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CALCOFI COORDINATOR George Hemingway

EDITOR Julie Olfe

SPANISH EDITOR Jesús Pineda

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**Michael Mullin
Richard Neal
Patricia Wolf**

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Part I

REPORTS, REVIEW, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE

The California Cooperative Oceanic Fisheries Investigations were begun in 1949 to answer the question, of great concern to the fishing industry and, therefore, the legislature: "Where have all the sardines gone, and what will bring them back?" The underlying question for population biologists was and is: "What are the causes of long-term, large-scale variation in population size of pelagic fish stocks?"

The labor for this research undertaking was divided between the California Department of Fish and Game, the Southwest Fisheries Science Center (NMFS/NOAA), and the Scripps Institution of Oceanography (UCSD). Each agency has contributed ships and scientific personnel to this project, so that the emerging understanding of the fishery oceanography of the California Current ecosystem is the product of dozens of principal investigators and hundreds of researchers over the decades. The knowledge gained in trying to understand what happened to one species has enlarged our understanding of the ecology and population dynamics of hundreds of species, in the waters of the Californias and throughout the world.

One of the greatest impediments to understanding change has been the lack of data on appropriate temporal and spatial scales. CalCOFI addresses that paucity of data in a number of ways. From studies of the deposition of fish scales in undisturbed marine sediments, we have begun to understand the time ranges of natural variations of pelagic fish populations, and how those variations relate to physical phenomena such as warming or cooling trends. Such studies, covering the last 2000 years, are being continued by Timothy Baumgartner of Mexico's Centro de Investigaciones Científicas y de Educación Superior de Ensenada, and Andrew Soutar of the Scripps Institution of Oceanography (SIO). Baumgartner and his student Diego Holmgren-Urba present a paper in this volume describing the population sizes of pelagic species in the Gulf of California during the past 250 years. One of their discoveries is that sardine populations seem to undergo natural fluctuations on the order of 50

100 years. Data from the Guaymas and Santa Barbara basins are being compared to other long time series, such as tree ring data. These comparisons may help explain the physical phenomena that cause biological responses in the sea.

Data collected by California Department of Fish and Game (CDFG), NMFS, and SIO personnel have shown that the Pacific sardine population in California coastal waters has increased during the past decade. Indeed, colleagues from the Pacific Biological Station at Nanaimo report that they captured sardines, ranging in age from 1 to 8 years, along the British Columbia coast from June through October 1992. These data may offer cause for optimism, but a new model, which used catch and age data from the United States and Mexico, and information from CalCOFI surveys and aerial spotters, suggests that the population has leveled off at between 100,000 and 220,000 metric tons (MT). This is relatively small when compared to the 2,000,000-MT biomass upon which the California sardine fishery was established near the turn of the century, and the estimated 5,000,000 MT in the sixth century A.D.

These data were presented at the fourth annual sardine management workshop, convened by the CDFG and involving state, federal, industrial, and Mexican federal biologists. As a result of these data, the U.S. harvest limit for 1993 was set at 22,000 MT, slightly lower than last year.

A team of federal and state scientists continued their work on a federal fishery management plan for coastal pelagic species (anchovy, sardine, Pacific mackerel, and jack mackerel) under the auspices of the Pacific Fishery Management Council. The team completed the fishery description, developed options for a license limitation program and an experimental offshore fishery, and began developing harvest strategies and definitions of overfishing. Relations between temperature and the recruitment and productivity of sardines continue to be studied. A newly developed high-speed trawl should make it possible for NMFS and CDFG to sample adult sardines and jack mackerel for stock assessment from their research vessels, and may make it practical to

use the daily egg-production method to estimate sardine biomass.

Scientists at NMFS completed new life-table models for anchovy, sardine, and Dover sole. These models yield new insights into the importance of different life stages in the recruitment process and of population growth rates. In addition, a new biomass estimation model was developed for the northern anchovy. This model is simpler than past models because it does not require age-structured information.

Researchers at NMFS continued studying the ecology of groundfish that inhabit the continental slope: Dover sole, sablefish, and long- and short-spine thornyheads. The work included field studies on recruitment processes; verification of the growth of Dover sole larvae and the determination that they live in the plankton for up to two years; initial sequencing of the mitochondrial DNA of these species for purposes of studying larval dispersion; and studies of Dover sole's physiological adaptations to the oxygen minimum zone.

Scientists from NMFS, CDFG, and Moss Landing Marine Laboratories have been investigating the distribution, abundance, age, and growth of pelagic juvenile rockfish relative to thermal fronts in Monterey Bay. Early results suggest that the juvenile fish are associated with areas of colder water.

Researchers in the NMFS climate project BURNM used immunoassay techniques to identify UV-induced damage in field-caught anchovy larvae. This work verifies earlier findings, based only on laboratory work, that atmospheric ozone levels are damaging the DNA of anchovy larvae.

Electronic and computer-facilitated data acquisition and processing continue to advance on the quarterly CalCOFI survey cruises of NOAA ship *David Starr Jordan* and the University of California ship *New Horizon*. A complete transition to a CTD rosette system for hydrographic sampling and measurement is anticipated by mid-1993.

As of this writing, warm-water phenomena are obvious in the California Current for a second consecutive year. For 20 of the past 21 months, the sea height at Scripps Pier in La Jolla has been higher than the 89-year mean sea height. The May 1993 sea height at La Jolla tied the May 1992 sea height for the highest May on record at La Jolla. In April, scientists on the quarterly CalCOFI survey cruise measured water temperatures on sections perpendicular to the California Current off Southern California, and found that waters even deeper than 50 m were anomalously warm by as much as 2°C. Pelagic red crabs (*Pleuroncodes*) have been abundant in the Southern California Bight in the first quarter of this year.

Investigators not normally associated with the CalCOFI program have joined CalCOFI survey cruises to test new techniques or collect data to supplement the customary data suite. Researchers often find that their data become more valuable when collected simultaneously with variables for which a very long (44-year) time series already exists, because it is possible to determine whether or not the conditions at the time of sampling are typical. These non-CalCOFI researchers can also reach desirable sampling sites without great cost in ship transit time, and have the help of a highly trained and competent CalCOFI technical team.

Izadore Barrett served as director of the Southwest Fisheries Science Center and as a member of the CalCOFI Committee from 1977 to 1992, when he retired from federal service. Iz was a strong supporter of CalCOFI's mission and helped the program remain current by periodically reevaluating its direction and accomplishments. Iz was instrumental, in 1987, in formalizing CalCOFI's longstanding relations with Mexican scientists into a cooperative fisheries research agreement with Mexico, called MEXUS-Pacífico. Iz served as cochair of MEXUS-Pacífico from its inception until his retirement. The Committee will miss his presence, his thoughtfulness, and his dry wit.

The Committee is pleased to announce the publication, in March of this year, of CalCOFI Atlas 31, *Distributional Atlas of Fish Larvae and Eggs in the California Current Region: Taxa with 1000 or More Total Larvae, 1951 through 1984*, by H. G. Moser, R. L. Charter, P. E. Smith, D. A. Ambrose, S. R. Charter, C. A. Meyer, E. M. Sandknop, and W. Watson. This atlas of the distributions of 110 fish taxa will be followed, in about a year, by another atlas describing the distributions of taxa with fewer than 1000 larvae collected between 1951 and 1984.

The CalCOFI Committee thanks the officers and crews of the fishing vessel *Good News*, the state of California vessel *Mako*, the NOAA ship *David Starr Jordan*, and the University of California ship *New Horizon* for their contribution to the success of the CalCOFI program. The Committee and the coordinator further thank all those who served as reviewers for this volume of *CalCOFI Reports*: Mark Abbott, Tom Barnes, Dudley Chelton, Tom Clark, Ed DeMartini, Bob Francis, John Govoni, Phillip Hastings, Dennis Hedgecock, Larry Jacobson, Tony Koslow, Nancy Lo, Ron Lynn, Alex MacCall, Rick Methot, Dick Parrish, Rick Prager, Paul Smith, Dan Ware, and Gary Winans; as well as the editor of *CalCOFI Reports*, Julie Olfe, and the Spanish-language editor, Jesús Pineda.

REVIEW OF SOME CALIFORNIA FISHERIES FOR 1992

CALIFORNIA DEPARTMENT OF FISH AND GAME
 Marine Resources Division
 411 Burgess Drive
 Menlo Park, California 90425

Total landings of fishes, crustaceans, echinoderms, and mollusks decreased 14% from 1991, marking the fourth consecutive year of lower annual landings.

Pelagic wetfish landings decreased 36% from last year's total. Pacific mackerel and squid landings fell dramatically, but Pacific sardine landings increased by 143% (table 1).

All-species groundfish landings decreased minimally, continuing a ten-year trend of diminishing catches. Landings of Dover sole, sablefish, and thornyheads rose in 1992, although most groundfish catches remained stable or declined. California halibut landings decreased moderately as the fishery shifted northward.

Despite a substantial drop in statewide landings, the sea urchin fishery remained one of California's largest and most economically valuable fisheries, with an ex-vessel value of \$29.3 million. Dungeness crab landings decreased throughout the central and northern California fishery. Total statewide all-species abalone landings were the third lowest in the history of the commercial fishery.

Swordfish landings increased substantially as El Niño conditions shifted the fishery north of San

Francisco. Fishers landed decreased tonnages of common thresher shark and shortfin mako shark into southern California ports during 1992.

Both the numbers of recreational fishers and the catch declined slightly in 1992, although southern California fishers benefited from increased availability of highly desirable, southerly species such as yellowtail, bluefin tuna, and barracuda.

PACIFIC SARDINE

In recent years, the population of Pacific sardine (*Sardinops sagax*) has expanded, and a fishery has been reestablished. The California Department of Fish and Game (CDFG) is required by law to set a quota of at least 1,000 short tons when the biomass exceeds 18,200 metric tons (MT). The quota may be increased, but only at a rate that allows further population growth. To this end, biomass estimates of the adult sardine population in 1992 were made at the third annual Pacific Sardine Resource Assessment and Management Workshop in October 1991 and were subsequently revised in July 1992. The revised assessment, using data for the entire year of 1991, was similar (339,000 MT) to the original.

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

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Pacific herring	Market squid	Total
1971	133	40,036	70	26,725	107	14,066	81,137
1972	166	61,680	48	22,814	56	9,640	94,404
1973	68	118,391	25	9,201	1,259	5,383	134,326
1974	6	73,810	60	11,362	2,348	12,901	100,486
1975	3	141,486	129	16,415	1,086	10,542	169,661
1976	24	111,503	293	19,882	2,151	9,063	142,915
1977	5	99,504	5,333	44,775	5,200	12,605	167,424
1978	4	11,253	11,193	30,755	4,401	16,869	74,476
1979	16	48,094	27,198	16,335	4,189	19,660	115,493
1980	34	42,255	29,139	20,019	7,932	15,136	114,514
1981	28	51,466	38,304	13,990	5,865	23,132	132,785
1982	129	41,385	27,916	25,984	10,106	16,023	121,543
1983	346	4,231	32,028	18,095	7,881	1,786	64,367
1984	231	2,908	41,534	10,504	3,786	555	59,518
1985	583	1,600	34,053	9,210	7,856	10,110	63,410
1986	1,145	1,879	40,616	10,898	7,502	20,935	82,975
1987	2,061	1,424	40,961	11,653	8,264	19,662	84,025
1988	3,724	1,444	42,200	10,157	8,677	36,632	102,835
1989	3,845	2,410	35,548	19,477	9,046	40,235	110,560
1990	2,770	3,156	36,716	4,874	7,978	27,989	83,483
1991	7,625	4,184	30,459	1,667	7,345	37,388	87,203
1992*	20,335	1,124	19,699	720	6,125	12,869	57,960

*Preliminary

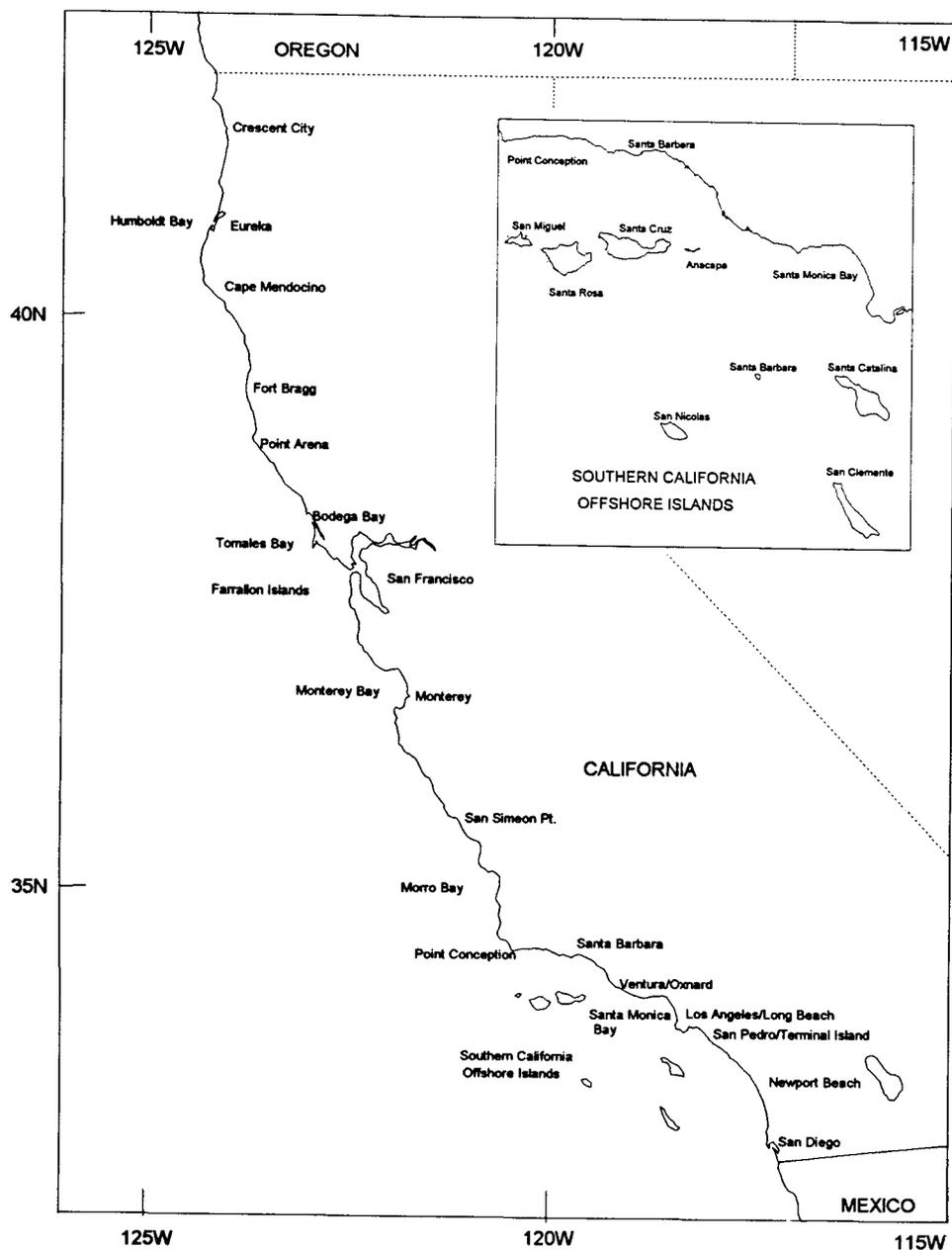


Figure 1. California ports and fishing areas.

For the 1992 season, a 10% harvest rate was continued, but projected Mexican landings of 12,220 MT were considered as the California quota was established. The CDFG allocated the 22,680-MT quota to an 18,600-MT directed fishery, a 2,720-MT reserve for incidental take, a 905-MT live bait fishery, and a 455-MT dead bait fishery. The directed-fishery allocation was divided geographically and temporally, with 6,200 MT allocated for landing at ports north of San Simeon Point after May 13, and

12,400 MT to the south commencing January 6 (figure 1).

Sportfishing vessels used many more small sardines as live bait in 1992 because of a shortage of anchovies. By midsummer the live bait catch of sardines had approached the 905-MT live bait allocation, and in October, CDFG increased the allocation to 1,810 MT by redistributing 905 MT of the incidental catch reserve. By year's end, 1,807 MT had been taken by the live bait fishery. Commercial fish-

ers landed only 65 MT of the total dead bait sardine quota of 455 MT.

Sardine landings into California and Mexico during the first half of 1992 fell below projected levels because of poor market conditions and the increased availability of squid. In early October, a major cannery in southern California reopened in response to improved market demand, and landings dramatically increased. The allocation for the southern area directed fishery was reached in late November, and CDFG applied the remaining 1,815-MT incidental catch reserve to increase the southern allocation to 13,610 MT and the northern allocation to 6,805 MT. The revised southern allocation was captured within two weeks of the adjustment, and the fishery closed on December 8 with total landings of 14,725 MT, or 108% of the allocation. After the closure, an additional 241 MT were landed incidentally to the mackerel fishery.

Almost one-half (3,255 MT) of the northern allocation of the directed quota was landed in the Monterey Bay area. Most of the sardines landed were small, probably young-of-the-year, and market demand was low.

The 1992 California landings total of 20,335 MT (90% of the statewide quota) greatly exceeded any annual figure for the last 20 years (table 1).

Sardine industry consultants introduced an integrated stock assessment model called CANSAR (catch-at-age analysis of sardines) at the fourth annual assessment workshop in October 1992. This model combines simulated population dynamics of the sardine resource with catch and age data and various measures of relative sardine abundance. The general linear model (GLM) used in 1991 includes only the indices of relative abundance. The CANSAR model indicated that the adult biomass was about 100,000 MT in 1992, and that the recovery of the sardine resource may have slowed or stopped. A reanalysis of the GLM, with the same version of the relative abundance indices that was used in CANSAR, reduced the GLM estimate to 256,000 MT, still higher than CANSAR. The apparent large change in the size of the sardine population is partly a result of the new model. Although the two models showed similar trends, the population estimates generated by CANSAR were consistently lower than those generated by the GLM.

Industry representatives, troubled by the low estimates of the CANSAR model, felt that it had not allowed for a northern expansion of the population. Warm water conditions over the past two years may have shifted the sardine population to the north, but the geographical range of the data used in the anal-

yses was largely limited to the area below Point Conception. Therefore, the models may have underestimated the true population biomass, since sampling areas did not cover the entire range of the sardine. The bycatch of sardines in the Pacific whiting trawl fishery off central Oregon from August to mid-October 1992 supports this contention.

PACIFIC MACKEREL

By January 1, 1992, 17,722 MT of Pacific mackerel (*Scomber japonicus*) had already been landed during the 1991–92 fishing season (July 1, 1991, through June 30, 1992). Current regulations authorize an open fishery when the Pacific mackerel biomass exceeds 136,080 MT (150,000 short tons), and no quota was imposed because biomass was estimated to be 173,000 MT.

Pacific mackerel landings of 6,004 MT during the first quarter of 1992 were similar to landings in the first quarter of 1991. In January, fishing effort was directed toward squid (*Loligo opalescens*) and Pacific sardines. But the fleet targeted Pacific mackerel during February and March, when the sardine market weakened and squid became less available to fishers.

Second-quarter landings totaled 3,024 MT, only 34% of the mean second-quarter landings for the previous five years, partly because a major Terminal Island cannery closed in mid-April as a result of financial problems. Some vessels that had formerly landed their fish at this cannery delivered to San Pedro fish markets instead.

The 1991–92 season ended on June 30, 1992, with a total catch of 26,275 MT of Pacific mackerel—the lowest seasonal catch since the 1979–80 season. The species composition of total statewide mackerel landings for the 1991–92 season was 71% Pacific mackerel, 4% jack mackerel (*Trachurus symmetricus*), and 25% Pacific sardine.

Although the sardine directed fishery was open most of the year, Pacific mackerel were taken when available, because mackerel brought a higher ex-vessel price (\$90–\$110 per MT) than sardines (\$70–\$100 per MT). However, warm water (El Niño) conditions displaced Pacific mackerel to the north, diminishing availability to southern California fishers. Despite this, only 2% of total Pacific mackerel landings was made in the Monterey Bay area.

The 1992–93 season opened on July 1, 1992, without quota restrictions, because total biomass was estimated to be 146,000 MT. In fishery samples, the 1990 and 1991 year classes constituted 31% and 36% of the catch. The Pacific mackerel biomass has declined over the last several years, and the midseason, revised biomass estimate in 1993 is expected to be

lower than 136,080 MT (150,000 short tons), necessitating a quota in the 1993–94 season.

Third-quarter landings totaled 8,817 MT, similar to the same period in the previous year. Landings increased from July to August as mackerel became more available, then decreased during September as market demand declined.

During October and November, Pacific mackerel landings continued their decline because fishers landed sardines instead. Total landings for the fourth quarter were 1,854 MT, a 79% decline from the same period in 1991.

By the end of the year, 10,671 MT of Pacific mackerel had been landed toward the 1992–93 season catch, a 39% decrease from the midseason landings in 1991–92 and less than half of the average midseason landings of the last five years. Pacific mackerel landings for 1992 totaled 19,699 MT, the lowest annual landings since 1978. A combination of warm water conditions (which displace fish to the north), the declining trend of the Pacific mackerel population over the last five years, and the closure of a major Terminal Island cannery contributed to low landings.

NORTHERN ANCHOVY

No landings of northern anchovy (*Engraulis mordax*) were made for reduction purposes in 1992 (table 2). The 1992 spawning biomass estimate of 220,000 MT was below the 300,000-MT minimum level required by the Anchovy Fishery Management Plan

for a reduction quota, therefore no take for reduction purposes was authorized during the 1992–93 season. This is the second consecutive year that no reduction quota has been allowed. The 1992–93 nonreduction harvest was set at 4,900 MT, with an unspecified amount for use as live bait.

A total of 1,124 MT of anchovy was landed for nonreduction use in 1992 (table 1), a 64% decrease from the previous year. A strong El Niño event persisted throughout the year and may have decreased the availability of anchovy in southern California. In addition, the early-season detection of domoic acid (a toxin that causes amnesic shellfish poisoning) in amounts above the alert level may have decreased demand for anchovy in 1992.

The anchovy live bait catch also declined; approximately 3,044 MT were caught in 1992, a 40% decrease from 1991. Anchovy were often unavailable to bait fishers off southern California, particularly in the San Diego area. As a result, bait fishers and sport anglers relied heavily on small Pacific sardines.

The anchovy reduction fishery in Mexico remained poor in 1992, primarily as a result of the reduced anchovy population.

PACIFIC HERRING

Annual statewide landings for the Pacific herring (*Clupea pallasii*) roe fishery were 6,125 MT in 1992, a decrease of 17% from the previous year (table 1). Statewide landings for the 1991–92 season (November to March) totaled 6,850 MT. The three gill net platoons in the San Francisco Bay fishery landed 4,974 MT—8% over their quota of 4,600 MT. Round haul (seine and lampara) permittees fishing in San Francisco Bay landed 1,747 MT—7% less than their 1,885-MT quota. Tomales–Bodega Bay permittees fell far short of their 182-MT quota, landing only 22 MT. The entire catch by Tomales–Bodega Bay permittees came from outer Bodega Bay; Tomales Bay remained closed to fishing because of low spawn escapement in the preceding year. Humboldt Bay permittees landed 56 MT, and Crescent City permittees landed 29 MT; each fishery exceeded its quota by 2 MT.

The price of roe herring rebounded from the low prices of the 1990–91 season to \$1,200 per short ton for gill net-caught herring with 10% roe recovery, and \$750 to \$800 per short ton for round haul-caught herring. The total ex-vessel value for statewide herring fisheries was approximately \$11 million.

Ten permittees in the San Francisco Bay herring roe-on-kelp fishery harvested 76.5 MT, which was 26.1% under their 104-MT quota.

Hydroacoustic and spawn-deposition surveys in

TABLE 2

California Anchovy Landings for Reduction (Metric Tons)

Season	Southern permit area	Northern permit area	Total
1972–73	66,404	2,135	68,539
1973–74	99,112	10,328	109,440
1974–75	99,757	6,053	105,810
1975–76	123,082	4,802	127,884
1976–77	92,058	4,544	96,602
1977–78	62,138	6,545	68,683
1978–79	47,825	1,065	48,890
1979–80	30,297	2,146	32,443
1980–81	56,415	4,298	60,713
1981–82	40,975	4,495	45,470
1982–83	4,470	1,153	5,623
1983–84	64	1,602	1,666
1984–85	71	0	71
1985–86	0	1,148	1,148
1986–87	0	38	38
1987–88	0	111	111
1988–89	0	234	234
1989–90	142	29	171
1990–91	182	856	1,038
1991–92	0	0	0
1992–93*	0	0	0

*Preliminary

San Francisco Bay detected a significant decrease in herring biomass for the second consecutive year. The spawning biomass estimate for the 1991–92 season was 42,400 MT, an 8.5% decrease from the previous season's level. Poor recruitment of two-year-old fish (1990 year class) was a major cause for the decline. Two-year-old fish typically constitute 35% of the spawning population, but made up only 3.1% of the spawning population in 1992. This biomass decline is expected to continue in the next several years, because 1991 and 1992 young-of-the-year (YOY) surveys in San Francisco Bay suggested that those year classes were also weak. While the YOY indexes for 1991 and 1992 were higher than the 1990 index, they fell considerably below the thirteen-year average for the index.

Tomales Bay and Bodega Bay herring are managed as one stock. During the 1991–92 season, the Department of Fish and Game surveyed spawn deposition in Tomales Bay, but not in Bodega Bay. The total biomass estimate for this stock was 1,125 MT, a 41.6% increase from the prior-year estimate, and the third year of increase since the dramatic plunge of 1988–89. Despite its recent resurgence, the Tomales Bay spawning population remained below the historic average of 4,500 to 5,500 MT.

The spawn deposition survey conducted in Humboldt Bay indicated that the 1991–92 biomass was 345 MT, similar to the 1990–91 estimate of 364 MT.

GROUNDFISH

California's 1992 commercial groundfish harvest was 34,478 MT, with an ex-vessel value of approximately \$28.2 million. Total 1992 landings decreased approximately 4%, or 1,285 MT, from the 1991 level, continuing a decline evident since 1982 (figure 2). Rockfishes (*Sebastes* spp.), Dover sole (*Microstomus*

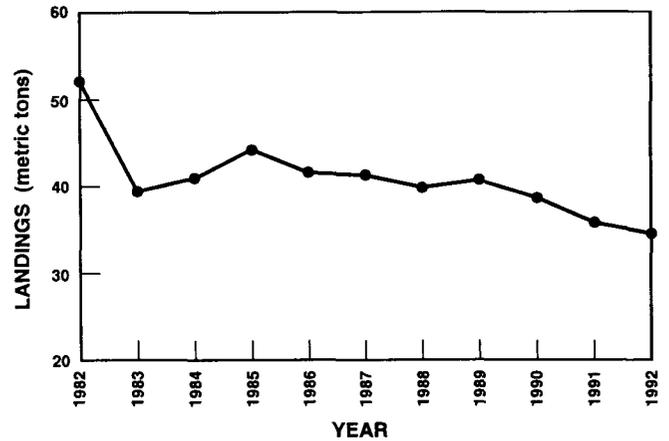


Figure 2. California groundfish landings, 1982–92.

pacificus), sablefish (*Anoplopoma fimbria*), thornyheads (*Sebastes* spp.), and Pacific whiting (*Merluccius productus*) were the principal species harvested. Dover sole, sablefish, and thornyhead landings rose in 1992, but most other groundfish landings declined (table 3).

Salmon stocks were again depressed in 1992, and the shift of effort to groundfish persisted into 1992. Incidental salmon catches by the offshore Pacific whiting fleet concerned the Pacific Fisheries Management Council (PFMC). Salmon bycatch in the spring 1992 whiting fishery for at-sea processors dropped to 0.0135 salmon per MT of whiting, compared with 0.0321 salmon per whiting MT in 1991, well below the PFMC target maximum of 0.05 salmon per MT of whiting. Bycatch of salmon by the at-sea processing sector was apparently higher in the fall, but remained below the 0.05-salmon/MT-whiting standard.

Bottom and midwater trawl landings continued to dominate total statewide landings, accounting for 75% of the total groundfish harvest in 1992, down 4% from 1991. The line portion of the catch continued its increase: from 6.6% in 1989, to 12.4% in 1990, to 14.0% in 1991, and to 17.7% in 1992. The trap and gill net components remained unchanged from 1991 at 1.2% and 5.9% of total landings.

The PFMC may establish a quota or harvest guideline for any species needing attention under the framework procedures established by Amendment 4 to the Fishery Management Plan (FMP). In 1992, guidelines were used to limit the total harvest of species or species groups, and trip or cumulative limits were used as the principal means of limiting landings in order to meet the PFMC objective of a year-round groundfish fishery.

For 1992 the PFMC set harvest guidelines, cumulative limits, and trip limits for the sablefish,

TABLE 3
 California Groundfish Landings (Metric Tons)

Species	1991	1992	Percent change
Dover sole	7,726	8,619	12
English sole	812	564	-31
Petrale sole	735	528	-28
Rex sole	621	439	-29
Other flatfish	880	520	-41
Widow rockfish	1,201	1,102	-8
Bocaccio	1,122	1,467	30
Other rockfish	8,586	7,396	-14
Thornyheads	2,864	4,328	51
Lingcod	786	604	-23
Sablefish	3,308	3,653	10
Pacific whiting	6,893	4,930	-28
Other groundfish	229	328	43
Total	35,763	34,478	-4

widow rockfish (*Sebastes entomelas*), bocaccio, thornyhead, Dover sole, and Pacific whiting fisheries. Most trawl trip limits (biweekly, weekly, and twice-weekly) in effect for 1991 were changed to cumulative vessel limits in 1992 to reduce regulation-caused discards and to reduce violations of trip limits. Cumulative two-week limits were enacted for the *Sebastes* complex (including bocaccio rockfish) and the deepwater complex (Dover sole, sablefish, and thornyheads), while a cumulative four-week limit was set for widow rockfish.

The Pacific whiting fishery in the Washington-Oregon-California (WOC) area opened on April 15. A 208,800-MT harvest guideline was apportioned 98,800 MT for processing at sea (domestic catcher/processors and motherships); 80,000 MT for processing shoreside; 30,000 MT was held in reserve for release to at-sea processing on September 1, if shoreside processors had not taken 60% (48,000 MT) of their allocation, or on October 1, if surplus to shoreside processing needs.

The at-sea processing fleet took its 98,800-MT initial allocation in a record three weeks. Because shore-based processors had taken considerably less than 48,000 MT of whiting by September 1, (approximately 32,000 MT through August 29), the 30,000-MT reserve was released for at-sea processing on September 4, 1992. An additional 24,000 MT of whiting surplus to shore-based processing needs was made available for at-sea processing on October 1, increasing the limit for at-sea processing to 152,800 MT. The fishery for the second release was closed on October 7. When the emergency-rule allocation expired on October 15, two at-sea processors reentered the fishery to use approximately 2,000 MT of their allocation that had not been taken before October 7. Both vessels left the fishery on October 21, when 152,800 MT was projected to have been taken by at-sea processors for the year. The shore-based fishery continued operating, taking close to 56,000 MT for the year. A 3,000-pound trip limit was imposed on October 31, when the 208,800-MT harvest guideline for whiting was projected to be reached.

Unlike 1991, all at-sea processing of whiting was restricted to waters north of 42° N. California's shoreside fishery landed and processed 4,930 MT, which was 1,963 MT less than the previous year. All California's shoreside whiting landings were made between the April opening and the end of June. The unavailability of whiting after June was probably related to unusually warm water (El Niño) conditions.

