

The plankton samples were preserved in a 5% buffered Formalin solution. One of each of the paired neuston and bongo samples was retained by the Americans and the other by the Soviets. The American plankton samples were processed by the Polish Plankton Sorting Center in Szczecin, Poland, and subsequently by the Northwest and Alaska Fisheries Center, Seattle. Fish eggs and larvae were removed from the samples, identified to the lowest taxonomic level possible, counted, and measured. Counts of fish eggs and larvae were converted to numbers per 10 m^2 of sea-surface area for the bongo samples and numbers per 1000 m^3 for the neuston samples.

OCEANOGRAPHIC ENVIRONMENT

The oceanography of the survey area is characterized by the California Current system, a typical eastern boundary current regime (Hickey 1979, 1989). The main California Current is slow, meandering, broad, and indistinct, and it proceeds southwards along the U.S. west coast (figure 2). Subcomponents of the California Current include the northward-flowing California Undercurrent and Davidson Current (Hickey 1989). The California Undercurrent consists of a jetlike poleward flow with a subsurface maximum. Its core appears to be confined to

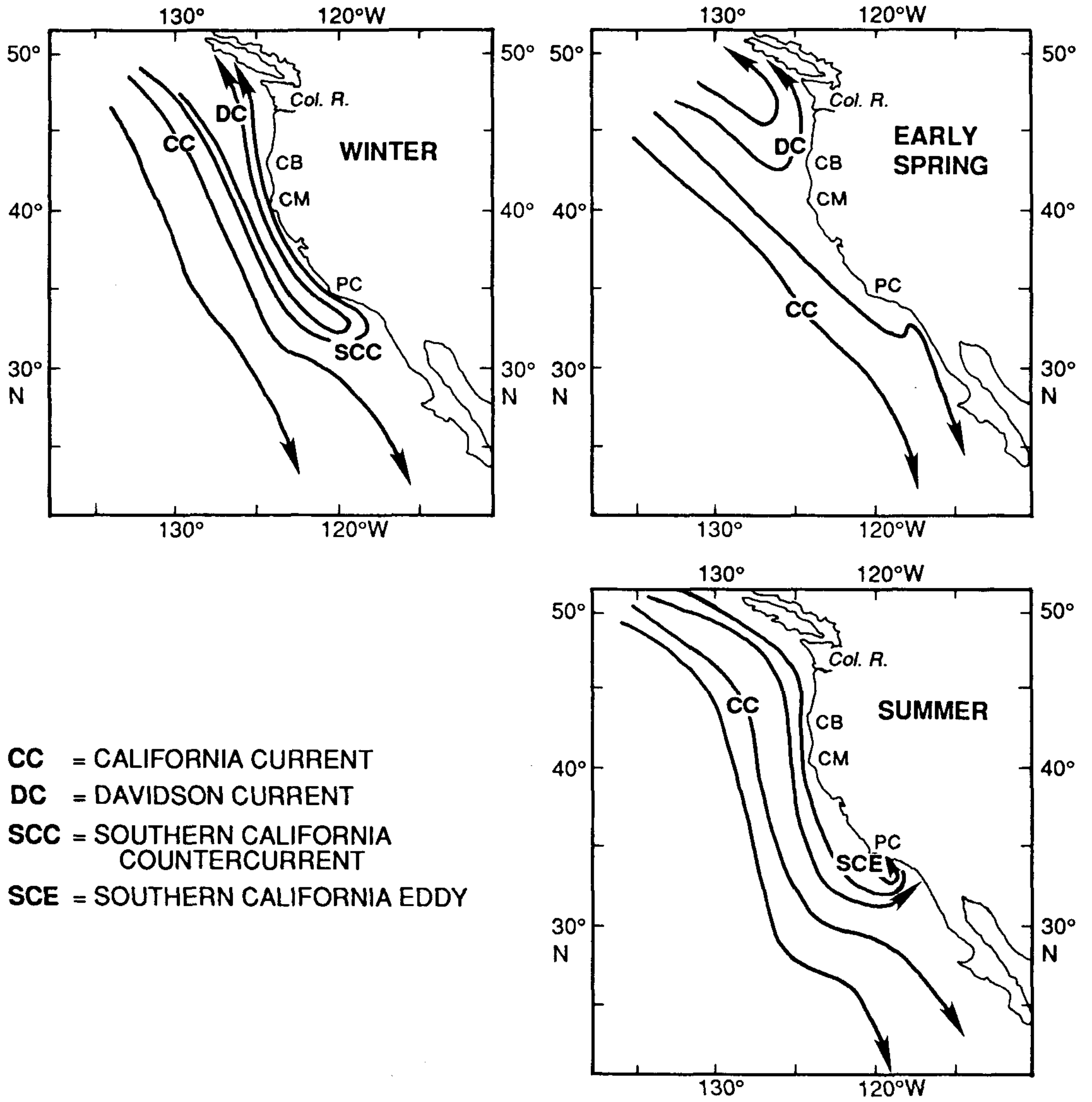


Figure 2. Seasonal variation in deep-ocean boundary currents off the U.S. west coast: Col. R. = Columbia River; CB = Cape Blanco; CM = Cape Mendocino; PC = Point Conception. From Hickey 1989.

the continental slope. The northward-flowing Davidson Current that prevails on the coastal side of the California Current during winter is a seasonal surface current (figure 2).

Coastal surface currents in this region are primarily wind-driven, with strong seasonal variability (Huyer et al. 1975; Hickey 1979; Strub et al. 1987). Spring and autumn transitions in prevailing winds and associated coastal currents are driven by large-scale changes in atmospheric pressure systems over the North Pacific. In winter, southerly winds result in the northward-flowing Davidson Current, onshore Ekman transport of surface water, and downwelling close to the coast. In spring the winds shift from southerly to northerly, and by summer the prevailing conditions include a southward-flowing coastal current, offshore Ekman transport, and upwelling of cold oceanic water close to the coast. The autumn transition from northerly to southerly winds leads back to the winter conditions.

The intensity of Ekman transport and associated upwelling varies along the coast. Mean monthly upwelling indices (derived from geostrophic wind stress; Bakun 1973) for four locations along the 125°W meridian — from northern Washington to northern California — show that the extent and intensity of upwelling increases from north to south (figure 3). Off Washington and northern Oregon, the upwelling season is confined largely to summer, whereas winter is characterized by vigorous downwelling. Along the northern California coast, winter downwelling is weaker and less extensive, and

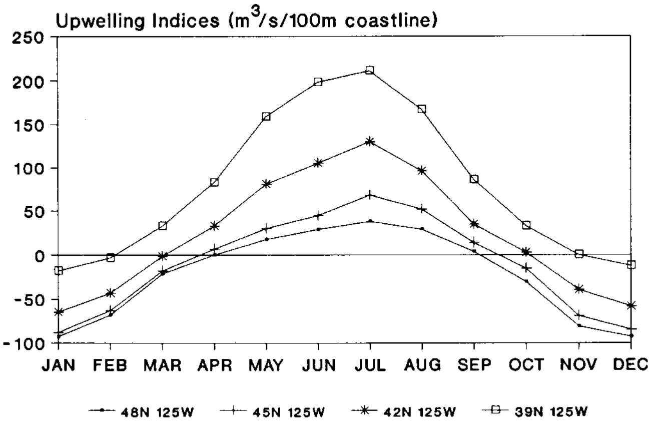


Figure 3. Monthly upwelling indices (Bakun 1973), mean of years 1946 to 1989, for four locations along the west coast. 48N = northern Washington; 45N = northern Oregon; 42N = Oregon/California border; 39N = northern California.

summer upwelling indices are considerably higher than off Washington and northern Oregon. The region of maximum upwelling along the U.S. west coast is between Cape Blanco in southern Oregon and Point Conception in southern California, with a local maximum at Cape Mendocino (Parrish et al. 1981).

The oceanography of waters off the U.S. northwest coast is modified significantly by the Columbia River, which divides the Washington and Oregon coastal regions (Hickey and Landry 1989). The Columbia River is the largest point source of freshwater flow into the eastern Pacific Ocean, and its water forms a low-salinity plume that extends outwards from the river mouth above a shallow halocline (<20 m; Fiedler and Laurs 1990). The extent and orientation of the plume is variable and subject to seasonal changes in runoff (peak period in June) and coastal circulation patterns.

RESULTS

Species Composition and Relative Abundance

Both fish eggs and larvae were abundant in neuston samples, but species diversity was lower than in the bongo samples. Twenty-five species of eggs representing 17 families were identified from neuston samples (table 2). In addition, three identifications were to generic level and five to family level. In terms of percentage occurrence and mean abundance in all samples, *Engraulis mordax*, *Trachipterus altivelis*, *Icichthys lockingtoni*, the paralichthyids, and the pleuronectids dominated. The paralichthyids (*Citharichthys* spp.) were outstandingly abundant, with a mean density of 389 eggs per 1000 m^3, even though they occurred in only 27% of neuston samples. The mesopelagic species *Chauliodus macouni* and *Icosteus aenigmaticus* were moderately abundant but occurred in approximately 10% of all samples.

Taxonomic diversity was higher for larvae in the neuston samples. Forty-six species were identified in a total of 24 families (table 3). Among the nine identifications to generic level, *Sebastes* spp., representing numerous rockfish, was most important. Species composition, and particularly relative abundance, differed greatly from that recorded for eggs in the neuston. *Engraulis mordax* was the only species for which both eggs and larvae were abundant. Although paralichthyid and pleuronectid larvae appeared in the neuston samples, occurrence and abundance were very low in comparison with their eggs. The numerically dominant taxa of larvae in the neuston included *Engraulis mordax*, *Cololabis saira*, *Sebastes* spp., *Anoplopoma fimbria*, *Hexagrammos decagrammus*, *Hemilepidotus spinosus*, and *Scorpaenichthys marmoratus*. Less abundant, but also well represented, were *Tarletonbeania crenularis*, *Hexagrammos lagocephalus*, *Ophiodon elongatus*, *Hemilepidotus hemilepidotus*, *Ronquilus jordani*, *Cryptacanthodes aleutensis*, and *Ammodytes hexapterus*.

Eggs of all species that were prominent in the neuston were also prominent in subsurface bongo samples (tables 4 and 5). Except for *Engraulis mordax*, larvae of the same species were absent or scarce in the neuston, but were generally prominent in the bongo collections. It seems, therefore, that species of fish eggs that are abundant in the neuston accumulate passively at the surface and on hatching into larvae migrate downwards into the subsurface zone.

In contrast, many of the larval species that were abundant in the neuston were absent or scarce in the bongo samples and therefore may be considered almost exclusively neustonic (obligate members of the neuston). These include *Cololabis saira*, *Anoplopoma fimbria*, the hexagrammids, the cottids, and *Cryptacanthodes aleutensis*. Because their eggs were absent from the neuston (table 2), these larvae must actively migrate to, and remain in the surface zone. *Ronquilus jordani* and *Ammodytes hexapterus* were recorded frequently in the bongo samples, although they were not abundant. Their incidence of occurrence in neuston samples was, however, higher than in the bongo samples. These larvae are considered to be more facultative than obligate neustonic types. The remaining taxa that were prominent in the neuston—including *Engraulis mordax*, *Tarletonbeania crenularis*, and *Sebastes* spp.—were also abundant, and had a higher incidence of occurrence, in the bongo samples, which indicates that they are essentially facultative in the neuston.

TABLE 2
Percentage Occurrence and Mean Abundance of All Taxa of Eggs in Neuston Samples Collected during All Cruises

Family	Species	% occurrence (all samples)	Mean no./1000 m^3 (all samples)
Unidentified	—	2.83	3.10
Engraulidae	*Engraulis mordax*	2.74	32.28
Argentinidae	Unidentified	0.19	0.02
	Nansenia candida	0.28	0.04
	Nansenia crassa	0.38	0.07
Bathylagidae	Unidentified	1.51	0.60
	Bathylagus spp.	1.42	0.26
	Bathylagus ochotensis	0.28	0.04
Chauliodontidae	*Chauliodus macouni*	10.21	2.23
Melanostomidae	*Tactostoma macropus*	2.65	4.88
Myctophidae	Unidentified	0.09	0.02
Gadidae	*Merluccius productus*	0.09	0.01
	Theragra chalcogramma	0.19	0.07
Scomberesocidae	*Cololabis saira*	1.04	2.70
Trachipteridae	Unidentified	0.66	0.12
	Trachipterus altivelis	39.98	37.77
Scorpaenidae	*Sebastolobus* spp.	1.51	57.49
Carangidae	*Trachurus symmetricus*	0.19	0.08
Icosteidae	*Icosteus aenigmaticus*	10.21	5.54
Ammodytidae	*Ammodytes hexapterus*	0.09	0.02
Centrolophidae	*Icichthys lockingtoni*	30.15	43.48
Tetragonuridae	*Tetragonurus cuvieri*	0.47	0.13
Paralichthyidae	*Citharichthys* spp.	27.03	389.37
Pleuronectidae	Unidentified	10.40	76.18
	Errex zachirus	8.88	13.05
	Hippoglossoides elassodon	0.57	0.13
	Pleuronectes isolepis	1.80	0.55
	Eopsetta exilis	5.86	4.13
	Microstomus pacificus	14.75	42.19
	Pleuronectes vetulus	3.50	3.13
	Platichthys stellatus	1.13	0.81
	Pleuronichthys coenosus	0.76	0.17
	Pleuronichthys decurrens	3.02	1.15
	Psettichthys melanostictus	4.44	3.43

Diel Variation in Catches of Larvae

For larvae in the neuston, it is important to consider diel variation in catches, especially for the facultative members that are only occasionally abundant in the surface layer. The pattern of diel variation in total catches differs significantly between the two sampling gears (figure 4). There is very little variation over 24 hours for the bongo samples, whereas in the neuston, catches were considerably lower during daylight than at night. Between 0800 and 1900 hours, catches in the neuston were always <3% of total catch; from 2000 to 0600, catches per hour ranged from approximately 5% to 12% of the total larval fish catch (figure 4a). Two possible factors may contribute to this diel pattern: (1) vertical migration of larvae into the neuston at night causes an increase in catches during darkness, and (2) enhanced avoidance of the neuston sampler during daylight reduces catches during the day. One or both of these factors may operate among the individual species of larval fish in the neuston.

There was little variation in catches of *Cololabis saira* over 24 hours, with only a slight reduction during daylight (figure 5a). Given that it occurred almost negligibly in the bongo samples (table 6), this species appears to be a permanent resident in the neuston. *Anoplopoma fimbria* larvae were less abundant in neuston samples during the day than at night (figure 5b), and their occurrence in bongo samples was, although low, higher than for *Cololabis saira* (table 6). There may be some migration of these larvae out of the immediate surface zone during the day.