Within the WOC area a 50,000-pound, 2-week

cumulative limit with no more than 10,000 pounds of bocaccio allowed was in effect all year for the *Sebastes* complex fishery. California's *Sebastes* complex landings dropped from 9,708 MT in 1991 to 8,863 MT in 1992. The 1992 rockfish harvest included nearly 1,467 MT of bocaccio. The commercial bocaccio harvest combined with an estimated 200 MT from the recreational fishery amounted to 1,767 MT, considerably more than the 1,100-MT harvest guideline. However, the PFMC reviewed a new bocaccio assessment and recommended that the 1993 harvest guideline be increased to 1,540 MT. This new assessment incorporates improved estimates of historical trawl, setnet, hook and line, and recreational catches.

For the deepwater complex, the two-week cumulative limit was initially set at 55,000 pounds, of which no more than 25,000 pounds could be thornyheads and no more than 25% or 1,000 pounds per trip (whichever is greater) could be sablefish. By midyear it became clear that the thornyhead cumulative limit would have to be reduced if a year-round fishery for that species were to be ensured. Consequently the cumulative two-week limit for thornyheads was reduced to 20,000 pounds on July 29. In order to further restrict thornyhead landings, the cumulative limit was reduced to 15,000 pounds and the deepwater complex limit to 50,000 pounds on October 7.

In the WOC area, thornyhead landings of 8,606 MT were up from 1991 landings and, in spite of the reduced cumulative limit, were 1,607 MT greater than the harvest guideline. An increased market demand is responsible for the surge in activity. California landed 4,328 MT, or 50%, of the WOC thornyhead catch.

The coastwide catch of Dover sole was 16,009 MT, a decrease of 2,194 MT from 1991 landings. The decrease primarily stems from reduced demand. California 1992 landings of 8,619 MT were 54% of total WOC landings, higher than the 42% share in 1991.

In the WOC area, the 1992 widow rockfish harvest guideline of 7,000 MT was unchanged from 1991. Vessels were at first limited to 30,000 pounds per 4-week period; on August 12, a 3,000-pound trip limit was implemented. By November, however, it was evident that the harvest guideline would not be reached by the end of the year, so the 30,000-pound, 4-week cumulative limit was reinstated for the month of December. The total 1992 landed catch of 6,010 MT in the WOC area was 85% of the harvest guideline. California landings of 1,099 MT were 18% of the WOC total.

Sablefish management in the WOC area during 1992 was similar to 1991, but with greater attention to setting the level of trip limits, because of the large increase in nontrawl vessels participating in the fishery. The 1992 harvest guideline of 8,900 MT was the same as in 1991. After a tribal set-aside of 300 MT was subtracted, 8,600 MT was allocated as follows: trawl, 4,988 MT (58%) and nontrawl, 3,612 MT (42%).

The PFMC adopted a framework allowing the WOC area unrestricted non-sablefish fishery to begin on May 12, three days before the opening of the Alaska sablefish fishery. Beginning on January 1, a 500-pound daily trip limit was allowed for incidental and small directed sablefish fisheries. The trip limit was set to increase to 1,500 pounds daily beginning March 1, and would run until the opening of unrestricted fishing or until 440 MT of the nontrawl sablefish harvest guideline had been taken. By March 21, the 440-MT limit was reached, and the trip limit was reduced to 500 pounds. A much higher than anticipated level of effort remained after the 1,500-pound trip limit was reduced to 500 pounds; as a result, the trip limit was further reduced to 250 pounds on April 17. The unrestricted fishery began on May 12 and was closed on May 27, leaving 300 MT to ensure that enough sablefish remained for a 250-pound trip limit to continue through the remainder of the year.

The total catch of sablefish landed in the WOC area in 1992 was 9,273 MT — 673 MT more than the harvest guideline. Nontrawl landings of 3,851 MT were 7% greater than the nontrawl allocation, and trawl sablefish landings were 5,422 MT, about 9% greater than the trawl allocation. California accounted for 3,652 MT, or 39%, of the total WOC area catch. Of the California total, trawlers landed 2,471 MT, and nontrawl gear took 1,181 MT.

For 1993 the PFMC has adopted a 7,000-MT sablefish harvest guideline. Size and age-composition data from the fishery during 1986–91 and data from NMFS synoptic trawl and sablefish pot surveys were used in a stock synthesis model to reassess the sablefish resource in 1992.

The limited entry plan for groundfish adopted by the PFMC in 1991 was approved by the National Marine Fisheries Service in 1992 and is scheduled for implementation on January 1, 1994. The plan requires that all trawl vessels and any longline or pot vessel fishing above some minimum level have a limited entry permit. Nontrawl vessels not qualifying for a limited entry permit will still be allowed to fish in the open-access fishery but will be constrained by small trip limits.

In 1992 the PFMC examined the feasibility of individual transfer quotas (ITQs) and decided to develop an ITQ program for nontrawl sablefish. For 1993 the PFMC will continue to narrow its focus in developing the program. In the future, ITQs may be set for other gears and species. Work also continued to develop a mandatory, coastwide, onboard observer program for groundfish vessels in the WOC area.

DUNGENESS CRAB

California Dungeness crab (*Cancer magister*) landings during the 1991–92 season were 4,446 MT, a decrease of 998 MT from the previous season (ten-year average = 3,448 MT).

The northern California season opened on December 1, 1991, but a price dispute kept fishers in port. On December 7, the commercial and recreational crab fisheries off Washington were closed in response to public health concerns about domoic acid levels in crab tissue samples. This naturally occurring toxin is produced by the diatom *Pseudo-nitzschia australis*, and can cause amnesic shellfish poisoning. Oregon officials temporarily closed their season on December 11 because of confusion over public health issues created by Washington's closure. The commercial and recreational crab seasons off northern California were suspended temporarily on December 14, pending domoic acid test results.

Laboratory testing by the California Food and Drug Administration confirmed that crabs off Del Norte, Humboldt, and Mendocino counties were safe for human consumption. Safe domoic acid concentrations were also found in crabs from Oregon waters; consequently, the California and Oregon crab seasons opened simultaneously on December 22.

A price settlement of \$1.20 per pound was reached on December 26, \$0.30 per pound lower than the 1990–91 season price. Approximately 3,902 MT of crab from 400 vessels were landed at the northern California ports of Crescent City, Trinidad, Eureka, and Fort Bragg during the 1991–92 season. The port of Crescent City accounted for 2,132 MT of the season total, followed by Eureka (1,316 MT), Trinidad (408 MT), and Fort Bragg (45 MT).

The San Francisco–area Dungeness crab season opened on November 12, 1991, with an ex-vessel price of \$1.85 per pound. Crab landings decreased by 100 MT from the previous season to a seasonal total of 522 MT. Crab fishers landed 186 MT at Bodega Bay and 263 MT at ports in the San Francisco area. Monterey and Morro Bay contributed 73 MT to the season total.

In June 1992, the Tri-State Dungeness Crab Com-

mittee, comprising crab fishers, processors, and state agency advisors from Washington, Oregon, and California, agreed to a coastwide management approach if soft-shell crabs (crabs recently molted and unmarketable) were commonplace. Should the season in Washington and northern Oregon be delayed because of soft-shell crabs (about one in ten years), the committee agreed to postpone the fishery throughout the range of the soft-shell condition.

The Tri-State Committee circulated a questionnaire to crab fishers in August 1992, and learned that 69% of respondents from the three states favored limited entry. On September 22, 1992, California Assembly Bill 3189 (Hauser) enacted a moratorium on new entrants into the fishery, pending a study of the need to limit entry. Only those fishers who landed crab in California between August 5, 1982, and August 5, 1992, were eligible for an annual Dungeness crab permit. This bill was crafted in response to industry action to establish fishery eligibility cutoff dates of September 15, 1991, in Washington, and August 15, 1991, in Oregon.

The Tri-State Committee also sent letters to the governors of the three states requesting that a unified sampling program be developed to determine levels of domoic acid in Dungeness crabs before the season, as well as to coordinate reporting of test results. As a consequence, a unified monitoring plan was enacted in 1992.

SWORDFISH AND SHARKS

Swordfish (*Xiphias gladius*) landings increased to 1,061 MT in 1992, nearly 50% more than in 1991 (table 4). Most of the catch (90%) was taken in the drift gill net fishery; another 5% was landed by the harpoon fishery, which registered the first landings increase in eight years. Three vessels, using longline gear outside of the U.S. Exclusive Economic Zone

(3–200 miles offshore), accounted for the remaining landings. Eureka and Fort Bragg became the major landing areas for swordfish, as fishing shifted northward due to El Niño conditions. Approximately 70% of statewide swordfish catches were landed north of San Francisco. Ex-vessel prices ranged from \$1.50 to \$7.00 per pound.

Common thresher shark (*Alopias vulpinus*) landings in 1992 decreased to 179 MT, the lowest level in twelve years (table 4). Immature fish continued to make up most of the catch. Fishers landed thresher shark predominantly at southern California ports, at ex-vessel prices from \$0.50 to \$2.50 per pound.

Shortfin mako shark (*Isurus oxyrinchus*) landings decreased by 36% to approximately 96 MT (table 4), partly because of the California Fish and Game Commission's decision to withhold permits for the experimental drift longline fishery. In past years, drift longline gear accounted for nearly one-third of mako shark landings (recreational and drift gill net fisheries accounted for the remaining catch). Market sampling data indicate that the mean age of landed mako sharks is under two years. Approximately 75% of the mako shark tonnage was landed at southern California ports, at ex-vessel prices from \$0.30 to \$2.50 per pound.

CALIFORNIA HALIBUT

California halibut (*Paralichthys californicus*) landings in 1992 were approximately 401 MT, a decline of 15% from the 472 MT landed in 1991 (figure 3). The largest annual halibut landings are usually made in the Santa Barbara area. In 1992, however, almost 60% of the total landings were made in more northerly ports (table 5). As in 1983, which was also the second year of an El Niño event, the 1992 fishery shifted northward; the San Francisco area accounted for almost a third of all halibut landings.

TABLE 4
 Landings of Swordfish and Selected Shark Species
 (Metric Tons)

	Swordfish	Thresher shark	Shortfin mako shark
1982	762.3	1089.5	239.5
1983	1182.5	782.8	146.8
1984	2013.4	755.7	149.9
1985	2362.1	700.4	102.5
1986	1748.2	275.7	215.3
1987	1245.9	238.7	274.0
1988	1129.3	249.8	221.9
1989	1295.8	295.1	176.5
1990	850.7	209.8	262.0
1991	711.2	344.0	150.6
1992*	1061.2	179.1	96.8

*Preliminary

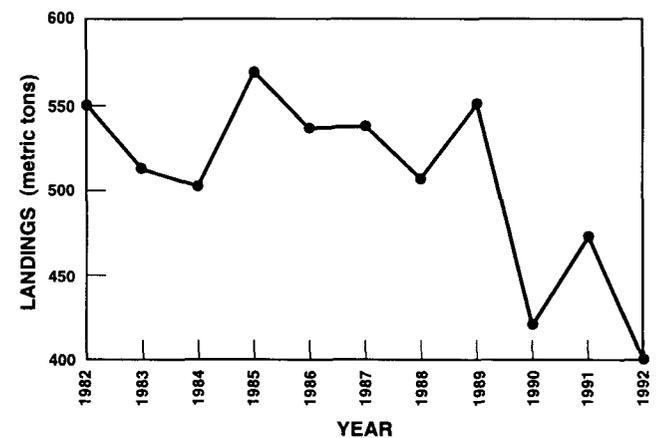


Figure 3. California landings of halibut, 1982–92.

TABLE 5
 1992 California Halibut Landings by Area

Area	Metric tons	% of total
Eureka	2.5	<1
San Francisco	153.9	38
Monterey	19.4	5
Morro Bay	62.8	16
Santa Barbara	94.1	24
Los Angeles	50.1	13
San Diego	17.1	4
Total	400.5	100

Peak landings of California halibut in 1992 were made from January through July. Trawl nets accounted for 52% of the catch, followed by entangling nets (33%), hook and line (9%), and miscellaneous and unspecified gears (6%). In the past, entangling nets (gill and trammel) harvested the largest proportion of all halibut taken. However, the Marine Resources Protection Act of 1990 (ballot initiative Proposition 132) prohibits the use of gill and trammel nets in state waters beginning on January 1, 1994, so some halibut fishers shifted to other gears in 1992.

Typically, fishers received \$2.25 to \$2.50 per pound for their catch, but live halibut commanded ex-vessel prices of \$3.00 to \$6.00 per pound.

ALBACORE

In 1992, albacore (*Thunnus alalunga*) landings in California totaled 1,257 MT. This was an increase over the last two years, but was still considerably below the 25-year average of 6,242 MT. Fleet size increased from 133 vessels in 1991 to 173 vessels in 1992, but only about half of the fleet landed at least one ton of albacore during the year. The increase in fleet size probably resulted when salmon trollers entered the fishery because albacore schools not normally within their range became available.

The Western Fishboat Owners Association and the canneries settled on a price of \$1,950 per short ton for albacore over nine pounds and \$740 per short ton for fish under nine pounds. In August the large-fish price rose briefly to \$2,100 per short ton, but returned to \$1,950 by season's end. Cannery competition for increased market shares inflated prices during the 1992 season. Albacore from northern Pacific waters commanded lower prices than fish from southern waters, to offset transshipment fees. A brief market developed for fresh albacore, and fishers received up to \$2,700 per short ton in some areas. Many fishers in Crescent City and Eureka marketed fish directly to consumers for about \$1.50 per lb.

The 1992 season began in July about 600 miles west of northern California and continued in north-

ern waters throughout much of the season. As the season progressed, vessels followed the fish eastward to the Mendocino Ridge area, and by August effort was centered 200–400 miles west of Fort Bragg. In September fishing spread north and east toward the coast from northern California to central Washington. Although fishing extended into November, weather conditions hampered fishing after late October.

During the 1992 season, vessels averaged 91 fish per day compared to 100 fish per day in 1991. Catch rates peaked at 150 fish per day in August. The mean size of landed albacore declined to 5.45 kg in 1992 from 5.68 kg in 1991.

Although the commercial catch of albacore was the highest in 4 years, it lagged far behind the 25-year average. The apparent shift in migration paths caused by warm water conditions in 1991 continued to keep most of the fishery to the north. The apparent lack of three- and four-year-old fish, which historically dominate the commercial catch, and a continued decline in the median size of the fish, may be causes for management concern. High recruitment of two-year-old fish, indicated by their dominance in the catch, may partially explain the decline in median size.

SEA URCHIN

Commercial urchin divers landed 14,655 MT of red sea urchin (*Strongylocentrotus franciscanus*) statewide in 1992—23% less than the 1991 total of 19,010 MT (figure 4). Red sea urchin landings into southern California and northern California ports declined by 20% and 28% from the previous year. Landings in the third and fourth quarters declined most steeply in both regions because an atypical statewide storm pattern disrupted fishing. Purple sea urchin (*Strongylocentrotus purpuratus*) landings in

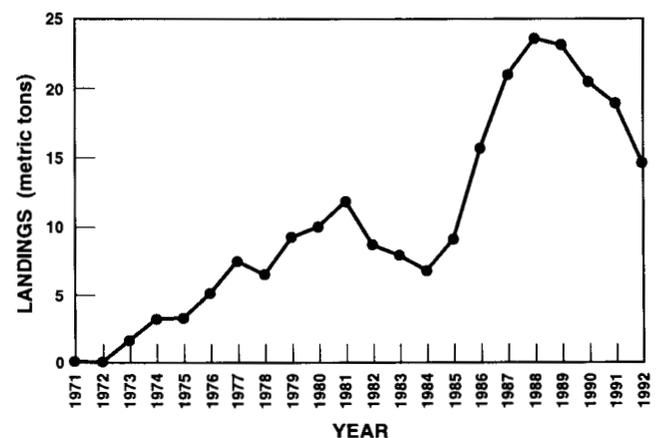


Figure 4. California landings of sea urchin, 1971–92.

1992 were 143 MT, compared to 133 MT in 1991. Average catch per unit of effort (CPUE), in urchin pounds per diving hour, continued its steady decline off northern California, to less than 136 kg (300 pounds) per hour. Southern California CPUE has remained steady at over 91 kg (200 pounds) per hour for the past several seasons.

The California Fish and Game Commission promulgated additional red sea urchin fishing restrictions in 1992 in response to a gradual shift of fishing effort from northern California to southern California waters and a further decline in the northern California sea urchin stock. The minimum size limit increased from 3.00 inches (76 mm) to 3.25 inches (83 mm) for southern California waters. A minimum size limit of 3.50 inches (89 mm) remained unchanged for northern California waters. The Commission further restricted fishing to two-day fishing weeks in July off southern California, three-day weeks in June and August, and four-day weeks in April and October for all state waters. Further regulatory changes are not anticipated for the 1993 season.

Despite the imposition of a limited entry system in 1987 to reduce effort in the fishery, numbers of standard and apprentice permits have diminished by only 9% since the 1988 season, to 625 permits.

In 1992, Department of Fish and Game scientists, using a Leslie depletion regression procedure, estimated historical red sea urchin biomass levels for the Fort Bragg area. From 1988 to 1992, fishers took 21,460 MT of sea urchin in this area of northern California. By regression of cumulative catch on annual mean CPUE, the model estimated a pre-1988 fishable biomass of 31,125 MT ($R^2 = 0.95$) along more than 20 miles of coastline in the Fort Bragg area. Using an estimated annual natural mortality rate of 7.4% (from studies in the unfished Point Cabrillo Marine Reserve near Fort Bragg), the Leslie model calculated a sustainable annual harvest for the Fort Bragg area of 725 MT beginning with the 1993 season. In 1992, approximately 1,588 MT were landed in this area.

ABALONE

Total statewide commercial abalone landings were 235 MT in 1992, an increase of 64 MT over 1991 (figure 5). The 1992 landings by species, with 1991 values in parentheses, were red abalone, 205 MT (149); black, 17 MT (12); pink, 8 MT (6); and green, 5 MT (4). Although the 1992 landings increased from the 1991 level, they are still the third lowest in the history of the fishery. Landings in southern California originated mostly from the Santa Barbara

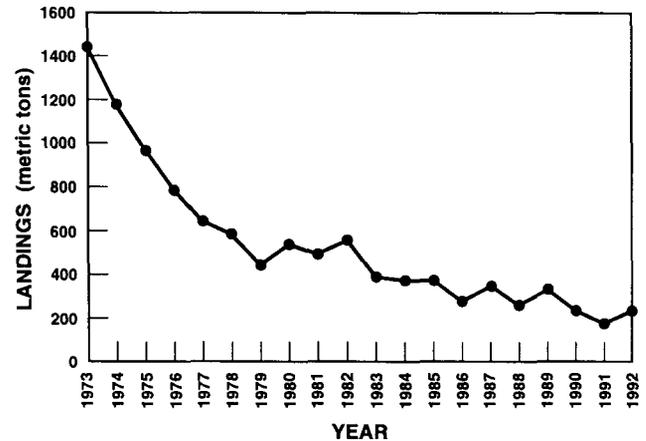


Figure 5. California landings of abalone, 1973–92.

Channel Islands; lesser quantities came from the Santa Barbara and San Diego mainland areas. Central California catches were from the Farallon Islands and the coastline of San Mateo and Santa Cruz counties. Portions of the red abalone landings in some central California ports were allegedly harvested from northern California areas that are closed to commercial harvest.

Eight species of abalones occur in California waters. All inhabit rocky bottoms, but specific distributions are generally related to ambient seawater temperatures and depth. Red (*Haliotis rufescens*), pink (*H. corrugata*), green (*H. fulgens*), and black (*H. cracherodii*) abalones support a commercial fishery in California. Stocks of all abalones increased after the near elimination of sea otters during the nineteenth century, providing a large, highly lucrative fishery with peak annual landings of over 2,270 MT in the 1950s. Landings have declined steadily to about 10% of historic levels as a result of continued harvest pressure, effort shifts, habitat destruction, and increased predation from sea otters as their range expands. In other abalone fisheries worldwide, stock depletion is commonly defined as a decline to 40% of the unfished biomass. The monetary value of abalone appears high enough to sustain fishing effort despite low abundance.

Red abalone are the largest and most desired of all abalones. They reach a maximum size of almost 12 inches, but usually are smaller than 10 inches. This species supported a large and valuable commercial fishery on the central California coast before being displaced by expansion of the sea otter range in the 1960s and 1970s. In northern and north-central California red abalone occur intertidally to depths of over 60 feet, but are found subtidally in southern California in areas where cool-water influences are consistent. North of Point Lobos in San Francisco

County, abalone harvest is restricted to recreational fishers. Most of the current total harvest occurs in southern California. Red abalone have been successfully cultured and are sold commercially at a size of 2 to 3 inches.

Pink abalone occur subtidally to 100 feet or deeper, from Point Conception into Mexico. Pink abalone were an alternative to red abalone in the southern California fishery, but stocks declined after the commercial red abalone fishery moved from central California to the Channel Islands when the sea otter's range expanded.

Green abalone range from Point Conception into Mexico. They are found in shallow subtidal areas often associated with surf grass. This species became commercially important when the pink abalone harvest declined.

Black abalone are an intertidal species ranging from Oregon into Mexico. As recently as 1990, they could be found in dense aggregations off the Channel Islands. Black abalone were not commercially fished until regulations enacted during the 1970s allowed export to Asian markets.

A limited-entry permit is required for commercial harvest of abalone; 123 permits were issued for the 1991–92 season. The target effort level is 70 or fewer permits, and until that number is reached, the permit is transferable, under specific conditions, on a two-for-one basis. Differential minimum harvest sizes exist for sport and commercial fisheries. Daily bag limits and seasonal closures are in effect for the sport fishery. Commercial regulations also include seasonal and area closures, bag limits, and gear restrictions.

In 1986, discolored, atrophied black abalone were first seen off several of the Channel Islands. These symptoms, now known as withering syndrome, eventually affected black abalone off all Channel Islands, killing up to 99% of the population. The cause of withering syndrome is still undetermined, and other species of abalones may be affected as well. Most populations of black abalone north of Point Conception were apparently unaffected. Withering syndrome has reduced black abalone landings from 309,000 pounds in 1987 to the current 37,000 pounds. A fishery closure for this species was under consideration in 1993 to protect remaining stocks.

CALIFORNIA SPINY LOBSTER

California spiny lobster (*Panulirus interruptus*) range from Monterey to Magdalena Bay, Baja California, and include a small population along the northwestern shore of the Gulf of California. Most of the population is found between Point Concep-

tion and Magdalena Bay. The present distribution suggests a historical range centered farther to the south, encompassing all of Baja California. California spiny lobster larvae spend six to nine months in the plankton and have been collected 530 km from shore. Recruitment of spiny lobster to California waters, from a population center south of the U.S.-Mexico border, is probably patchy, especially at the northern end of the range. Scientists have estimated only 415 square miles of adult lobster habitat along the California coast. Only a small fraction of this habitat contains surfgrass beds—the primary area of larval settlement. Anomalous ocean currents, such as those in El Niño events, could cause poor and sporadic recruitment, because larvae may never reach typical areas of settlement.

A total of 268 MT was landed during the 1991–92 commercial spiny lobster season in southern California (first Wednesday in October to first Wednesday after March 15). This total was 19% less than the 1990–91 total of 331 MT (figure 6).

Landings have generally increased since the paltry 1974–75 season value of 69 MT to a peak of 332 MT during the 1989–90 season. Lobster landings in southern California reached a historic high of 499 MT during the 1949–50 season. From 1989 to 1992, lobster landings have greatly exceeded the past 18-year average of 212 MT.

Landings typically peak during the first month of the season, suggesting heavy fishing pressure on a limited resource. Since 1970, October landings have constituted 40% of seasonal landings; November landings, 22%; December, 15%; January, 11%; February, 8%; and March, 4%.

Since 1965, when the Department instituted a commercial lobster trap permit, the number of permittees has varied from a low of 180 in the 1970–71 season to 614 in 1968–69. The number of permittees

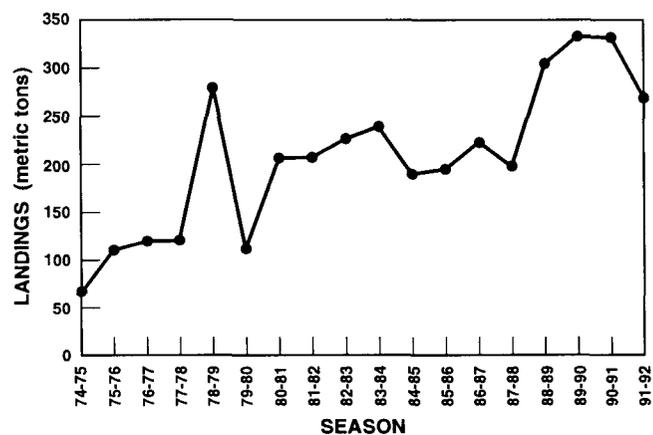


Figure 6. California landings of spiny lobster, 1974–92.

has been relatively stable over the past decade (average = 369).

From 1952 to 1970, the seasonal ex-vessel value of the commercial lobster fishery remained relatively stable, varying from \$250,000 to \$500,000. Since that time, however, the value has steadily increased, and in 1991-92 reached approximately \$4 million. The ex-vessel price in 1992 was \$6.60 per pound. Live shipments to markets in Asia have created increased demand and higher prices for California spiny lobsters.

SALMON

In 1992, California commercial salmon fishers landed slightly over 728 MT of chinook salmon (*Oncorhynchus tshawytscha*) and approximately 4.6 MT of coho salmon (*Oncorhynchus kisutch*) for an estimated 19,800 days fished. California recreational anglers caught 72,100 chinook salmon and 11,600 coho salmon on 123,600 trips (table 6).

Both commercial and recreational ocean salmon landings reflected the disastrous impact of six years of drought. Very restrictive regulations were therefore necessary to meet the annual escapement goals

(numbers of salmon returning for in-river spawning) for the Klamath and Sacramento fall chinook stocks, which constitute most of California's ocean salmon landings. The annual minimum escapement goal for Klamath River fall chinook was 35,000 natural spawners; the minimum goal for Sacramento River fall chinook was 122,000 adult fish.

The commercial fishery north of Point Arena was closed in 1992. South of Point Arena, fishing for chinook was permitted on an intermittent basis from May 1 through September 30 under quota restrictions above Point San Pedro in San Mateo County. No quota restrictions were imposed for the fisheries south of Point San Pedro. Coho fishing was allowed south of Cascade Head in Oregon on June 1 under a catch ceiling, which was reached on August 7.

Ex-vessel prices for salmon, which are landed in eviscerated, head-on form, were \$2.73 per pound for chinook and \$1.66 per pound for coho, for total ex-vessel values of \$4.4 million for chinook and \$17,000 for coho.

The recreational salmon fishery, like the commercial fishery, operated under catch quotas from the California-Oregon border to Point San Pedro; some of these quotas were very restrictive. Recreational anglers were not subject to quotas in waters south of Point San Pedro. The length of the fishing season varied in different parts of the state; the season opened as early as February 15 and closed as late as November 15.

LIVE-FISH FISHERY

The live-fish fishery has grown rapidly in California. Statewide landings for live fish in 1992 were estimated to be approximately 335 MT (table 7). This fishery began about five years ago to supply the California Asian community's demand for live fish. Many Asian restaurants allow patrons to select an entree from aquaria before cooking. The most popular species are those that can withstand the rigor of capture and transportation and are bright red in color. Thus the most important species are various nearshore rockfishes (*Sebastes* spp.), California sheephead (*Semicossyphus pulcher*), California

TABLE 6
 Commercial Landings of Chinook and Coho Salmon,
 1980-92 (Metric Tons)

Year	Chinook	Coho
1980	2,593	137
1981	2,511	217
1982	3,380	250
1983	973	121
1984	1,189	158
1985	2,050	36
1986	3,356	91
1987	4,105	111
1988	6,548	145
1989	2,491	105
1990	1,870	142
1991	1,469	208
1992	728	5

Recreational Landings of Chinook and Coho Salmon,
 1980-92 in Numbers of Fish × 1,000

Year	Chinook	Coho
1980	85.2	21.2
1981	84.0	10.6
1982	138.7	26.7
1983	63.8	27.3
1984	87.8	19.0
1985	171.1	15.8
1986	141.6	18.7
1987	192.5	47.3
1988	171.4	34.7
1989	186.6	49.6
1990	139.8	51.6
1991	80.8	69.3
1992	72.1	11.6

TABLE 7
 Preliminary 1992 Landings of Live Fish (Metric Tons)

	Monterey northward	South of Monterey
All species	139.5	195.9
All rockfishes	134.0	109.0
Red and gopher rockfishes	71.9	14.0
California sheephead	0	74.8

scorpionfish (*Scorpaena guttata*), lingcod (*Ophiodon elongatus*), and cabezon (*Scorpaenichthys marmoratus*). The fish are caught year-round, but especially in summer. The preferred weight range for live fish is 1-2 pounds, which serve well for a single entree. Finfishes brought aboard a vessel are quickly stowed in live wells. At the dock, fish are offloaded directly into trucks equipped with tanks and are delivered to brokers or restaurants. Statewide ex-vessel prices ranged from \$1.00 to \$6.00 per pound, substantially more than the \$0.40 to \$1.00 per pound for dead fish.

The primary fishing gears employed in this fishery are traps and various hook-and-line gears, including rod-and-reel with multiple-hook gangions, set lines, and vertical longlines. Live-fish traps resemble modified lobster traps, with double compartments and two entrance funnels on either side. Preferred baits are whole or freshly crushed rock and spider crabs, mussels, and squid. Gill nets and trawls have also been used for flatfish, primarily California halibut (*Paralichthys californicus*).

The fishery from Monterey northward employs line gear, primarily vertical longlines, for rockfish and lingcod along nearshore rocky reefs and offshore banks. The San Francisco and Monterey areas are the most active fishing ports; there is little activity in the Crescent City, Eureka, and Bodega Bay areas. The principal target rockfish species include canary (*Sebastes pinniger*), vermilion (*S. miniatus*), yelloweye (*S. ruberrimus*), gopher (*S. carnatus*), brown (*S. auriculatus*), china (*S. nebulosus*), copper (*S. caurinus*), and quillback (*S. maliger*).

The live-fish fishery to the south of Monterey uses both hook-and-line and trap gears. Trap use is moderate from Morro Bay to Ventura and increases from Los Angeles to San Diego. Greatest fishing activity takes place in the Santa Barbara area, followed by Los Angeles. Target species include California sheephead; California scorpionfish; cabezon; and treefish (*S. serriceps*), kelp (*S. atrovirens*), brown, grass (*S. rastrelliger*), and gopher rockfishes.

Monitoring and management of this evolving fishery have been a pronounced challenge. Accurate catch accounting is hampered by inconsistent or inaccurate species identification, the rapid removal of fish from landing sites, and the lack of a live-fish designation on state landing receipts. The mobile nature of both the landing and marketing has hampered biological sampling. The Department of Fish and Game has recently changed sampling protocol and the landing receipt system to respond to this challenge.

The bycatch of juvenile fish and nontarget species, and additional fishing mortality on slow-growing,

TABLE 8
 1992 Commercial Passenger Fishing Vessel Catch

Species/species group	Thousands of fish	Rank
Rockfishes	2,008	1
Kelp bass	458	2
Barred sand bass	361	3
Pacific mackerel	305	4
Barracuda	247	5
Bonito	114	6
Sculpin	76	7
Salmon	43	8
Lingcod	43	9
Halfmoon	42	10
Ocean whitefish	39	11
Yellowtail	39	12
California sheephead	25	13
Jack mackerel	17	14
Bluefin tuna	8	15
Flatfish (misc.)	6	16
Striped bass	5	17
Cabezon	5	18
Croaker	5	19
California halibut	4	20
All others	164	—
Total	4,016	—

long-lived rockfishes have aroused considerable concern among Department scientists.

RECREATIONAL FISHERY

California's large, diverse marine recreational fishery includes skiff, beach-and-bank, pier, and commercial passenger fishing vessel (CPFV) modes. The CPFV fleet accounts for a substantial proportion of California's recreational landings and is the subject of this summary (table 8). In southern California, traditional CPFV targets include pelagic species such as albacore (*Thunnus alalunga*), Pacific bonito (*Sarda chiliensis*), yellowtail (*Seriola lalandei*), California barracuda (*Sphyrnaea argentea*), yellowfin tuna (*Thunnus albacares*), bluefin tuna (*Thunnus thynnus*), Pacific mackerel (*Scomber japonicus*), rockfishes (*Sebastes* spp.), barred sand bass (*Paralabrax nebulifer*), and kelp bass (*Paralabrax clathratus*). In central and northern California, CPFVs target salmon (*Oncorhynchus* spp.), striped bass (*Morone saxatilis*), rockfishes (*Sebastes* spp.), lingcod (*Ophiodon elongatus*), and white sturgeon (*Acipenser transmontanus*).

CPFV catches were affected by above-normal sea-surface temperatures (El Niño) and drought conditions during 1992. Warm waters displaced subtropical species to the north, and CPFV operators south of Point Conception benefited. Fishing for yellowtail, bluefin tuna, yellowfin tuna, dolphinfish (*Coryphaena hippurus*), and barracuda increased from 1991 values. Operators from northern California were adversely affected by drought conditions. The 1992

salmon catch, in an already declining trend, was the poorest since 1961.

A total of 629,564 CPFV anglers landed 4.02 million fish in 1992 (table 8). Angler numbers declined by 4.3% from last year, and landings declined by 5.0%. Landings of only two of the top ten species increased in 1992: kelp bass (up 42%) and California barracuda (up 39%). Species with lower landings were Pacific bonito (down 2%), rockfishes (down 3%), lingcod (down 14%), barred sand bass (down 27%), sculpin (*Scorpaena guttata*) (down 57%), Pacific mackerel (down 30%), salmon (down 19%), and halfmoon (*Medialuna californiensis*) (down 55%).

Sturgeon (*Acipenser* spp.; down 72%) and sablefish (*Anoplopoma fimbria*; down 97%) showed the most dramatic declines in CPFV landings.

Contributors:

<i>K. Barsky, California halibut</i>	<i>E. Konno, Pacific mackerel</i>
<i>D. Busatto, recreational</i>	<i>L. Laughlin, swordfish/shark</i>
<i>R. Dixon, salmon</i>	<i>K. McKee, live fish</i>
<i>T. Foreman, sardine</i>	<i>R. Rodriguez, albacore</i>
<i>P. Haaker, abalone</i>	<i>C. Ryan, herring</i>
<i>S. Harris, lobster</i>	<i>D. Thomas, groundfish</i>
<i>F. Henry, editor</i>	<i>G. Walls, anchovy</i>
<i>P. Kalvass, sea urchin</i>	<i>R. Warner, crab</i>

PRELIMINARY OBSERVATIONS OF THE 1991-1992 EL NIÑO IN THE CALIFORNIA CURRENT

THOMAS L. HAYWARD

Marine Life Research Group
Scripps Institution of Oceanography
University of California, San Diego
9500 Gilman Drive
La Jolla, California 92093-0227

ABSTRACT

The successful prediction that an ENSO (El Niño Southern Oscillation) event would occur in the equatorial Pacific during 1991, and the timely and widespread distribution of coastal temperature and sea-level data have increased public interest in understanding how El Niño affects the California Current. The effects of El Niño were apparent in the California Current during late 1991 and early 1992. Sea-surface temperatures (SST) and sea level were elevated, and there was a strong poleward counter-current along the coast. Maximum sea-level anomalies at La Jolla were similar to values observed during the 1982-83 El Niño. Chlorophyll and primary production were low during the period of elevated sea level. The 1991-92 event was relatively short, with elevated sea level lasting about 8 months, and it appeared to end abruptly. There was a rapid change in structure in April-May 1992. Sea level (at least at La Jolla) rapidly decreased; the strong southward flow of the California Current returned; and chlorophyll and primary production increased. This appeared to mark the decline of El Niño. However, SST remained anomalously high over much of the California Current throughout 1992. Observation of the change in structure associated with El Niño may yield insights into the physical processes that enrich this system and the ways in which the system may respond to global change. (A note added in proof indicates that El Niño conditions were again present in the California Current in late 1992 and early 1993, and that it was premature to describe the change in structure which took place in April-May 1992 as the decline of El Niño.)

RESUMEN

El interés público por entender como los eventos tipo "El Niño" afectan a la corriente de California aumentó debido al éxito de la predicción que un evento "El Niño-La Oscilación del Sur" ocurriría en el Pacífico ecuatorial en 1991, y a la ocurrencia oportuna y amplia distribución geográfica de la

temperatura y nivel del mar. Los efectos de El Niño se notaron a finales de 1991 y principios de 1992. Los valores de temperatura superficial y nivel del mar fueron elevados, y hubo una fuerte corriente paralela a la costa hacia el polo. Las máximas anomalías del nivel del mar en La Jolla tuvieron valores similares a las de El Niño 1982-83. Los valores de clorofila y producción primaria fueron bajos durante el período de nivel del mar alto. El evento de 1991-92, con nivel del mar alto durante 8 meses, fué relativamente corto y al parecer finalizó abruptamente. Hubo un cambio rápido de la estructura en Abril-Mayo de 1992. El nivel del mar bajó rápidamente (por lo menos en La Jolla); de nuevo, hubo un flujo intenso de la corriente de California hacia el norte, y además, hubo un incremento de clorofila y producción primaria. Esto parecía haber marcado el final de El Niño. Sin embargo, en una gran porción de la corriente de California, las anomalías de temperatura superficial permanecieron altas durante 1992. Observaciones sobre el cambio de estructura asociado con El Niño podrían ayudar a vislumbrar los procesos físicos que enriquecen el sistema y la manera en que éste pudiera responder al cambio global. (Una nota añadida en capilla indica que las condiciones El Niño se habían presentado de nuevo a finales de 1992 y principios de 1993, y que fué prematuro haber descrito el cambio de estructura que ocurrió en Abril-Mayo 1993 como el fin de El Niño.)

INTRODUCTION

There is considerable public interest in understanding the effects of El Niño in the California Current because of recent successful predictions of the 1991-92 equatorial ENSO event (e.g., on computer bulletin boards); widespread distribution of coastal temperature and sea-level data (e.g., the CoastWatch Program); and hopes that the onset of El Niño would signal the end of drought in California. El Niño events can represent large perturbations in the environmental structure of the California Current (Chelton et al. 1982; Simpson 1983; McGowan 1984).

Although individual events differ, several structural aspects appear characteristic of El Niño in the California Current. Sea-surface temperature (SST) is typically elevated over a broad area (Simpson 1983, 1992). However, not all "warm events" in the California Current are associated with ENSO events (e.g., Fiedler et al. 1986). SST anomalies are associated with a deepening of the mixed layer and thermocline. Sea level, as measured from coastal tide gages (Lyles et al. 1988; Roemmich 1992), rises during El Niño; this elevation is associated, in turn, with a strong poleward countercurrent in the coastal zone (Lynn 1983; Huyer and Smith 1985). Range extensions of, especially, southern warm-water species are observed (Brinton and Reid 1986; Pearcy and Schoener 1987), presumably due to a combination of advection and a changed habitat structure. The deeper thermocline is also reflected in a deeper nutricline (McGowan 1984), apparently reducing the nutrient supply to the euphotic zone. Lower primary production and lower phytoplankton and macrozooplankton biomass values are observed (Chelton et al. 1982; Fiedler 1984; McGowan 1984). The biomass and production of the upper trophic levels may also be affected, and abundance both declines and increases (Stewart et al. 1984; Fiedler et al. 1986).

This report presents preliminary observations of the effects of the 1991-92 El Niño in the California Current and compares these effects to patterns observed during prior events.

METHODS

Time series of data collected at the Scripps Institution of Oceanography (SIO) pier, and plots of property distributions from eight CalCOFI survey cruises conducted during 1991 and 1992 are presented. The sampling plan, analytical methods, and raw data are listed in the data reports of individual cruises (Scripps Institution of Oceanography 1991, 1992a, 1992b). Primary production data are presented in units of $\text{mg C m}^{-2} \text{ half-day}^{-1}$ to allow comparison with data collected by similar methods in the central North Pacific. Cruise mean values of vertically integrated chlorophyll, vertically integrated primary production, and macrozooplankton biomass were calculated as the average of all measurements made on a cruise. There were typically about 75 stations per cruise for chlorophyll and macrozooplankton, and about 12 stations for primary production. Pattern in the seasonally corrected anomalies from long-term mean distributions (e.g., 1916-91 for SIO pier temperature or 1950-92 for

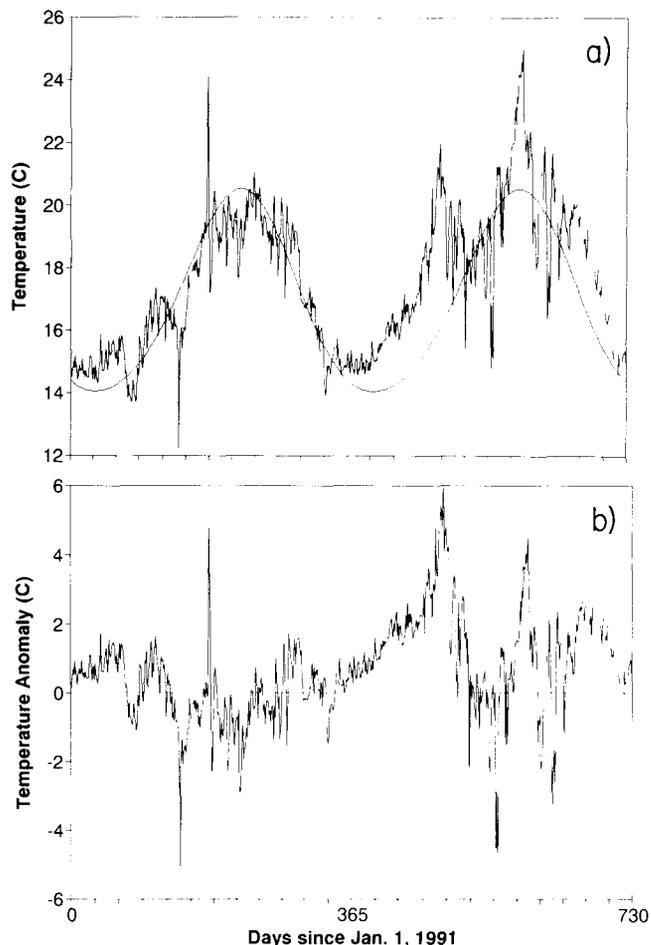


Figure 1. Sea-surface temperature and long-term (1916-91) harmonic mean temperature (a), and temperature anomalies (b) at the SIO pier for 1991 and 1992.

CalCOFI hydrographic data) are shown for several properties.

RESULTS

Extensive regions of positive SST anomalies are commonly considered to be indicators of El Niño. SST at the SIO pier was near the long-term mean throughout 1991 (figure 1). Temperature anomalies at the SIO pier began to increase steadily in January 1992, and they reached a maximum of over 4°C in April. The SST anomalies decreased rapidly in early May; June and July had nearly normal temperatures. Anomalously high temperatures were again measured at the SIO pier in the fall and winter of 1992. Large-scale SST maps, distributed by the Coast-Watch Program, showed anomalously high SST values throughout the California Current for most of 1992 (figure 2). These large-scale warm anomalies persisted until the end of 1992.

Sea-level (tide-gage) data are collected at several stations along the California coast. There has been a

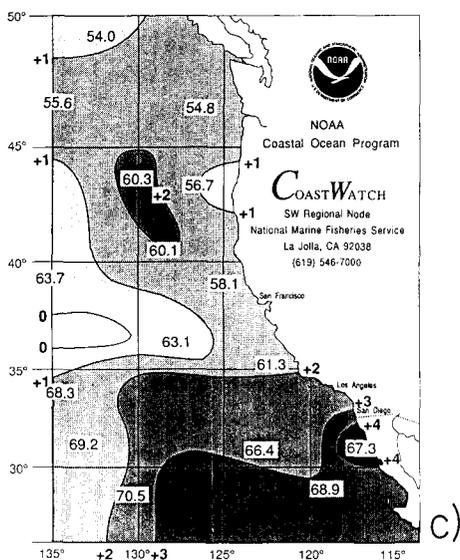
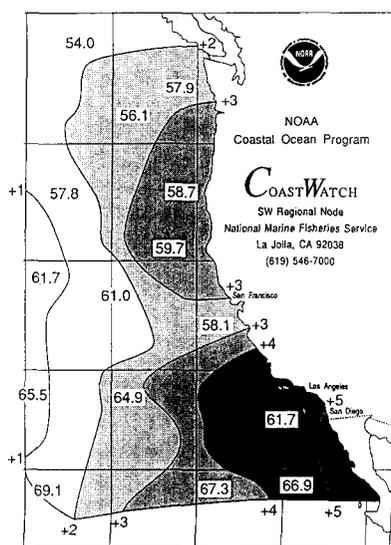
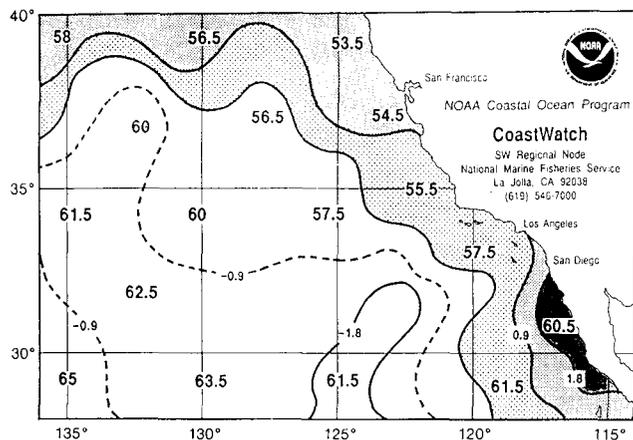


Figure 2. SST (°F) and anomaly field for the California Current during (a) January, (b) June, and (c) November 1992 (distributed by the CoastWatch Program). Note that the contour intervals differ between panels.

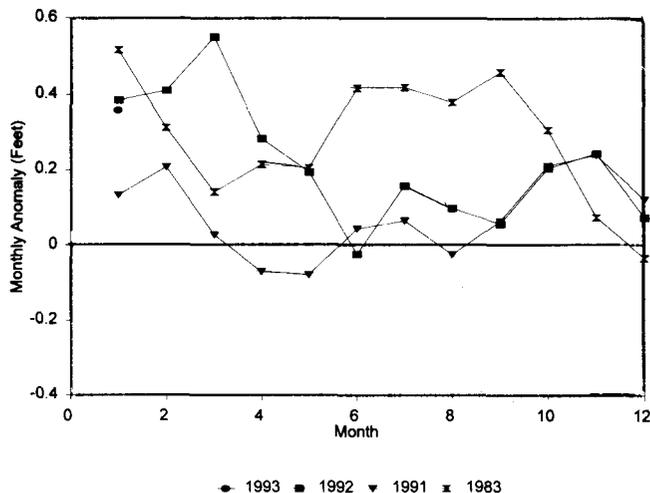


Figure 3. Monthly sea-level anomalies for La Jolla for 1983, 1991, 1992, and January 1993. The anomalies have been corrected for the secular rise in sea level.

secular increase in sea level at La Jolla of about 2.5 mm per year over the last 65 years (Roemmich 1992), and calculations of monthly anomalies from the long-term mean have been corrected for this. Corrected sea level at La Jolla (SIO pier) began to show positive anomalies starting in September 1991 (figure 3). High values persisted until March 1992, when sea level began to decline rapidly. Sea level was near normal from June through September, but anomalously high again in October, November, and December 1992. The maximum sea-level anomalies during 1992 were similar in magnitude to those observed during the 1982-83 El Niño (about 12-18 cm). However, the 1991-92 El Niño event, at least as defined in terms of sea-level anomalies, was much shorter than the 1982-83 event (8 months versus 14 months).

Data from CalCOFI cruises are used to examine pattern in circulation, vertical distributions, and biological structure. The change in structure associated with the onset of El Niño is not well resolved because no CalCOFI cruises were scheduled between March and August 1991, the period immediately preceding the rise in sea level. There was a strong poleward countercurrent in the coastal region and equatorward flow offshore during CalCOFI cruises 9108, 9110, and 9202 (figures 4 and 5). Comparison of the 9202 dynamic height map with the long-term mean dynamic height field (figure 5) shows that the anomalies are greatest in the coastal region and that the change in pattern from the long-term mean represents an increase in the strength and spatial extent of the coastal countercurrent. Poleward flow in the coastal region of northern California was also observed during March 1992 on the

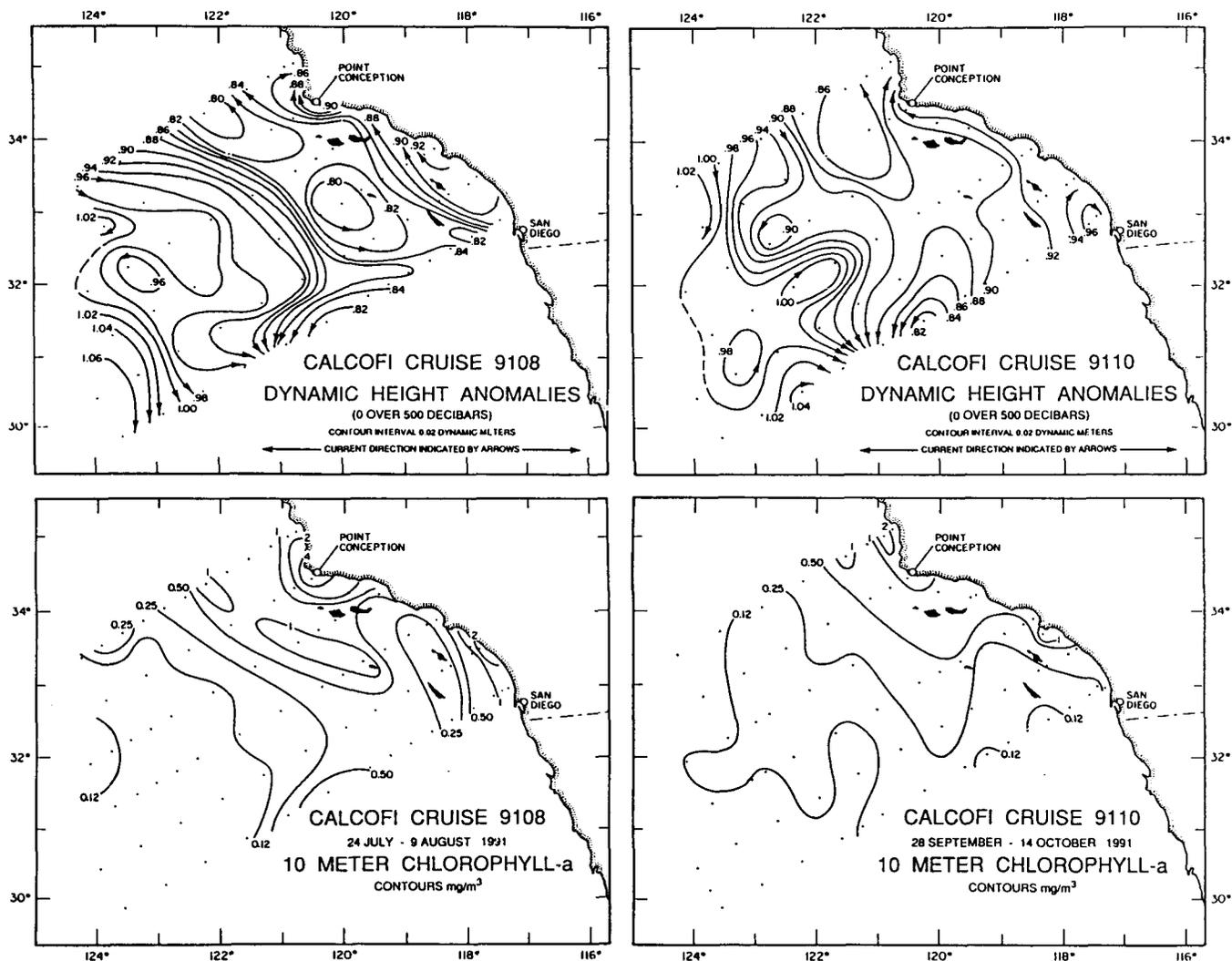


Figure 4. Spatial maps of dynamic height anomaly (0 over 500 db) and surface chlorophyll for CalCOFI cruises 9108 and 9110. The dynamic height anomaly indicates the total geostrophic flow in the upper 500 m, not the seasonally corrected anomaly from the long-term mean. (Figures from Scripps Institution of Oceanography, 1992a.)

PreFORAGE cruise (9203, unpublished observations). This coastal countercurrent is characteristic of El Niño (Lynn 1983; Huyer and Smith 1985). Cruise 9108 took place while sea level was beginning to rise at La Jolla, and 9110 and 9202 while sea level was high. Data from the 9204 CalCOFI cruise, which coincided with the drop in sea level, showed that the system had also returned to a more typical circulation pattern, with strong equatorward flow of low-salinity water in the coastal region. This circulation pattern was also evident on cruises 9207 and 9210.

Sections made along line 90 from CalCOFI cruises 9202 and 9204 show the change in vertical structure associated with El Niño and its decline in the southern California region. Cruise 9202 took place while SST and sea level were high, and there

was anomalous poleward flow. There was only slight shoaling of the pycnocline and nutricline in the coastal region on this cruise, and chlorophyll was relatively low (figures 6 and 7). On cruise 9204 the pycnocline sloped more strongly, and the nutricline was about 25 m shallower in the coastal region. Shoaling of the pycnocline and nutricline was associated with the return of southerly flow, and coincided with much higher chlorophyll values ($>4 \mu\text{g chl l}^{-1}$) in the coastal region. Temperature anomaly sections from both cruises showed that the maximum anomalies occurred at depths that would normally correspond to the upper thermocline, as was the case during the 1982-83 El Niño (Simpson 1983, 1992). However, in contrast to the 1982-83 event, the salinity sections did not show large anomalies in the coastal region (data not shown).

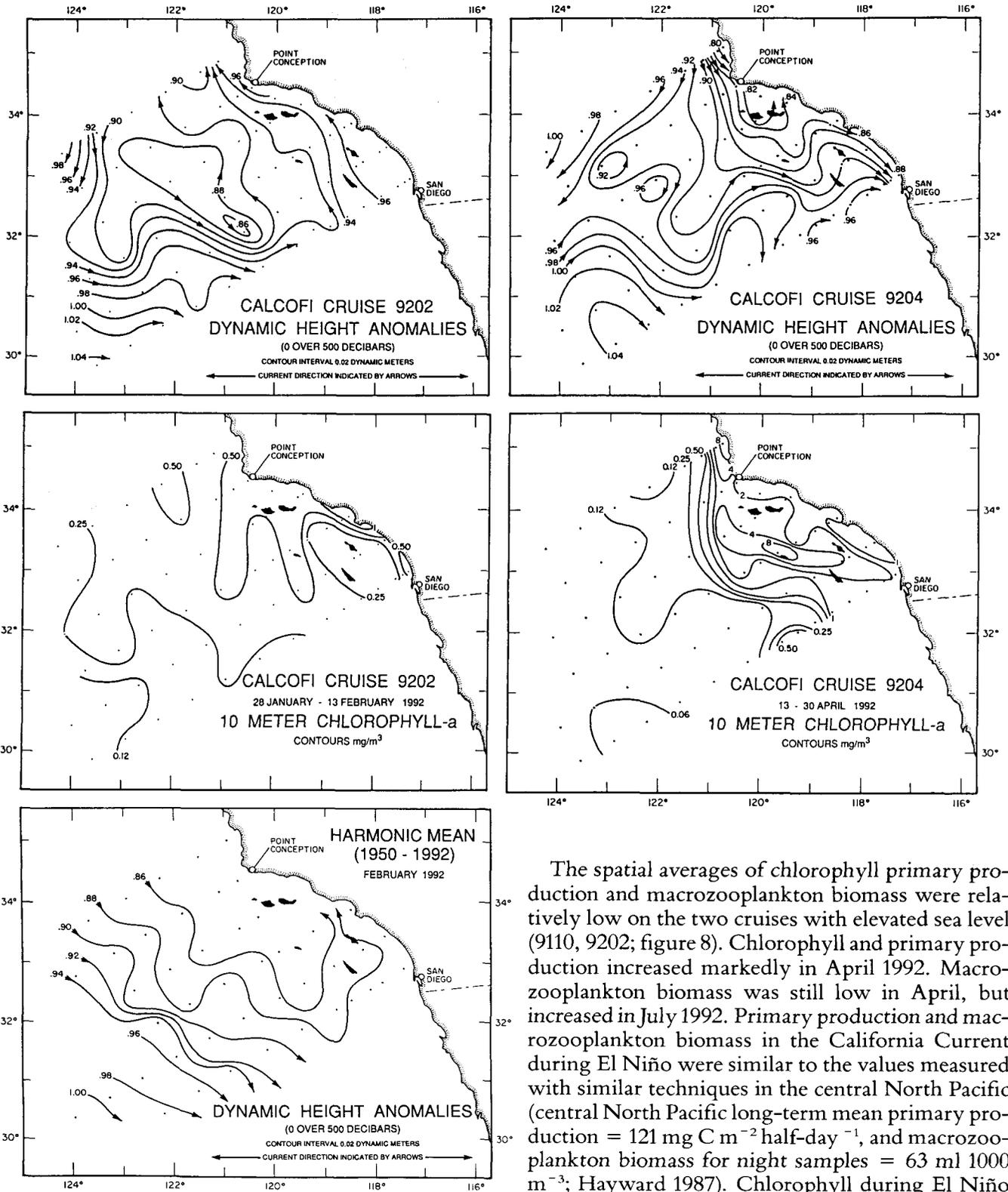


Figure 5. Spatial maps of dynamic height anomaly (0 over 500 db) and surface chlorophyll for CalCOFI cruises 9202 and 9204, and long-term harmonic mean dynamic height anomaly for cruise 9202. The dynamic height anomaly indicates the total geostrophic flow in the upper 500 m, not the seasonally corrected anomaly from the long-term mean. (Figures from Scripps Institution of Oceanography 1992b.)

The spatial averages of chlorophyll primary production and macrozooplankton biomass were relatively low on the two cruises with elevated sea level (9110, 9202; figure 8). Chlorophyll and primary production increased markedly in April 1992. Macrozooplankton biomass was still low in April, but increased in July 1992. Primary production and macrozooplankton biomass in the California Current during El Niño were similar to the values measured with similar techniques in the central North Pacific (central North Pacific long-term mean primary production = $121 \text{ mg C m}^{-2} \text{ half-day}^{-1}$, and macrozooplankton biomass for night samples = $63 \text{ ml } 1000 \text{ m}^{-3}$; Hayward 1987). Chlorophyll during El Niño was only slightly greater than in the oligotrophic central North Pacific ($22 \text{ mg chl-a m}^{-2}$; Venrick et al. 1987).

The wind field implied by the spatial pattern in sea-level atmospheric pressure also changed abruptly in

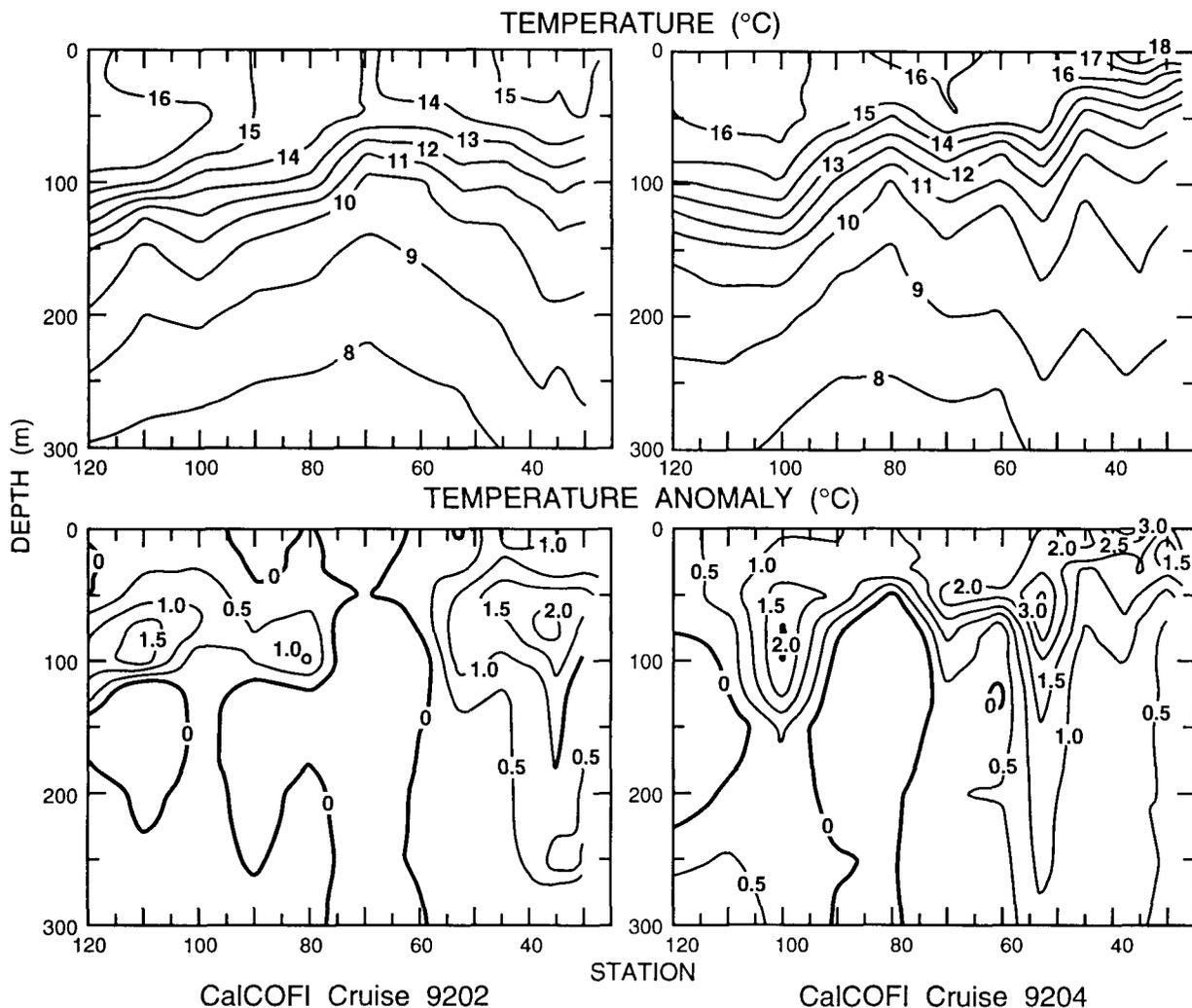


Figure 6. Vertical sections of temperature and temperature anomalies along line 90 for CalCOFI cruises 9202 and 9204.

May 1992. The pattern in sea-level-pressure anomalies changed from one of anomalously weak northerly winds (winds from the north) during April and the several preceding months, to a pattern with anomalously strong northerly winds in May and for the several following months (figure 9). This pattern was superimposed upon the normal annual cycle of the spring transition (Strub et al. 1987), during which the wind field changes from one of episodic winter storms to spring conditions of more regular, northerly, upwelling-favorable winds. The change in the sea-level-pressure anomaly field in April is consistent with intensification of coastal upwelling and increased southerly transport of the California Current.