The incidence of occurrence of hexagrammid larvae in bongo samples was very low (<1%) or, in the case of *Hexagrammos lagocephalus*, zero (table 6), implying that they are obligate neustonic species. Diel variation in catches, however, indicates that these larvae were slightly more abundant at night than during daylight (figure 5c–e). The cottid *Hemilepidotus spinosus*, which accounted for approximately 25% of all larvae caught in the neuston (table 6), was considerably more abundant in nighttime neuston

TABLE 3
Percentage Occurrence and Mean Abundance of All Taxa of Larvae in Neuston Samples Collected during All Cruises

Family	Species	% occurrence (all samples)	Mean no./1000 m^3 (all samples)
Clupeidae	*Clupea harengus pallasi*	0.58	0.19
Engraulidae	*Engraulis mordax*	3.88	9.99
Osmeridae	Unidentified	1.23	1.07
Argentinidae	*Nansenia candida*	0.09	0.01
Bathylagidae	Unidentified	0.09	0.02
	Bathylagus spp.	0.09	0.02
	Bathylagus ochotensis	1.13	0.25
Myctophidae	Unidentified	0.19	0.02
	Ceratoscopelus townsendi	0.09	0.02
	Diaphus theta	0.28	0.04
	Lampanyctus regalis	0.09	0.02
	Protomyctophum crockeri	0.19	0.05
	Protomyctophum thompsoni	0.09	0.01
	Stenobrachius leucopsarus	1.42	0.65
	Symbolophorus californiense	0.19	0.03
	Tarletonbeania crenularis	5.95	5.56
Merluccidae	*Merluccius productus*	0.09	0.02
Gadidae	*Microgadus proximus*	0.09	0.01
	Theragra chalcogramma	0.09	0.01
Scomberesocidae	*Cololabis saira*	31.29	16.71
Scorpaenidae	Unidentified	0.09	0.19
	Sebastes spp.	18.05	19.86
	Sebastolobus spp.	0.09	0.05
Anoplopomatidae	*Anoplopoma fimbria*	22.02	26.46
Hexagrammidae	Unidentified	0.19	0.14
	Ophiodon elongatus	4.16	3.39
	Pleurogrammus monopterygius	0.19	0.04
	Hexagrammos spp.	0.19	0.06
	Hexagrammos decagrammus	19.01	15.16
	Hexagrammos lagocephalus	5.01	1.61
	Hexagrammos stelleri	0.09	0.04
Cottidae	Unidentified	0.28	0.04
	Artedius fenestralis	0.28	0.08
	Artedius harringtoni	0.28	0.08
	Cottus asper	0.09	0.01
	Hemilepidotus hemilepidotus	3.02	1.24
	Hemilepidotus spinosus	13.14	40.84
	Leptocottus armatus	0.76	0.21
	Radulinus spp.	0.09	0.16
	Radulinus asprellus	0.09	0.01
	Scorpaenichthys marmoratus	16.54	8.38
Agonidae	Unidentified	0.09	0.01
Cyclopteridae	Unidentified	0.94	0.16
Carangidae	*Trachurus symmetricus*	0.09	0.09
Bathymasteridae	*Bathymaster* spp.	0.19	0.03
	Ronquilus jordani	3.49	1.75
Stichaeidae	Unidentified	0.09	0.22
Cryptacanthodidae	*Delolepis gigantea*	0.09	0.01
	Cryptacanthodes aleutensis	1.42	1.83
Pholidae	*Pholis* spp.	0.09	0.02
Ammodytidae	*Ammodytes hexapterus*	4.06	7.11
Centrolophidae	*Icichthys lockingtoni*	0.39	0.07
Paralichthyidae	*Citharichthys* spp.	0.57	0.44
	Citharichthys sordidus	0.19	0.03
	Citharichthys stigmaeus	1.51	0.24
Pleuronectidae	*Eopsetta jordani*	0.28	0.09
	Errex zachirus	0.09	0.43
	Pleuronectes isolepis	0.28	0.22
	Microstomus pacificus	0.19	0.03
	Pleuronectes vetulus	1.42	0.44
	Platichthys stellatus	0.19	0.02
	Pleuronichthys decurrens	0.28	0.35
	Psettichthys sp.	0.09	0.01
	Psettichthys melanostictus	0.28	0.06

TABLE 4
Dominant Ichthyoplankton Taxa in Neuston and Bongo Samples Collected during All Cruises

Family	Species	Neuston Eggs	Neuston Larvae	Bongo Eggs	Bongo Larvae
Engraulidae	*Engraulis mordax*	x	x	x	x
Osmeridae	Unidentified				x
Bathylagidae	Unidentified			x	
	Bathylagus spp.			x	
	Bathylagus ochotensis			x	x
	Bathylagus pacificus				x
Chauliodontidae	*Chauliodus macouni*	x		x	x
Melanostomidae	*Tactostoma macropus*	x			
Myctophidae	Unidentified			x	x
	Diaphus theta				x
	Protomyctophum crockeri				x
	Protomyctophum thompsoni				x
	Tarletonbeania crenularis		x		x
	Stenobrachius leucopsarus				x
Scomberesocidae	*Cololabis saira*		x		
Trachipteridae	*Trachipterus altivelis*	x		x	
Scorpaenidae	*Sebastes* spp.		x		x
	Sebastolobus spp.				x
Anoplopomatidae	*Anoplopoma fimbria*		x		
Hexagrammidae	*Hexagrammos decagrammus*		x		
	Hexagrammos lagocephalus		x		
	Ophiodon elongatus		x		
Cottidae	*Hemilepidotus hemilepidotus*		x		
	Hemilepidotus spinosus		x		
	Scorpaenichthys marmoratus		x		
Bathymasteridae	*Ronquilus jordani*		x		
Cryptacanthodidae	*Cryptacanthodes aleutensis*		x		
Icosteidae	*Icosteus aenigmaticus*	x		x	
Ammodytidae	*Ammodytes hexapterus*		x		
Centrolophidae	*Icichthys lockingtoni*	x		x	
Paralichthyidae	*Citharichthys* spp.	x		x	
	Citharichthys sordidus				x
	Citharichthys stigmaeus				x
Pleuronectidae	Unidentified	x		x	
	Errex zachirus	x		x	x
	Eopsetta exilis	x		x	x
	Microstomus pacificus	x		x	
	Pleuronectes vetulus	x		x	x
	Psettichthys melanostictus	x		x	x

TABLE 5
Relative Abundance of Dominant Taxa of Eggs in Neuston Samples

Family	Species	Common name	% total egg abundance	% occurrence (all samples) Neuston	Bongo
Engraulidae	*Engraulis mordax*	Northern anchovy	4.44	2.74	2.17
Chauliodontidae	*Chauliodus macouni*	Pacific viperfish	0.30	10.21	20.69
Melanostomidae	*Tactostoma macropus*	Longfin dragonfish	0.69	2.65	2.17
Scomberesocidae	*Cololabis saira*	Pacific saury	0.36	1.04	0.94
Trachipteridae	*Trachipterus altivelis*	King-of-the-salmon	5.19	39.98	32.61
Scorpaenidae	*Sebastolobus* spp.	Thornyheads	7.93	1.51	0.76
Icosteidae	*Icosteus aenigmaticus*	Ragfish	0.76	10.21	13.04
Centrolophidae	*Icichthys lockingtoni*	Medusafish	5.99	30.15	20.71
Paralichthyidae	*Citharichthys* spp.	Sanddabs	56.28	27.03	26.00
Pleuronectidae	Unidentified	Righteye flounders	10.48	10.40	11.91
	Eopsetta exilis	Slender sole	0.55	8.88	15.12
	Errex zachirus	Rex sole	1.79	5.86	21.83
	Microstomus pacificus	Dover sole	5.80	14.75	14.37
	Pleuronectes vetulus	English sole	0.93	3.50	3.59
	Psettichthys melanostictus	Sand sole	0.42	4.44	4.82

Based on data from all cruises.

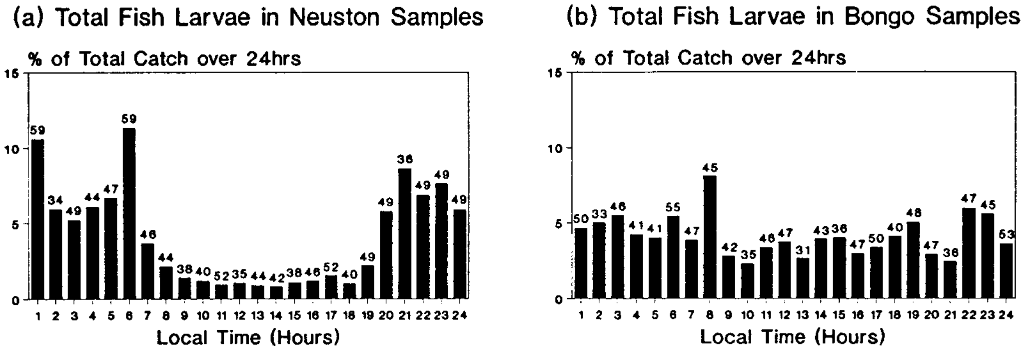


Figure 4. Diel variation in total catch of fish larvae in neuston (*a*) and bongo (*b*) samples. For each hourly interval over 24 hours, abundance was summed for all stations (10 cruises combined) where larvae were found. The percentage of total catch (24 hours combined) accounted for by each hourly interval was then calculated. Numbers above the bars are the total number of samples collected during each hourly interval.

samples than in daytime ones (figure 5f), indicating a possibly significant migration out of the surface layer. The incidence of occurrence of *H. spinosus* larvae in the bongo samples was still low (approximately 1.9%), however, but higher than for the obligate neustonic species (table 6). An unusual pattern of diel variation was apparent for the cottid *Scorpaenichthys marmoratus* (figure 6a). Its larvae were most abundant in the neuston after midnight until early afternoon (1400 hours); after that, hourly catches made up less than 3% of the total catch. These larvae may migrate out of the neuston during the latter period.

Diel variation in larval abundance was most dramatic for *Ronquilus jordani*, *Engraulis mordax*, *Tarletonbeania crenularis*, *Sebastes* spp., and *Ammodytes hexapterus* (figure 6b–f). Daytime catches of these larvae were usually insignificant. It seems that high numbers of these larvae migrate into the surface zone at night, which indicates a facultative association with the neuston. For *E. mordax*, *T. crenularis*, and *Sebastes* spp., this facultative association is further emphasized by the much higher occurrence and abundance of these larvae in the bongo samples than in the neuston collections (tables 4 and 6). *Ronquilus jordani* and *A. hexapterus* occurred in fewer bongo than neuston samples, and their overall abundance in the bongo samples was low (tables 4 and 6).

Categories of Neustonic Ichthyoplankton

The patterns of occurrence and abundance of eggs and larvae in the neuston collections, and the diel variation in catches indicate three categories of neustonic occurrence for west coast ichthyoplankton (table 7).

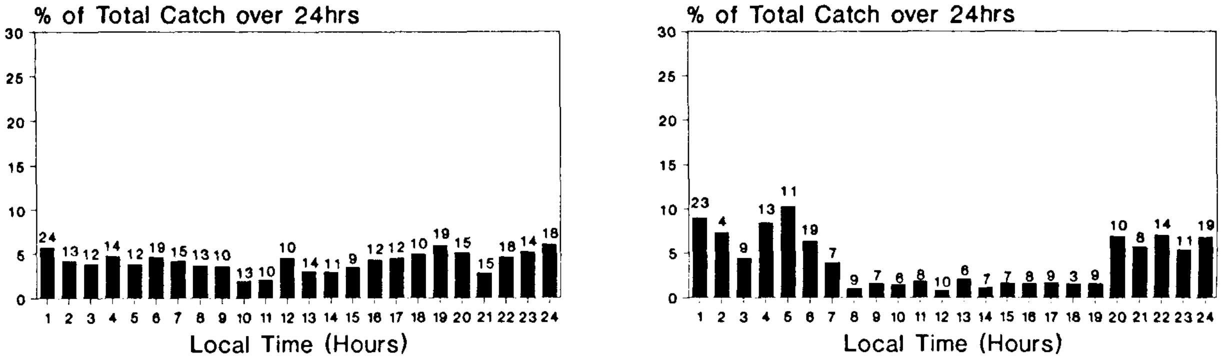
Obligate members of the neuston permanently live in the surface zone. Among the west coast ichthyoplankton, larvae and early juveniles of the species *Cololabis saira*, *Anoplopoma fimbria*, *Hexagrammos decagrammus*, *H. lagocephalus*, *Ophiodon elongatus*, *Hemilepidotus hemilepidotus*, *H. spinosus*, *Scorpaenichthys marmoratus*, and *Cryptacanthodes aleutensis* are assigned to this category (table 7).

Facultative members of the neuston are occasionally abundant in the surface layer. In the study area, larvae and early juveniles of *Engraulis mordax*, *Tarletonbeania crenularis*, *Sebastes* spp., *Ronquilus jordani*, and *Ammodytes hexapterus* belong to this category. They are abundant in the neuston only at night and migrate vertically in a diel pattern, remaining in the subsurface zone during daylight.

A third category of neustonic ichthyoplankton, "strays," includes a wide variety of fish eggs and larvae. Most of the species assigned to this category were most abundant in the subsurface zone of the water column, but some also appeared in the neuston. The species listed in tables 2 and 3 but not included in tables 4–6 (dominant neustonic taxa) are considered strays. In contrast, several species of eggs accumulate passively and abundantly in the surface zone. They float to the surface because they are positively buoyant. Eggs of the paralichthyids *Citharichthys* spp. are the most prominent members of this category, accounting for over 50% of all eggs in the neuston collections (table 5). Other species of eggs that were relatively abundant in the neuston included *Engraulis mordax*, *Trachipterus altivelis*, *Sebastolobus* spp., *Icichthys lockingtoni*, and various pleuronectids.

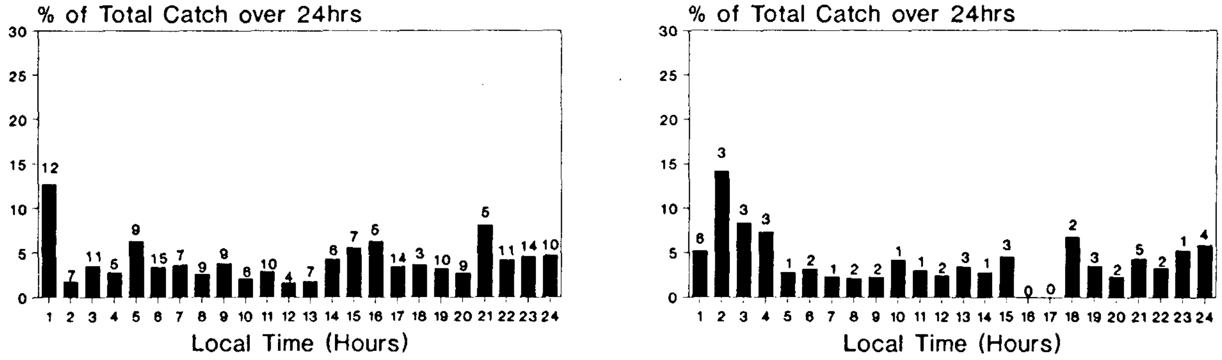
Horizontal Patterns of Distribution

Patterns of distribution described here for neustonic fish larvae are based on data combined for the ten sampling cruises; no adjustment is made for day-night differences in catches. The distribution maps represent general patterns of horizontal distribution



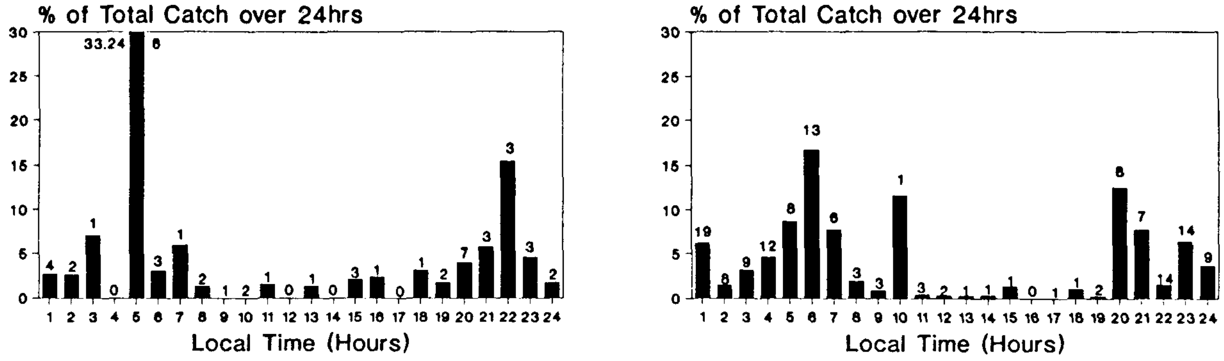
(a) *Cololabis saira*

(b) *Anoplopoma fimbria*



(c) *Hexagrammos decagrammus*

(d) *Hexagrammos lagocephalus*



(e) *Ophiodon elongatus*

(f) *Hemilepidotus spinosus*

Figure 5. Diel variation in catches of fish larvae in neuston samples. For each hourly interval over 24 hours, abundance was summed for all stations (10 cruises combined) where larvae were found. Numbers above the bars are the total number of stations at which fish larvae were caught (with either gear) during each hourly interval. The total number of neuston samples collected during each hourly interval is given in figure 4a.

in the sampling area rather than accurate plots of mean larval abundance. Most taxa of fish larvae occurred close to the coast over the shelf and slope and were absent or scarce in the deepest part of the oceanic zone (figures 7 and 8). This is true of the pelagic *Engraulis mordax* and the demersal hexagrammids, cottids, *Ronquilus jordani*, *Cryptacanthodes aleutensis*, and *Ammodytes hexapterus*. Adult populations of these species are essentially coastal. Some, such as *Hexagrammos decagrammus*, *H. lagoce-*

TABLE 6
Relative Abundance of Dominant Taxa of Larvae in Neuston Samples

Family	Species	Common name	% total larval abundance	% occurrence (all samples)	
				Neuston	Bongo
Engraulidae	*Engraulis mordax*	Northern anchovy	5.96	3.88	5.67
Osmeridae	Unidentified	Smelts	0.26	1.23	4.91
Myctophidae	*Tarletonbeania crenularis*	Blue lanternfish	3.33	5.95	34.40
	Stenobrachius leucopsarus	Northern lampfish	0.26	1.42	56.33
Scomberesocidae	*Cololabis saira*	Pacific saury	10.08	31.29	0.47
Scorpaenidae	*Sebastes* spp.	Rockfish	11.99	18.05	43.57
Anoplopomatidae	*Anoplopoma fimbria*	Sablefish	15.97	22.02	1.23
Hexagrammidae	*Hexagrammos decagrammus*	Kelp greenling	9.15	19.01	0.66
	Hexagrammos lagocephalus	Rock greenling	0.91	5.01	0.00
	Ophiodon elongatus	Lingcod	1.95	4.16	0.47
Cottidae	*Hemilepidotus hemilepidotus*	Red Irish lord	0.74	3.02	0.28
	Hemilepidotus spinosus	Brown Irish lord	24.65	13.14	1.89
	Scorpaenichthys marmoratus	Cabezon	5.06	16.54	0.85
Bathymasteridae	*Ronquilus jordani*	Northern ronquil	1.05	3.49	2.08
Cryptacanthodidae	*Cryptacanthodes aleutensis*	Dwarf wrymouth	1.00	1.42	0.19
Ammodytidae	*Ammodytes hexapterus*	Pacific sandlance	4.16	4.06	1.80

Based on data from all cruises.

TABLE 7
Categories of Neustonic Ichthyoplankton

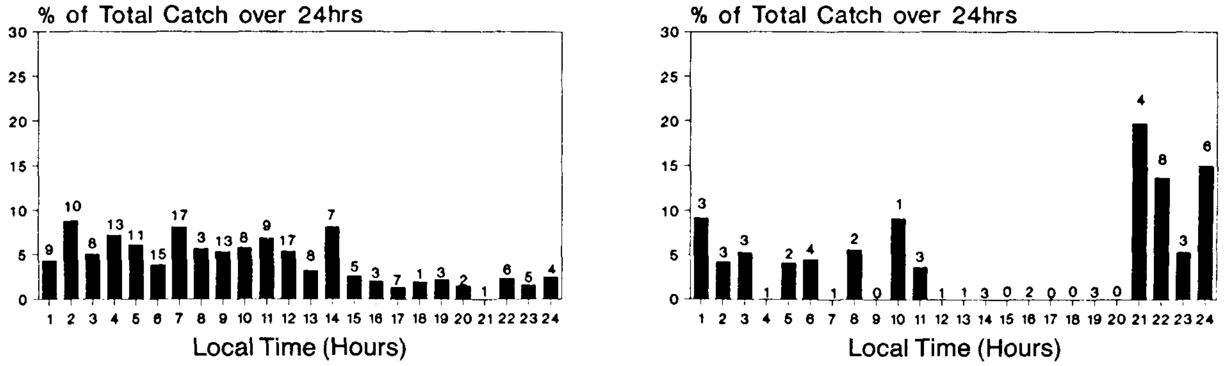
Obligate	Facultative	Strays
Permanently in the neuston — most abundant in the surface zone. Neustonic larval niche.	Occasionally abundant in the neuston because of diel vertical migration.	Accumulate passively in the neuston because of neutral or positive buoyancy, or because of occasional forays to the surface.
Larvae and juveniles of: *Cololabis saira* *Anoplopoma fimbria* *Hexagrammos decagrammus* *Hexagrammos lagocephalus* *Ophiodon elongatus* *Hemilepidotus hemilepidotus* *Hemilepidotus spinosus* *Scorpaenichthys marmoratus* *Cryptacanthodes aleutensis*	Larvae and juveniles of: *Engraulis mordax* *Tarletonbeania crenularis* *Sebastes* spp. *Ronquilus jordani* *Ammodytes hexapterus*	Eggs of: *Engraulis mordax* *Trachipterus altivelis* *Sebastolobus* spp. *Icichthys lockingtoni* *Citharichthys* spp. Pleuronectidae Other less abundant eggs and larvae of various species.

phalus, *Hemilepidotus spinosus*, and *Scorpaenichthys marmoratus*, are most abundant close to shore, where they spawn from the intertidal zone to a maximum depth of 100 m (Hart 1973; Matarese et al. 1989). It seems unusual, then, that the larval distribution of *S. marmoratus* extends as far offshore as it does, with occurrences over the slope and adjacent deep water and sometimes over the deepest water of the sampling grid (figures 7f,g and 8b,c). Obviously larval drift is extensive; larvae in the neuston are subject to wind-generated transport as well as the prevailing patterns of water circulation. Because the station grid began three miles offshore, the highest larval densities of the shallow-water species were probably missed by this sampling program.

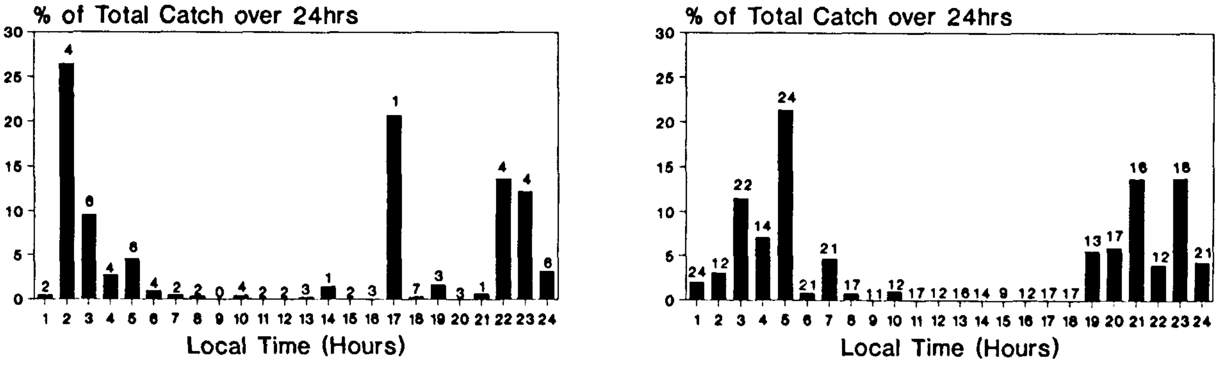
The occurrence of highest densities of *Engraulis mordax* larvae over the shelf, slope, and immediate deepwater zone off Washington and northern Oregon (figure 7a) reflects the known association of this species with the Columbia River plume. The northern subpopulation of *E. mordax* spawns in the near-surface waters of the Columbia River plume during summer (Richardson 1980).

Larvae that occurred extensively in the neuston of the shelf, slope, and oceanic zones include the myctophid *Tarletonbeania crenularis* (figure 7b), the Pacific saury (*Cololabis saira*; figure 7c), the rockfish complex (*Sebastes* spp.; figure 7d), and the sablefish (*Anoplopoma fimbria*; figure 7e). Larval distribution accurately reflected the distribution of adult popu-

(a) *Scorpaenichthys marmoratus* (b) *Ronquilus jordani*



(c) *Engraulis mordax* (d) *Tarletonbeania crenularis*



(e) *Sebastes* spp. (f) *Ammodytes hexapterus*

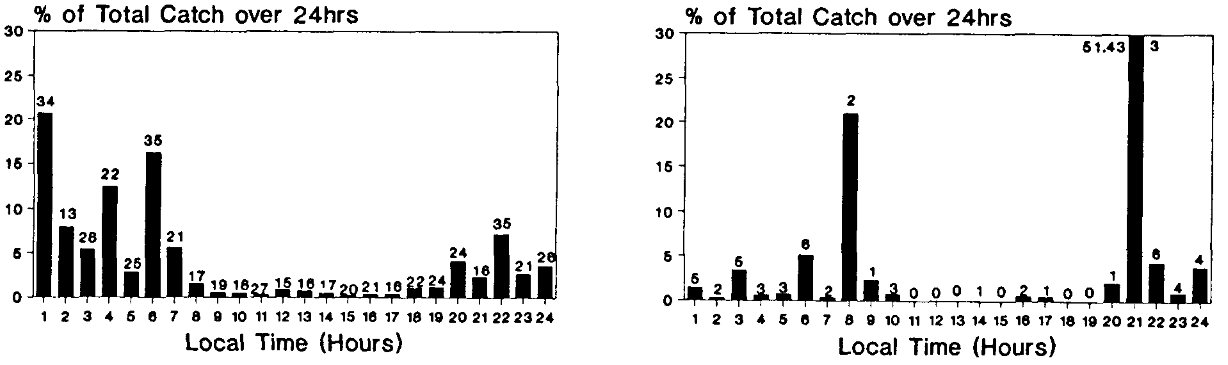
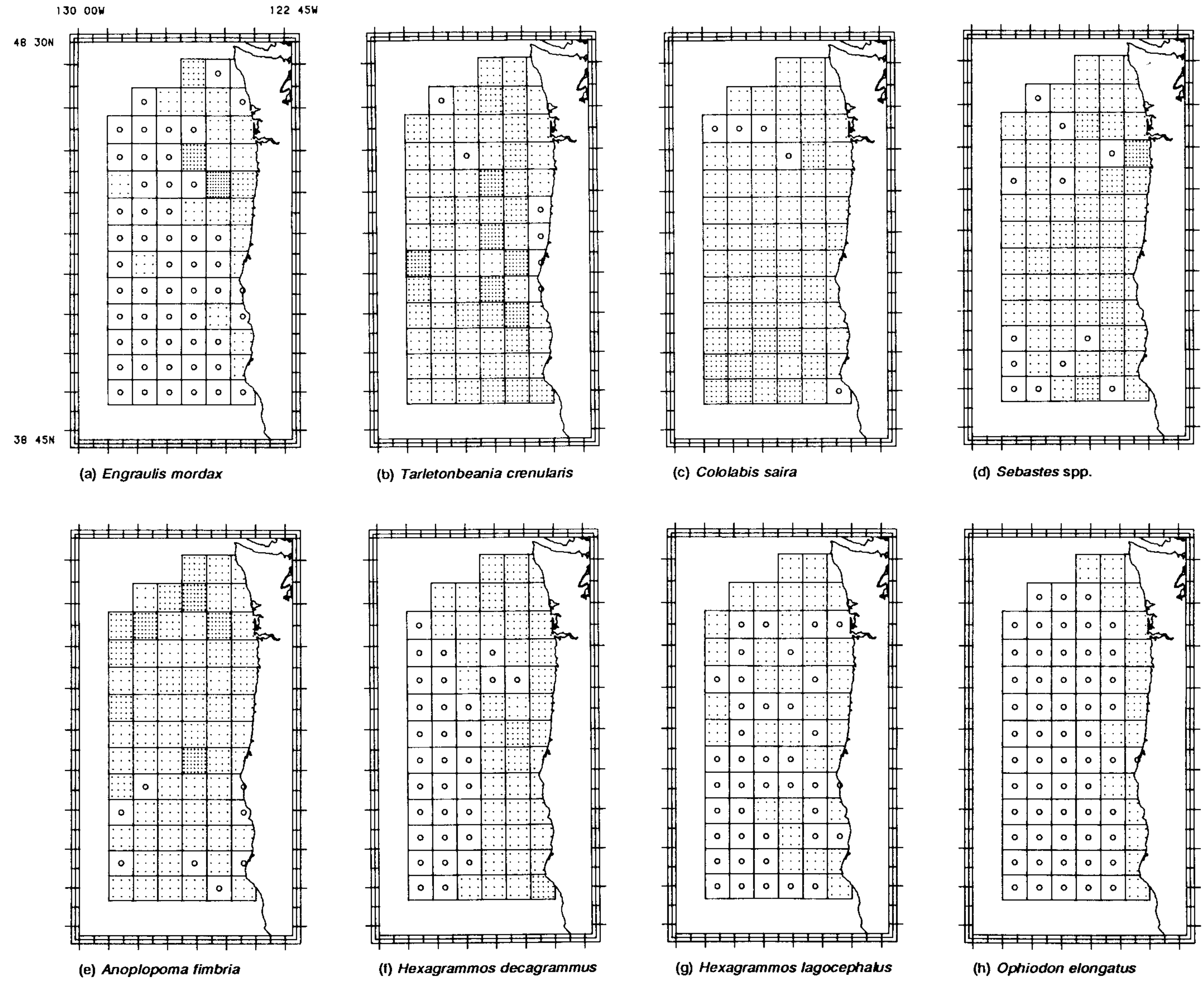


Figure 6. Diel variation in catches of fish larvae in neuston samples (continued). For each hourly interval over 24 hours, abundance was summed for all stations (10 cruises combined) where larvae were found. Numbers above the bars are the total number of stations at which fish larvae were caught (with either gear) during each hourly interval. The total number of neuston samples collected during each hourly interval is given in figure 4a.

lations only in the case of the mesopelagic *T. crenularis*, which is an oceanic species. *Sebastes* spp., *C. saira*, and *A. fimbria* are most abundant as adults along the outer shelf and over the slope, and their larvae are advected extensively into deep water.