DISCUSSION

The data presented here are sufficient for a preliminary description of the 1991-92 El Niño event in

the California Current. This description may require revision as more information becomes available. The changes in structure in the California Current during the 1991-92 El Niño event (SST, sea level, poleward flow, reduced plankton populations, and reduced primary production) were qualitatively similar to patterns observed during prior events. The 1991-92 event was relatively short, and it appeared to end abruptly. The anomalies in sea level and SST during the short period of maximum anomalies (3 months) were comparable to those reported during the strong 1982-83 El Niño event in the California Current. The rise and decline in sea-level anomalies preceded the rise and decline in SST anomalies (figures 1 and 3). Sea-level anomalies thus seemed to be a more reliable indicator of other aspects of El Niño (circulation pattern and primary production) than were SST anomalies during this event. Chelton (1981) also observed that low-fre-

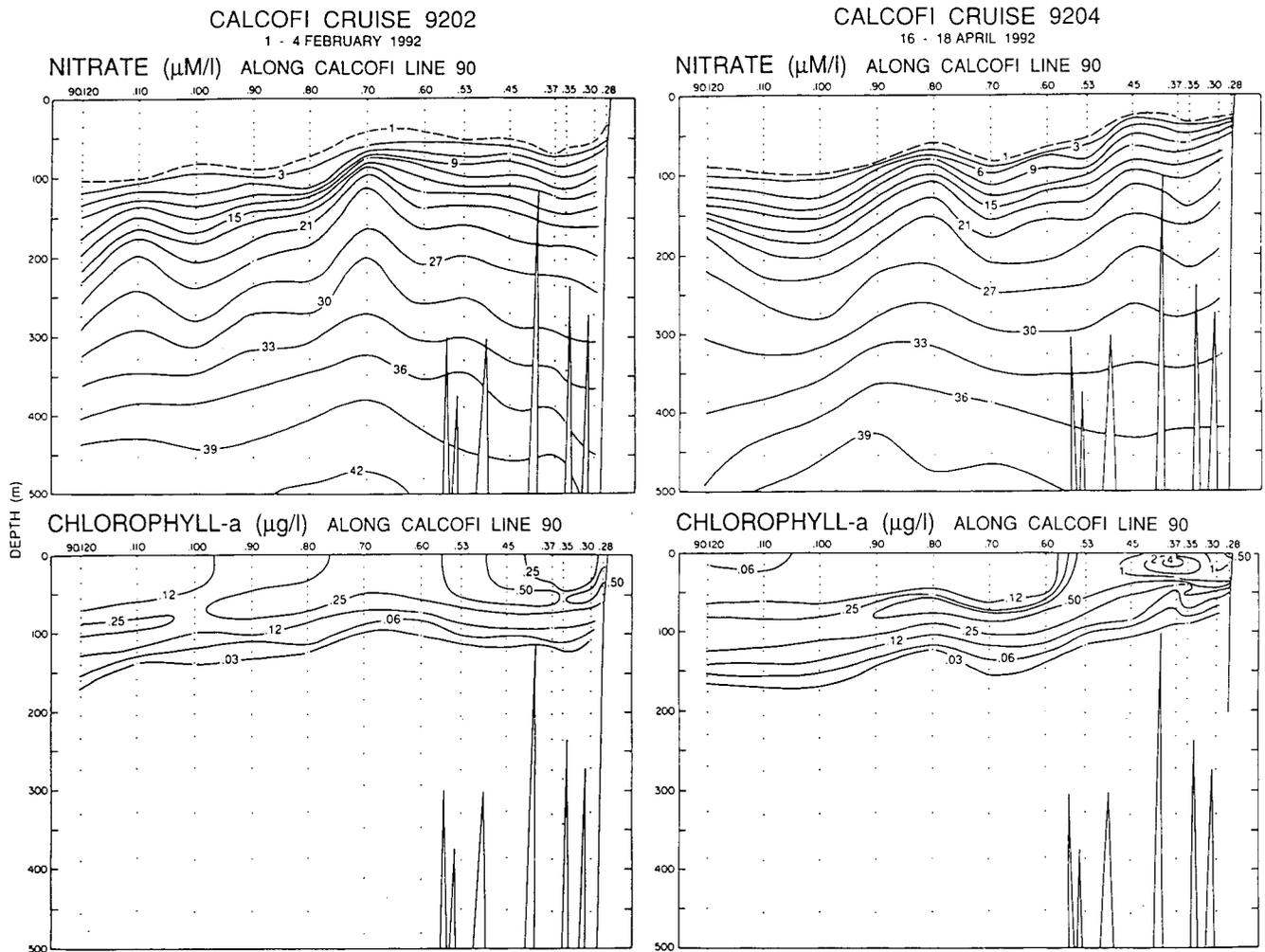


Figure 7. Vertical sections of NO_3 and chlorophyll along line 90 for CalCOFI cruises 9202 and 9204.

quency variability in zooplankton biomass in the California Current is more closely related to sea-level anomalies than to SST anomalies.

Observation of events such as El Niño may foster understanding of the mechanisms linking environmental structure with population dynamics of the upper trophic levels. This, in turn, is an important aspect of understanding and predicting the consequences of global change. Global change will first be detected in those properties for which long time series exist (e.g., SST or sea level; Roemmich 1992). But the ecological consequences of change in properties such as SST are difficult to predict because the direct effects upon organisms are generally small, and because it is uncertain how the distribution of properties (e.g., nutrients) that more directly influence ecosystem structure will be affected. Correlations between low-frequency changes in temperature and sea level and the population dynamics

of pelagic systems have been documented in some cases, and mechanisms linking these correlations have been proposed (Chelton et al. 1982; Smith and Eppley 1982; Mysak 1986). The effects of global increase in temperature upon the upper trophic levels of eastern boundary currents have also been predicted in the context of a mechanism linking circulation and production (Bakun 1990). Understanding the observed correlations and testing such predictions will require additional observations of events such as El Niño where large changes take place, and a better understanding of the mechanisms linking physical and biological structure.

The change in the pattern of circulation, sea level, and primary production in April-May 1992 is interesting because it was both abrupt and strong. It may be easier to relate cause and effect under such circumstances. Although this change in structure may have marked the regional decline of El Niño, it

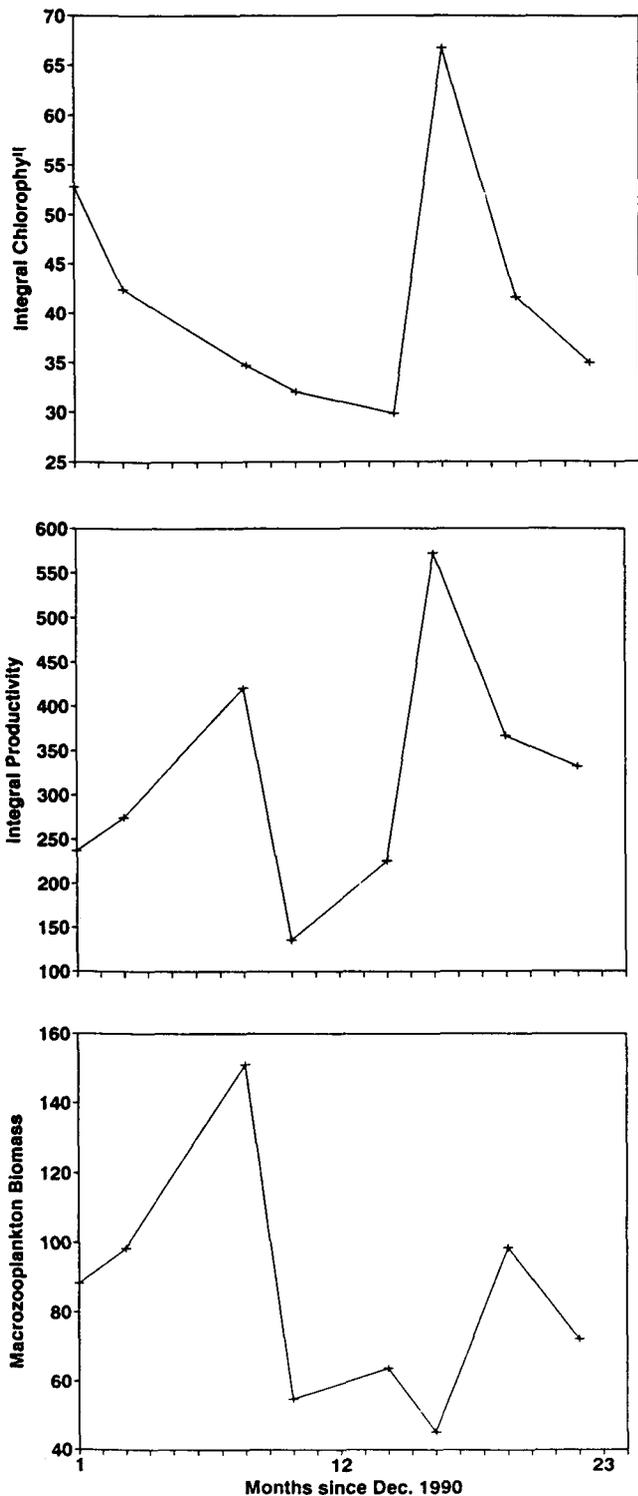


Figure 8. CalCOFI cruise mean values of vertically integrated chlorophyll (mg chl-a m^{-2}), vertically integrated primary production ($\text{mg C m}^{-2} \text{ half-day}^{-1}$), and macrozooplankton biomass ($\text{ml } 1000 \text{ m}^{-3}$) for 1991 and 1992.

seems likely that some component can also be attributed to the annual cycle which is observed in, at least, the wind field (Strub et al. 1987) and macrozooplankton biomass (Chelton et al. 1982). Further

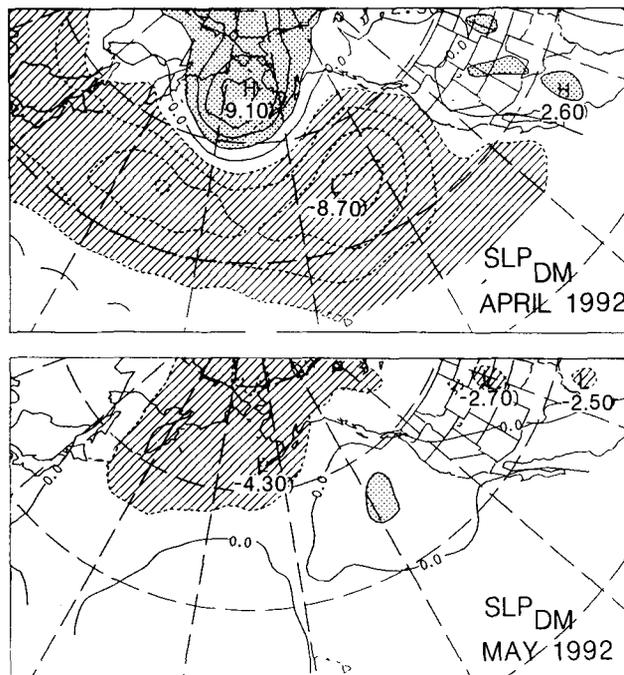


Figure 9. Monthly sea-level atmospheric-pressure anomaly field (mb) for April and May 1992.

study is needed to separate the effects of processes on these two time scales. The mechanism linking increased primary production and plankton biomass with the rise in sea level and the return of southerly flow was probably an increase in the nutrient supply to the euphotic zone due to shoaling of the nutricline. The nutrient input due to coastal upwelling and related processes should be greater when the nutricline is shallower.

Note Added in Proof

This manuscript derives from a talk presented on November 4, 1992, at the CalCOFI conference, and it is based upon the data that were processed and available at that time. Additional data collected in late 1992 and early 1993 suggest that some aspects of this early interpretation were incorrect. In spite of this, I did not substantially change the text of the manuscript that went out for review, because the structure of the California Current continues to evolve rapidly and in unexpected ways, and a synthesis is premature. I have, however, modified figures 1, 2, and 3 to include the latest information available. Large positive SST anomalies were again present at the SIO pier in late 1992 (figure 1), and sea level at La Jolla also began to rise in the fall of 1992 (figure 3). The pattern in sea level in late 1992 and January 1993 was remarkably similar to that seen during the winter of 1991-92. Thus it now appears to have been premature to attribute the change in

structure in the spring of 1992 to the decline of the 1991–92 El Niño.

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The data shown here were collected and processed by CalCOFI technical staff, and I thank them for timely data processing and rapid preparation of preliminary data reports and anomaly fields. I also thank Arnold Mantyla and Ken Plummer for help with processing and interpreting the data, Ron Lynn for the long-term harmonic means for CalCOFI hydrographic data, Dan Cayan for the sea-level-pressure anomaly fields, and Pat Walker for the SIO pier data. Helpful comments from two reviewers improved the manuscript. The data analysis was supported by the Marine Life Research Group of SIO, and the Office of Naval Research.

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Part II

SYMPOSIUM OF THE CALCOFI CONFERENCE

Pacific Grove, California

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**SATELLITE REMOTE SENSING IN THE CALIFORNIA
CURRENT AND ITS UTILITY IN FISHERY OCEANOGRAPHY**



SEASONALITY OF CHLOROPHYLL CONCENTRATIONS IN THE CALIFORNIA CURRENT: A COMPARISON OF TWO METHODS

GIULIETTA S. FARGION
Department of Marine Biology
Texas A & M University
P.O. Box 1675
Galveston, Texas 77553

JOHN A. MCGOWAN
Scripps Institution of Oceanography
University of California, San Diego
9500 Gilman Drive
La Jolla, California 92093-0228

ROBERT H. STEWART
Department of Oceanography — 3146
Texas A & M University
College Station, Texas 77843

ABSTRACT

We have compared estimates of seasonal variations in chlorophyll concentrations in the California Current as derived from a large series of *in situ*, water-column, measures and from the Coastal Zone Color Scanner—West Coast Time Series (WCTS) in both original and corrected forms. We find substantial differences between the two methods, satellite and *in situ*. The original WCTS showed winter to be the peak season for pigment concentration everywhere, but the *in situ* data did not. A previous study of the corrected WCTS data found “a strong seasonal cycle with a spring summer maximum,” but the *in situ* data contained no convincing evidence for a “strong” cycle when all of the data were examined. Some individual years (e.g., 1984) do have clear spring maxima, particularly very near shore, but most do not. There are extensive interannual variations.

The overall relation between surface *in situ* (or 0–20 m) pigment concentrations and integrated, *in situ* water-column (0–150 m) concentrations is very uncertain in terms of mean concentrations per unit volume, spatial heterogeneity, and temporal change.

RESUMEN

Comparamos estimaciones de la variación estacional de clorofila en la Corriente de California: observaciones *in situ* (en la columna de agua, datos provenientes de una gran serie de datos) y observaciones de la Serie de Tiempo de la Costa Oeste (“WCTS”) obtenidas con el Sensor a Color de la Zona Costera (series “corregida” y “original”). Encontramos diferencias substanciales entre los dos métodos, *in situ* y por satélite. La serie WCTS original mostró un máximo en la concentración de pigmentos en invierno (en todos los sitios), pero no así los datos *in situ*. Un estudio anterior de la serie WCTS corregida encontró “un ciclo estacional pronunciado con un máximo en primavera-verano”; sin embargo, al examinar todas las observaciones *in situ*, los datos no mostraron evidencia convincente de un ciclo “pronunciado”. Algunos años (por ejemplo 1984) mostraron claramente máximos en pri-

mavera, particularmente muy cerca a la costa, pero la mayoría no. Hubo gran variabilidad interanual.

Considerando todas las observaciones, la relación entre las concentraciones de pigmento superficiales (o de 0 a 20 m) *in situ* y las concentraciones integradas *in situ* en la columna de agua (0 a 150 m) son muy inciertas en cuanto a las concentraciones medias por unidad de volumen, heterogeneidad espacial y cambio temporal.

INTRODUCTION

One of the most well known and recognizable changes in the environment is seasonality. Any method used to study change (in time and space) should be able to detect a seasonal signal, if it occurs and if it is strong with respect to changes on other frequencies.

Because the ocean and its populations vary considerably on many time-space scales, there are many opportunities for sampling error. In addition, when indirect or remote methods are used, measurement error may become a serious problem. In practice, both sources of error are usually present, but some methods may suffer from one source more than the other. The nature of the error from either source is often difficult to determine. It is useful then, to compare two quite different methods to assess the extent of their agreement. If there is substantial agreement, then we may have some (limited) assurance that our understanding of change is reasonably good in spite of not knowing the exact nature of the errors.

The following study is a comparison between a large series of *in situ* measurements of chlorophyll and those made remotely by the Coastal Zone Color Scanner (CZCS) in the California Current. The larger question is: What is the seasonal change? But the immediate question, treated here, is: How do the two methods compare?

Measurements spanning forty years have shown clear and unambiguous seasonal changes in the physical structure and mass transport of the California Current system (Reid et al. 1958; Eber 1977; Hickey 1979; Lynn et al. 1982; Chelton and Davis

1982; Jackson 1986; Reid 1987; Lynn and Simpson 1987; and many others). This seasonal variation may be sharply differentiated from variations on other frequencies (Chelton 1984). Although the entire physical system has a strong seasonal component to its variability, many authors also define three spatial domains: oceanic, coastal, and a large zone between these. This "in-between" zone is centered about 200–300 km offshore, parallels the coast, and is considered to be the "core," or main body, of the California Current. The flow is equatorward and is strongest in spring and summer; off Baja California it bends inward towards the coast. In the coastal zone there is a strong poleward counterflow, especially in fall and winter. This counterflow weakens in the spring. South of Point Conception it appears as a large, geographically fixed cyclonic eddy over the shallow offshore banks in the Southern California Bight (Lynn and Simpson 1987). Thus the seasonal patterns of water movement inshore in the coastal zone and in the main body of the current, especially south of Point Conception, are not the same. These differences have led to somewhat different areal, seasonal patterns and ranges of the local temperature and density structure (Lynn and Simpson 1987). These features show up in the long-term means; thus they are not transient or vague.

Relatively fewer studies of biological seasonality in this system have been based on such large data sets. But in spite of very large interannual variations, Smith (1971), Colebrook (1977), Chelton et al. (1982), and McGowan (1985) have shown that mean macrozooplankton biomass changes seasonally in all sectors. Once again, however, there are near-shore-offshore, north of Point Conception–south of Point Conception differences in the patterns of seasonality. In all sectors summer is the maximum and winter the minimum, but the offshore waters have a greatly damped cycle (Bernal and McGowan 1981), as do the sectors off Baja California (Chelton et al. 1982).

If these systematic, seasonal patterns in zooplankton biomass result from local trophodynamics or from the transfer of energy from *in situ* primary production, we might expect a spring or early summer productivity maximum of phytoplankton and perhaps a phytoplankton biomass bloom. This expectation may also come from the application of the Sverdrup critical depth model for the initiation of the spring bloom (Sverdrup 1953). This model depends strongly on the depth of light penetration (deeper with increasing sun angles, as in the spring) and changes in the depth of vertical mixing which, in turn, depends on the degree of vertical density

stratification (i.e., warming of the upper layer, as in the spring). This model assumes that nutrients are not limiting, and predicts only the onset of the spring bloom. Smetacek and Passow (1990) have reviewed the frequent misuse of this model but conclude that in its original form it is "logically sound." They suggest that the model be limited to a period of stabilization of a shallow layer long enough to permit algal growth rates to exceed the death rates due to grazing. Whether the original version, the misinterpreted version, or the Smetacek–Passow version is used, this model predicts a late spring–early summer bloom of phytoplankton in the California Current, because that is when the stability maximum shoals in all zones and intensifies in the nearshore (Lynn et al. 1982).

Are there studies to validate these two independent predictions (zooplankton bloom and Sverdrup model), both of which agree on the seasonal timing of the phytoplankton bloom, namely late spring? The assumption behind both predictors is that local, rather than horizontal, advective processes are responsible.

Quite different kinds of measurements are available to test these predictions. Direct *in situ* water-column measurements of chlorophyll have been made by the Southern California Bight Study (SCBS) group (Carlucci et al. 1986). In the lexicon of Lynn, Simpson, Reid, Jackson, etc. the SCBS area is not in the "main body" of the California Current but rather in the coastal domain of the southern California borderland, often called the Southern California Bight. Eppley et al. (1985) have reviewed the SCBS measurements and conclude that the chlorophyll concentrations ". . . exhibit a significant seasonal variation," being lowest in summer and highest in winter. Mullin (1986), on the other hand, using the same data, could detect no seasonal signal in chlorophyll or primary production. In the very nearshore, at the Scripps Institution of Oceanography pier, spring appears to be the time of maximum diatom and dinoflagellate abundance (Allen 1941; Tont 1989).

Much additional *in situ* data come from the California Cooperative Fisheries Investigations (CalCOFI), which have measured water-column chlorophyll concentrations at a large number of stations in the main body of the California Current and the bight since 1969.

A second method of assessing how plant biomass changes in time and space is by studying remotely sensed concentrations of plant pigments as measured by the Coastal Zone Color Scanner (Smith and Baker 1982; Eppley et al. 1985; Peláez and McGowan

1986; Abbott and Zion 1987; Balch et al. 1989). Using 129 images from the West Coast Time Series (WCTS; Abbott and Zion 1985) for the period from 1979 to 1981, Michaelsen et al. (1988) studied seasonal variability of "pigment biomass" in a series of "boxes" of about 10,000 km² each, selected to represent areas both onshore and offshore north of Point Conception, in the Southern California Bight, and south of San Diego. Their "nearshore" areas were centered about 150 km off the coast in what they call the "mainflow" of the California Current; the "offshore" areas were 300 km away from the coast in what they called "oceanic water." They also used the SCBS, shipboard data (i.e., *in situ* water-column measurements) from the "inner portion" of the Southern California Bight, but "only those observations obtained from stations at least 10 km from the coast." These data were used for comparison with the satellite data. Michaelsen et al. found that "Annual cycles in upper layer chlorophyll," as measured by either satellite or ship, show winter maxima and summer minima, but the "total" (i.e., in the entire water-column) "as measured from ships, on the other hand, peaks in early summer." They attribute this to the seasonal development of "strong sub-surface maxima and surface minima." They clearly imply that these "shipboard" observations and their interpretations apply throughout the entire study area even though the measurements came only from the "inner portion" of the Southern California Bight.

Strub et al. (1990) studied seasonality of satellite-derived surface pigment concentration over a much larger area of the California Current. They too used the West Coast Time Series of satellite data to determine seasonal patterns. However, they identify an error in the processing of these data where the single-scattering Rayleigh algorithm that was used produces winter values "known" to be too high (no citation given). They point out that the symptoms of this sort of error should be "uniformly increasing chlorophyll with latitude with a seasonal maximum in winter." This point was also made by Gordon et al. (1988), who implied that the algorithm should be valid for solar zenith angles less than 50°–55°, which corresponds to latitudes of 26.5°–31.5° in late December. Thomas and Strub (1990) state "The algorithm used to correct these images for atmospheric (Rayleigh) scattering is known to produce artificially high values of pigment concentrations in regions of high zenith angle. This pigment concentration estimated by the CZCS at high latitudes during winter cannot be trusted." They nevertheless used values up to a latitude of 47°N, which has a

solar zenith angle of around 70° in late December; we will use data as far south as 28°N and as far north as 39°20'.

Although no *in situ* validation of the seasonal change in direction of error or its magnitude is given by Strub et al. (1990) they do suggest an algorithm correction that appears to bring the data into "conformity" with another algorithm (Gordon et al. 1988) and to produce a "strong" seasonal cycle with a spring-summer maximum outside of the Southern California Bight, a northward progression of high pigment concentrations, and—within the bight—low seasonality with a "relative minimum" in late summer. They point out that in regions "where previous work has been done" (presumably the *in situ* studies of Eppley et al. 1985 in the Southern California Bight) "there is general agreement with the seasonal cycles found here."

Thus there is disagreement among authors as to the direction and magnitude of the seasonal changes in plant biomass as measured by chlorophyll content, whether this was measured directly *in situ*, or remotely by satellite. Some of the error of satellite-derived measurements of chlorophyll in the California Current has been addressed by Balch et al. (1989), who used *in situ* measurements. But they did not report a seasonal change in the direction of error, as did Strub et al. (1990). Although Gordon et al. (1988) adjusted the algorithm used to process the original WCTS data, and Strub et al. (1990) introduced their own correction, there remain the issues of what the extensive *in situ* CalCOFI data say about how well this correction depicts seasonality in areas outside of the Southern California Bight and what a more extensive data set (CalCOFI plus SCBS) says about it within the bight. Neither the Gordon et al. (1988) nor Strub et al. (1990) "corrections" have been validated against seasonal *in situ* chlorophyll data.

Further, there are the very nearshore areas (less than 10 km) to consider. These are of some concern because here is where people have their most intimate contact with the ocean, where pollutants are discharged, and where society, in general, is most concerned with "changes." We have some right to expect that the tempo and mode of phytoplankton population biology here differs from the offshore (Allen 1941), and that this observation needs to be validated with more modern data in order to compare with satellite-derived information. Although there are recognized potential errors in remotely sensed pigment estimates from very nearshore pixels (class II error, Gordon and Morel 1983), these too need validation from *in situ* data. The immediate nearshore zone is too important to ignore. We also

will test the idea that the error is greatest at higher latitudes.

METHODS

We began our study (Fargion 1989) before becoming aware of the ongoing work of Michaelsen et al. (1988), Strub et al. (1990), or Thomas and Strub (1990), and yet we treated the WCTS data similarly. We too examined the seasonal, remotely sensed, signal in a set of "boxes" both nearshore and offshore, north and south in the California Current, as did Michaelsen et al. (1988). Thus our results can be compared to theirs. We also tried to determine the larger-scale, satellite-derived, seasonal signal from the WCTS, as did Strub et al. (1990). We differ from these studies in that we also examined the very nearshore satellite signal where we had a relatively extensive high-frequency time series of chlorophyll measurements (over 1000) and where the water column is almost always well mixed. We also differ in that we used the very extensive CalCOFI time/space series of over 958 *in situ* water-column chlorophyll measurements (12 to 14 depths each) for areas both within the bight and well outside of it to validate the remote sensing data. The years covered by these 58 cruises are 1969, 1972, 1978, and 1983 through 1991. These measurements are particularly apt because they may be directly related to the extensive hydrographic and biological studies of the California Current cited earlier.

The satellite scenes and numerical values are from the Nimbus 7 Coastal Zone Color Scanner and were processed to gridded and earth-navigated images of nearsurface pigment concentrations by Mark Abbott and Philip Zion. The processed images were provided by the NASA Ocean Data System of the Jet Propulsion Laboratory. We used these satellite data at three different spatial scales (one of which was rather large), so it was important to select relatively cloud-free, large, individual images. Between the years 1979 and 1985 we found 190 suitable images. We used no spatial composite images.

We first determined the seasonal cycle of satellite-derived color from the WCTS at nearshore, mid-stream, and offshore locales (1 × 1 mosaic pixels 7.1 km on a side) nearest to CalCOFI oceanographic stations 60, 80, and 110 on seven CalCOFI lines from 40°N to 30°N, a distance of some 1080 km (figures 1 and 2). We then selected six smaller areas, or "boxes," similar to those of Michaelsen et al. (1988). These were 162 km by 162 km and represented the nearshore and offshore regimes off San Francisco, Point Conception, and San Diego (figure 3). We space-averaged the numerical data from within each

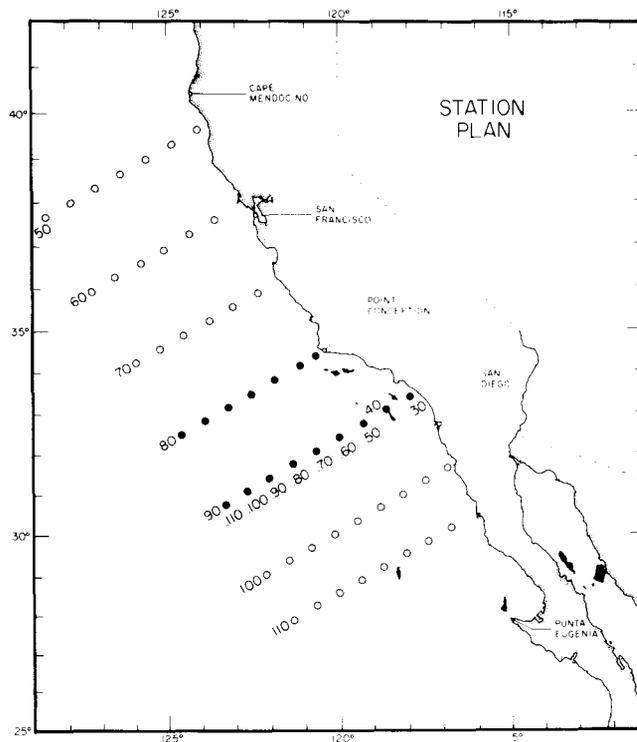


Figure 1. The pattern of CalCOFI stations used in this study. The open circles are stations on cardinal lines 50 through 110 and are the locales for the seasonal satellite study shown in figure 2. The closed circles on cardinal lines 80 and 90 are the locations of the *in situ* chlorophyll measurements shown in figures 6, 7, 9, and 10. Stations are numbered .50 through .120. For example, the nearest station to the shore on line 90 is station 90.50; the farthest offshore is 90.110.

of these boxes for each of the available monthly images (figure 4). Thus this aspect of our study resembles that of Michaelsen et al. (1988).

Finally we looked at the satellite monthly means from 1979 to 1985 from a single pixel nearest the end of the ocean pier at Scripps Institution. This was in order to compare the satellite results with a high-frequency (paired samples, two times per week), long-term (six years) time series of chlorophyll measurements taken here. This latter part of our study has the additional benefit of introducing a different system, the very nearshore (class II) environment, into the comparison of satellite with *in situ* results—a system in which we have a large background of information and where the water column is very shallow and almost always very well mixed (figure 5).

The data from Scripps Pier resulted from filtration and extraction of paired 50-ml samples taken just beneath the surface. Our other more oceanic water column data come exclusively from the SCBS and CalCOFI programs. Both of these used the same extraction and analysis procedures and are

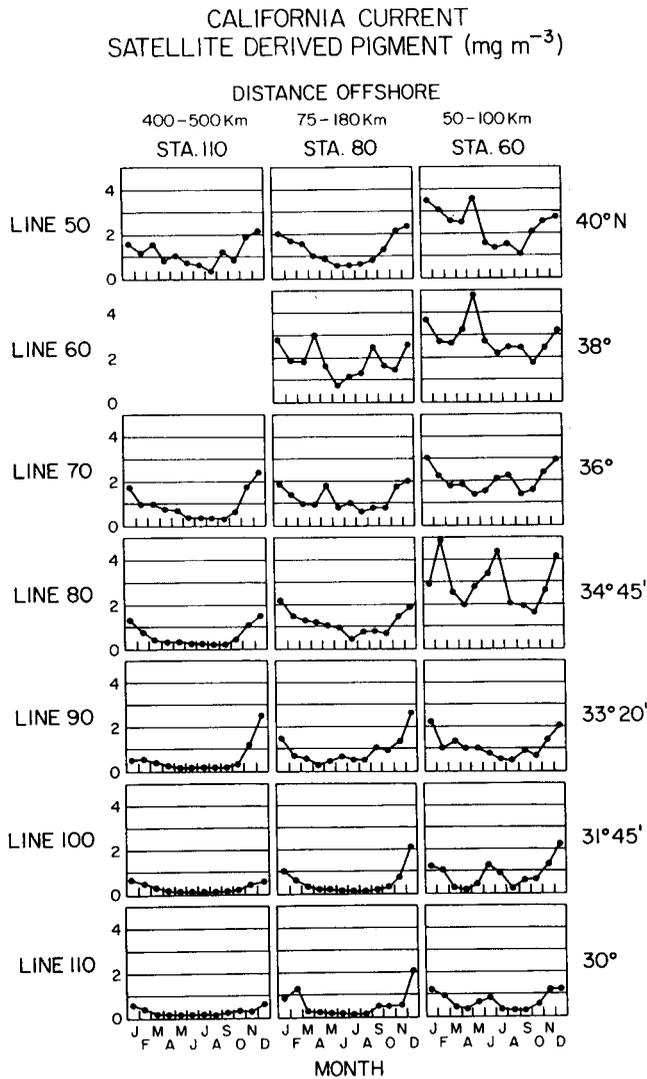


Figure 2. Satellite-derived (uncorrected WCTS) estimates of chlorophyll concentrations. These are averaged from 1×1 mosaics (7.1 km on a side) nearest to CalCOFI stations offshore .110, mid-current .80, and nearshore .60, on seven cardinal lines between 40°N and 30°N (see figure 1).

identical with the Scripps Pier procedures (Venrick and Hayward 1984).