Early Life-History Characteristics for Species with Neustonic Larvae

Larval length distributions are compared between the neuston and bongo collections for the facultative neustonic species with larvae abundant in the water

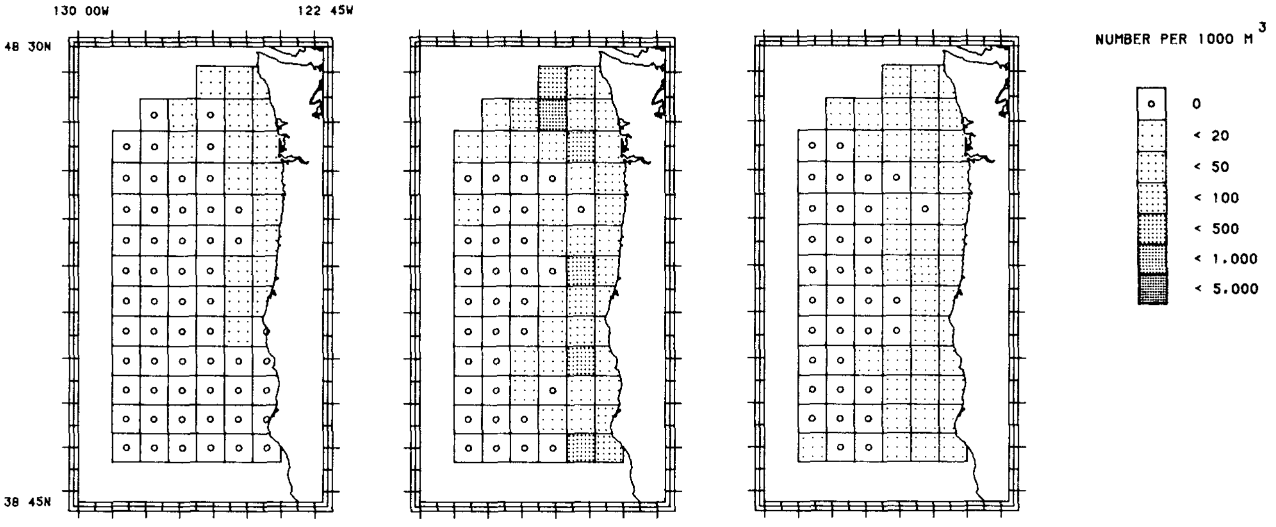


(a) *Engraulis mordax* (b) *Tarletonbeania crenularis* (c) *Cololabis saira* (d) *Sebastes* spp. (e) *Anoplopoma fimbria* (f) *Hexagrammos decagrammus* (g) *Hexagrammos lagocephalus* (h) *Ophiodon elongatus*

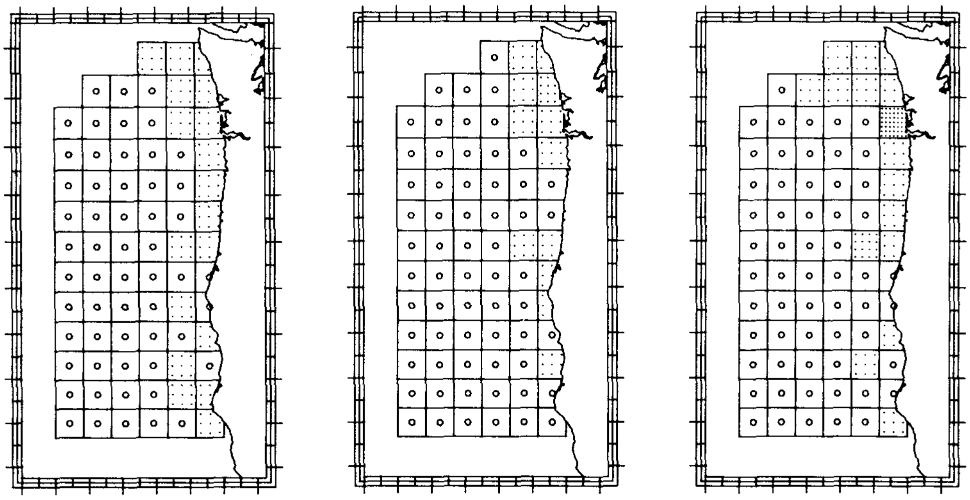
Figure 7. Patterns of distribution for dominant taxa of fish larvae in the neuston. Data are combined for 10 cruises, and mean abundance of larvae (no./1000 m^3) is calculated for each grid square.

column (figure 9a–j). A broader size range of specimens was encountered in the neuston than in the bongo samples. Neustonic specimens were significantly larger, and many were juveniles. Most of the larvae taken in the bongo samples were less than 10 mm long, or in the case of *A. hexapterus* less than 15 mm, whereas neustonic larvae were mostly longer than 10 mm (figure 9). The difference was greatest for *Tarletonbeania crenularis*: its smallest neustonic specimens were 19 mm (figure 9c,d). Length at transformation for this species is given at 19–21 mm (Matarese et al. 1989). It seems, therefore, that among the facultative neustonic species, mainly the well-developed, large larvae and young juveniles migrate to the surface zone at night.

Among the obligate neustonic species, a wide size range of larvae and early juveniles was encountered, and most larvae were larger than 10 mm (figure 10a–i). Catches of early juveniles varied among species. Length at transformation to juvenile stage varies among these species. For some, such as the hexagrammids and cottids, the transition stage is prolonged, and a prejuvenile, neustonic stage is



(i) *Hemilepidotus hemilepidotus* (j) *Hemilepidotus spinosus* (k) *Scorpaenichthys marmoratus*



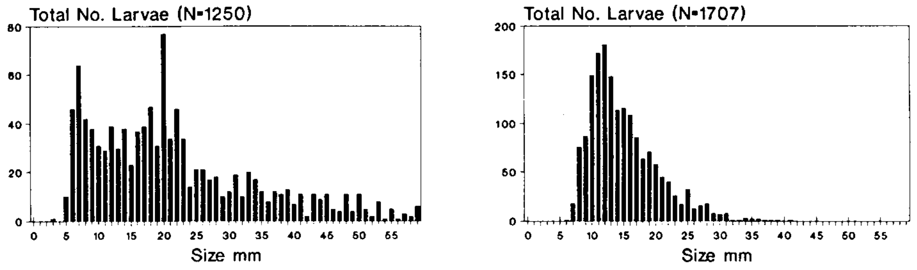
(l) *Ronquilus jordani* (m) *Cryptacanthodes aleutensis* (n) *Ammodytes hexapterus*

Figure 8. Patterns of distribution for dominant taxa of fish larvae in the neuston (continued). Data are combined for 10 cruises, and mean abundance of larvae (no./1000 m^3) is calculated for each grid square.

recognized (Kendall et al. 1984). This prejuvenile stage differs from both the larval and the adult stage, and the morph resembles a herring, with silvery sides.

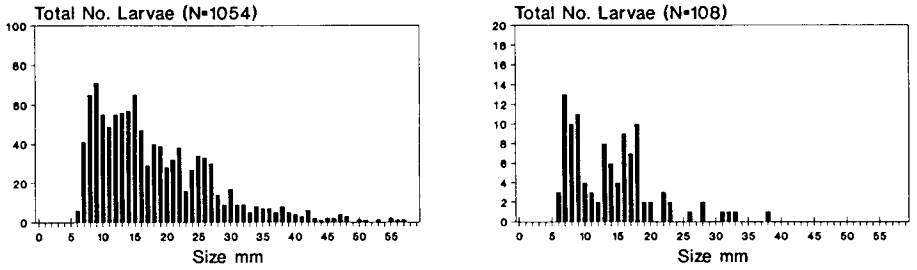
By the time *Cololabis saira* have reached a body length of 25 mm, most adult characters are present. These juveniles (>25 mm) were well represented in the catches, although less abundant than the larval stages (figure 10a). Large larvae and early juveniles (>30 mm) were scarce for *Anoplopoma fimbria* (figure 10b). Prejuvenile stages (>20–25 mm) for the hexagrammids *Hexagrammos decagrammus*, *H. lagocephalus*, and *Ophiodon elongatus* were present but in low concentrations, and specimens longer than 40 mm were rare. Lengths at transformation for the cottids *Hemilepidotus hemilepidotus* (19–23 mm), *H. spinosus* (19 mm), and *Scorpaenichthys marmoratus* (14 mm) are less than for the hexagrammids (Matarese et al. 1989). Prejuveniles of these species were scarce, and specimens longer than 40 mm were absent from the neuston samples (figure 10f–h).

Obligate neustonic larvae and larvae that are abundant deeper in the water column differ strikingly in their levels of pigmentation, particularly on the dorsal surface (Zaitsev 1970; Hempel and Weikert 1972; Moser 1981). The obligate neustonic larvae (*Cololabis saira*, *Anoplopoma fimbria*, hexagrammids, cottids, and *Cryptacanthodes aleutensis*) all have heavy melanistic pigmentation along the dorsal surface, particularly at the late larval and juvenile stage (Matarese et al. 1989). The intensity of pigmentation and beginning of its development, how-



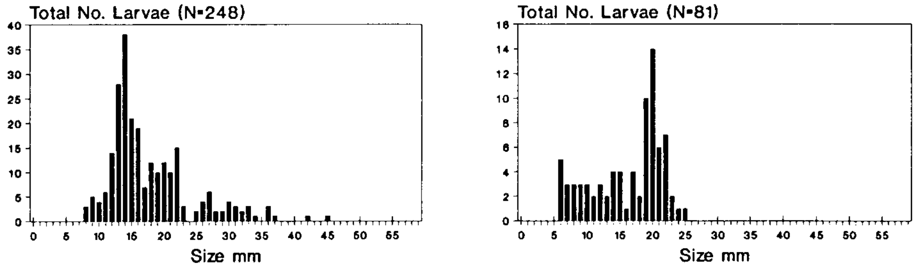
(a) *Cololabis saira*
Neuston samples

(b) *Anoplopoma fimbria*
Neuston samples



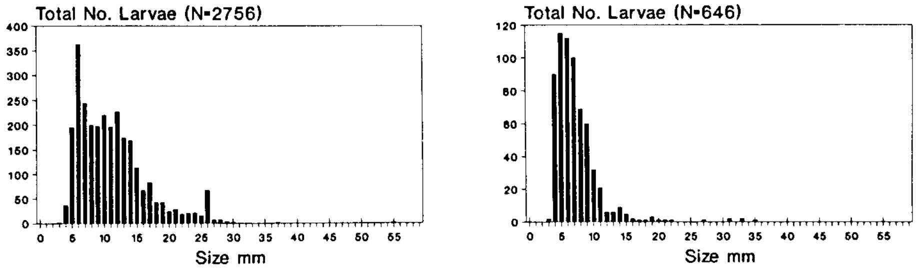
(c) *Hexagrammos decagrammus*
Neuston samples

(d) *Hexagrammos lagocephalus*
Neuston samples



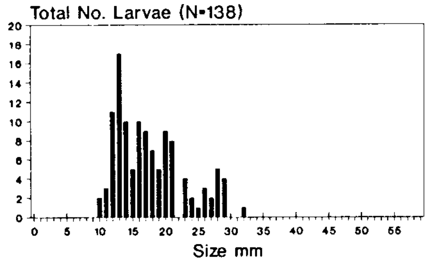
(e) *Ophiodon elongatus*
Neuston samples

(f) *Hemilepidotus hemilepidotus*
Neuston samples



(g) *Hemilepidotus spinosus*
Neuston samples

(h) *Scorpaenichthys marmoratus*
Neuston samples

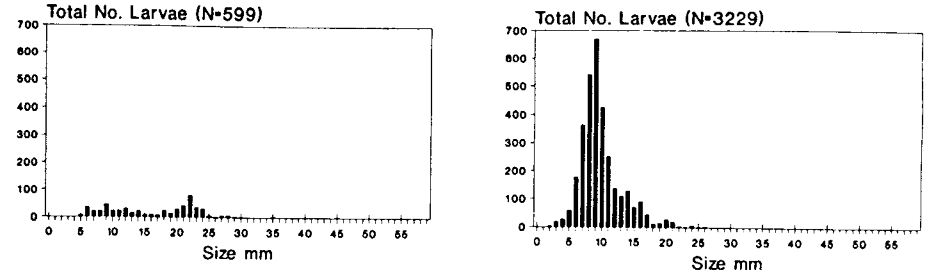


(i) *Cryptacanthodes aleutensis*
Neuston samples

Figure 9. Length-frequency distributions among obligate neustonic fish larvae and juveniles in neuston samples. Catches combined for 10 cruises. N = total number of larvae caught for each species.

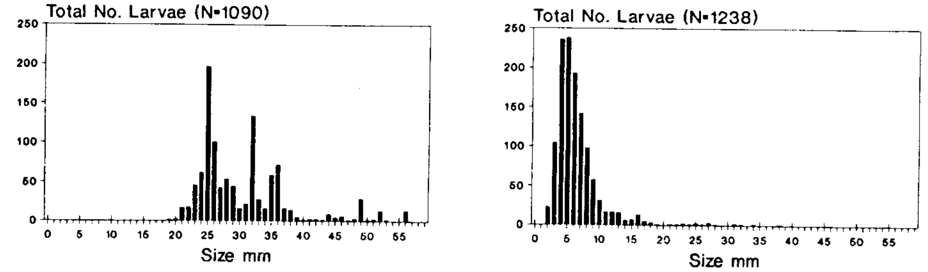
(a) *Engraulis mordax*
Neuston samples

(b) *Engraulis mordax*
Bongo samples



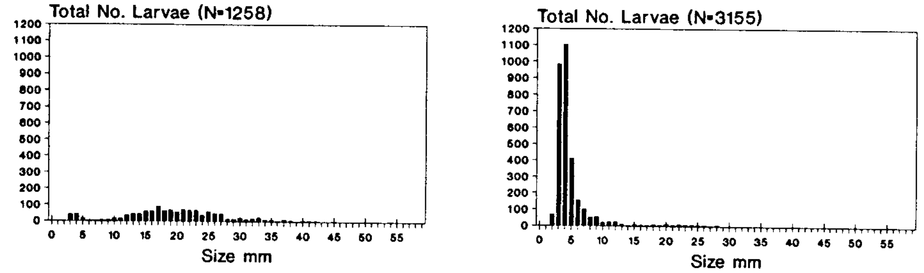
(c) *Tarletonbeania crenularis*
Neuston samples

(d) *Tarletonbeania crenularis*
Bongo samples



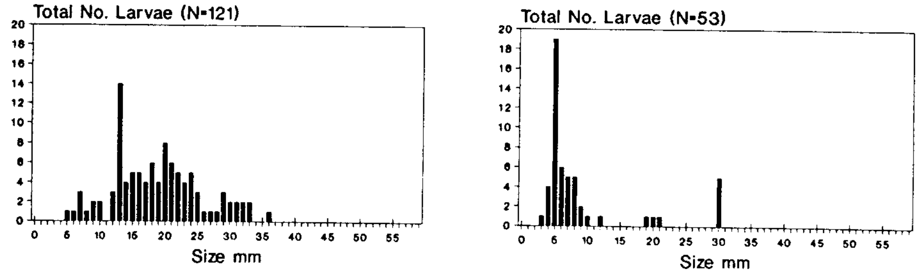
(e) *Sebastes* spp.
Neuston samples

(f) *Sebastes* spp.
Bongo samples



(g) *Ronquilus jordani*
Neuston samples

(h) *Ronquilus jordani*
Bongo samples



(i) *Ammodytes hexapterus*
Neuston samples

(j) *Ammodytes hexapterus*
Bongo samples

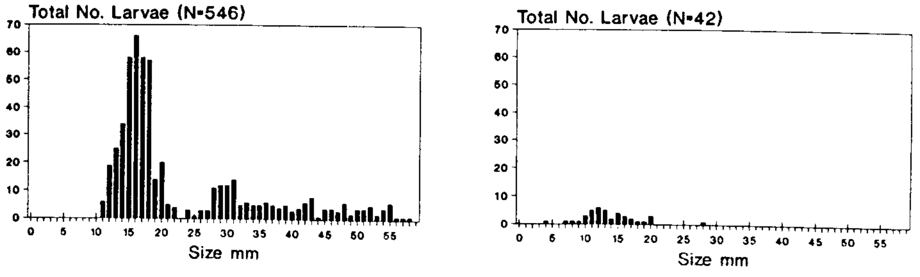


Figure 10. Length-frequency distributions among facultative neustonic fish larvae and juveniles in neuston and bongo samples. Catches combined for 10 cruises. N = total number of larvae caught for each species.

TABLE 8
Habitat and Spawning Strategies among Species with Obligate Neustonic Larvae

Species	Habitat	Spawning season	Spawning mode	Larval hatch size (mm)
Cololabis saira	Epipelagic Shelf and slope	Winter–autumn Peak: Feb.–July	Epipelagic, eggs attached to flotsam	6–8.5
Anoplopoma fimbria	Semidemersal Shelf and slope	Winter–spring Peak: Feb.–March	Bathypelagic	6
Hexagrammos decagrammus	Demersal Coastal–inshore	Autumn–spring Peak: Dec.	Demersal, shallow water, adhesive eggs	7–9
Hexagrammos lagocephalus	Demersal Coastal–inshore	Autumn–winter Peak: Dec.–Jan.	Demersal, shallow water, adhesive eggs	7–9
Ophiodon elongatus	Demersal Coastal and shelf	Winter–spring Peak: Dec.–Feb.	Demersal, shallow water, adhesive eggs	7–10
Hemilepidotus hemilepidotus	Demersal Coastal and shelf	Winter–spring Peak: Dec.–Jan.	Demersal, shallow water, adhesive eggs	5–6
Hemilepidotus spinosus	Demersal Coastal–inshore	Winter–spring Peak: Dec.–Feb.	Demersal, shallow to moderately deep water	5
Scorpaenichthys marmoratus	Demersal Coastal–inshore	All year Multiple spawning	Demersal, shallow water, adhesive eggs	4–6
Cryptacanthodes aleutensis	Epi/meso-benthal Shelf and slope	Winter–spring Peak: Jan.–March	Demersal, moderately deep water	10?

Life-history information from Matarese et al. 1989.

ever, varies among species. In contrast, in the facultative neustonic larvae identified here dorsal melanistic pigmentation is poorly developed.

Habitat and spawning strategies among the west coast species with obligate neustonic larvae are similar (table 8). Except for *Cololabis saira*, which is epipelagic, all live on or close to the bottom, mainly in coastal waters. *Cololabis saira*, *A. fimbria*, and *C. aleutensis* extend into deeper water than the other species, and they are common near the slope. The spawning season for most species is short, with a winter peak, usually from December to March. In contrast, *C. saira* has an extended spawning period from winter to autumn, with a peak from February to July, and *Scorpaenichthys marmoratus* is a multiple spawner throughout the year. *Cololabis saira* and *A. fimbria* are the only species that do not have demersal eggs. Eggs of *C. saira* are epipelagic and are usually attached to flotsam, whereas *A. fimbria* eggs are bathypelagic. Hexagrammids and cottids tend to have adhesive eggs that are attached to the substratum, either rocks or seaweed. Size at hatching among the obligate neustonic larvae is greater than 5 mm, and may be up to 10 mm, except for *S. marmoratus*, which hatches at a minimum size of about 4 mm. These sizes are relatively large in comparison with most species that hatch at sizes <5 mm. For instance, *E. mordax* hatches at 2.5–3 mm and *T. crenularis* at <3 mm (Matarese et al. 1989). Obligate neustonic larvae therefore tend to be relatively well developed at hatching.

DISCUSSION

Data from this study and from previous ichthyoplankton investigations indicate a neustonic assemblage of fish eggs and larvae off the coasts of Washington, Oregon, and northern California (Richardson[1]; Ahlstrom and Stevens 1976; Gruber et al. 1982; Brodeur et al. 1987; Shenker 1985, 1988). This assemblage is most diverse over the shelf and continental slope, but several species are also distributed throughout the oceanic zone.

The three categories of neustonic occurrence among the ichthyoplankton follow the general classification scheme for neustonic organisms (Zaitsev 1970; Hempel and Weikert 1972; Peres 1982). Obligate and facultative members of the neuston include larvae and early juveniles that actively seek out the surface zone.

The nine species of fish larvae assigned here to the obligate neustonic category appear to live permanently in the surface zone. These species occupy an exclusively neustonic niche during their larval and early juvenile or prejuvenile stages. Their larvae are scarce or absent in subsurface ichthyoplankton collections from coastal and oceanic waters off Washington, Oregon, and northern California (Richardson 1973; Richardson and Pearcy 1977; Richardson et al. 1980; Boehlert et al. 1985; Brodeur

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[1] S. L. Richardson. 1975. Oregon's coastal ichthyoneuston: a preliminary report. Unpublished report presented at American Society of Ichthyologists and Herpetologists, Williamsburg, Virginia.

et al. 1985; Doyle et al. in press). The reduced abundance of some of these larvae in neuston samples collected during daylight is attributed primarily to their visual avoidance of the sampling gear. It is also possible, however, that some larvae migrate vertically out of the surface layer during the day.

The facultative members differ from the obligate members in that they do not remain permanently in the neuston but migrate vertically in a diel pattern, moving up to the surface around dusk and remaining there until the onset of daylight.

Fish eggs are present in the neuston as "strays," accumulating at the surface because of positive buoyancy. Also included in this category are many species of larvae that appear frequently in the neuston but are much more abundant in the subsurface zone. For these species, the neuston represents the upper extreme of their vertical range.

In their review of the neuston of the subtropical and boreal northeast Atlantic Ocean, Hempel and Weikert (1972) documented the scarcity of very young fish larvae in the surface zone. Their neuston net caught mainly late larval and juvenile stages. The same was true for Shenker's (1985, 1988) ichthyoneuston collections off the Oregon coast. Comparing the length-frequency distributions of larvae caught in the bongo samples with those of the neuston collections in this study, I found that neustonic larvae are generally larger than those in the subsurface zone. The difference was particularly striking among the facultative larvae, indicating that those that migrate to the surface at night are well-developed larvae and early juveniles. Tully and O'Ceidigh (1989a) made the same observation for facultatively neustonic species of fish larvae in Galway Bay on the west coast of Ireland.

The scarcity of larvae less than 10 mm long among the obligate ichthyoneuston can be related to the strategies displayed by these species. Except for *Cololabis saira*, which is an epipelagic spawner, these species either deposit their eggs on the bottom — frequently in gelatinous masses that adhere to rocks or weed — or spawn bathypelagic eggs, e.g., *Anoplopoma fimbria* (Matarese et al. 1989). After hatching, larvae migrate to the surface, and small yolk-sac larvae are therefore likely to be dispersed throughout the water column rather than concentrated in the neuston. Their scarcity in the bongo samples may be attributed to the inefficiency of the gear in sampling relatively low densities of larvae scattered throughout the water column, in comparison with neuston nets, which efficiently sample larvae that are concentrated at the surface. Fecundity is also relatively low among the species with obligate neustonic larvae, and the larval hatch size is correspondingly high (Matarese et al. 1989), further contributing to the larger larval sizes in the neuston.

The implication from these length-frequency observations is that it is advantageous for larvae in the neuston to be well developed. With increasing size, fish larvae become more agile at seeking food and avoiding predators, thus enhancing their chances of survival. The size range of available food organisms also expands with increasing larval size. Hempel and Weikert (1972) observed that because phytoplankton seems to be scarce in the immediate vicinity of the surface, neustonic fish larvae are carnivorous or omnivorous. On depletion of the yolk sac, small first-feeding larvae may therefore be more vulnerable to starvation than they would be deeper in the water column.

Eggs that adhere to the substratum help retain young fish close to the adult habitat. The commencement of a planktonic existence is postponed to the larval phase, considerably reducing the period of drift in the plankton. It therefore seems contradictory that the dominant hexagrammid and cottid species inhabiting the coastal and inshore zone off Washington, Oregon, and northern California have larvae that are essentially neustonic. Their presence in the neuston subjects them to wind transport as well as to surface currents. In the dynamic surface zone they are much more likely to be widely dispersed away from suitable habitats for settlement than if they were concentrated deeper in the water column. The distribution patterns documented for all the neustonic larval species during this study indicate that larval drift is generally extensive in the surface zone of this region. Even among some of the inshore species such as *Hexagrammos decagrammus*, *H. lagocephalus*, and *Hemilepidotus spinosus*, the distribution of neustonic larvae extends well into the slope and oceanic zone. Larvae of these species encountered over deep water probably are lost to the adult populations and do not survive to recruitment. The widespread dispersal of larvae in the neuston may be facilitated by various mesoscale oceanographic features as well as wind transport and prevailing patterns of circulation. Eddies, offshore jets, meanders in the alongshore currents, and surface slicks associated with internal waves may contribute significantly to the onshore-offshore dispersal of ichthyoplankton (Shanks 1983; Kingsford and Choat 1986; Shenker 1988).

The prevalent spawning season among species with obligate neustonic larvae, however, is such that the larvae are most abundant when Ekman surface transport is onshore, and downwelling is occurring along the coast. The peak period of spawning for most species is winter; for the coastal species this favors retention of their larvae in the coastal zone, in the vicinity of the adult habitats. In their review of reproductive strategies among fish species in the California Current system, Parrish et al. (1981) observe a correspondence to the major features of surface transport that minimizes larval advection out of suitable habitats. Richardson et al. (1980) and Doyle et al. (in press) document a coastal assemblage of fish larvae in the plankton along the Washington, Oregon, and northern California coasts. This assemblage is present during winter and spring and, for the most part, absent from summer to autumn, when upwelling and offshore Ekman transport prevail. The spawning seasons among species with exclusively neustonic larvae therefore reflect the general correspondence between spawning strategies in this region and the prevailing circulation patterns.

By the time the neustonic larvae have developed to the juvenile stage, the transition to offshore Ekman transport and upwelling of oceanic water may have taken place along the coast. If young juveniles are still present in the neuston, they are likely to be transported away from the coastal zone. Postlarvae and juveniles of *Cololabis saira* and *Anoplopoma fimbria* remain at the surface (Hart 1973; Kendall and Matarese 1987) and therefore are widely distributed in deep water as well as along the coast. Among coastal and inshore hexagrammids and cottids, there is some evidence to suggest that large prejuveniles and juveniles migrate out of the neuston with the onset of upwelling, thus largely avoiding offshore transport. Shenker (1985, 1988) documented the disappearance of hexagrammid and cottid juveniles from neuston collections off Oregon in association with the beginning of upwelling and offshore Ekman transport. He proposed that upwelling triggers these fishes' settlement to the demersal habitat used by older juveniles and adults and that a possible stimulus for this transition is the breakdown of the thermocline.

Several factors that may limit the successful habitation of the neuston by fish eggs and larvae characterize the surface layer (Zaitsev 1970; Hempel and Weikert 1972). They include high levels of UV radiation, which may cause physiological stress or genetic damage; intensive wave action, which may cause mechanical damage to organisms; and a reduced biota, which may mean a diminished availability of prey. In addition, the high light intensity at the surface during the day is likely to make neustonic fish eggs and larvae more visible to predators. Surface transport mechanisms that disperse larvae away from a suitable adult habitat are another disadvantage associated with the neuston.

Adaptations to these potentially adverse factors are, however, apparent among neustonic ichthyoplankton in general (Zaitsev 1970; Hempel and Weikert 1972; Moser 1981) and specific to the U.S. west coast. For instance, the heavy melanistic pigmentation on the dorsal surface of larvae and early juveniles in the obligate neustonic category is considered to be a protective adaptation in response to high light intensity and associated UV radiation. Mechanical resistance of fish eggs is high, and eggs are believed to be endangered by wave action only during the first few hours after spawning (Hempel 1979), when they are deeper in the water column. Recently hatched larvae are likely to be much more vulnerable to mechanical damage, but — as observed off the U.S. west coast and elsewhere (Hempel and Weikert 1972) — in most species these larvae are absent from the neuston. The well-developed nature of neustonic larvae may be adaptive both in terms of seeking prey — which may be scarce in the neuston — and avoiding predators, to which they may be more visible than if they were deeper in the water column. As mentioned previously, the detrimental effects of surface transport along the west coast are reduced by the synchrony of spawning seasons. The demersal spawning mode is also an adaptive feature in this respect.

Given the hazardous conditions that may prevail in the sea-surface layer, it is interesting that certain species of fish along the U.S. west coast use this biotope as the ecological niche for their young. Advantages to a neustonic existence for ichthyoplankton may include enhanced growth and reduced levels of predation. For instance, accelerated embryogenesis is characteristic of fish eggs in the neuston, where temperatures are higher because of the intensive absorption of solar radiation in the upper 10 cm of the water column (Zaitsev 1970; Peres 1982). Positive buoyancy among certain species of fish eggs, resulting in their concentration in the neuston, may therefore be considered adaptive. Larval growth is also likely to be enhanced at the surface, shortening the most vulnerable early stage. For example, *Anoplopoma fimbria* larvae are known to grow rapidly (up to 2 mm per day) during spring off the U.S. west coast (Kendall and Matarese 1987). Hempel and Weikert (1972) propose that the surface layer of the ocean serves as a refuge from predators, particularly during the daytime, because of the relative scarcity of invertebrates and fishes, making it a less attractive hunting area for large predators. Hempel and Weikert suggest that the few enduring neustonic metazoa, including fish larvae, encounter relatively little predatory pressure during the daytime.

Based on their investigations of feeding among fish larvae and juveniles in the neuston of Galway Bay (west coast of Ireland), Tully and O'Ceidigh (1989b) conclude that feeding conditions at the surface are unique and that neustonic species are adapted to feed more successfully in this environment. It is likely that the most important advantage to a neustonic existence for fish larvae is the suitability of the surface layer as a trophic niche. Evidence that facultatively neustonic species of fish larvae migrate to the surface with the onset of darkness and return to deeper layers in the morning supports this hypothesis. A feature common to all investigated regions in the world ocean is that many plankton organisms migrate into the surface zone as daylight fades, thus making the neuston a much richer biotope at night, with higher concentrations of food suitable for fish larvae (Zaitsev 1970; Hempel and Weikert 1972; Peres 1982; Holdway and Maddock 1983a, b).

Apart from the high densities of zooplankton that may occur in the neuston at night, mesoscale physical features such as fronts, convergence zones, and surface slicks can cause aggregations of plankton at the surface, bringing high concentrations of fish larvae together with high concentrations of suitable prey. Kingsford and Choat (1986) found that small fish and zooplankton from surface waters off New Zealand were denser in slicks than in the rippled waters adjacent to them. Off Oregon, Shenker (1988) documented aggregations of Dungeness crab megalopae and fish larvae and juveniles in association with nearshore surface convergence zones and the periphery of the Columbia River plume. High concentrations of neustonic ichthyoplankton and zooplankton have also been found in association with the frontal structure around the discharge plume of the Mississippi River (Grimes and Finucane 1991). Clearly, the neuston biotope offers unique trophic conditions for young fish, and Moser (1981) proposes that the neustonic zone may be a permanent food patch available to larval fish. The feeding habits of the neustonic fish larvae described in the present study need to be investigated thoroughly, however, for a more complete understanding of the neustonic realm's importance in the early life history of fishes off the U.S. west coast.