RESULTS

Satellite-Derived Pigment Seasonality

Our large-scale study of the original, uncorrected, 1988 WCTS data show essentially what Strub et al. (1990) have suggested about the sense of the error. That is, in the nearshore (the sta. 60 N-S line) and in midstream (the sta. 80 N-S line) chlorophyll generally increases from south to north. Offshore (the sta. 110 N-S line) this trend is less evident. But because these same north-south trends may be present in some of the larger spatial maps of *in situ* water-column chlorophyll from CalCOFI cruise re-

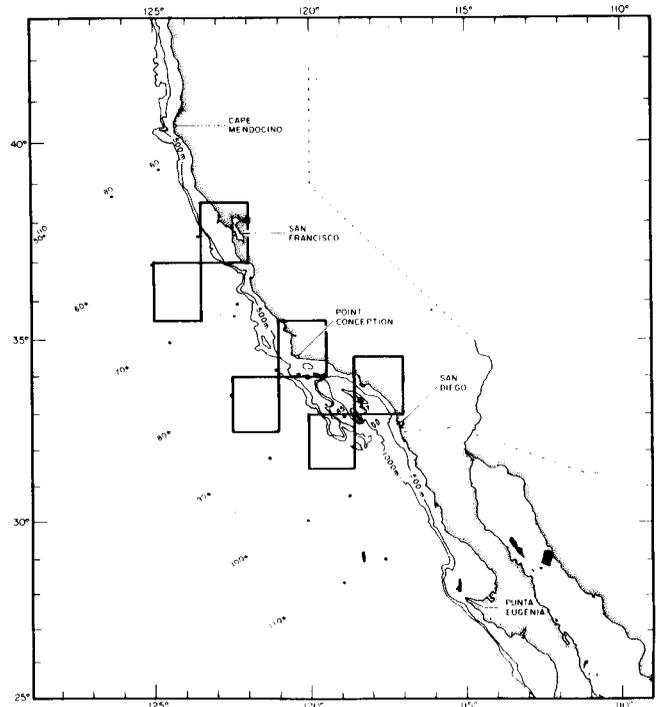


Figure 3. Six "boxes" of $162 \text{ km} \times 162 \text{ km}$ where satellite-derived chlorophyll concentrations (uncorrected WCTS) were space-averaged by month for the years 1979 to 1985.

ports (SIO 1984a,b) and atlases (Owen 1974) it is not quite clear that the observation can be considered to represent an algorithm error or a satellite measurement error. What is evident, however, is that in virtually all of the sectors, most of the WCTS-derived graphs indicate that peak concentrations occur in the winter months of December and January even as far south as 28°N , station 110 on line 110 (figure 2). Offshore and in the Southern California Bight (south of line 80) midsummer generally appears to be the time of minima in WCTS estimates of chlorophyll concentration. Midsummer secondary maxima occur nearshore, north of Point Conception (line 80, figure 2). Thus our satellite determinations of "seasonality" agree with Michaelsen et al. (1988) and with the uncorrected data of Strub et al. (1990) and Thomas and Strub (1990). This suggests that wintertime errors in the satellite algorithm may be important for solar angles as small as 51.5° .

In our study of the boxes, for which a large amount of space-time averaging was done, the seasonal trends provided by WCTS do not differ strongly from the above (figure 4), in spite of the spatial smoothing. Here again we see winter maxima everywhere, and midsummer minima in the offshore and in the San Diego inshore boxes. Secondary summer highs are present in the inshore Point Conception and San Francisco sectors. The

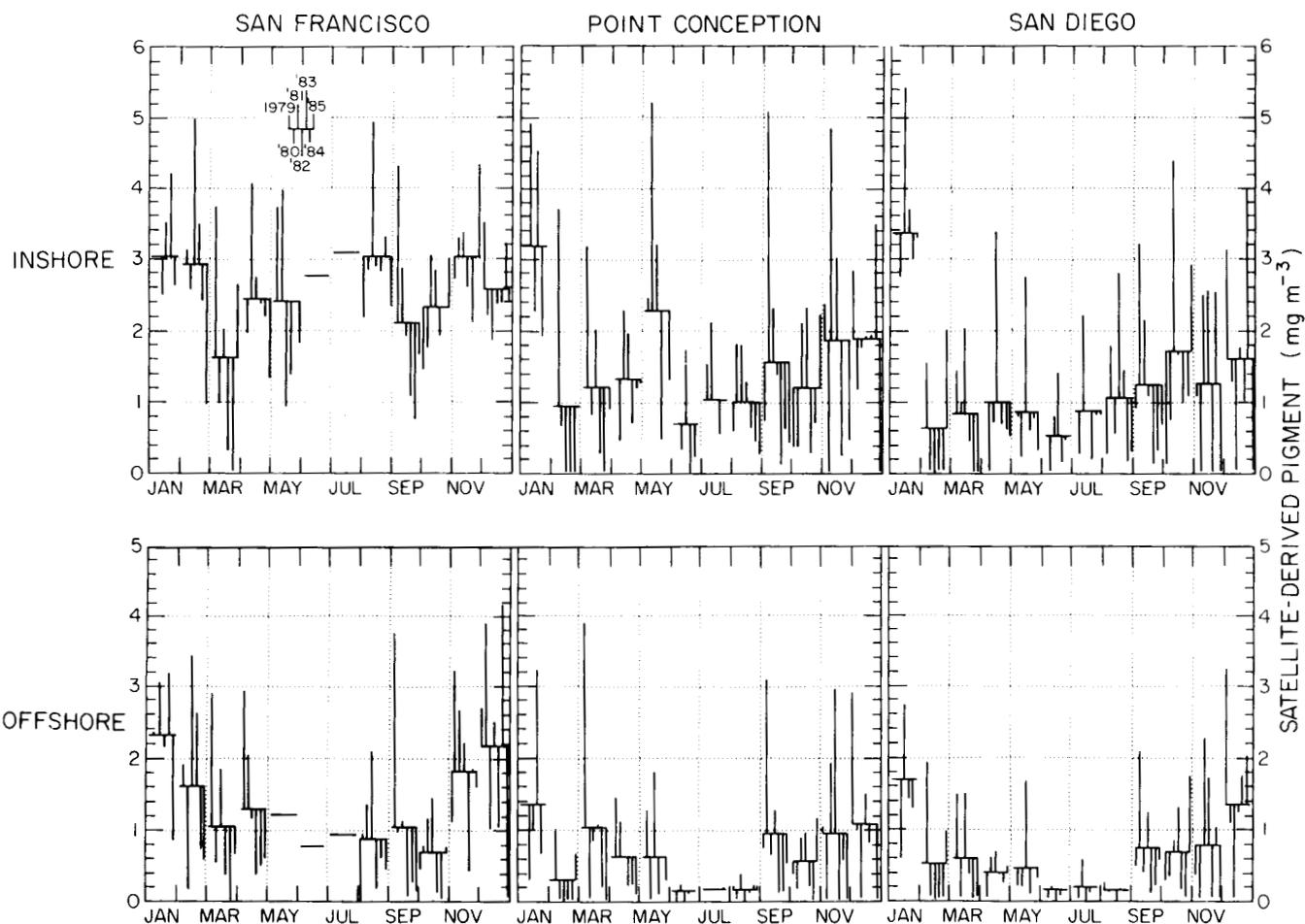


Figure 4. Monthly means of chlorophyll estimates (mg/m^3) in the six boxes shown in figure 3. The horizontal bars are the overall monthly means; the vertical bars are the monthly values from individual years (uncorrected WCTS).

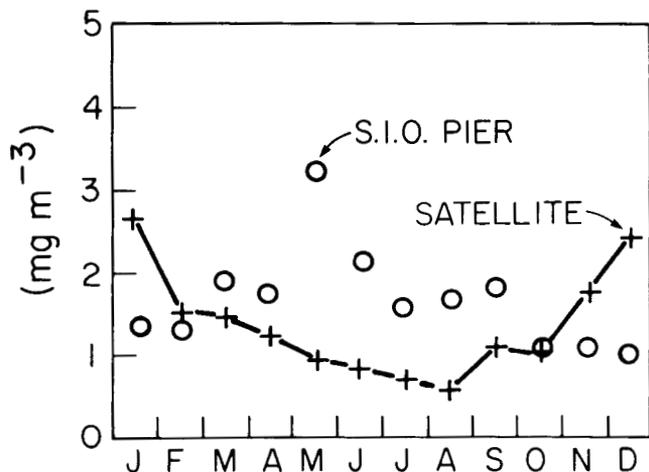


Figure 5. Circles, the concentrations by month of surface chlorophyll plus phaeopigments (mg/m^3) from twice-weekly sample pairs from Scripps Pier (1983–85). Crosses, satellite-derived (uncorrected WCTS) estimates from the nearest pixel.

major new aspect in this part of our study is the large interannual signal seen in all six sectors.

Finally we examined the mean seasonal signal from a pixel nearest the Scripps Pier (figure 5). Here there is a clear winter (Dec.–Jan.) maximum and a midsummer (Jul.–Aug.) minimum in the WCTS, satellite-derived estimates. So far we are in total agreement with Strub et al. (1990), who first mentioned this important error in the open scientific literature: that the uncorrected (as of 1990) WCTS showed strong, regular, winter blooms of phytoplankton in the California Current.

Satellite–In Situ Comparisons

In the following sections we will show extensive *in situ* water-column data. These contain no evidence for winter peaks in the concentrations of chlorophyll anywhere in the California Current. We will also examine how surface *in situ* or 0–20-m *in situ* estimates of chlorophyll abundance relate to complete (0–150-m) water-column measurements and

will show that their patterns of change in space and time do not agree. Note that where there is a well-developed mixed layer, changes in surface chlorophyll should reflect changes in 0–20-m integrated chlorophyll abundance. That is the depth range generally thought to be well represented by CZCS color measurements.

There are too few large-scale surveys of the chlorophyll content of all the sectors of the California Current, particularly in the north, so we cannot map large-scale spatial, seasonal changes with great confidence, especially because of aliasing by other frequencies. The few seasonal maps that do exist (Owen 1974) do not confirm the broad-scale WCTS, satellite estimates of the seasonal directions of change. But we do have more extensive water column data from farther south on CalCOFI lines 80 and 90 (figure 1) and from the bight, especially during the time that the CZCS operated. We can look for the nearshore-offshore seasonal signals off of Point Conception, well south of it, and in a large amount of space-averaged data from the combined SCBS-CalCOFI time series within the bight.

CalCOFI line 80 runs normal to the coastline and transects our two Point Conception boxes and those of Michaelsen et al. (1988) (figure 1). The means of integrated, (0–150 m) water-column chlorophyll from stations in the inner 120 km of this line show only a weak “seasonal” peak in April–May means, with a minimum in the fall season. It is evident that there are large variations about these monthly means and that some springs have much less chlorophyll than some winters (figure 6 and table 1). Offshore on this line the overall mean concentration decreases considerably; there are broadly overlapping standard deviations (table 1); and there is no convincing evidence for a regular seasonal cycle. As with the nearshore data, the nonseasonal variations are large. If one integrates only through the upper 20 m in an attempt to emulate the optical depths over which the radiometer in the CZCS is thought to accurately estimate chlorophyll pigment concentration, a seasonal picture is even less evident (figure 6). Over this depth range there is still no strong seasonal signal, but the May mean is the maximum and the October the minimum. These two means differ significantly

TABLE 1
 Monthly Means, Medians, Ranges, Standard Deviations, and Coefficients of Variability, Nearshore (<Sta. 70) and Offshore (Sta. 70 and Greater) for the Near-Surface (0–20 m) and Water-Column (0–150) *In Situ* Chlorophyll Measurements (mg m^{-2}) on CalCOFI Line 80, 1969–91

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Nearshore 0–20 m												
Mean mgm^{-2}	38.38	23.99	21.58	44.77	46.28		35.01	29.75	29.68	17.07	18.69	
SD	44.71	17.01	12.65	58.34	29.79		34.31	20.73	28.52	12.25	9.59	
N	17	8	12	17	18	0	14	11	6	8	20	0
MD	24.73	19.25	19.55	24.32	45.30		19.76	28.00	23.00	14.70	17.20	
MIN	5.25	2.96	6.11	2.75	4.03		1.74	4.55	3.40	3.19	3.47	
MAX	168.80	51.51	50.38	218.39	105.16		108.14	74.45	72.60	44.16	45.95	
SD/ \bar{x}	1.16	0.71	0.59	1.30	0.64		0.98	0.70	0.96	0.72	0.51	
Nearshore 0–150 m												
Mean mgm^{-2}	74.63	59.06	79.30	91.98	96.39		84.46	76.54	69.51	41.50	46.43	
SD	71.27	41.24	87.16	98.25	53.58		83.05	64.97	42.73	18.69	22.71	
N	16	8	12	17	18	0	14	12	6	8	20	0
MD	50.85	52.39	60.07	52.60	92.20		55.71	56.30	66.66	35.83	44.71	
MIN	16.57	17.48	26.13	15.46	20.33		13.08	26.58	26.57	18.98	10.49	
MAX	271.82	143.06	348.30	350.85	241.64		335.53	248.08	116.80	73.99	104.11	
SD/ \bar{x}	0.95	0.70	1.10	1.07	0.56		0.98	0.85	0.61	0.45	0.49	
Offshore 0–20 m												
Mean mgm^{-2}	10.14	5.34	5.70	5.19	4.72		8.22	4.03	2.43	3.46	7.17	
SD	5.90	5.90	5.85	7.86	5.51		14.01	3.79	1.07	1.93	5.74	
N	18	9	12	9	23	0	16	15	9	9	21	0
MD	9.19	3.20	3.32	2.20	2.16		2.95	2.30	2.76	2.65	5.98	
MIN	2.38	0.50	1.55	1.27	1.14		0.54	1.00	1.30	1.91	1.62	
MAX	23.17	16.36	18.99	25.70	23.77		56.93	14.20	3.70	8.06	26.22	
SD/ \bar{x}	0.58	1.10	1.03	1.51	1.17		1.70	0.94	0.44	0.55	0.80	
Offshore 0–150 m												
Mean mgm^{-2}	37.48	24.20	39.18	32.89	27.74		33.89	24.47	23.38	25.01	30.82	
SD	16.18	13.70	37.95	19.40	10.49		23.06	7.72	5.78	6.44	14.79	
N	18	9	12	9	23	0	16	15	9	9	21	0
MD	36.92	22.84	30.53	24.87	24.57		26.73	20.75	21.13	26.87	26.90	
MIN	14.63	2.89	12.52	13.19	14.88		10.68	15.30	17.68	11.39	13.86	
MAX	67.43	49.85	155.96	68.05	57.80		113.51	36.19	35.17	32.89	81.25	
SD/ \bar{x}	0.43	0.57	0.97	0.59	0.38		0.68	0.32	0.25	0.26	0.48	

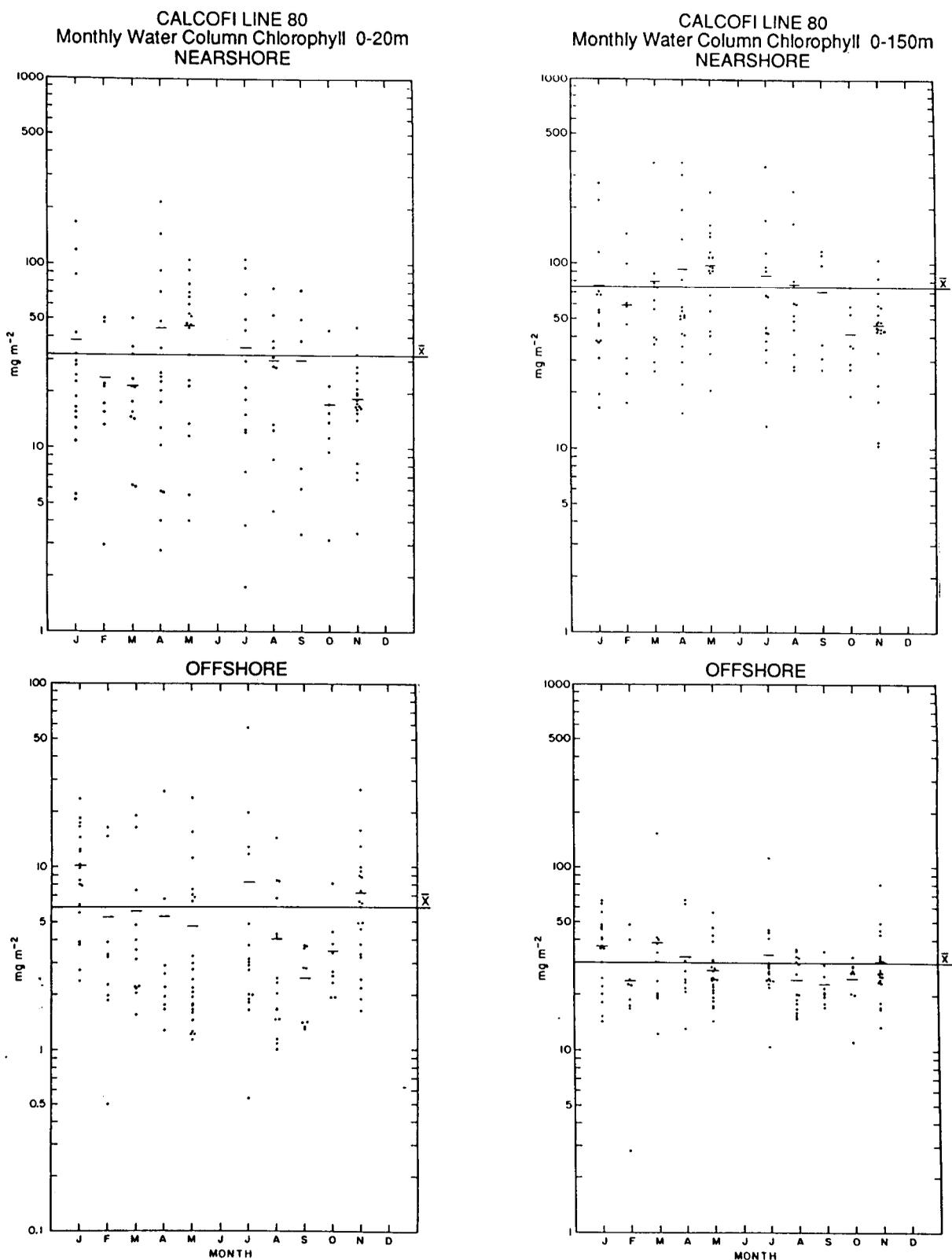


Figure 6. Integrated *in situ* water-column measurements of chlorophyll on cardinal line 80. There are three "nearshore" and three to six "offshore" stations. Station 70 (see figure 1) was taken as the breakpoint between nearshore and offshore. Each dot represents the integral of either depths over 0–20 m or depths over 0–150 m. Horizontal bars are long-term monthly means. Data are from 1969, 1972, 1978, and 1984–91.

TABLE 2
 Monthly Means, Medians, Ranges, Standard Deviations, and Coefficients of Variability, Nearshore (<Sta. 70) and
 Offshore (Sta. 70 and Greater) for the Near-Surface (0–20 m) and Water-Column (0–150) *In Situ* Chlorophyll
 Measurements (mg m^{-2}) on CalCOFI Line 90, 1969–91

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Nearshore 0–20 m												
Mean mgm^{-2}	12.43	10.62	13.26	17.38	15.76	9.75	9.96	10.24	7.24	6.35	5.10	6.69
SD	8.47	7.75	25.90	23.45	18.87	7.27	12.44	13.20	11.31	6.94	3.79	4.21
N	44	35	43	48	56	14	38	36	27	36	48	15
MD	9.68	8.70	6.88	8.74	9.06	7.62	5.41	4.58	2.95	3.52	4.07	4.48
MIN	2.05	2.03	2.07	2.19	1.53	1.90	1.90	1.85	2.05	1.91	1.00	2.60
MAX	30.66	36.14	165.95	94.05	111.40	25.72	65.86	51.41	52.40	38.22	25.10	17.08
SD/ \bar{x}	0.68	0.71	1.95	1.35	1.20	0.75	1.25	1.29	1.56	1.09	0.74	0.63
Nearshore 0–150 m												
Mean mgm^{-2}	37.51	39.09	42.31	56.09	50.13	37.23	48.87	35.74	35.57	33.51	29.45	30.04
SD	12.05	15.97	27.42	47.94	34.58	17.64	42.38	17.77	12.40	20.09	9.02	11.84
N	42	34	42	48	56	14	37	37	26	35	48	15
MD	35.95	33.35	35.09	35.27	37.70	31.11	34.96	29.90	31.39	26.98	27.78	27.81
MIN	14.19	21.43	20.94	22.15	17.93	17.06	12.90	14.44	21.60	8.19	10.52	13.96
MAX	64.75	82.76	184.31	233.25	199.98	75.32	203.75	101.63	74.07	116.37	61.59	50.53
SD/ \bar{x}	0.32	0.41	0.65	0.85	0.69	0.47	0.87	0.50	0.35	0.60	0.31	0.39
Offshore 0–20 m												
Mean mgm^{-2}	4.24	2.78	3.13	3.79	2.61	9.67	2.44	1.67	1.80	1.80	2.57	4.04
SD	2.75	2.04	3.17	6.49	2.81	3.86	2.12	1.25	1.40	0.68	1.72	1.03
N	40	23	30	28	35	5	27	24	12	19	33	7
MD	3.26	1.99	2.05	2.05	1.60	8.09	1.82	1.30	1.42	1.89	1.95	3.89
MIN	1.16	1.05	0.84	1.00	0.93	6.36	0.31	0.14	1.00	0.40	1.04	2.88
MAX	12.41	8.07	13.45	26.25	15.10	16.00	10.89	6.34	6.05	2.71	9.44	5.83
SD/ \bar{x}	0.65	0.73	1.01	1.71	1.08	0.40	0.87	0.75	0.78	0.38	0.67	0.25
Offshore 0–150 m												
Mean mgm^{-2}	25.58	22.58	23.36	31.97	26.66	37.03	33.66	20.53	21.36	24.61	22.51	23.15
SD	9.44	8.69	8.20	22.47	11.92	8.62	44.68	6.65	4.41	4.27	5.24	3.99
N	37	15	29	28	32	5	25	22	12	12	31	7
MD	23.44	20.34	22.20	26.29	22.92	37.60	26.01	18.86	19.90	23.16	21.84	23.24
MIN	14.02	13.53	14.87	17.19	12.20	25.58	5.40	8.40	15.84	19.47	15.91	17.07
MAX	61.16	48.20	49.38	109.02	61.18	48.67	245.43	39.00	30.93	33.90	39.83	27.80
SD/ \bar{x}	0.37	0.38	0.35	0.70	0.45	0.23	1.33	0.32	0.21	0.17	0.23	0.17

($p < .05$). There are even fewer reasons to claim an offshore 0–20-m water-column seasonal signal (figure 6, table 1).

Farther south, along CalCOFI line 90 (figure 7 and table 2) we have done a similar study. The “nearshore” stations are within the bight, and the “offshore” stations are in the main body of the California Current. The median and mean values of integrated, (0–150) water-column chlorophyll within the bight on this transect show some evidence of a seasonal signal, with the April–May means well above the overall mean. A test of the April, May, and June means against those of December, January, and February, with the null hypothesis of “no difference” was rejected ($p < .005$). But the very broad scatter of points and the large standard deviations indicate a strong nonseasonal component to the variability. Again the offshore data are even less seasonal, and a similar test with an identical null hypothesis could not be rejected. If, as with the more northerly stations on line 80, we integrate through only the upper 20 m, we see that the monthly scatter of points increases greatly, making it even more difficult to de-

tect a regular seasonal pattern, and making it quite clear that variations on frequencies other than seasonal are very large (figure 7, table 2). Inspection of both figures reveals that many of these monthly means are skewed upwards by a few very high outliers. These outliers do, however, tend to fall between March and September. Perhaps it is only in this sense that we can see an occasional “strong” seasonal cycle with a “spring-summer” maximum (Strub et al. 1990; Thomas and Strub 1990).

Because the line 90 data present such an indeterminate picture, we used the combined CalCOFI-SCBS data to space-average by month over the entire bight in the hope that averaging a larger number of stations here ($n = 700$) would reduce some of the ambiguity. But neither the monthly, bightwide, space-averaged, integrated chlorophyll nor the surface, space-averaged data showed a clear seasonal pattern (figure 8).

Finally we examined the six-year, twice-weekly measurements from Scripps Pier for the presence of a seasonal signal, and compared it to the nearest pixel satellite data (figure 5). Although this locale is

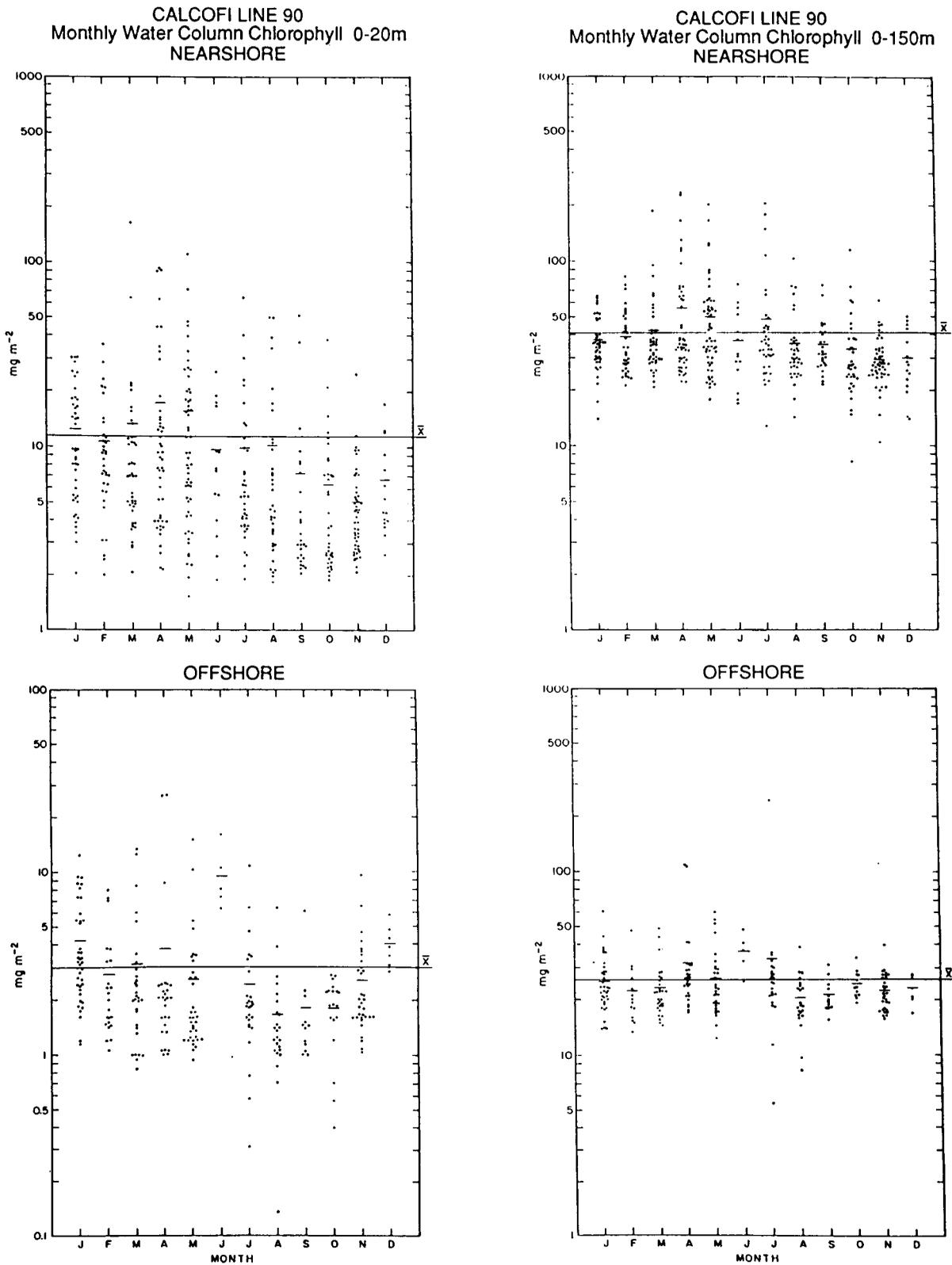


Figure 7. Integrated *in situ* water-column measurements of chlorophyll on cardinal line 90. There are from five to ten "nearshore" and six (except in 1983) offshore stations. Each dot represents the integral of either 3 depths over 0–20 m or 12 depths over 0–150 m. Horizontal bars are the monthly means. Data are from 1969, 1972, 1978, and 1983–91.

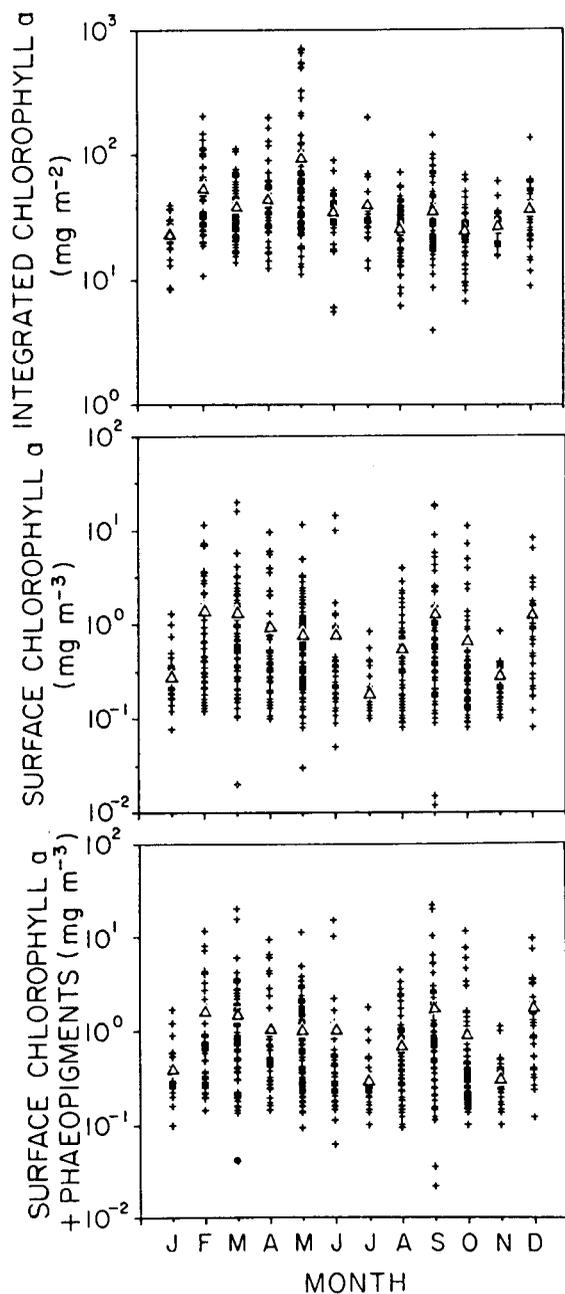


Figure 8. Integrated chlorophyll to the 1% light level, surface chlorophyll, and surface chlorophyll plus phaeopigments. These data are from SCBS (1974–87) and CalCOFI (1969–86) measurements taken in the Southern California Bight. Triangles are monthly means.

very nearshore and the satellite data may suffer from the class II sediment interference problem (Gordon and Morel 1983), cell counts and chlorophyll from simultaneous sampling indicate that this may not be a serious source of error (Reid et al. 1985). Further, sediment input from runoff at this locale is very small, episodic, and limited to the winter months. Here there was an evident seasonal maximum, May–June, in the *in situ* data, and although this maximum

is due mainly to one particular year it does agree with previous studies of phytoplankton species abundance at this locale (Allen 1941; Tont 1989). Unfortunately the uncorrected satellite data are in broad disagreement. Not only are the satellite winter values large overestimates as compared to the *in situ* data, but the May–June means are underestimates by factors of two or three.