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GROWTH AND LARVAL DEVELOPMENT OF *NYCTIPHANES SIMPLEX* IN LABORATORY CONDITIONS

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ABSTRACT

Larvae of *Nyctiphanes simplex* were reared in the laboratory from second and third calyptopis stages (C_2 and C_3) to juvenile. Effects of three different diets were observed: the microalgal flagellate *Tetraselmis suecica*, nauplii of the brine shrimp *Artemia franciscana*, or a mixture of the two. Larvae receiving *Artemia* showed longer pathways of development and longer intermoult periods. The age of larvae at the start of experiment (C_2 compared with C_3) affected patterns of pleopodal development. Rate of growth (body-length increment) decayed exponentially as estimated by von Bertalanffy equation: 0.010 d^{-1} for larvae fed either microalgae or the mixture, and 0.034-0.050 d^{-1} for larvae fed only *Artemia*.

RESUMEN

Larvas de *Nyctiphanes simplex* fueron cultivadas en laboratorio a partir de los estadios caliptopis segundo y tercero (C_2 y C_3) hasta juvenil. Se observó el efecto de tres diferentes tipos de dietas en el crecimiento: el microflagelado *Tetraselmis suecica*, nauplios de *Artemia franciscana*, o una mezcla de los dos. Las larvas que recibieron *Artemia* tuvieron vías de desarrollo más largas y periodos de intermuda más prolongados. La edad de la larva al inicio del experimento (C_2 comparado con C_3) afectó los patrones de desarrollo pleopodal. La tasa de crecimiento (incremento en longitud corporal) decayó exponencialmente según estimación con la ecuación de Bertalanffy: 0.010 d^{-1} para larvas alimentadas con microalgas o la mezcla, y de 0.034-0.050 d^{-1} para larvas alimentadas con *Artemia*.

INTRODUCTION

Nyctiphanes simplex is the most abundant euphausiid in nearshore waters of the eastern subtropical Pacific, including the Gulf of California (Brinton and Townsend 1980; Lavaniegos et al. 1989). In the season of intense upwellings, larvae of this species can average more than 50 ind/m^3 over distances of hundreds of km (Brinton 1967, 1973). However, little attention has been paid to the species' population dynamics and trophic role in the pelagic ecosystem. Boden (1951) described larval development of *N. simplex* from field samples. He found great variability in number of pleopods and terminal telson spines among furcilia specimens. A detailed study of *Nyctiphanes australis* showed that variant forms could not be considered a distortion of a single, basic pathway of development, since the dominant forms can differ from one place to another (Sheard 1953). Hedgpeth (1957) pointed out that all species of the genus occupy similar subtropical warm-temperate ecological situations.

Variability in larval development has been considered an effect of environmental variability, since it is observed most frequently in species distributed through coastal or continental slope areas (Mauchline and Fisher 1969). Influences of food type on larval development and growth rate were tested in the laboratory for *Nyctiphanes couchii* from the coast of France (Le Roux 1973). In that work there was a lower growth rate and greater variability in pathways of development in larvae on a diet of the diatom *Phaeodactylum tricornutum* than in larvae on diets of mixed microalgae or *Artemia* nauplii. Similar results were obtained for *Nyctiphanes capensis* from South Africa (Pillar 1985). Though healthy individuals tended to go through particular pathways of development, no clearly dominant pathway could be traced.

Euphausiids go through three larval phases: nauplius, calyptopis, and furcilia. In the furcilia phase there may be conspicuous variation in the addition and development of the five pairs of abdominal swimming appendages, or pleopods, and in the reduction in the number of terminal telson spines. The pleopods are added in sequence from anterior to posterior abdominal segments; each pair appears first as nonsetose rudiments which become setose and functional at the next moult (Fraser 1936; Mauchline and Fischer 1969). The number of terminal telson spines decreases from seven to one through a variable number of moults. The extreme variability in larval development that characterizes *Nyctiphanes* makes it difficult to describe an onto-

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genic sequence. An approximation of developmental sequence is crucial to the determination of age and estimation of growth.

For this study I analyzed the larval development and growth in *Nyctiphanes simplex* exposed to different feeding conditions. The following terms describe furcilia development: *phase* is the complete sequence of events in furciliar development; *instar* is the form of larva between successive moults. The following furcilia stages are used:

Furcilia 1: forms with 0–4 pairs of nonsetose pleopods.

Furcilia 2: forms with any combination of nonsetose and setose pairs of pleopods.

Furcilia 3: forms with five pairs of setose pleopods and seven terminal telson spines.

Furcilia 4: forms with five pairs of setose pleopods and five or six terminal telson spines.

Furcilia 5: forms with five pairs of setose pleopods and 2–4 terminal telson spines.

Furcilia 6: forms with five pairs of setose pleopods and one terminal telson spine.

There may be one or more instars within each stage. All furcilia forms have three pairs of posterolateral telson spines. The juvenile has only two pairs of posterolateral telson spines.

METHODS

Larvae of *N. simplex* were collected on February 9, 1990, near Todos Santos Islands, Baja California (31°49'N; 116°49'W), with a net of .333-mm-mesh width. They were transferred immediately to laboratory containers. Calyptopis stages 2 and 3 (C_2 and C_3) were sorted out. Groups of 20 larvae were placed in 200-ml beakers containing 150 ml of filtered seawater (10 μm) which had been sterilized by ultraviolet light. Beakers were kept in the dark at 14 ± 0.5°C. The larvae were fed the microalga *Tetraselmis suecica*, nauplii of the brine shrimp *Artemia franciscana*, or a mixture of the two (table 1). The content of carbon in one cell of *T. suecica* is approximately $0.8 \cdot 10^{-4}$ μg (Parsons et al. 1961); in one *Artemia* nauplii it is 0.9 μg (Bruggeman et al. 1980). Therefore, when the experiment started the amount of carbon per larva was 2.7 μg in *Artemia*-fed animals and 120 μg in *Tetraselmis*-fed animals. In addition, two lots of larvae were given no food.

The seawater was changed and the food provided daily. Microalgal culture was grown in F/2 medium under constant white light at 14 ± 0.5°C. *Artemia* nauplii were hatched every day in filtered seawater at 20°C. Body lengths of *Nyctiphanes* larvae were measured daily (in a welled slide), from tip of rostrum to end of telson (including spines) with an ocular micrometer. The number of pleopods and telson spines, and the dates of moulting were recorded. Larvae in stage C_2 at the start of the experiment are designated cohort 1, and those starting at C_3 are designated cohort 2.

TABLE 1

Food Given to Larvae of *Nyctiphanes simplex* in Each Experimental Unit*

Initial stage	Diet type	Daily ration	Replicates
C_2	Without food		2
C_2	*Tetraselmis suecica*	$2 \cdot 10^5$ cel/ml	2
C_2	*Artemia franciscana*	60 nauplii	2
C_2	*T. suecica* + *A. franciscana*	$2 \cdot 10^5$ cel/ml + 60 naup.	2
C_3	*Tetraselmis suecica*	$2 \cdot 10^5$ cel/ml	1
C_3	*Artemia franciscana*	60 nauplii	1

*150 ml of filtered seawater with 20 larvae
C_2 = calyptopis 2; C_3 = calyptopis 3.

RESULTS

Survival and Duration of Development

During the first week of the experiment half of the larvae died. Only a quarter of the total remained alive into the juvenile phase. Some of the starved larvae (table 2) started pleopodal development, but none completed it. Larvae with the best survival rate were in the cohort 2 lot receiving the *Tetraselmis* diet; 10% of the initial number died before entering the furcilia phase, and 10% more died when moulting to juvenile phase. There was high mortality (40%–60%) for all other fed larvae entering the furcilia phase. Differences in survival in relation to kind of diet were important only in the moult from last furcilia stage to juvenile.

Juveniles first appeared in lots fed *Tetraselmis* or the mixed diet, after 25 days in cohort 1 and 20 days in cohort 2 (table 3). Since furcilia first appeared in the cohort 1 after 7 days and in cohort 2 after 4 days,

TABLE 2

Survival (Percentage) of *Nyctiphanes simplex* Larvae on Different Diets at Four Levels of Development

Diet type	Initial stage	First furcilia instar	First instar with 5"	First instar with 1 t.t.s.	First juvenile instar
Starved	C_2	27.5	0.0	0.0	0.0
Tetraselmis	C_2	55.0	47.5	47.5	37.5
Artemia	C_2	40.0	35.0	25.0	7.5
Mixed	C_2	47.5	35.0	35.0	35.0
Tetraselmis	C_3	90.0	90.0	90.0	80.0
Artemia	C_3	60.0	40.0	40.0	15.0

5" = 5 pairs setose pleopods.
1 t.t.s. = 1 terminal telson spine.
C_2 = calyptopis 2; C_3 = calyptopis 3.

TABLE 3

Mean Time Elapsed (Days) ± Standard Deviation from the Beginning of Experiment for *Nyctiphanes simplex* Larvae on Different Diets at Four Levels of Development

Diet type	Initial stage	First furcilia instar	First instar with 5″	First instar with 1 t.t.s.	First juvenile instar
Starved	C_2	7±2	—	—	—
Tetraselmis	C_2	7±1	16±2	22±2	25±2
Artemia	C_2	7±1	19±5	26±2	33±0
Mixed	C_2	7±1	16±2	21±2	26±3
Tetraselmis	C_3	4±1	13±2	17±3	20±1
Artemia	C_3	3±0	14±2	22±2	33±2

5″ = 5 pairs setose pleopods.
1 t.t.s. = 1 terminal telson spine.
C_2 = calyptopis 2; C_3 = calyptopis 3.

the furcilia phase lasted 17–19 days. The *Artemia* diet produced longer periods of furcilia development (26 days for cohort 1 and 30 days for cohort 2).

Development of Pleopods

The high variability in pleopod development during the furcilia phase that characterizes other species of the genus *Nyctiphanes* was also observed in *N. simplex* (figure 1). Of the possible pleopod combinations, only forms 5′ (5 nonsetose pleopods) and 2″3′ (2 setose and 3 nonsetose pleopods) did not occur. Forms present in all lots, including starved larvae, were 0, 1′, 2′, 3′, 1″3′, and 4″1′. Considering only the lots with food, the minimum number of forms was observed in the lots receiving the mixed diet, and the maximum number in the lot of cohort 2 receiving the *Artemia* diet. However, differences in type and proportions of forms were greater between cohorts than among diets.

Of 98 larvae starting pleopodal development, 74% completed it through 25 different pathways (table 4). Only the pathway 1′ → 1″3′ → 4″1′ → 5″ was common to all treatments; it occurred in 32.9% of the larvae. However, this pathway is considered dominant only in cohort 1 (40.4% of larvae).

In cohort 2, pathways consisting of the sequence 2′ → 2″2′ → 4″1′ → 5″ or 2′ → 2″ → 2″2′ → 4″1′ → 5″ were more common (34.6% versus 6.4% in cohort 1). Another important difference between cohorts was the proportion of pathways starting with form 0 (furcilia without pleopods): 9 pathways (46.8% of cases) in cohort 1, and 2 pathways (11.5%) in cohort 2.

The number of instars per pathway was similar in the two cohorts, with feeding conditions clearly determining the pathway. Larvae fed *Tetraselmis* tended to follow shorter pathways (table 4) than larvae fed only *Artemia*.

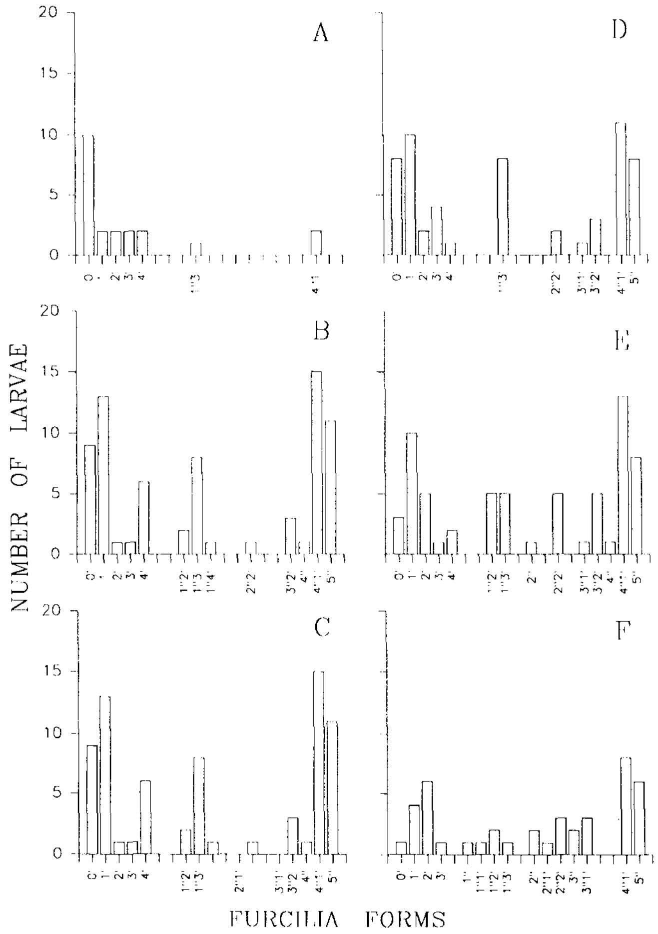

Figure 1. Frequency of furcilia forms of pleopod development in *Nyctiphanes simplex* kept under different feeding conditions: starved (*A*); *Tetraselmis* diet (*B*,*E*); *Artemia* diet (*C*,*F*); mixed diet (*D*). *A–D* are from cohort 1; and *E–F* are from cohort 2. (′) denotes a pair of nonsetose pleopods and (″) a pair of setose pleopods. All forms have seven terminal telson spines.

Reduction in Number of Terminal Telson Spines

Of 73 larvae in the first instar with five pairs of setose pleopods, 67 survived to complete the reduction of terminal telson spines (from 7 to 1). Twenty-eight larvae fed microalgae started this reduction without passing through F_3. All six possible reduced numbers of terminal telson spines (6, 5, 4, 3, 2, 1) occurred in each of the four groups that received food, with odd numbers of spines being more frequent. Most larvae required only 2 or 3 instars for complete spine reduction from 7 to 1 (table 5). Seventeen different pathways were observed in this part of development. Three pathways (7 → 5 → 3 → 1, 7 → 5 → 1, and 7 → 3 → 1) dominated, occurring in 58.2% of larvae. Sequence 7 → 3 → 1 appeared only in cohort 1.

Number of Instars in Furcilia Phase

Considering both pleopod development and the reduction of terminal telson spines, the total number

TABLE 4
Effect of Diet on Pathways of Pleopodal Development in Laboratory-Reared *Nyctiphanes simplex* Furcilia Stages 1, 2, and 3*, with Frequency Observed for Kind of Diet

Cohort 1

Instar number					Diet type and number of larvae				
1	2	3	4	5	*Tet*	*Art*	Mix	Total	%
4′	→4″1′	→5″			1	1		2	34.0
1′	→1″4′	→5″			1			1	
1′	→1″3′	→4″1′			4		3	7	
0	→ 4′	→4″1′			3	1	1	5	
0	→ 3′	→3″2′					1	1	
3′	→3″1′	→4″1′	→5″				1	1	55.3
1′	→1″3′	→4″1′	→5″		3	5	4	12	
1′	→1″2′	→3″2′	→5″		1			1	
0	→ 4′	→4″1′	→5″		2	2		4	
0	→ 3′	→3″2′	→5″		1	3	2	6	
0	→ 2′	→2″2′	→4″1′				1	1	
0	→ 1′	→1″2′	→3″2′		1			1	
1′	→1″3′	→4″	→4″1′	→5″	1			1	10.6
0	→ 4′	→4″	→4″1′	→5″		1		1	
0	→ 2′	→2″2′	→4″1′	→5″	1		1	2	
0	→ 1′	→1″2′	→3″1′	→4″1′		1		1	

Cohort 2

Instar number						Diet type and number of larvae			
1	2	3	4	5	6	*Tet*	*Art*	Total	%
3′	→3″1′	→4″1′				1		1	30.8
2′	→2″2′	→4″1′				3		3	
1′	→1″3′	→4″1′				2		2	
1′	→1″2′	→3″2′				2		2	
2′	→2″2′	→4″1′	→5″			1	2	3	50.0
2′	→2″	→2″2′	→4″1′			1	1	2	
1′	→1″3′	→4″1′	→5″			2	1	3	
1′	→1″2′	→3″2′	→5″			2		2	
0	→ 4′	→4″1′	→5″			2		2	
0	→ 1′	→1″2′	→3″2′			1		1	
2′	→2″1′	→3″	→3″1′	→4″1′			1	1	15.4
2′	→2″	→2″2′	→4″1′	→5″			1	1	
1′	→1″3′	→4″	→4″1′	→5″		1		1	
1′	→1″1′	→2″2′	→4″1′	→5″			1	1	
1′	→1″2′	→3″	→3″1′	→4″1′	→5″		1	1	3.8

*Includes all larvae with 7 terminal telson spines.
(′) = pair nonsetose pleopods; (″) = pair setose pleopods.

of developmental pathways was 52. The number of furcilia instars most frequently observed was 6 for *Tetraselmis*-fed larvae and 7 for *Artemia*-fed larvae (table 6). Statistical comparison of the number of instars (two-way analysis of variance) with factors cohort and diet, showed significant differences only for diet ($F = 8.68$, $p = 0.005$). *A posteriori* multiple range test (Student-Newman-Keuls) for means at 95% confidence interval indicated a difference ($p = 0.015$) only between the means for *Tetraselmis*-fed larvae (6.2 ± 0.3 instars) and those fed *Artemia* (6.9 ± 0.4 instars) and not between larvae fed the mixed diet and the other diets. All the larvae fed microalgae showed one instar in F_6. Only six of the *Artemia*-fed larvae reached the juvenile phase (i.e., reduction of posterolateral telson spines from three pairs to two), and they required two or three instars within F_6.

Intermoult Period and Moulting Rate

The average intermoult period for all larvae was 3 days. In each feeding treatment some extremely short or long periods occurred. Long periods were most common in *Artemia*-fed and starved larvae (figure 2). Nonparametric comparison of intermoult periods among diets, using Kruskall-Wallis test (rank sums) showed significant differences ($p < .001$) only in cohort 1. For all treatments, the intermoult period remained approximately constant through successive moults.

Regression analysis of cumulative intermoult period on number of moults (table 7; figure 3) indicated a slower moulting rate for *Artemia*-fed animals of cohort 1, but very similar rates among other diet groups (mixed diet is omitted in figure 3, since it is almost identical to *Artemia* diet). Moulting rate is

TABLE 5

Effect of Diet on Pathways of Reduction in Terminal Telson Spines in Laboratory-Reared *Nyctiphanes simplex*

Cohort 1

	Instar number				Diet type and number of larvae				
	1	2	3	4	*Tet*	*Art*	Mix	Total	%
	3	→1			5	1	3	9	40.5
	4	→1			1			1	
	5	→1			3	2	2	7	
	4	→2	→1			1		1	54.8
	5	→2	→1		1	1		2	
7→	5	→3	→1		4	3	2	9	
	5	→4	→1				1	1	
	6	→2	→1		2		1	3	
	6	→3	→1		1		4	5	
	6	→4	→1			1	1	2	
	5	→3	→2	→1	1			1	4.8
	6	→4	→3	→1	1			1	

Cohort 2

	Instar number				Diet type and number of larvae			
	1	2	3	4	*Tet*	*Art*	Total	%
	4	→1			2	1	3	52.0
	5	→1			6	2	8	
	6	→1			2		2	
7→	5	→2	→1		1	1	2	44.0
	5	→3	→1		3	3	6	
	6	→2	→1		2		2	
	6	→3	→1			1	1	
	5	→4	→2	→1	1		1	4.0

TABLE 6

Effect of Diet on Number of Instars in Furcilia Phase of *Nyctiphanes simplex*

		Number of instars				
Diet type	Cohort	5	6	7	8	9
Tetraselmis	1	3	9	6	1	
Artemia	1		4	5		
Mixed	1	1	7	6		
Tetraselmis	2	5	7	4	1	
Artemia	2		2	3	2	1
Total		9	29	24	4	1

In *Artemia* diet only the first instar in F_6 (1 t.t.s.) is included because most of the larvae died before the moult to juvenile phase.

TABLE 7

Regression Parameters of Cumulative Intermoult Period on Moult Number for Larvae of *Nyctiphanes simplex*

Diet type	Cohort	*a*	Moulting rate (days/moult)	r^2
Tetraselmis	1	0 ± 1.5	2.90 ± 0.03	0.941
Artemia	1	0 ± 1.9	3.69 ± 0.04	0.942
Mixed	1	0 ± 1.4	2.82 ± 0.03	0.951
Tetraselmis	2	0 ± 1.6	2.64 ± 0.04	0.898
Artemia	2	0 ± 3.3	2.88 ± 0.09	0.819

Forcing intercept (*a*) to zero; slope = moulting rate.

defined here as number of days elapsed per moult. The regression for *Artemia*-fed larvae of cohort 2 had the poorest fitting, with the last instars sometimes showing prolonged intermoult periods, and sometimes showing short intermoult periods but more moults. Juveniles appeared first in the *Tetraselmis* diet (figure 3).

Growth Rate

Increments in body length were consistently higher in the *Tetraselmis*-fed larvae. Mean body length for furcilia forms is shown in tables 8 and 9. A comparison among forms and treatments could not be made because there were too few measurements for many of the forms and heteroscedasticity. However, for larvae with form 5″ and 7 terminal telson spines (when the development of pleopods was complete), the statistical comparison of body-length measurements among diets and cohorts produced significant differences ($F = 31.54$, $p < 0.001$; one-way analysis of variance) among treatments. *A posteriori* multiple range test (Student-Newman-Keuls) for means resulted in two groups: the diets including microalgae and the diet of *Artemia* only. A similar comparison among treatments of larvae with

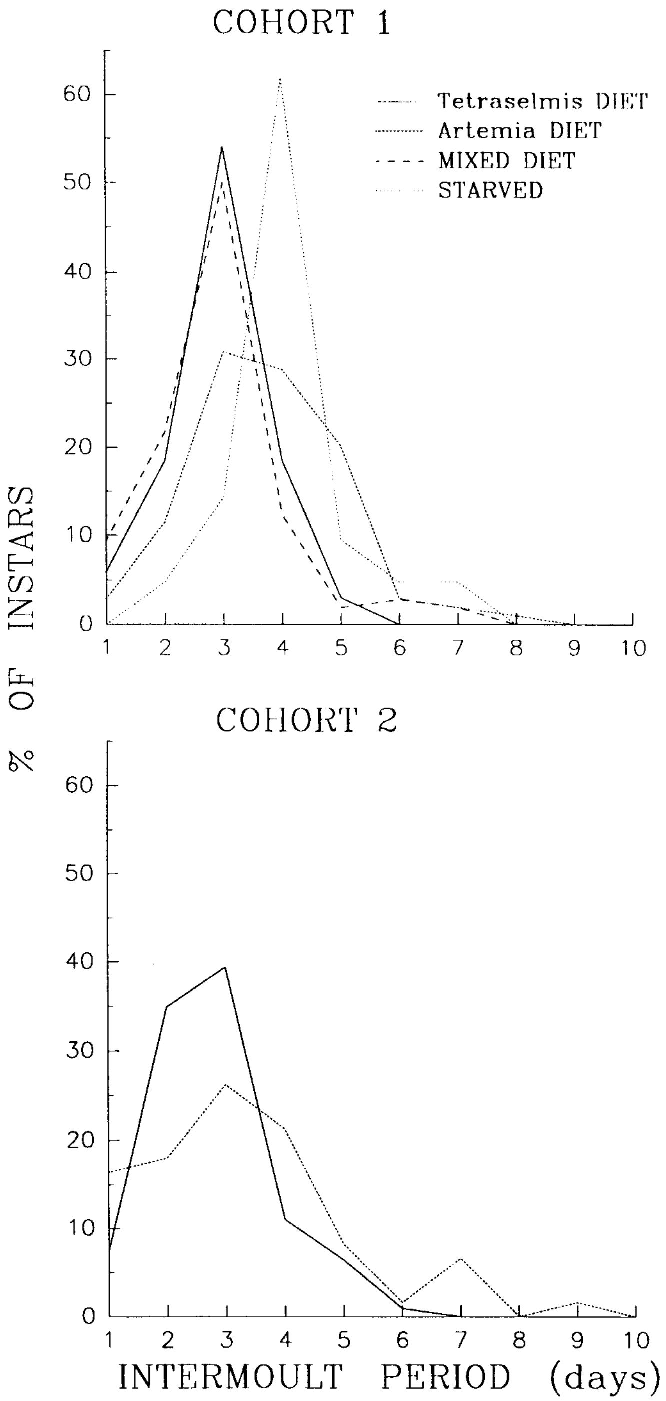

Figure 2. Relative frequency of furcilia instars having different durations in *Nyctiphanes simplex* under different feeding conditions.

the form 1 terminal telson spine (when reduction in number was complete) showed significant differences also ($F = 163.27$, $p < 0.001$), and again one homogeneous group of means for microalgal diets. *Artemia*-fed larvae, however, did not form a homogeneous group, which suggests differences between cohorts.

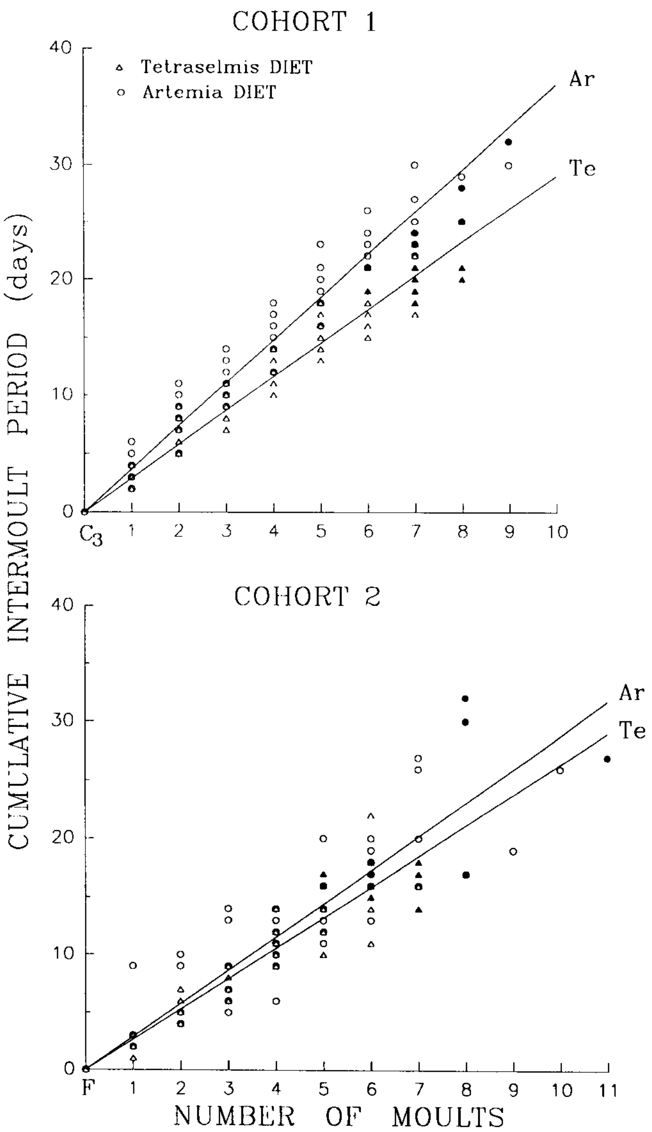

Figure 3. Cumulative intermoult period on successive number of moults for *Artemia*-fed and *Tetraselmis*-fed larvae. Mixed diet had similar values to *Tetraselmis* diet. Closed symbols indicate the appearance of juveniles. Lines are predicted values from regression analysis (Ar, *Artemia*-fed; Te, *Tetraselmis*-fed).

The increment in body length on time was not linear, suggesting an exponential decay (instantaneous growth rate). The von Bertalanffy growth curve was used to estimate growth:

$$L_t = L_{\text{inf}}[1 - e^{-K(t-t_0)}]$$

where L_t = length of animal at age t; L_{inf} = asymptotic maximum length; K = instantaneous growth rate; and t_0 = age of animal when L_t is zero. In order to eliminate the last parameter to make the curves for different diets comparable, t_0 is taken equal to zero. Therefore a constant value of 8.5 days was added to values of t in cohort 1, and of 11.5 days in

TABLE 8
Effect of Diet on Mean Body Length (mm) ± Standard Deviation of *Nyctiphanes simplex* of Cohort 1

		Diet type			
Stage	Form	Starved	*Tetraselmis*	*Artemia*	Mixed
Calyptopis 2		1.5 ± 0.1	1.6 ± 0.1	1.6 ± 0.1	1.6 ± 0.1
Calyptopis 3		1.9 ± 0.1	2.1 ± 0.1	2.0 ± 0.1	2.1 ± 0.1
Furcilia 1	0	2.3 ± 0.2	2.6 ± 0.2	2.4 ± 0.1	2.6 ± 0.1
	1′	2.5 ± 0.1	2.7 ± 0.2	2.6 ± 0.2	2.7 ± 0.1
	2′	2.6 ± 0.2	3.0	2.8	2.8 ± 0.1
	3′	2.8 ± 0.1	3.4	2.9 ± 0.1	3.0 ± 0.2
	4′	3.0 ± 0.1	3.3 ± 0.1	3.0 ± 0.2	3.4
Furcilia 2	1″2′	—	3.1 ± 0.2	2.7	—
	1″3′	2.8	3.3 ± 0.2	3.2 ± 0.1	3.3 ± 0.1
	1″4′	—	3.5	—	—
	2″1′	—	—	2.8	—
	2″2′	—	3.3	—	3.3 ± 0.3
	3″1′	—	—	2.9	3.3
	3″2′	—	3.6 ± 0.3	3.2 ± 0.1	3.5 ± 0.2
	4″	—	3.4	3.1	—
	4″1′	3.0 ± 0.2	3.9 ± 0.2	3.4 ± 0.2	3.8 ± 0.2
Furcilia 3	7 t.t.s.	—	4.3 ± 0.3	3.6 ± 0.3	4.2 ± 0.3
Furcilia 4	6 t.t.s.	—	4.4 ± 0.2	3.4 ± 0.1	4.3 ± 0.1
	5 t.t.s.	—	4.4 ± 0.1	3.8 ± 0.3	4.4 ± 0.3
Furcilia 5	4 t.t.s.	—	4.5 ± 0.1	3.9 ± 0.2	4.9 ± 0.1
	3 t.t.s.	—	4.8 ± 0.2	4.0 ± 0.3	4.6 ± 0.2
	2 t.t.s.	—	4.8 ± 0.2	4.1 ± 0.2	4.9
Furcilia 6	1 t.t.s.	—	5.0 ± 0.3	4.3 ± 0.3	5.1 ± 0.3
Juvenile 1*		—	5.4 ± 0.3	4.9 ± 0.1	5.5 ± 0.3

(′) = pair nonsetose pleopods; (″) = pair setose pleopods; (t.t.s.) = terminal telson spines.
*For *Tetraselmis* and mixed diets, measurements after day 24 (when 50% larvae had moulted to juvenile) are excluded.