The Strub et al. (1990) and Thomas and Strub (1990) studies of seasonality of phytoplankton pigment concentrations in the California Current did not use winter data because it was “unreliable” or “suspect.” In spite of that they conclude that north of the Ensenada Front at about 32°N (Peláez and McGowan 1986) and “outside” of the Southern California Bight there is a “strong” seasonal cycle with a spring–summer maximum. We have already shown there is only a very ill-defined seasonal cycle nearshore in either depth range (0–20 m or 0–150 m) and none at all offshore (i.e., outside the bight).

To visualize the temporal/spatial changes in the *in situ* data and to compare with satellite imagery, we have contoured about eight years of these *in situ* data of chlorophyll plus phaeopigment, by stations, integrated 0–20 m, from lines 80 and 90 (figures 9 and 10). The first three years of the line 80 data do show either spring (for 2 yrs.) or summer (for 1 yr.) peaks very near shore. In the remaining four years, high values occur most of the year except for autumn. Line 90 data are similar in that the spring or summer peaks occur only in the first three years and are only very near shore. The remaining five years of line 90 data seem to have prolonged, nearshore highs most of the year, again excepting the autumn. The lines 80 and 90 data from 1969, 1972, and 1978 have been treated in an identical way. There are no offshore seasonal signals in any of these data. Nearshore, there are no regular temporal patterns, although 1978 did have four stations with high values in July (out of a total of 29 in the entire data set). Neither line of stations shows a very coherent or consistent cycle of change at the station-70 meridian or at greater distances offshore at any time between 1969 and 1991. It is evident from an examination of these plots that the meridional line along station 70 chosen by Thomas and Strub (1990) to sea truth their corrected WCTS data does not accurately represent the sequence of large temporal changes taking place primarily inshore of this meridional line.

There are clear interannual differences to be seen in all of these *in situ* studies, and both Strub et al. (1990) and Thomas and Strub (1990) have emphasized this. But their failure to use winter data from any of the years they studied makes their observa-

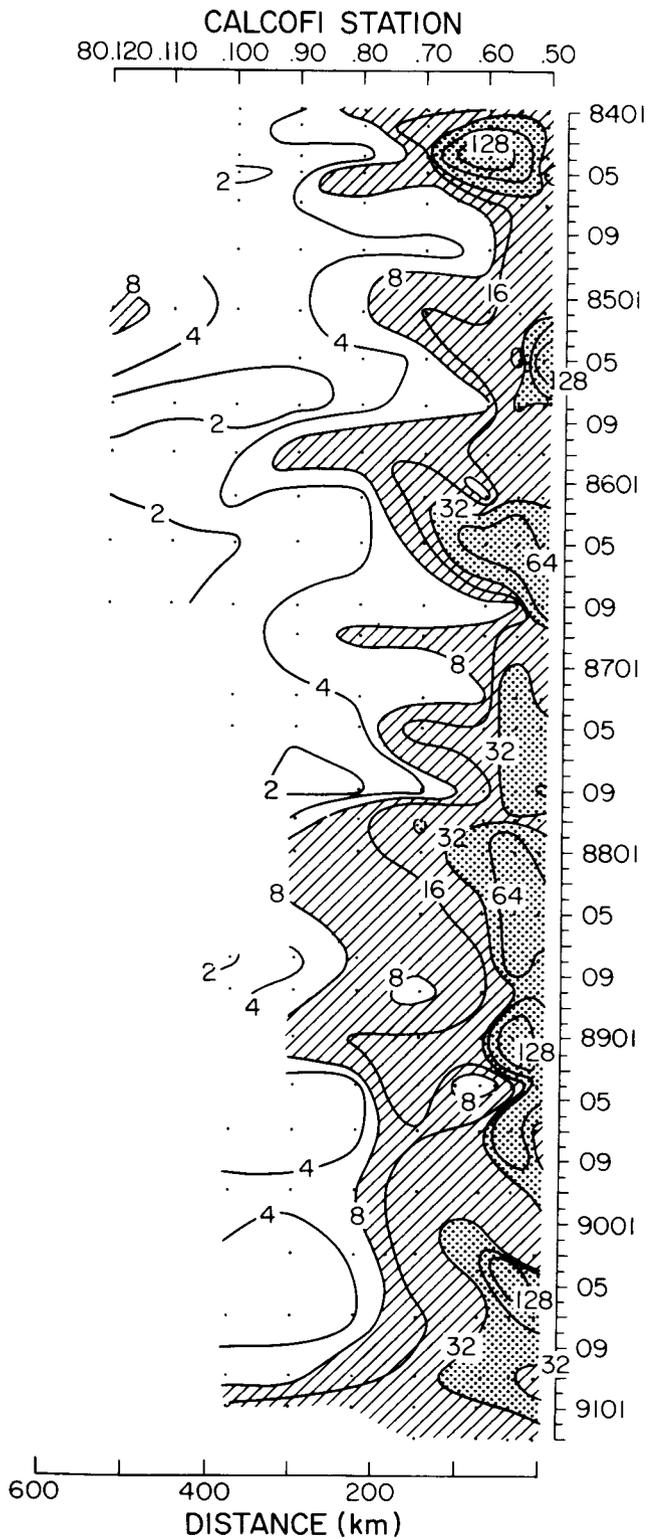


Figure 9. Time-space contours of *in situ* chlorophyll plus phaeopigments integrated over the depth range 0–20 m on CalCOFI line 80. Three samples over this depth range were generally taken.

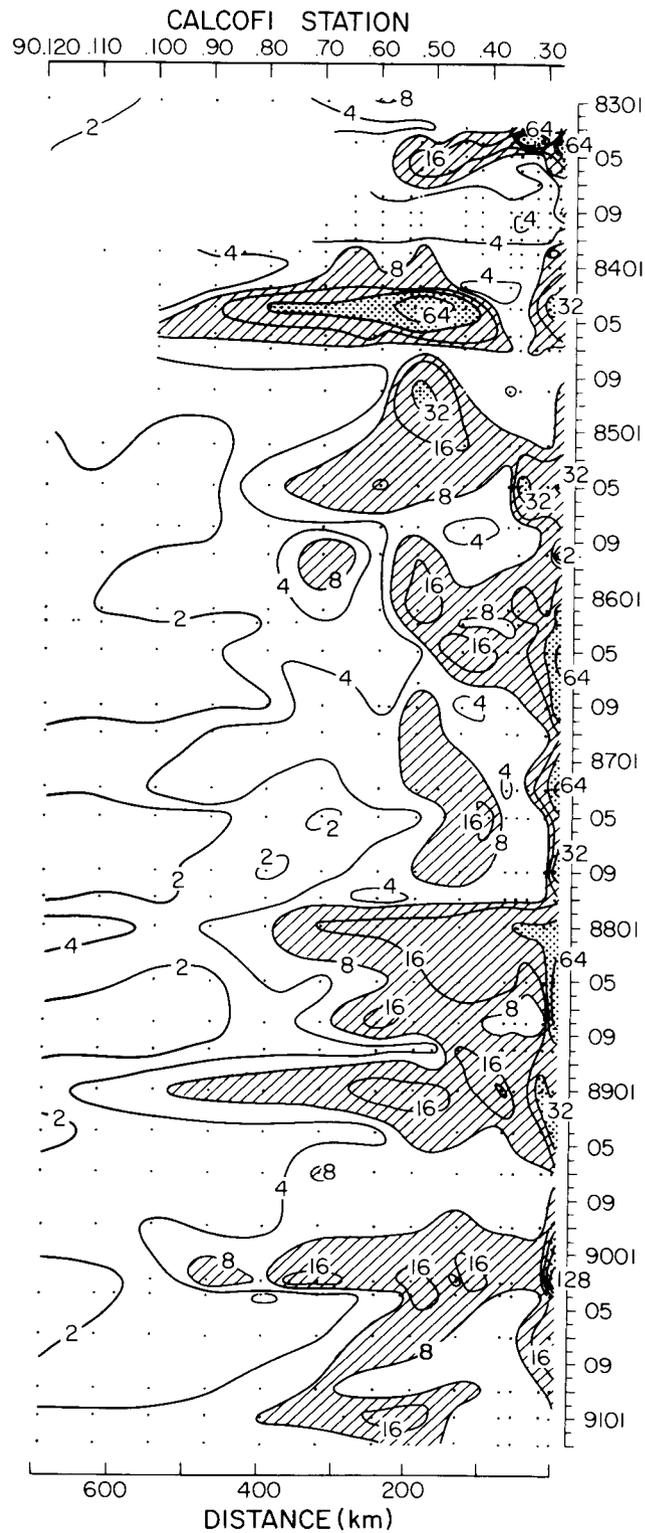


Figure 10. Time-space contours of *in situ* chlorophyll plus phaeopigments integrated over the depth range 0–20 m on CalCOFI line 90. Three samples over this depth range were generally taken.

tions somewhat dubious. Further, the well-known decline in phytoplankton standing crop during the 1983 El Niño (Fiedler 1984; McGowan 1985) accounts for most of their "interannual" changes. Thus the view that there is a "strong seasonal cycle with a spring-summer maximum" outside the bight is not supported by these *in situ* studies; at best the signal is only nearshore, inconsistent, and quite weak.

CONCLUSIONS

The West Coast Time Series in its original version, based on a single-scattering Rayleigh algorithm, provided data that systematically overestimated winter chlorophyll values in the California Current as compared to our *in situ* data. There is clear evidence from the very near shore that it also underestimated late spring and summer concentrations. This calls into question the results of many previous (before 1990) California Current studies based on these uncorrected WCTS data. The studies are, to an unknown extent, biased because of the strong seasonal error in the data. Strub et al. (1990) attempted to correct the error in the WCTS single-scattering algorithm by assuming that *in situ* chlorophyll values are low and essentially nonseasonal "some" distance from the coast. This assumption may be validated by our *in situ* data, depending on just how far off the coast one looks (figures 9 and 10). Along line 90, chlorophyll values can be substantial even 400 km offshore, and although not seasonal, they certainly vary with time. Strub et al. (1990) derived a correction function dependent on month and latitude, based on their assumption, and subtracted it from the monthly CZCS-WCTS data. They checked this correction against West Coast values from the multiple-scattering "global CZCS" data. They state that this comparison of annual cycles based on the two data sets (corrected WCTS and "global CZCS") indicates that "major conclusions about the March-through-October cycle in the California Current" will not be "changed" when the new WCTS is available. This may very well be true for some researchers, but the fact remains that our extensive *in situ* data provide no convincing evidence for a general summer maximum outside of the Southern California Bight and only weak evidence within the bight itself. The only "strong" *in situ* seasonal mean signal is at Scripps Pier, where May, on average, is high. The magnitude of this peak is due mainly to an unusual red tide in May 1985.

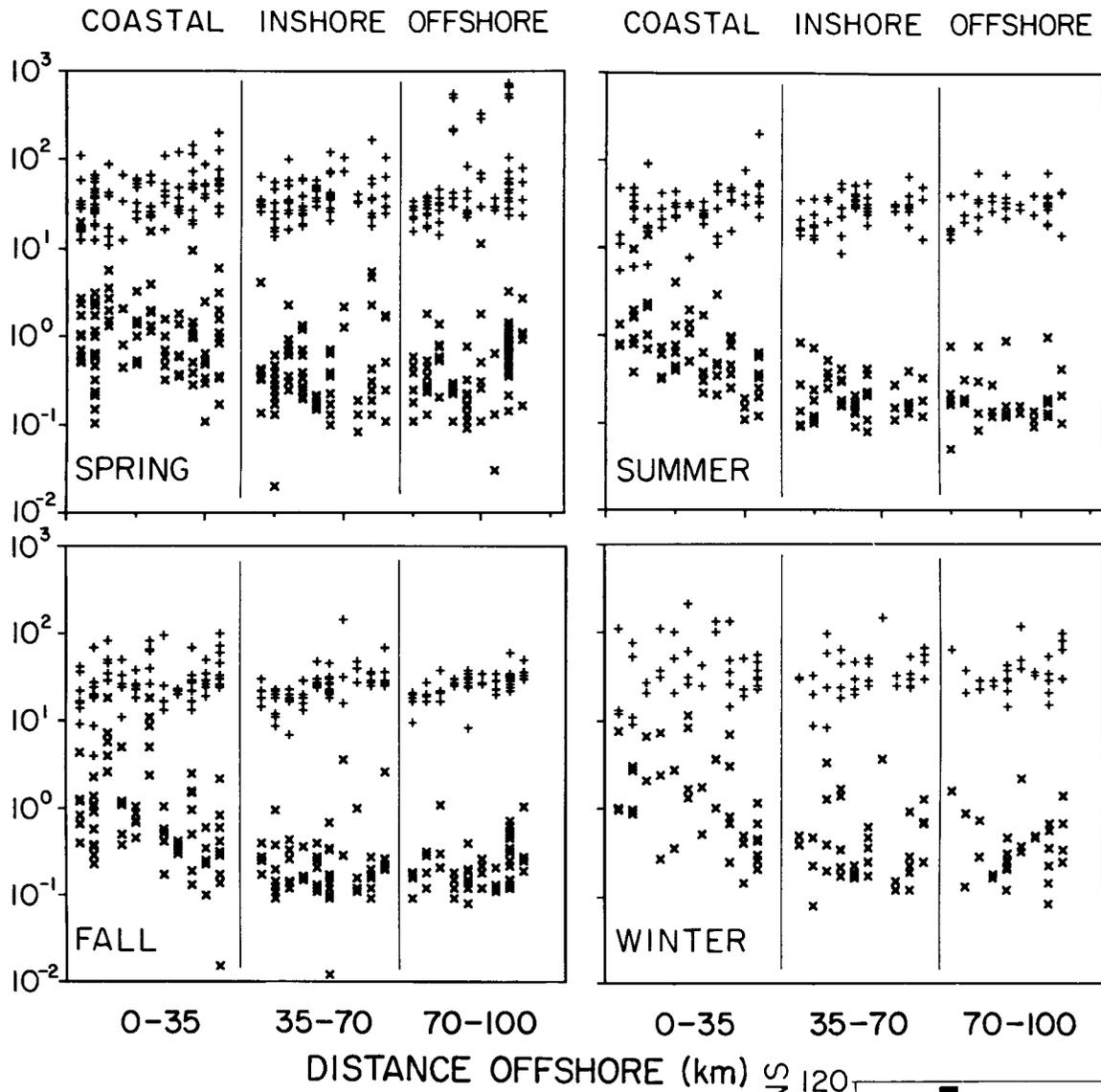
Michaelsen et al. (1988) — in order to explain their results of winter maxima and summer minima in

the upper layer, although water column chlorophyll peaks in early summer — have suggested that strong subsurface maxima and surface minima develop during the "spring upwelling season." The satellite radiometer would, in this case, be unable to detect the deep chlorophyll maximum. When we separate our combined CalCOFI-SCBS data into coastal, mid-bight, and outer bight and compare integrated to surface chlorophyll by season (figure 11), we see little support for this hypothesis. There is, however, an onshore-offshore trend in all seasons for surface chlorophyll to be higher in the very near coastal zone (within 10 km) than in mid or outer bight. This is also a consistent feature of all satellite images. There are well-developed, offshore, deep chlorophyll maxima (Venrick et al. 1973), but as yet no extensive study of their changes with time has been made.

Finally, the overall relation between *in situ* measured surface pigments and integrated water-column concentrations is not very useful for predictive purposes (figure 12). Even in winter, where the slope of the regression line is strongly positive, the main body of the data varies by a factor of over 5.

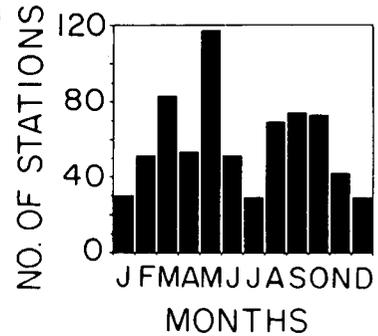
This uncertain relationship is also seen in the 0–20-m *in situ* concentrations and the 0–150-m data (tables 1 and 2; figures 6 and 7) where there is agreement only about half of the time on which months are above the annual mean. Further, the ranges, standard deviations, and coefficients of variability (SD/\bar{x}) differ considerably between the two data sets. Even if the satellite did a perfect job of estimating the concentration of chlorophyll in the upper 20 m, it would not be a good estimator of water-column concentrations and their variability, a fact pointed out by Hayward and Venrick (1982) some time ago.

Throughout this paper we have emphasized the lack of correspondence between the satellite determination of space-time patterns and those measured *in situ*. We have implied that the differences are due solely to error in the satellite-derived data. This may not be entirely the case. In their discussion of the sources of error in satellite color data, Chelton and Schlax (1991) point out that small-scale, horizontal heterogeneity is "effectively averaged out by the 1km footprint size of the CZCS." But this averaging out is not the case with our *in situ* measurements. We mentioned earlier that we have observed "outliers" in our data set, particularly during summers. If there are patches of high concentrations that are relatively small and well separated in space, then "outliers" like this can be expected. The question is, have we effectively sampled them? Our cruises were separated in time by quarterly intervals, or greater, and



+ INTEGRATED CHLOROPHYLL a (mg m^{-2})
 x SURFACE CHLOROPHYLL a (mg m^{-3})

Figure 11. The combined SCBS (5 depths) and CalCOFI (12 depths) integrated chlorophyll and surface chlorophyll by season, 1974-87.



our stations by about 72 km, so there is plenty of opportunity (except in the Scripps Pier data) for aliasing due to high-frequency variability in time and space. Because of this it is possible, but rather unlikely, that we have systematically underestimated the summer *in situ* concentrations. Only a

high-frequency, oceanic measurement program carried out for several years, such as the one at Scripps Pier, can give us much insight into this problem.

Satellite remote sensing of phytoplankton biomass is a potentially powerful tool for studying some aspects of oceanic biological systems. But we

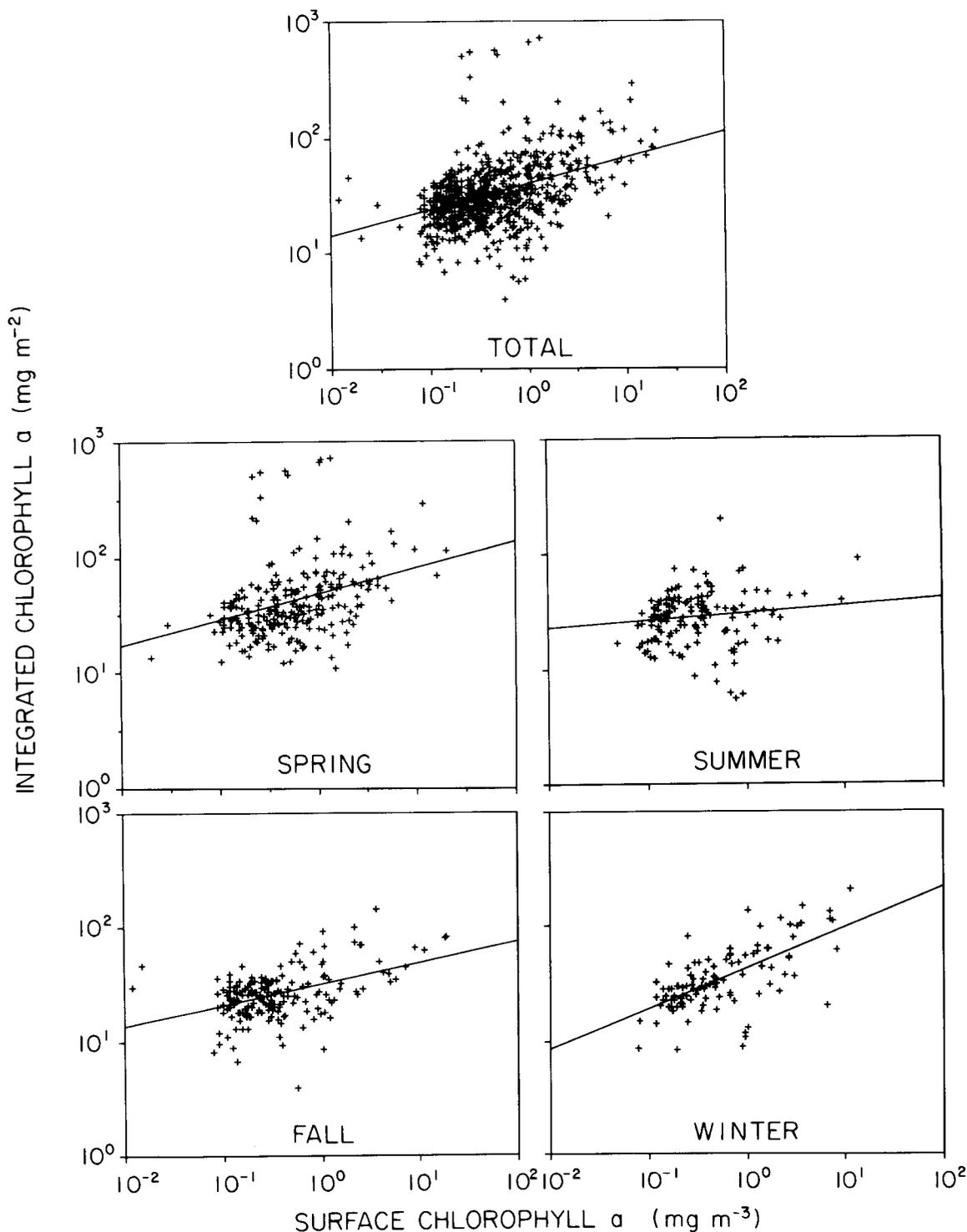


Figure 12. Scatter diagrams of integrated CalCOFI (1969–86) plus SCBS (1974–87) chlorophyll versus surface chlorophyll in the Southern California Bight by season, and overall.

must improve both precision and accuracy if we are to describe and understand the large-scale population biology of phytoplankton from the proxy measurements provided by this tool. Much better ground truthing is called for.

ACKNOWLEDGMENTS

The *in situ* chlorophyll measurements, made over the years by the CalCOFI and SCBS programs were the work of a number of dedicated marine technicians, and we are indebted to them. The Scripps Pier

measurements were made mostly by P. Walker, who also processed the data and originated tables 1 and 2 and figures 6, 7, 9, and 10. We received much good help from the staff at the Jet Propulsion Laboratory, who provided us with the CZCS-WCTS data. We are also grateful to M. M. Mullin and A. Tubbs for their help. This work was supported, in part, by NASA grant NAGW-1237, and in part by the Marine Life Research Group, Scripps Institution of Oceanography, University of California, San Diego.

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A CONCEPTUAL FRAMEWORK FOR THE OPERATIONAL FISHERIES OCEANOGRAPHY COMMUNITY

JAMES J. SIMPSON
Marine Life Research Group
Scripps Institution of Oceanography
University of California, San Diego
9500 Gilman Drive
La Jolla, California 92093-0237

ABSTRACT

A conceptual framework is developed for interactions among the diverse groups involved in operational fisheries oceanography: fishing industry, basic and operational researchers, and tactical and strategic stock assessment managers. These interactions originate in a need for accurate and timely information, information so complex and diverse that no single sector of the community can efficiently and economically satisfy its own information requirements. Some methods of gathering and analyzing presently available remotely sensed data to provide such information are discussed.

RESUMEN

Se desarrolla un marco conceptual de las interacciones entre los grupos que participan en los aspectos operativos de la oceanografía pesquera: industria pesquera, investigadores "básicos" e investigadores enfocados en aspectos operativos, y administradores de la evaluación de los "stocks", tácticos y estratégicos. Las interacciones se originan de la necesidad de información precisa y oportuna; la información es tan compleja y diversa que ningún sector de la comunidad por separado puede satisfacer de manera eficiente y económica sus propios requerimientos (de información). Se discuten algunos de los métodos actuales de coleccionar y analizar los datos usados para proveer la susodicha información; los datos se obtuvieron de sensores remotos y se encuentran disponibles actualmente.

INTRODUCTION

Since about 1979, remote sensing has played an increasing role in both the management and utilization of marine fisheries. Remote-sensing products have been used to (1) assist both the commercial and sports fishing industries in harvesting fish from the sea (e.g., Svejksky 1989); (2) provide marine resource managers with information useful for assessing the survival of fish eggs and larvae to the juvenile stage within a given year class (e.g., Pelaez and McGowan 1986; Simpson 1987); and (3) indicate the onset of major interannual events (e.g., ENSO and

associated mid-latitude warming events) that may threaten a local fishery (e.g., Fiedler 1984). Likewise, there has been an increased awareness of the importance of both remotely sensed and *in situ* environmental data for understanding the scientific basis of marine fisheries (e.g., Lasker 1975; Parrish *et al.* 1981; Leggett 1984; Simpson 1987), as well as for the intelligent management (e.g., Tillman 1968; Ushakov and Ozhigin 1987), and use (e.g., Laevastu and Bax 1989; Hogan and Clarke 1989) of the marine fisheries resource. Moreover, recent advances in data acquisition, digital mass storage of data and communications technologies, coupled with more powerful analysis methods, indicate that satellite and environmental oceanography will play a considerably expanded role over the next decade in all aspects of marine fisheries, especially in terms of near-real-time support of actual fishing activity. This paper presents some of the benefits to be gained from the increased use of remote sensing in operational fisheries oceanography.

AN INTERACTION MATRIX

In this section an attempt is made to describe some activities of the various sectors of the operational fisheries oceanography community (i.e., fishing industry, tactical and strategic stock assessment managers, and basic and operational researchers) and to identify common needs and linkages between these sectors.

Fishing Industry

The fishing industry's primary concern should be to harvest economically a given resource from the sea in such a way as to insure its continued, long-term use (figure 1). Thus, the fishing industry should constantly try to optimize catch per unit of effort without jeopardizing the fecundity of the stock. Unfortunately, this has not always been the case: in some circumstances (e.g., the California sardine fishery) the desire for short-term economic gain, coupled with inadequate resource management and an inability to properly observe and recognize early, major, interannual, environmental

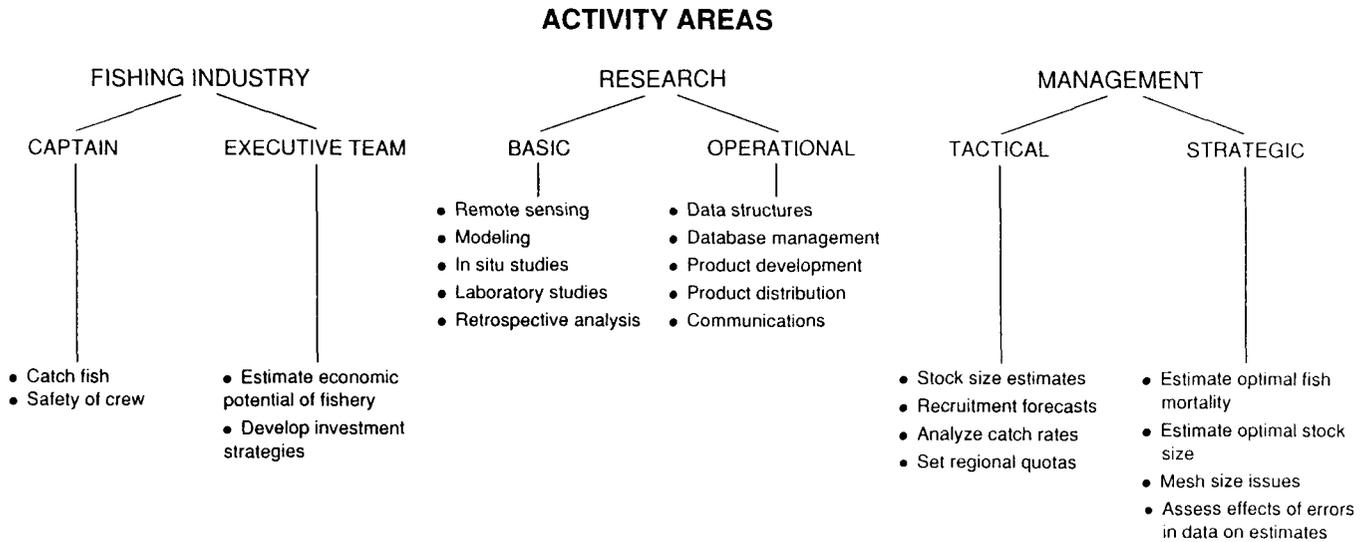


Figure 1. Conceptualization of the various sectors involved in operational fisheries oceanography and some of the functions performed by each.

changes in the fishery (e.g., the 1940–41 ENSO mid-latitude warming event), has led to the collapse of a fishery.

Most offshore fishing can be profitable only on aggregations such as shoals, or where the density of fish per unit area is high (Laevastu and Bax 1989). Fish aggregations may be purposeful (i.e., for spawning), or may be associated with feeding and migration. Major environmental factors that tend to produce aggregation are temperature, coastal and bathymetric boundaries, currents, and salinity. Thus, fish often aggregate near oceanic fronts; that is, at boundaries between water types and currents. Satellite data and modern methods of digital image analysis make it possible to accurately detect the near-surface expression of these boundaries, follow their evolution in space and time, and determine the velocity and current shears associated with them. Advances in communications technology make such information available in near-real time to help optimize fishing operations. Remotely sensed data also can be used to monitor storms and, in polar regions, to identify sea ice–ocean boundaries. These latter two analyses can lead to a safer fishing environment (e.g., in the North Atlantic cod fishery).

Most captains of fishing vessels do not have the time or training to obtain and analyze, in a state-of-the-art fashion, satellite or *in situ* oceanographic data. Moreover, the economics of fishing, of which the need for prorated capitalization (e.g., vessel, processing plant costs) is only one factor, should motivate commitment to conservation on the part of the fishing industry (figure 1). This commitment to conservation can be effective even if it is better expressed as a desire on the part of the fishing indus-

try for good (i.e., technically sound and informed) counsel from stock assessment managers. Ultimately, the quality of such counsel is critically dependent upon the availability of reliable, near-real-time data on catch: data that can come only from the fishing industry. Thus the exchange of accurate information between members of the fishing industry and stock assessment managers represents the only practical way to insure a long-term, economically viable fishery. Efforts must be made to educate the fishing industry of the benefits to be obtained from such an exchange of information.

Fisheries Management

Fisheries management often consists of groups of fisheries biologists and stock assessment personnel who are required to monitor or predict fish stocks and recommend total allowable catch (TAC) on a species-by-species basis (figure 1). The basis for management of a given fishery usually involves an estimate or prediction of mortality and/or recruitment. (Recruitment is taken as a measure of variable year-class strength established by the time of the juvenile stage.) The ratio of the importance of the two measures (mortality vs. recruitment) is species dependent, with relative importance being determined largely by how long the fish lives. For squid, which live for only one year, recruitment is the key to management success; for rockfish, which live to 70 years and hence have many year classes in the fishery, recruitment data are tactically less important than mortality data for good management of the stock.

Accurate estimates of either mortality or recruitment are difficult to make because data are limited

and the scientific basis for the tactical estimate is uncertain. For example, observationally based estimates of mortality are often determined empirically (e.g., Reed et al. 1989), depend upon assumed or measured patch size (McGurk 1986), and may have regional dependencies. Such estimates describe only observed change and do not distinguish between contributions from physical processes (e.g., advection, temperature) and mortality; thus a decrease in concentration can serve as an estimate of mortality only if one assumes no significant physical change (Reed et al. 1989). In general, however, such an assumption is not likely to be valid. For example, advection affects both mortality and recruitment because it can carry eggs and larvae into areas poor in food, rich in predators, or both. Conversely, water movement can carry eggs and larvae into areas rich in food, poor in predators, or both. The precise effects of water motion on a biological population depend upon the detailed phase relation (where and when) between the space-time history of the population and the environmental factors that form its habitat (Simpson 1987). English sole off Oregon (Kruse and Tyler 1989) and the cod fishery of Hecate Strait, British Columbia (Tyler and Westrheim 1986; Tyler and Crawford 1991) illustrate the importance of transport.