TABLE 9
Effect of Diet on Mean Body Length (mm) ± Standard Deviation of *Nyctiphanes simplex* of Cohort 2

		Diet type	
Stage	Form	*Tetraselmis*	*Artemia*
Calyptopis 3		2.1 ± 0.1	2.2 ± 0.1
Furcilia 1	0	2.5 ± 0.2	2.2
	1′	2.6 ± 0.2	2.4 ± 0.2
	2′	2.7 ± 0.2	2.5 ± 0.2
	3′	2.5	2.5
	4′	3.2 ± 0.1	—
Furcilia 2	1″	—	2.7
	1″1′	—	2.7
	1″2′	3.1 ± 0.2	2.9 ± 0.1
	1″3′	3.2 ± 0.3	3.1
	2″	3.0	2.8 ± 0.1
	2″1′	—	2.8
	2″2′	3.3 ± 0.2	3.0 ± 0.2
	3″	—	2.8
	3″1′	3.3	3.1 ± 0.2
	3″2′	3.6 ± 0.2	—
	4″	3.1	—
	4″1′	3.8 ± 0.2	3.4 ± 0.2
Furcilia 3	7 t.t.s.	4.3 ± 0.3	3.8 ± 0.3
Furcilia 4	6 t.t.s.	4.2 ± 0.2	3.6
	5 t.t.s.	4.4 ± 0.2	3.8 ± 0.1
Furcilia 5	4 t.t.s.	4.2 ± 0.4	3.9
	3 t.t.s.	4.7 ± 0.1	3.8 ± 0.1
	2 t.t.s.	4.6 ± 0.3	4.1
Furcilia 6	1 t.t.s.	5.1 ± 0.3	4.0 ± 0.3
Juvenile 1*		5.2 ± 0.4	4.5 ± 0.2

(′) = pair nonsetose pleopods; (″) = pair setose pleopods; (t.t.s.) = terminal telson spines.
*For *Tetraselmis* diet, measurements after day 20 (when 50% of larvae had moulted to juvenile) are excluded.

cohort 2. These values are assumed to be the mean ages for stages C_2 and C_3 respectively, from hatching to the midpoints of C_2 and C_3, assuming that (1) the larvae had spent one day becoming metanauplii after leaving the maternal ovisacs in the form of pseudometanauplii, and (2) each successive instar of the calyptopis phase lasted 3 days. When parameters L_{inf} and K were estimated for each treatment (table 10; figure 4) there was a remarkable similarity in K for the *Tetraselmis*-fed larvae and those fed the mixed diet, indicating a reduced growth rate of 0.01 per day. The asymptotic body length predicted for these treatments is consistent with the maximum sizes occasionally found in field samples of adults (17–19 mm). In contrast, the *Artemia*-fed and starved larvae showed a drastic decay in growth rate and a small asymptotic body length, indicating that such larvae would probably die in subsequent larval or juvenile stages.

A duration of 4–5 weeks for the larval phase is predicted by von Bertalanffy's equation under optimal feeding conditions (from pseudometanauplius to the first juvenile). The *Artemia*-fed larvae could require 7–8 weeks. The number of moults produced with a constant moulting rate is 12 in the first case. For *Artemia*-fed larvae of cohort 2 the estimated number of 18 moults could be too high, indicating that a constant moulting rate should not be assumed.

TABLE 10

Parameters of von Bertalanffy's Growth Equation, and Age Estimated at End of Larval Phase (L_t = Body Length of First Juvenile Stage)

Diet	Cohort	L_{inf} (mm)	K (d^{-1})	r^2	Larval phase	
					Days	Moults*
Tetraselmis	1	18.6	0.010	0.929	34	12
Artemia	1	5.8	0.034	0.864	56	15
Mixed	1	20.2	0.009	0.953	35	12
Starved	1	3.4	0.067	0.729	—	—
Tetraselmis	2	19.6	0.010	0.890	31	12
Artemia	2	4.9	0.050	0.847	52	18

*Number of moults is calculated with moulting rates from table 7.

DISCUSSION

The influence of feeding conditions on larval growth and development of other *Nyctiphanes* euphausiids reared in the laboratory (Le Roux 1973, 1974; Pillar 1985) indicates that the environment does indeed affect ontogenesis, as suggested by the many studies of euphausiid furcilia of various genera based on field samples (Lebour 1926; Macdonald 1927; Rustad 1930; Fraser 1936; Boden 1951; Sheard 1953; Mauchline 1965; Mauchline and Fisher 1969). However, variation in pathways of pleopodal development is not exclusive to larvae subjected to poor feeding conditions, as observed here for *Nyctiphanes simplex* and previously for *N. couchii* (Le Roux 1973) and *N. capensis* (Pillar 1985). The number of larvae handled in experiments of this kind may be inadequate for extracting general conclusions as to dominant pathways, but the results still indicate that, under controlled conditions, there are several preferential routes. Furthermore, dominant pathways in *N. simplex* following different experimental starting points (cohorts C_2 and C_3) were more different than in groups distinguished by diet. Whether developmental pathways are affected by the precapture history of larvae or differing adaptations to laboratory conditions is difficult to answer.

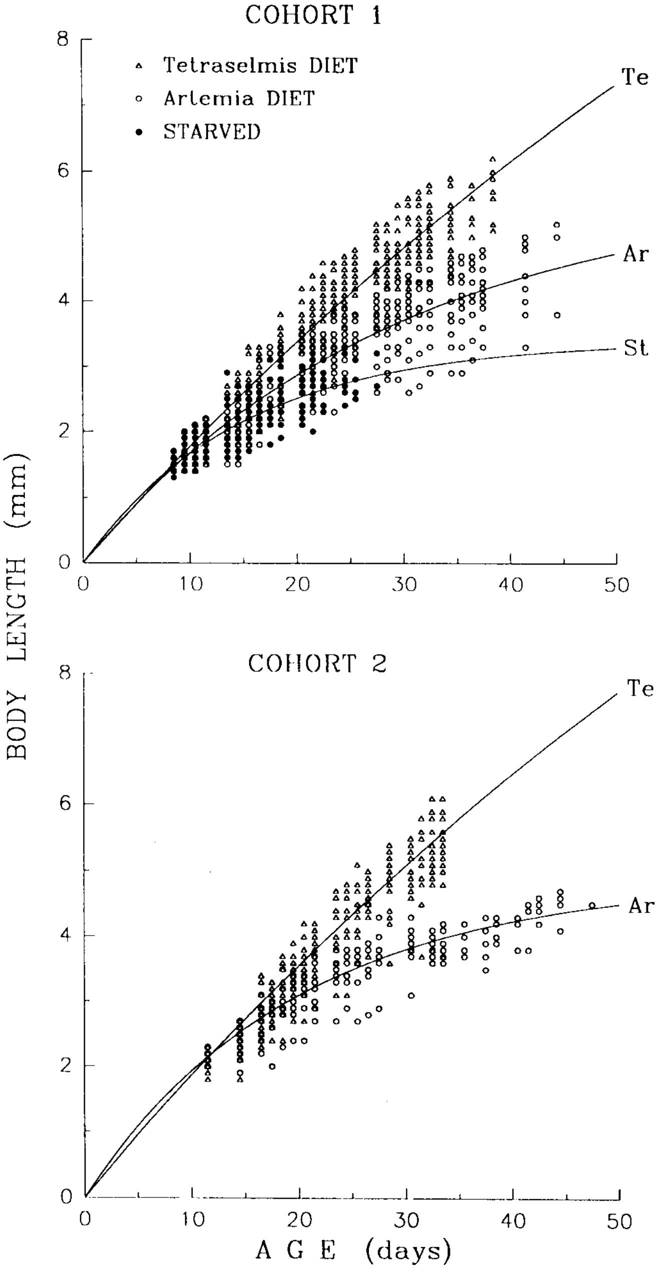

Figure 4. Body length of *Nyctiphanes simplex* larvae reared under different feeding conditions (*symbols*) and von Bertalanffy growth curves (*lines*) estimated for *Tetraselmis*-fed (Te), *Artemia*-fed (Ar), and starved (St) larvae. Mixed diet had similar values to *Tetraselmis* diet.

Feeding history was reflected more in the duration than in the route of pathways. Healthy larvae of *N. simplex* seem to require 6 or 7 instars in the furcilia phase for developing pleopods and reducing the number of terminal telson spines before moulting to juvenile. Boden (1951) described six furcilia stages, two based on pleopodal development (with variable number of forms) and four based on reduction in number of terminal telson spines, as well as segmentation of the second antennal endopod (table 11). In this study, spine reduction was usually completed in 2–3 instars; only three larvae required 4 instars (table 5). Experimental results for *N. capensis* indicated a dominant sequence of 3 instars to reduce the number of terminal telson spines; no sequences of only 2 instars were noted (Pillar 1985). In *N. couchii* (Le Roux 1973) a 2-instar sequence was more frequent. Boden (1951) used segmentation of the antennal endopod to separate furcilia stages of *N. simplex* (table 11). In the experiment reported here, segmentation occurred when larvae moulted from penultimate to last furcilia instar (68% of the larvae) — i.e., when terminal telson spines were reduced to one, independently of the precedent form. Because this anatom-

TABLE 11
Diagnostic Characters Used to Classify Furcilia Stages of Development

Furcilia stages	Boden (1951)	This study
F_1	Forms with nonsetose pleopods; 7 terminal telson spines. 2nd antennal endopod unsegmented.	Forms with nonsetose pleopods; 7 terminal telson spines.
F_2	Combination of nonsetose and setose pleopods or all setose; 7 terminal telson spines. 2nd antennal endopod unsegmented.	Combination of nonsetose and setose pleopods; 7 terminal telson spines.
F_3	Five setose pleopods; 5–6 terminal telson spines. 2nd antennal endopod unsegmented.	Five setose pleopods; 7 terminal telson spines.
F_4	Five setose pleopods; 3–4 terminal telson spines; 2nd antennal endopod unsegmented.	Five setose pleopods; 5–6 terminal telson spines.
F_5	Five setose pleopods; 3–4 terminal telson spines; 2nd antennal endopod segmented.	Five setose pleopods; 2–4 terminal telson spines.
F_6	Five setose pleopods; 1–2 terminal telson spines; 2nd antennal endopod segmented.	Five setose pleopods; 1 terminal telson spine.

ical feature does not synchronize with telson spine reduction, I have omitted it in the diagnosis of furcilia forms.

A major advance in our understanding of moulting processes is needed to explain why, under poor feeding conditions, some larvae lengthen the intermoult period and others increase the number of moults. The intermoult period observed for healthy larvae of *N. simplex* is similar to that for *N. couchii* under temperatures of 15°–16°C (Le Roux 1973). In *N. capensis* a long intermoult period (5 days) was recorded most frequently at 12°C (Pillar 1985). Longer intermoult periods in *N. couchii* and *Meganyctiphanes norvegica* were found to be induced by limited food and low temperatures (Le Roux 1973, 1974).

The condition of larvae is expressed here by body length. Size differences among specimens of a particular form seem to depend on each individual's place in its pathway of development, since significant differences between diets were more important than between cohorts. Experimental studies permit us to know exact ages and to estimate growth rates. A constant growth rate was assumed by Le Roux (1973) for *N. couchii*, with estimates of 0.10–0.13 mm/d for larvae fed abundant *Artemia*. Similar values were estimated for *N. capensis* larvae fed *Artemia* mixed with copepod nauplii or microalgae (Pillar 1985); when both species were reared with a diet of the diatom *Phaeodactylum tricornutum* mean growth was only 0.05 mm/d. Differing growth rates among species of *Nyctiphanes* fed only *Artemia* may have resulted from the amount of this food offered to the larvae. In the experiment discussed in this paper, the ration offered (60 larvae per lot per day) was always completely consumed; thus the diet's effect may have resulted from its quantity as well as quality.

Body-length growth cannot be assumed constant, and the logarithm of length regressed on moult number (Mauchline 1977) has been used to estimate growth rate in several species. Fitting of data to this model seems inadequate in some cases, including *Nyctiphanes simplex*. The von Bertalanffy equation provides a better fit. For larvae of cohort 1 fed *Tetraselmis* ($K = 0.010\ d^{-1}$; $L_{inf} = 18.6$ mm), ages predicted for average sizes of C_3, F_3, F_6, and juvenile are 12, 26, 31, and 34 days, respectively; this means pleopodal development takes 14 days (mean growth = 0.159 mm/d); reduction of terminal telson spines takes 5 days (mean growth = 0.138 mm/d); and advance to the juvenile phase takes 3 days (mean growth = 0.137 mm/d). Similar calculations for *Artemia*-fed larvae ($K = 0.034\ d^{-1}$; $L_{inf} = 5.8$ mm) result in periods of 17 days for pleopodal development, 11 days for reduction of terminal telson spines, and 16 days for advance to juvenile phase (mean growth being 0.098, 0.062, and 0.040 mm/d, respectively). Mean growth rates for *Tetraselmis*-fed larvae of *N. simplex* are higher than those recorded for furcilia stages of another California Current euphausiid species, *Nematoscelis difficilis* (0.10–0.12 mm/d reared on *Artemia* mixed with diatoms; Gopalakrishnan 1973). However, *N. difficilis* needs only 3 furcilia-phase moults to reach the juvenile form, though with somewhat longer intermoult periods.

Considering the mean length of an immature adult (males with petasma scarcely apparent and females with ovaries not showing oocytes) of *Nyctiphanes simplex* to be 7.5 mm, its age estimated from the von Bertalanffy equation with parameters $K = 0.010\ d^{-1}$ and $L_{inf} = 18.6$ mm is 52 days, indicating a short juvenile phase of only 18 days. A maximum size of 17 mm (though the most frequently observed value has been 14 mm) would require 245 days. Therefore, at most, the adult phase would last 6–7 months. One-year-old individuals should be considered exceptionally long-lived. Whether or not the decay in growth rate (K) adequately expresses the use of energy for reproduction instead of increasing body length needs to be explored. Cohort analysis of field samples of larvae, juveniles, and adults of *N. australis* from southeastern Tasmania indicated a life span of approximately 140 days for a 14-mm adult, and 240 days for a 17-mm adult (Ritz and Hosie 1982). A similar study by Gros and Cochard (1978) using only adults suggested an average of one year of life for *N. couchii*, and perhaps two years for the largest specimens. The latter period seems improbable because growth rates estimated from laboratory experiments with *N. couchii* and its congeners *N. capensis* and *N. simplex* and from field samples of *N. australis* point to a shorter life span.

CONCLUSIONS

Growth and larval development of *Nyctiphanes simplex* were followed for the first time in the laboratory. A diet of the microalga *Tetraselmis suecica* produced better growth and shorter developmental pathways than a diet of *Artemia* nauplii. According to the van Bertalanffy growth equation, the time required to reach the juvenile phase was 31–34 days with the first diet and 52–56 days with the second diet. The average life span predicted by this model is 6 or 7 months. This short life span may be an adaptation to coastal upwelling ecosystems where production of food is irregular.

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