Spawner-recruitment models also have been used to estimate fish mortality between spawning and recruitment (e.g., Rothschild 1986). Wooster and Bailey (1989) point out that the most common models are those of Richer (1954) and Beverton and Holt (1957); both models contain density-dependent and density-independent terms. The density-dependent term, through compensatory mortality, has the effect of reducing recruitment with increasing stock size. Although compensatory mortality acts on new recruits in both models, the mechanism of interaction is interpreted differently. The Richer model emphasizes the role of predation (e.g., predators and cannibalism), whereas the Beverton and Holt model emphasizes starvation (i.e., pre-recruits increase with increasing spawner abundance, but the amount of available food per fish decreases). The underlying assumptions of such models, however, are far from universally accepted. Jones and Henderson (1985) conclude that, in general, little evidence exists for a significant relation between spawners and recruits in fish species. Other studies (e.g., Hollowed and Bailey 1989; MacCall 1990) find some density-dependent spawner-recruit relations but have difficulty separating these relations from density-independent effects. Thus the job of stock assessment managers to establish, on a species-by-species basis, realistic

and profitable TACs to ensure resource fecundity is an unenviable task limited by both inadequate near-real-time observations and an inadequately developed scientific basis for management. Present and planned remote-sensing instrumentation, improved methods of digital image analysis, and the development of meaningful environmental/biological indices using satellite data (i.e., those that relate directly to stock assessment) provide a means of mitigating one of these handicaps; namely, the lack of adequate, near-real-time observations.

Mortality and recruitment data, however, are not solely related to the conservation side of stock management. In fact, accurate estimates of both mortality and recruitment can help insure more efficient harvesting of a given stock through improved estimates of abundance (e.g., Wooster and Bailey 1989). Stock assessment managers should use this latter relation to educate and encourage the fishing industry (i.e., it's in their own best interests) to provide accurate catch statistics for management use.

Finally, a distinction should be made between tactical and strategic management of a given fisheries resource (figure 1). Tactical management (e.g., Megrey and Wespestad 1990; Stocker and Leaman 1990; Anthony 1990) estimates stock size for the current year, forecasts recruitment, and analyzes catch rates and events in the fishery. This information is used to decide on quotas, establish allowable fishing areas, and determine the opening and closing times of the fishery. Strategic management (e.g., Cook and Copes 1987; Murphy et al. 1990; Zhang and Gunderson 1990) is concerned with mesh size, optimal fishing mortality given growth and natural mortality, optimal stock size for maximal recruitment, and how to handle errors in measured data and derived fishing indices. Clearly, a well-managed fishery is guided by closely coordinated tactical and strategic stock assessment decisions.

Research

Research activity can broadly be divided into basic and operations research. Both require environmental information and catch statistics that, in part, must be supplied by the fishing industry (figure 1).

Basic research addresses questions that can provide a better scientific basis for operational fisheries oceanography. Clearly, improved understanding of the environmental and biological processes that influence both recruitment and mortality is a central concern of basic fisheries research—a concern that relates directly to both the tactical and strategic needs of stock assessment (figure 1). For example, basic research must develop a theoretically sound

means for determining the temporally and spatially varying relative importance of advection (e.g., Parrish et al. 1981; Simpson 1987) vs. starvation (e.g., Hjort 1914; Lasker 1975) vs. predation (e.g., Hunter 1981; Parsons et al. 1984) in the recruitment process of a given fishery. Also, methods need to be developed for separating the effects of density-dependent vs. density-independent factors in spawner-recruitment models used to estimate mortality. Basic research advances in these two areas alone will directly improve the ability of stock assessment personnel to develop better strategies and improved tactical indices for monitoring and managing a given fish stock.

The examples cited above are only two of the many fundamental environmental-biological questions that need to be studied if the complex interactions between fish and environment are to be clearly understood. Basic questions such as these, however, require a broad spectrum of research activity for proper resolution: (1) process-oriented experiments (e.g., Checkley et al. 1988; Rose and Leggett 1988); (2) laboratory studies (e.g., Theilacker 1986); (3) numerical models (e.g., Murdie and Hassell 1973; MacCall 1980); and (4) biogeographic and population dynamics studies (e.g., MacCall 1990). Remote-sensing analyses can provide real-time guidance for process-oriented experiments, some of the initial and boundary conditions needed by numerical models, data for validating the prognostic capabilities of such models, and data useful in biogeographical and population dynamics studies of marine fishes.

Operations research is concerned with the design of data structures that can provide an efficient and compact representation for environmental and biological data used in operational fisheries oceanography (figure 1). Such data structures are required to meet the ever-growing near-real-time support needs of a typical operational fishery, especially given the constraints and costs of present-day ship-to-shore communication networks. These data structures, in turn, are needed to build data bases to be used in developing and validating operational products useful to the community.

Operations research has many activity areas. This diversity is largely determined by the near-real-time needs of both the fishing industry and marine resource managers for data (e.g., catch statistics) or for operational products derived from data (e.g., sea-surface temperature charts) or models (e.g., wind-field analysis, marginal ice-zone analysis, fish mortality and recruitment analysis). Thus operations research activity includes, but is not limited to,

real-time data acquisition (e.g., satellite data); archiving and distribution (including near-real time and ship-to-shore) of processed data sets to support fishing activity; and the design and implementation of computer-assisted decision-making tools to help prevent information overload to bridge personnel. Operations research also should provide the focal point (figure 2) for the collection of information from the fishing fleet (e.g., length of fish, gonad statistics, infestation data) and the subsequent distribution of this information to other sectors of the fisheries community (e.g., stock assessment personnel). Moreover, this information provides the basis for both the validation and refinement of operational products supplied to the fishing fleet and for the development and refinement of basic research concepts.

Community Interactions

The basis for interactions among the various sectors of the operational fisheries oceanography community is a need for accurate and timely information. The information is so diverse and complex that no single sector of the community can effectively and economically gather all of the information it needs. In a very real sense, the information imperative translates into a pragmatic necessity; the various sectors will hang together (i.e., communicate and share data) or hang separately (not meet their respective objectives). The vehicle for interaction is a communications network. Operations research, by virtue of its functions (figure 1) and its position within the framework of the entire community (figure 2), is the logical sector to develop and maintain the communications network. These are the premises under which the following matrix of interactions for an operational fishery was developed.

The fishing industry uses information at two primary levels: (1) the executive team and (2) the captain, or skipper-group (Hogan and Clarke 1989). The executive team (figure 1) uses information to formulate strategies, policies, capital investments, and other corporate decisions that affect the socio-economic life of a fishing region (e.g., the Newfoundland cod fishery). These corporate decisions and actions are made within the framework of estimating the opportunities deemed to exist in the resource (i.e., the regional fish stocks) and the environmental factors governing their exploitation. Thus the fishing industry is critically dependent upon the stock assessment sector of the community to properly set TACs. A TAC that is set too high can result in an underutilized stock and probably economic hardship for the fishing region. Likewise, a

INFORMATION COMMUNICATIONS NETWORK

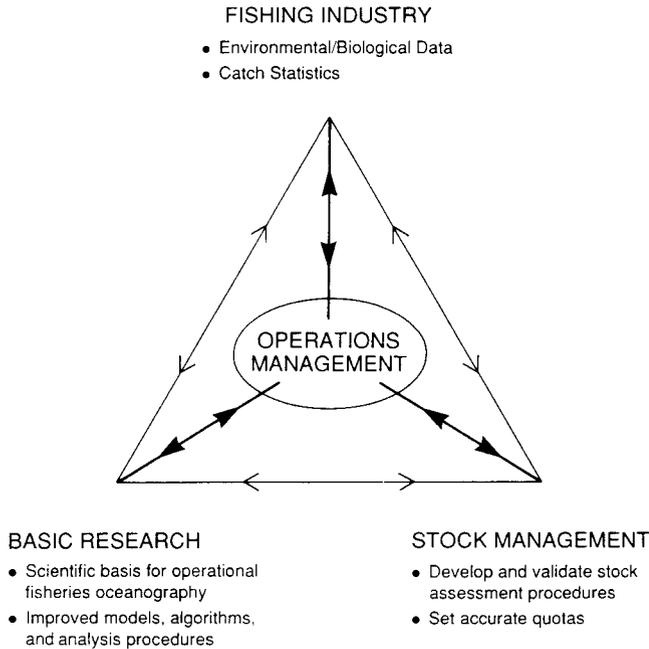


Figure 2. Conceptualization of the major types of communication linkages needed for a successful regional operational fisheries oceanography program. *Bold lines* indicate primary communications links via an operations research center. *Lighter lines* indicate secondary communications links.

TAC that is too low can result in an overutilized resource with potential long-term ecological and economic damage to the regional fishery. The captain, or skipper-group (figure 1) needs near-real-time information to make decisions and implement actions that affect the safety of crews and the efficiency of the fishing effort.

Traditionally, the fishing industry has been perceived as the “consumer” of information; the industry’s potentially important role as a data source for the rest of the community has largely been ignored (figure 2). A fishing vessel, which is at sea for well over 200 days a year, is virtually a floating information-collection platform (Hogan and Clarke 1989). At the least, estimates of catch per unit of effort can be made from fishing industry data. But the prospects for additional information are more exciting. Consider the Newfoundland cod fishery, in which cod are normally eviscerated upon catch. Evisceration makes it possible to collect gonad statistics and to estimate predator-prey relations; for example, cod gut contents (redfish, capelin, or sand lance) can be determined, and fish preying on the cod are hauled in with the cod and can be counted. Infestation data, discards of other biota, sightings of ceta-

ceans, the activity of foreign vessels in the regional fishery, and environmental data are additional types of information that other sectors of the fisheries oceanography community can glean from the fishing industry.

Both the strategic and tactical aspects of fisheries management need environmental and biological information. Strategic management issues (e.g., mesh size, estimation of optimal stock size, optimal fishing mortality, adult behavioral studies, and recruitment research) directly involve some aspect of operational fisheries oceanography. Tactical management issues — e.g., gathering indices of recruitment and mortality including ocean model predictions, survey design and covariates analysis, interpretation of events (varying catch rates) in the fishery caused by environmental factors (e.g., ENSO activity in the Northeast Pacific or severe winters in the Northwest Atlantic) — also require large amounts of high-quality environmental and biological data.

At present, the strategic side of fisheries management uses significantly more data than the tactical side. The tactical side of fisheries management, however, can reduce risk and uncertainty in a given fishery by more aggressively incorporating various oceanographic indices (developed in cooperation with basic fisheries research efforts) into assessment analyses. Remote sensing products developed within the context of operations research provide a basic source of information for such indices; planned instrumentation for the 1990s (e.g., SeaWiFS, MODIS) will expand this capability. The potentially diverse sets of fishing industry and historical data, collected and distributed via a communitywide communications network developed and maintained by operations research efforts, provide another source of data for developing and evaluating tactical fishing indices.

Two primary goals of basic fisheries oceanography research are (1) to provide a better scientific basis for both the use and management of an operational fishery; and (2) to develop improved algorithms and analyses for efficiently representing the state of a fishery from the large, diverse, and complex data sets needed to understand that fishery. Within this context the need for high-quality environmental and biological data is clear. Ultimately, the objective should be to translate advances in basic fisheries research into operational products that can improve both the use and management of the resource. Such products normally would be developed, evaluated, distributed, and maintained by operations researchers working in close collabora-

tion with the fishing industry and stock assessment managers.

The communications network, complete with products, historical data bases, current data bases, satellite data, and geographical reference data, provides feedback mechanisms for the entire operational fisheries oceanography community (figure 2). Operations research centers, funded jointly by government and industry, must be created to develop and maintain the required data bases, operational products, and communications network. These concepts, together with an extensive set of examples using remotely sensed data, are discussed in Simpson 1992, MS¹ and the references contained therein.

ACKNOWLEDGMENTS

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Part III

SCIENTIFIC CONTRIBUTIONS

A 250-YEAR HISTORY OF PELAGIC FISH ABUNDANCES FROM THE ANAEROBIC SEDIMENTS OF THE CENTRAL GULF OF CALIFORNIA

DIEGO HOLMGREN-URBA AND TIM R. BAUMGARTNER

División de Oceanología
Centro de Investigación Científica y de
Educación Superior de Ensenada
Ensenada, Baja California, México

ABSTRACT

The recent appearance of significant numbers of northern anchovy in the Gulf of California, along with the recent decline in sardine biomass, has prompted the fishing industry, agencies of the Mexican government, and the research community to ask whether similar events have occurred in the past. Are these events connected, and are they part of some long-term pattern? In order to answer such questions, we sampled and counted the fish scales in an 85-cm box core from the anaerobic varved sediments of the central Gulf of California. This core was collected from an area underlying one of the principal sardine spawning regions of the gulf. On the basis of these counts, we reconstructed time series of scale-deposition rates for Pacific sardine, northern anchovy, Pacific mackerel, Pacific hake (or a close variant), and an undifferentiated group of myctophids. The time series are resolved into 10-year sample blocks and extend from approximately 1730 to nearly 1980. These reconstructions show a strongly negative association between the presence of sardines and anchovies, with anchovies dominating throughout the nineteenth century, and with only two important peaks of sardine scale deposition—one in the twentieth century and one at the end of the eighteenth century. Both the mackerel and the myctophid group vary more like sardines than like anchovies (with the hake intermediate between anchovies and sardines). This suggests an overall coherent pattern in changing ecosystem structure that operates over a period of about 120 to 140 years.

By comparing the sardine and anchovy series from the Gulf of California to information from the California Current, we can examine this variability within a geographic as well as a temporal framework. Reference to the Northern Hemisphere air temperature adds another dimension to our interpretations of the inferred variability. The regional differences and relations to climate suggest that the populations (or stocks) of both species from the dif-

ferent regions do not vary independently through time. The concentrations of fish shift from one region to another over periods of several decades. The relation to climate is not yet clear, but altogether, the information here suggests that climate does mediate population sizes, but this process is still subject to strong filtering through biological interactions among species.

RESUMEN

Dos hechos recientes—la aparición de cantidades considerables de anchoveta noroesteña en el Golfo de California y la declinación de la biomasa de sardina—produjeron que tanto la industria como varias dependencias gubernamentales mexicanas y la comunidad científica se preguntaran si en el pasado ocurrieron eventos similares. ¿Cuál es la relación entre ambos sucesos? ¿Encajan en algún patrón a largo plazo? Para contestar estas preguntas, hicimos un muestreo y conteo de escamas de peces en un “núcleo-caja” de 85 cm, obtenido en sedimentos laminados anaeróbicos del Golfo de California central. El área donde se obtuvo el núcleo se encuentra en una de las principales zonas de desove de sardina en el golfo. Basándonos en estos conteos, reconstruimos series de tiempo de tasas de depositación de escamas de sardina Monterrey, anchoveta noroesteña, macarela, merluza (o una variedad afín), y un grupo de mictófididos. (Los mictófididos se analizaron en conjunto.) Las series de tiempo incluyen de 1730 hasta casi 1980, y tienen una resolución de bloques de muestro de 10 años. Las series muestran una correlación muy negativa entre la sardina y anchoveta. Las anchovetas dominan en el siglo diecinueve; en las tasas de depositación de escamas de sardina, solo hubo dos máximos, uno en el siglo veinte y otro a finales del siglo dieciocho. La variación de la macarela y los mictófididos se asemejó mas a la de la sardina que a la de la anchoveta. (La variación de la merluza fué intermedia, entre la de la sardina y la de la anchoveta.) Esto sugiere que el patrón de cambio en la estructura del ecosistema es coherente (con un período de 120 a 140 años).

Las series de sardina y anchoveta del Golfo de California pueden compararse con información

de la corriente de California para examinar la variación geográfica y temporal; la temperatura del aire del Hemisferio Norte añade otra dimensión a la interpretación de la variabilidad. Las diferencias regionales y la relación con el clima sugieren que las poblaciones (o stocks) de ambas especies de las dos regiones no varían independientemente en el tiempo. Las concentraciones de peces se desplazan de una región a otra en períodos de varias décadas. El papel del clima es aún poco claro; sin embargo, en conjunto, la información que aquí se presenta sugiere que el clima interviene en los tamaños poblacionales, pero que este proceso es filtrado por interacciones inter-específicas (y quizá intra-específicas).

INTRODUCTION

More than 25 years ago, Ahlstrom (1967) wrote, "The northern anchovy, a somewhat more temperate species [compared to the Pacific sardine] does not occur in the Gulf [of California] . . .". With what now seems an almost offhand comment, he relegated the problem of co-occurrence and/or alternation of the Pacific sardine with the northern anchovy in the Gulf of California to a "nonquestion" of the kind described by Oliver (1991, p. 43). In 1986, however, an unexpected catch of more than 2,000 MT of northern anchovy by the gulf sardine fleet (Hammann and Cisneros 1989) quickly made this an important issue, not only because of its implications for the commercial fishery, but for our understanding of the structure and stability of the gulf's pelagic ecosystem. By the end of 1992 the catch of Pacific sardine had plummeted from a 1988–89 peak greater than 250,000 MT (Cisneros et al. 1991) to 6,400 MT¹. Accompanying this dramatic decline in sardine catch, a significant by-catch of northern anchovy has persisted. In 1991–92 this by-catch nearly equaled the sardine catch, reaching a total of approximately 5,200 MT.

Industrial-scale exploitation of the Pacific sardine in the Gulf of California began in 1969, after exploratory fishing by the Ensenada fleet first detected significant volumes in 1967–68 (Solis-Villa 1981). The history of direct observations for the sardine is thus limited mainly to a 23-year time series of catch data. Fundamental questions arising from the appearance of the northern anchovy and the current decline of the Pacific sardine in the gulf are difficult to address with this 23-year data set; the changes appear unique in this time series but may not be unusual from the

perspective of variability over decadal-to-centennial time scales. Setting aside the uncertainty of whether the immediate cause of the sardine decline was overfishing, we should first determine whether or not we should have been surprised by these developments, from the perspective of a longer history of the ecosystem.

As the initial phase in reconstructing such a history, we have inventoried scale deposition in the anaerobic sediments of the central Gulf of California since the early part of the eighteenth century. Our initial motivation for this work was the need to address two specific questions about the pelagic fish populations. First, we wanted to know whether there is evidence for any significant earlier presence of northern anchovy in the gulf. Our second question was whether the population of Pacific sardine has gone through periods of decline during the past 250 years that may have been similar to the current decline. Our work has answered these two questions and led to a broader description of the pelagic populations by revealing not only the relationships between sardine and anchovy, but also their relationships with hake, mackerel, and myctophids. In our discussion we provide a larger context for considering the results by comparing the sardine and anchovy records from the Gulf of California with observations from the California Current and with a generalized history of global climate change since the mid-nineteenth century.

Although no prior attempt has been made to use the natural record of scale deposition in the Gulf of California to detect changes in fish populations, the value of such work for documenting and understanding pelagic fish populations has been established by the studies of Soutar and Isaacs (1969, 1974) and Baumgartner et al. (1992) on the anaerobic sediments of the Santa Barbara Basin off southern California. Deposition of distinct seasonal laminae several millimeters thick in both the Santa Barbara Basin and the gulf provide the natural calendars needed for the high-resolution reconstruction of scale deposition. The annual layers (known as varves) in the Gulf of California are preserved along the continental slopes where bioturbation is inhibited within the midwater oxygen minimum (Calvert 1964).

MATERIALS AND METHODS

Material used for this study was retrieved in the summer of 1978 with an open-vented Soutar box corer measuring 30 × 30 × 100 cm; the core was frozen on board ship. The coring site (7807–1305) lies approximately 650 m deep on the continental

¹Nevárez, M. O., M. Martínez, R. Morales, and P. Santos. 1992. Analisis comparativo de la pesquería de sardina en el Golfo de California; temporadas de pesca 1990/91 y 1991/92. CalCOFI program and abstracts, Annual Conference, Asilomar, Calif.

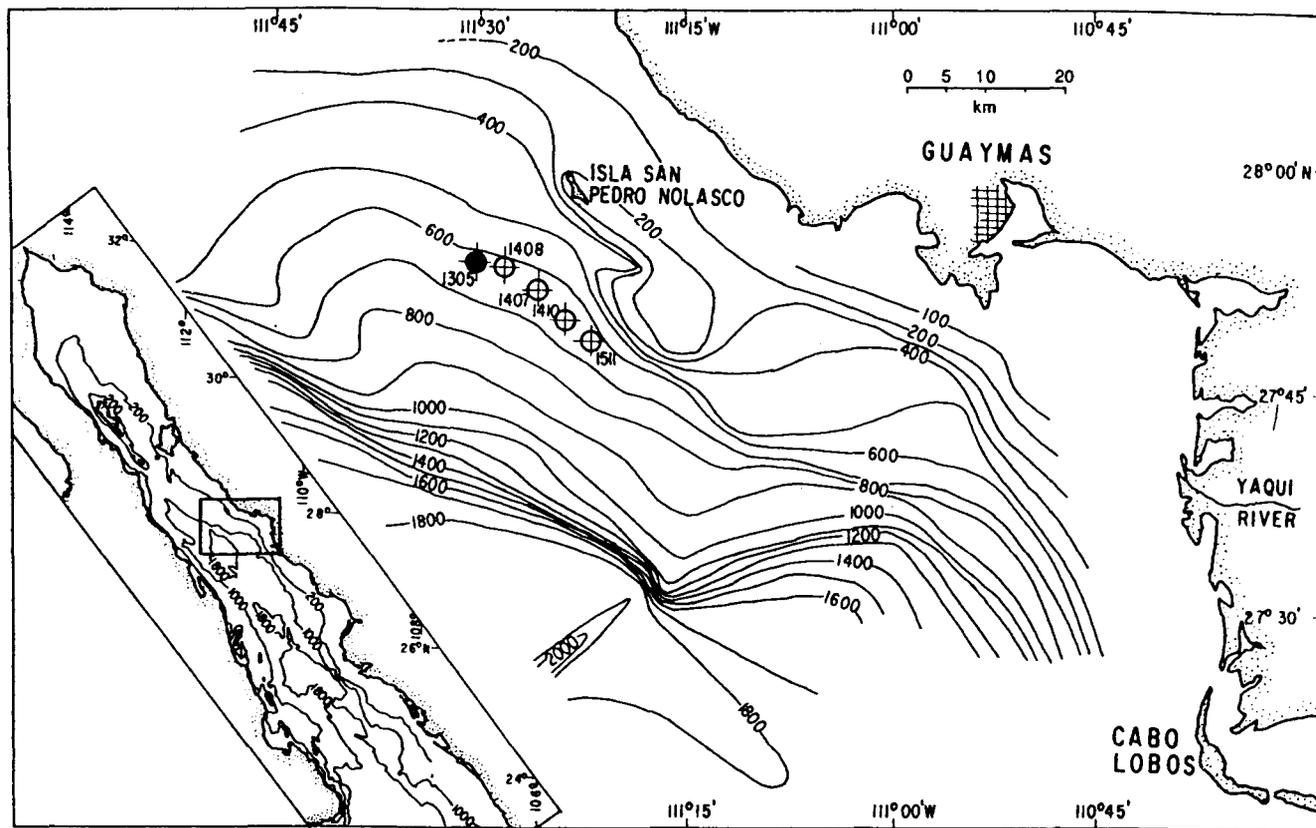


Figure 1. Solid circle, location of box core 7807-1305 on continental slope of the central Gulf of California. Open circles are locations of box cores used for reconstructing the twentieth-century varve chronology (Baumgartner et al. 1991).

slope off Guaymas, Sonora (figure 1), and is located within the Pacific sardine's principal spawning grounds in the gulf (Hammann et al. 1988). The core is approximately 85 cm long and represents sedimentation since the beginning of the eighteenth century. Coring and handling procedures are described in Baumgartner et al. 1991.

A sediment column equivalent to one-quarter of the core was dedicated to the analysis of fish scales; this represents an area of deposition of approximately 200 cm². The abrupt decrease in depositional area for the upper two samples (table 1) is due to deformation and loss of material associated with freezing of the core, which caused vertical doming in the laminae in the center of the core (more pronounced near the top of the core). Individual samples for scale counts constitute a continuous series of 10-year intervals cut from the sediment column; varve boundaries were identified visually from photographs of the exposed faces of the sediment column.

A detailed master chronology for the Guaymas Slope was developed for the twentieth century by Baumgartner et al. (1991) from cross-correlation and independent radiometric dating of the five (in-

cluding core 1305 used in this study) taken from the sites shown in figure 1. Although varve preservation is excellent over the past 250 years, the lateral continuity of the varves along the slope is occasionally disrupted by small-scale, secondary mass movement (described in Baumgartner et al. 1991). This has delayed development of a well-constrained, year-by-year chronology like that attained for the period after A.D. 1910. For the period before 1910 our chronology is based only on varve counts from core 1305 (as opposed to cross-dating among the five available box cores). We estimate the resulting chronological uncertainty to be approximately 10 years at the bottom of the core, which is dated to the nearest 5 years as A.D. 1735.

Each of the 25 samples was thawed and washed through 500- and 250- μ m sieves with the aid of a dispersant (Kodak Photo-Flo) in order to separate the fish scales and other remains from the sediment. The sieved residue was preserved in a solution of 60% ethanol. We used a Wild stereo microscope to identify the fish scales, and counted them from both size fractions of the wet subsamples. Identifications were made with the aid of the reference collection

TABLE 1
 Fish-Scale Data by Sampling Interval Based on Preliminary Varve Chronology of Box Core 7807-1305,
 Central Gulf of California

Sample interval	Area cm ²	Anchovy		Sardine		Hake		Mackerel		Myctophids	
		N	SDR	N	SDR	N	SDR	N	SDR	N	SDR
1970-80	61.3	0	0.0	0	0.0	0	0.0	0	0.0	4	8.7
1960-69	61.3	0	0.0	2	3.3	1	1.6	3	4.9	25	40.8
1950-59	186.3	0	0.0	3	1.6	1	0.5	2	1.1	95	51.0
1940-49	186.3	0	0.0	13	12.1	3	1.9	1	1.0	58	56.5
1930-39	177.1	0	0.0	4	1.7	0	0.1	2	1.9	119	108.3
1920-29	222.2	0	0.4	1	0.3	1	0.9	8	3.6	454	165.9
1910-19	168.4	3	1.8	0	0.0	4	2.4	6	3.6	64	38.0
1900-09	175.9	7	4.0	0	0.0	1	0.6	0	0.0	94	53.4
1890-99	192.5	10	5.2	0	0.0	2	1.0	0	0.0	44	22.9
1880-89	202.7	7	3.5	0	0.0	1	0.5	0	0.0	67	33.1
1870-79	194.7	114	58.5	0	0.0	3	1.5	4	2.1	69	35.4
1860-69	206.9	21	10.1	0	0.0	1	0.5	1	0.5	54	26.1
1850-59	224.9	20	8.9	0	0.0	3	1.3	0	0.0	30	13.3
1840-49	192.2	0	0.0	0	0.0	0	0.0	0	0.0	15	7.8
1830-39	216.2	5	2.1	0	0.0	0	0.0	0	0.0	17	7.1
1820-29	203.6	2	2.5	0	0.0	0	0.0	0	0.0	55	67.5
1810-19	197.5	1	0.5	0	0.0	0	0.0	0	0.0	99	50.1
1800-09	205.6	0	0.0	0	0.0	0	0.0	0	0.0	8	3.9
1790-99	184.0	1	0.9	4	5.0	0	0.0	10	9.1	262	237.3
1780-89	197.5	4	2.0	1	0.5	0	0.0	13	6.6	118	59.7
1770-79	204.2	5	2.4	2	1.0	0	0.0	0	0.0	69	33.8
1760-69	214.0	5	2.3	0	0.0	0	0.0	0	0.0	3	1.4
1750-59	197.8	2	1.0	0	0.0	1	0.5	0	0.0	14	7.1
1740-49	197.8	7	3.5	0	0.0	1	0.0	1	0.5	100	50.5
1730-39	197.8	4	3.4	0	0.0	1	0.8	2	1.7	40	33.7

Area = measured depositional surface of each sample. N = number of scales in 10-year interval. SDR = scale-deposition rate per year normalized to depositional area of 1000 cm². Note that where sample intervals do not encompass a full 10 years of deposition (i.e., first and last intervals, 1734-39, 1970-78; and intervals interrupted by hiatuses: 1820-29, 1940-49), the SDR values are still normalized to represent a 10-year interval.

assembled by A. Soutar at the Scripps Institution of Oceanography complemented by a collection assembled at CICESE.

It is important to note that these data were obtained from a single box core and, for now, must be considered without recourse to replicates from the same core or from other cores within the study area. However, the 200-cm² sample of depositional area provides a considerably higher margin of reliability for the scale counts than for any single sample in previously published work (cf. Soutar and Isaacs 1974). Careful analysis by Baumgartner et al. (1992) has shown that counts made for sampled areas as small as 30 cm² yield between-core results that are reproducible over distances of approximately 7 kilometers in the Santa Barbara Basin.

RESULTS

In addition to scales of *Sardinops sagax*, significant numbers of scales of Pacific mackerel (*Scomber japonicus*) and a large number from *Engraulis mordax* were found. There also is a significant presence of hake (*Merluccius angustimanus*?) with scales indistinguishable from Pacific hake, *M. productus*. Difficulty in distinguishing among scales of the various myctophids led us to lump all mesopelagic species of this

group into a single category of "undifferentiated myctophids." Holmgren-Urba (1993), however, shows that most of the variation in the myctophid group can be explained by *Benthosema panamense* and *Diogenichthys laternatus*.

The data needed to reconstruct scale-deposition rates are given in table 1. These include the measured area of depositional surface for each sample and the number of scales found in each 10-year sample block. Scale-deposition rates (SDR's) are reported as number of scales per 1,000 cm² per year to allow direct comparison with plots in Soutar and Isaacs 1974 and Baumgartner et al. 1992. We emphasize here that the dates of the sample intervals are based upon a preliminary chronology that we expect to refine in the future. However, we do not expect accumulative changes downcore to be greater than about 10 years.

Scale-deposition rates for each of the five species or groups are plotted in figure 2. This figure provides a clear and resounding answer to the question of whether the northern anchovy has been present prior to its appearance in the late 1980s. The data plotted in figure 2 demonstrate that *Engraulis mordax* was sufficiently abundant to leave a record of its scales from the early part of the eighteenth century

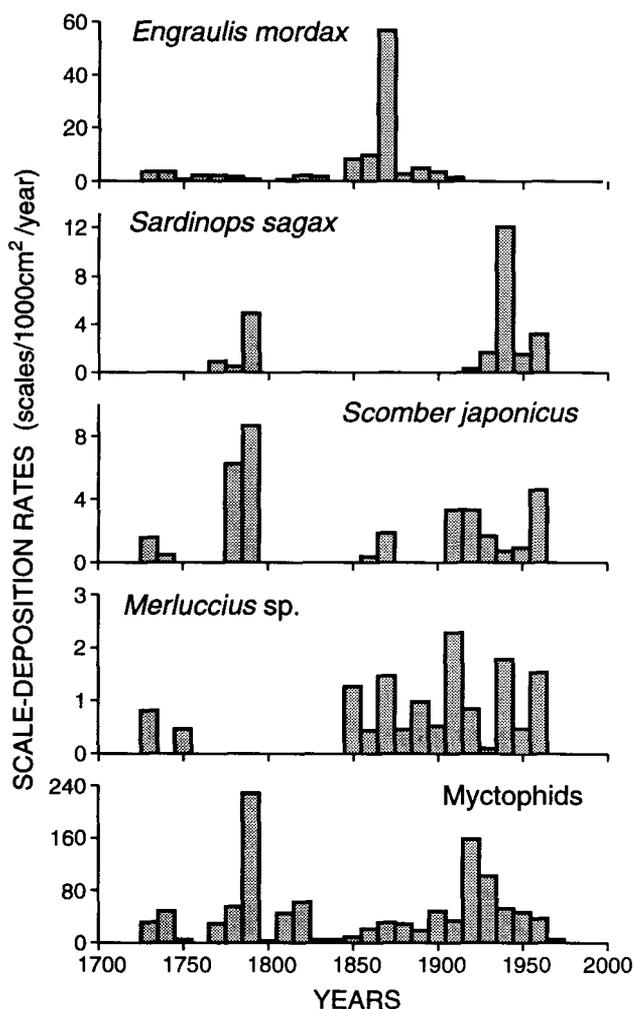


Figure 2. Time series of scale-deposition rates of *Engraulis mordax*, *Sardinops sagax*, *Scomber japonicus*, *Merluccius* sp., and the myctophid group reconstructed from box core 7807-1305 collected from the Guaymas Slope in the central Gulf of California. The time series covers the period from 1730 through 1980 and is resolved into 10-year intervals. Note that the chronology below 1910 is preliminary and has an associated uncertainty of approximately ± 10 years.

and persisted through the decade of the 1920s. The large peak in the anchovy SDR's suggests an abrupt expansion followed by an equally abrupt decline of the anchovy biomass in the gulf around the decade of the 1870s.

Looking beyond the presence of the anchovy, we find the pattern of sardine presence/absence adds another very important aspect to this history by its striking relationship to the anchovy record. The two episodes of sardine scale deposition occur virtually 180° out of phase with anchovy scale deposition. Table 1 and figure 2 show that the major transition between anchovy and sardine scale deposition in the early twentieth century occurred with only one decade of overlap (the 1920s). The peak of sardine scale deposition at the end of the eighteenth century was

accompanied by a measurable decrease in the anchovy SDR followed by a decade of no anchovy scales (1800–1809; see table 1).

The record of mackerel scale deposition is much more similar to the sardine pattern than to the anchovy pattern. This is seen in the strong peak of mackerel SDR in the late eighteenth century, its poor representation during the nineteenth century, and its return in the twentieth century (displaying, however, a locally inverse relationship with the sardines between 1910 and 1970).

The pattern of the myctophid record also resembles the sardine series. In particular, the two very large peaks in myctophid scale deposition occur in almost perfect synchronicity with the increase in sardine scale deposition of the late eighteenth and early twentieth centuries. Like the sardines, the myctophid group also appears to vary roughly 180° out of phase with the anchovies.

The hake record in figure 2 is the most different from all other records of scale deposition and thus adds another dimension to the information from the scales. We can characterize the hake from another approach by noting the presence of hake scales during the anchovy peak of the 1870s, during the sardine-anchovy transition (reaching a maximum value during the decade of crossover between the anchovies and sardines), and continuing into the twentieth century with the sardines.

The relations among the five time series are summarized more succinctly in figures 3 and 4. These figures show the plots of the cross-correlation functions for each pair of the species in figure 2. The correlations have been calculated with the log-transformed data (natural logarithm) of the original series. This provides smoother curves of the lagged correlations and more emphasis on the negative correlations without altering the overall pattern (see Holmgren-Urba 1993). Because the effects of autocorrelation (relative to the length of the series) severely reduce the effective degrees of freedom, these figures should be used more to describe and compare the associations among the species than to determine absolute measures of significance. Of course, the degrees of freedom are also decreased with the increasing lags. Correlation values of approximately 0.5, in the neighborhood of 0-lag are, however, significant at a level of 95% confidence.

The plots in figures 3 and 4 are grouped according to distinct patterns of the cross-correlation functions. The plots in the left-hand column of figure 3 exhibit a pattern similar to that of a sine wave. This pattern is best developed for the comparison between the anchovy and sardine, with the best fit

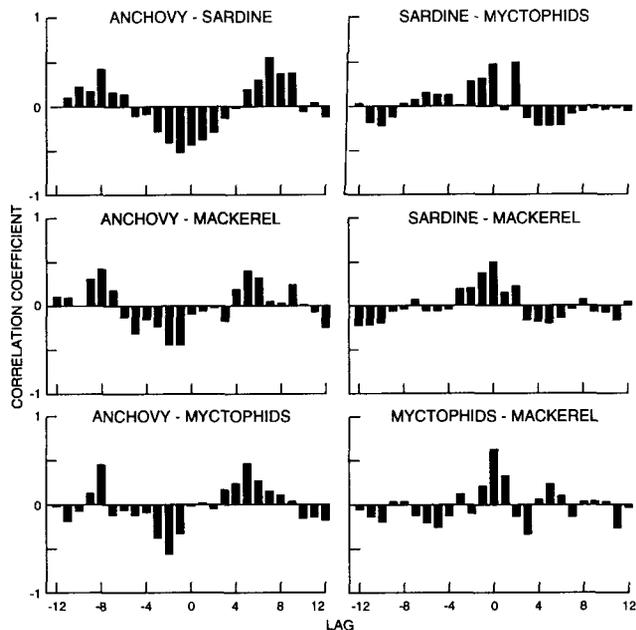


Figure 3. Cross-correlation functions of the time series of pairs of taxa formed from the combinations of the anchovy, sardine, mackerel, and myctophids in figure 2. Correlations have been calculated for the log transformations of the data in the figure 2 series. Plots are arranged in two columns according to the characteristics of the cross-correlation functions.

occurring when the anchovy series lags the sardine series by one decade. The cross-correlation also measures the period between the two peaks of the sardine series and that of the anchovy as 80 years (anchovy lags) and 70 years (sardine lagging the anchovy series).

The cross-correlation functions for comparisons between anchovy and mackerel and between anchovy and myctophids (lower two plots in left-hand column of figure 3) are very similar to that of the anchovy-sardine pair. These patterns highlight the basic similarity of the sardine, mackerel, and myctophid series and their common inverse relation to the anchovy. The three plots in the right-hand column of figure 3 directly illustrate the correlation structure among the sardine, mackerel, and myctophid series. The plots in figure 4 constitute a separate group composed of the correlations between hake time series and the other four time series.

DISCUSSION

For a broader context, we can compare the scale-deposition data from the Gulf of California with data from two nearshore sites in the California Current. The northern site is the Santa Barbara Basin just south of Point Conception. The southern site is the Soledad Basin off southern Baja California, just north of Magdalena Bay. For a reference to global climate, we have also included in this comparison

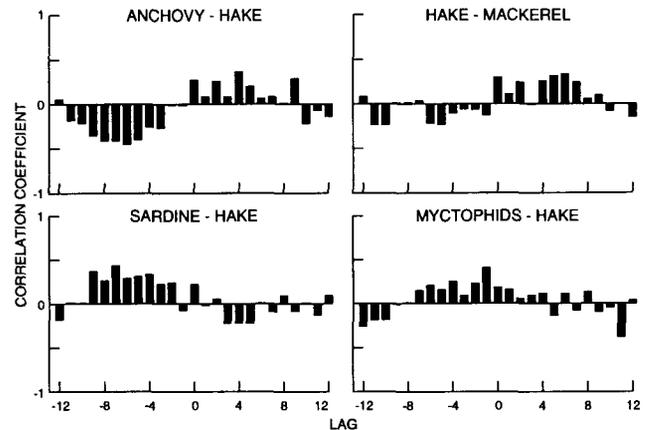


Figure 4. Cross-correlation functions calculated from the combinations of hake with the four taxa of anchovy, sardine, mackerel, and myctophids.

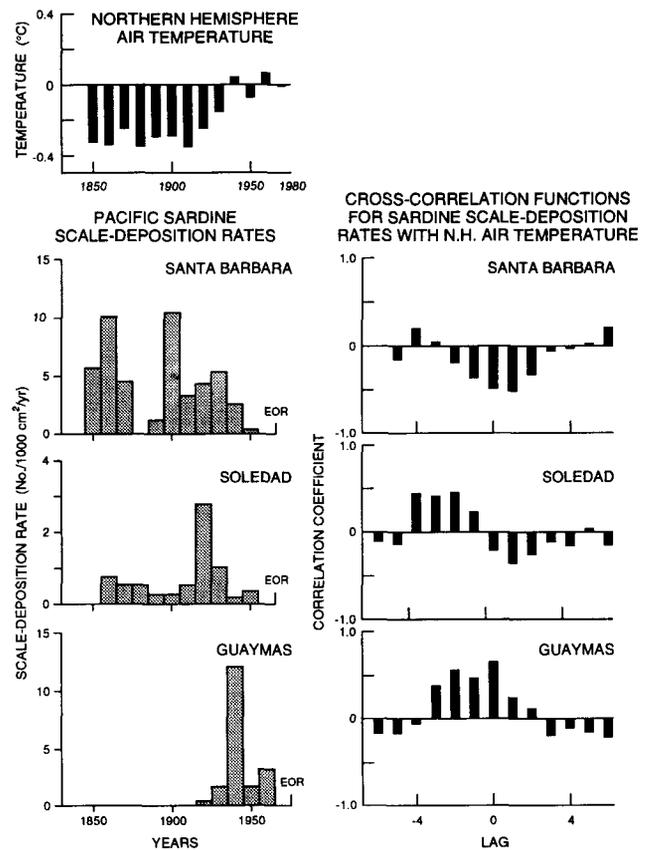


Figure 5. Plots of the time series of scale-deposition rates from A.D. 1850 for Pacific sardine from Santa Barbara Basin, Soledad Basin, and Guaymas Slope (lightly shaded bars in column at left of figure) compared with the Northern Hemisphere record of air temperature from Jones and Kelly (1988). The three plots to the right of the SDR series are the cross-correlation functions calculated from comparison of each series with the Northern Hemisphere air-temperature record.

Jones and Kelly's (1988) now familiar record of air temperature over the Northern Hemisphere.

Figure 5 contains the plots of the Pacific sardine records from the Santa Barbara Basin, the Soledad

Basin, and the Guaymas Slope. Figure 6 shows the plots of the northern anchovy from these three areas. The two California Current sites have been used to compare the histories of the northern and southern stocks of the sardine and anchovies (Soutar and Isaacs 1974), which are centered around the Southern California Bight and the area around Punta Eugenia in central Baja California. In figures 5 and 6 the Northern Hemisphere air-temperature record is aligned with the three scale-deposition plots. The beginning of the records has been set at 1850 to coincide with the start of the temperature record. The SDR records from the Santa Barbara and Soledad basins are reported as 5-year averages by Soutar and Isaacs (1974). We have modified both the SDR records of Soutar and Isaacs (1974) and the air temperature record to yield 10-year averages for this comparison. The right-hand columns in figures 5 and 6 show the cross-correlations between the Northern Hemisphere air-temperature curve and each of the sardine and anchovy series.

Intercomparison of the sardine series shows an intriguing pattern of successive 20-year displacements of the recent major peaks in these three regional "populations." We refer to the peak centered at 1900–10 in Santa Barbara, at 1920–30 in the Soledad Basin, and at 1940–50 in the Guaymas records. It is also worth noting that the earlier high sardine abundance in the Santa Barbara record (1850–80) is not obvious in the Soledad record, although scale deposition did occur in the Soledad Basin in a pattern that might be consistent with a 10–20-year lag of lowered deposition in Santa Barbara. From the Guaymas record we learn that the earlier peak in Santa Barbara, which is markedly lower in Soledad Basin, is completely absent in the central Gulf of California.

Intercomparison of the three regional northern anchovy populations (figure 6) indicates a decidedly different pattern than for the sardine. The anchovy series show that the major peak of abundance in the Gulf of California (1870–80) co-occurs with the major peak in the sediments of the Soledad Basin. These two coinciding peaks show a moderately inverse relationship to the pattern in Santa Barbara with its major peak in 1870–80.

The relations between the Northern Hemisphere air temperature and both sets of scale-deposition series are equally intriguing. The more readily interpretable relation is that of the Santa Barbara anchovy record and the air temperature (figure 6). This shows a well-knit pattern of cross-correlation, indicating a strong negative association between anchovy and temperature, with strong correlation at 0-lag. Thus

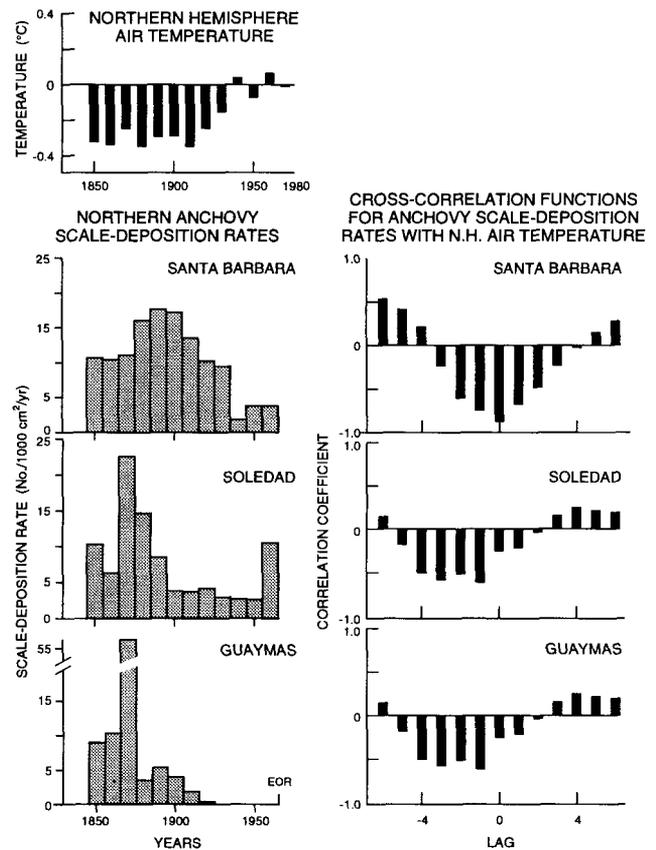


Figure 6. Plots of the time series of scale-deposition rates from A.D. 1850 for northern anchovy from Santa Barbara Basin, Soledad Basin, and Guaymas Slope (lightly shaded bars in column at left of figure) compared with the Northern Hemisphere record of air temperature from Jones and Kelly (1988). The three plots to the right of the SDR series are the cross-correlation functions calculated from comparison of each series with the Northern Hemisphere air-temperature record.

the anchovy maximum coincides with the cool period of the nineteenth century, whereas the decline and minimum abundance coincide with the period of global warming into the twentieth century. The Soledad Basin and Guaymas records are also negatively correlated with the temperature record (figure 6), but the decline in both areas began before the global warming began.

The relation between hemispheric air temperature and the regional sardine records is more difficult to interpret. The successive displacement of the population maxima between Santa Barbara and Guaymas results in a reversal in the correlation structure plotted in figure 6. Guaymas shows a well-defined positive relationship compared to hemispheric temperature; the Santa Barbara record is negatively correlated to the temperature, although not in the degree shown by the anchovy. Interestingly enough, the Soledad Basin, which is geographically intermediate, is also a transition between the Santa Bar-

bara and the Guaymas relations to hemispheric air temperature.

CONCLUSIONS

The scale-deposition data (table 1, figure 2) indicate that northern anchovy played a significant role in the pelagic ecosystem of the Gulf of California. The importance of the anchovy in the gulf seems to have been unsuspected until only a few years ago (cf. Ahlstrom 1967; Hammann and Cisneros 1989). The record also demonstrates a clear tendency for the anchovy to fluctuate out-of-phase with the sardine over a long cycle of roughly 150 years (figure 3). Moreover, there appears to be a broader pattern of coherence among the sardine, mackerel, and the myctophids (figure 3), resulting in a generally negative or inverse relation with the abundance of anchovies. The interrelations among the sardine, anchovy, mackerel, and myctophids (figure 3) are not shared with the hake (figure 4).

It is difficult to ignore the parallels between the recent collapse of the sardine population in the Gulf of California and the collapse in the California Current during the late 1940s and 1950s. Both populations declined under heavy fishing pressure (Barnes et al. 1992) superimposed on broad, natural, decadal-to-centennial-scale biomass fluctuations (Soutar and Isaacs 1974). Both declines appear to be accompanied by an increasing population of northern anchovy (cf. MacCall and Praeger 1988).

From figure 2, however, we see that the alternation or replacement of populations may occur in the gulf without fishing pressure. This has apparently happened repeatedly in the California Current through the past 1700 years over time scales of 50 to 100 years (Baumgartner et al. 1992). The time scale for a full cycle of alternation between the populations in the gulf is of the order of 120 to 140 years (i.e., 1790 to 1940). However, the much shorter record from the gulf (compared to that from Santa Barbara) allows us to sample at best only two major events. Thus we have few degrees of freedom with which to judge the confidence of a typical time scale of the changing ecosystem structure inferred from the scale-deposition series in figure 2.

Comparison of the sardine and anchovy series in the Gulf of California to those in the California Current provides a wider geographic context for interpreting and understanding data not only for the Gulf of California, but also for the entire region of the California Current-Gulf of California. Making these comparisons with reference to Northern Hemisphere air temperature (figures 5 and 6) allows us to consider the geographic differences in the in-

ferred population variability in the light of global climate change. The regional differences and relationships to climate suggest that regional populations (or stocks) of both species probably do not vary independently through time. There are indications of migrational shifts from one region to another over periods of several decades. The relation to climate is not yet clear, but altogether, the information here suggests that climate does mediate population sizes, but this process is still subject to strong filtering through biological interactions among species.

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THE ENSENADA FRONT: JULY 1985

LOREN R. HAURY, ELIZABETH L. VENRICK,
CONNIE L. FEY, JOHN A. MCGOWAN
Marine Life Research Group
Scripps Institution of Oceanography
University of California, San Diego
9500 Gilman Drive
La Jolla, California 92093-0218

PEARN P. NIILER
Physical Oceanography Research Division
Scripps Institution of Oceanography
University of California, San Diego
9500 Gilman Drive
La Jolla, California 92093-0230

ABSTRACT

The surface signature of the relatively cool, fresh, eutrophic waters of the southeastward-flowing California Current end abruptly off northern Baja California, Mexico, in a persistent, interannually variable feature we call the Ensenada Front. A detailed study of the front in July 1985 showed that it comprised a complex set of flows, some of which fed into eddies and others that may have been subducting under the warm, oligotrophic waters to the south. The frontal region was characterized by low gradients in physical, chemical, and biological properties. The nutricline was about 35 m deep north of the front and 100 m deep south of it. Integrated primary production to the north was three times that to the south; productivity was not enhanced in the jets. Integrated euphotic-zone chlorophyll showed no significant change across the front; an area northeast of the front with a strong, deep chlorophyll maximum (DCM) underlying a pool of warm, low-chlorophyll water had the highest integrated chlorophyll in the study region. Chlorophyll concentrations increased in the high shear zones between strong jets. The highest values of surface chlorophyll and primary production tended to correspond to regions of lowest geopotential anomaly, not to regions of low temperatures and positive divergence. Wet displacement volumes of zooplankton in the upper 210 m were three times higher to the north of the front, and in the upper 100 m were four times higher; the change occurred relatively abruptly over a distance of about 15 km. Zooplankton biomass varied directly with integrated chlorophyll in north-south sections across the southeast-trending front, but varied inversely with chlorophyll on a west-east section that ended in the warm pool with the strong DCM. Fish eggs and larvae were less abundant in the waters north of the front.

RESUMEN

Las aguas superficiales de la corriente de California que fluyen hacia el sureste se caracterizan por ser

relativamente eutróficas, frías y menos salinas. Las aguas superficiales cambian abruptamente de características frente al norte de Baja California, México. La zona de cambio, que aquí denominamos el Frente de Ensenada, es persistente y varía de año a año. En Julio de 1985 se realizó un estudio que mostró que el frente estaba formado por un intrincado conjunto de corrientes. Algunas de éstas corrientes alimentaban remolinos, mientras que otras podrían haber estado encajándose bajo aguas tibias y oligotróficas que se encontraban hacia el sur. El frente se caracterizó por gradientes poco intensos en las propiedades físicas, químicas y biológicas. La nutraclina se encontraba a 35 m de profundidad al norte del frente, mientras que al sur, se encontraba a 100 m. Hacia el norte del frente la producción primaria integrada fue tres veces mayor que al sur. La productividad no incrementó en los chorros. La clorofila (integrada para la zona eufótica) no varió significativamente a través del frente. Los valores máximos de clorofila (integrada para la zona eufótica) ocurrieron en una zona al noreste del frente; en ésta zona, se encontró un máximo-profundo de clorofila bajo una parcela de agua tibia (con concentraciones bajas de clorofila). Las concentraciones de clorofila incrementaron en las zonas de mayores gradientes horizontales de velocidad entre los chorros. En general, los valores más altos de clorofila superficial y producción primaria coincidieron con las regiones de menor anomalía geo-potencial y no con las zonas de temperaturas bajas y divergencia positiva. En los 210 m más someros de la columna de agua, el volumen húmedo desplazado de zooplancton fue tres veces mayor al norte del frente; en los 100 m más someros, cuatro veces. Estos cambios ocurrieron con relativa rapidez en una distancia de 15 km. El frente tendía al sureste, y mientras que en transectos norte-sur la biomasa de zooplancton varió directamente con la clorofila integrada, la variación fue inversa en un transecto oeste-este. Al final de éste último transecto fue cuando se encontró la parcela de agua tibia con un elevado máximo-profundo de clorofila. La abundancia de huevos y larvas de peces fue menor en aguas al norte del frente.

INTRODUCTION

It has been known for more than fifty years that the generally southeastward-flowing California Current turns shoreward toward northern Baja California in the vicinity of 32°N (Sverdrup and Fleming 1941; Wyllie 1966; Hickey 1979; Lynn and Simpson 1987; Pares-Sierra and O'Brien 1989). Some of the onshore flow turns north to form part of the cyclonic Southern California Eddy and Southern California Countercurrent (Jackson 1986); the remainder turns southward along the northern Baja California coast. The shoreward flow is also associated with a broad faunal boundary between pelagic organisms of northern (cool eutrophic water) and southern (warm oligotrophic water) affinities (e.g., Brinton 1976; Sette and Ahlstrom 1948).

Only within the last fifteen years, however, has the detailed physical and biological structure of this flow begun to be resolved. Satellite infrared images from 1975 and 1976 showed a recurring oceanic frontal zone in the region (Bernstein et al. 1977; Legeckis 1978) and Coastal Zone Color Scanner (CZCS) imagery showed a persistent, interannually variable front in chlorophyll between 1979 and 1982 (Pelaez and McGowan 1986; Thomas and Strubb 1990). The front is detectable much of the year, but is most strongly developed from late March to early June. The surface expression of the northern California eutrophic waters disappears in the frontal region, but the water parcels continue moving southward. The considerable warming and loss of surface pigment occurs rapidly perpendicular to, and along the path of, the frontal flow.

Niiler et al. (1989) studied the three-dimensional mesoscale physical dynamics of the flow associated with the front. They showed the presence of a narrow (about 50 km), surface-intensified jet to at least 300 m, with velocities in excess of 25 cm s⁻¹; the core of the flow had upwelling estimated to be about 50 cm day⁻¹. They also suggested that the abrupt disappearance of the cold, pigment-rich water along the front is due in part to subduction of these waters to the southwest. Chereskin and Niiler¹ describe in more detail similar circulation features observed in the frontal region in September 1988.

Thomas and Strub (1990) used the CZCS West Coast Time Series (1979–83 and 1986) to describe in more detail the seasonal and interannual temporal and spatial variability of the front's phytoplankton pigment signature. Seasonality in pigment concen-

tration is weak to the south and strong to the north. In the north, pigments have two peaks—in late spring and early fall. High pigment concentrations extend farther offshore (150–300 km) in the spring and early summer than in the mid to late summer. Interannual variability in latitudinal position of the front was about 150 km. In June of El Niño year 1983, the front was detectable for only a short time.

In this report we describe the physical, chemical, and biological characteristics of this front off northern Baja California, Mexico, using data collected during and shortly after the period of Niiler et al.'s (1989) synoptic study of the shoreward flow and mesoscale features of the front. The front has been called the East Pacific Subtropical Front (Legeckis 1978), a name which has also been applied to a more oceanic feature (e.g., Saur 1980; Lynn 1986). To avoid confusion we have called this feature the Ensenada Front (Haury et al. 1990; Venrick 1990) in recognition of its geographical location.

METHODS

The data were collected from 1 to 23 July 1985 on the two legs of the FRONTS 85 cruise on RV *New Horizon*; the ship track and station positions for Leg I are shown in figure 1a. The sampling pattern was located on the basis of an AVHRR satellite image received on the first day of the leg and modified as *in situ* data became available. During the second leg, cloud cover precluded further use of satellite imagery; hence the station plan was oriented according to the earlier images and Leg I information. Three replicate north-south (N-S) transects were made across the front followed by a west-to-east (W-E) section (figure 1b). On either side of the front at the ends of each N-S transect, a 24-hour station was occupied on each of two days, four days apart. Replicate observations made at these stations allowed characterization of the two types of water constituting the front, and of small-scale heterogeneity within the two types.

Details of most of the sampling methods, data handling, and accuracies are presented in Haury et al. 1986, with additional information in Niiler et al. 1989; the following is a summary of these techniques and others not previously described. Leg I data consisted of 81 Neil Brown CTD lowerings to 300 or 500 m, 90 XBT drops, 20 ARGOS-tracked drifters drogued at 15 m (Niiler et al. 1987) deployed at CTD stations from 8 to 10 July, and 8 hydrocasts collecting water at six depths to measure chlorophyll and primary production (¹⁴C incubation, noon to sunset). The ship's uncontaminated seawater system was used for underway measurements of 3-m tem-

¹Chereskin, T. K., and P. P. Niiler. Circulation in the Ensenada Front: September 1988. MS submitted to Deep-Sea Res.

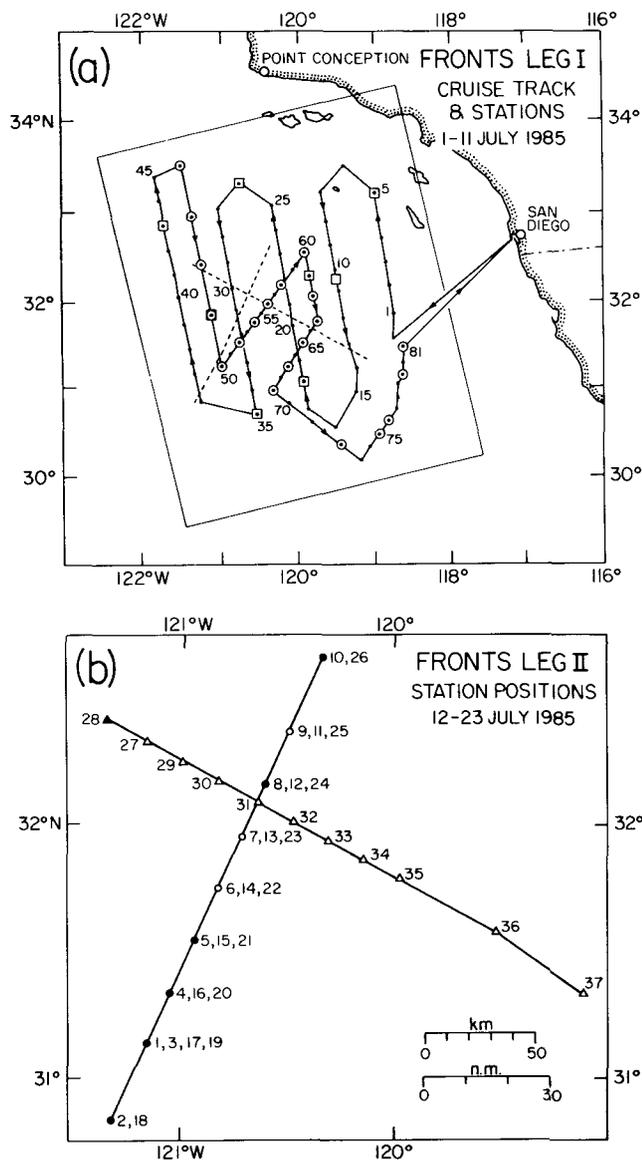


Figure 1. a, Cruise track and station positions for FRONTS 85 Leg I. Small black dots indicate CTD casts; circled dots, ARGOS-tracked drifter deployments; squares, primary productivity measurements. The boxed area denotes the region studied and illustrated in Niiler et al. 1989 and used in figure 4. The dashed lines indicate the transects detailed in b, which shows the station positions for FRONTS 85 Leg II, numbered by order of occupation. Filled circles and triangles indicate stations where at least one measurement of primary productivity was made.

perature and chlorophyll fluorescence at 5-minute intervals.

Leg II data were obtained from 40 hydrocasts with 20 Nansen bottles to a maximum depth of 1000 m. Temperature, salinity, oxygen, and nutrients were determined from all depths sampled; chlorophyll and phaeopigments were determined from the top 12 depths. Nine casts for primary production and underway temperature and chlorophyll data were collected as during Leg I. One or more macrozooplankton samples were obtained at each station

during Leg II (54 total) with oblique bongo net tows to 210 m using the standard CalCOFI procedures described in Kramer et al. (1972).

A twenty-net MOCNESS system (1-m² mouth, 333- μ m mesh; Wiebe et al. 1985) was used to take replicate samples of day and night vertical distributions of macrozooplankton at the ends of the N-S sections. Wet displacement volume measurements (after removal of organisms >5 ml) of all macrozooplankton samples are presented here, together with counts of fish eggs and larvae, provided courtesy of G. Moser, NOAA NMFS Southwest Fisheries Science Center, La Jolla. Moser and Smith (in press) describe in detail the taxonomic composition, abundance, and distribution of fish larvae. The data presented here for the bongo net tows combine the average values from the two sides. Night-to-day ratios of the bongo net macrozooplankton displacement volumes and counts of fish eggs and larvae (based on 29 daytime samples and 25 night samples) were 1.4 for eggs, and 1.6 for larvae. These ratios have been applied as a correction to the daytime samples for graphing and further analysis.

RESULTS

Physical Structure and Dynamics

AVHRR imagery from 1 July (figure 2) showed the Ensenada Front in the survey area as a sinuous

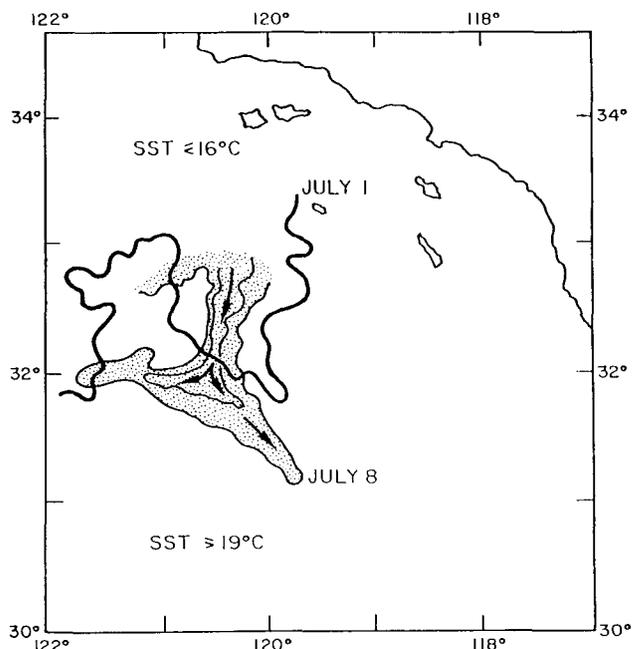


Figure 2. The location of the main gradient of sea-surface temperature, indicative of the Ensenada Front, on 1 July (heavy black line) and 8 July (thin black line) 1985. The frontal shapes were traced from AVHRR images; the arrows denote flow after 8 July as indicated by drifter tracks (see figure 3).

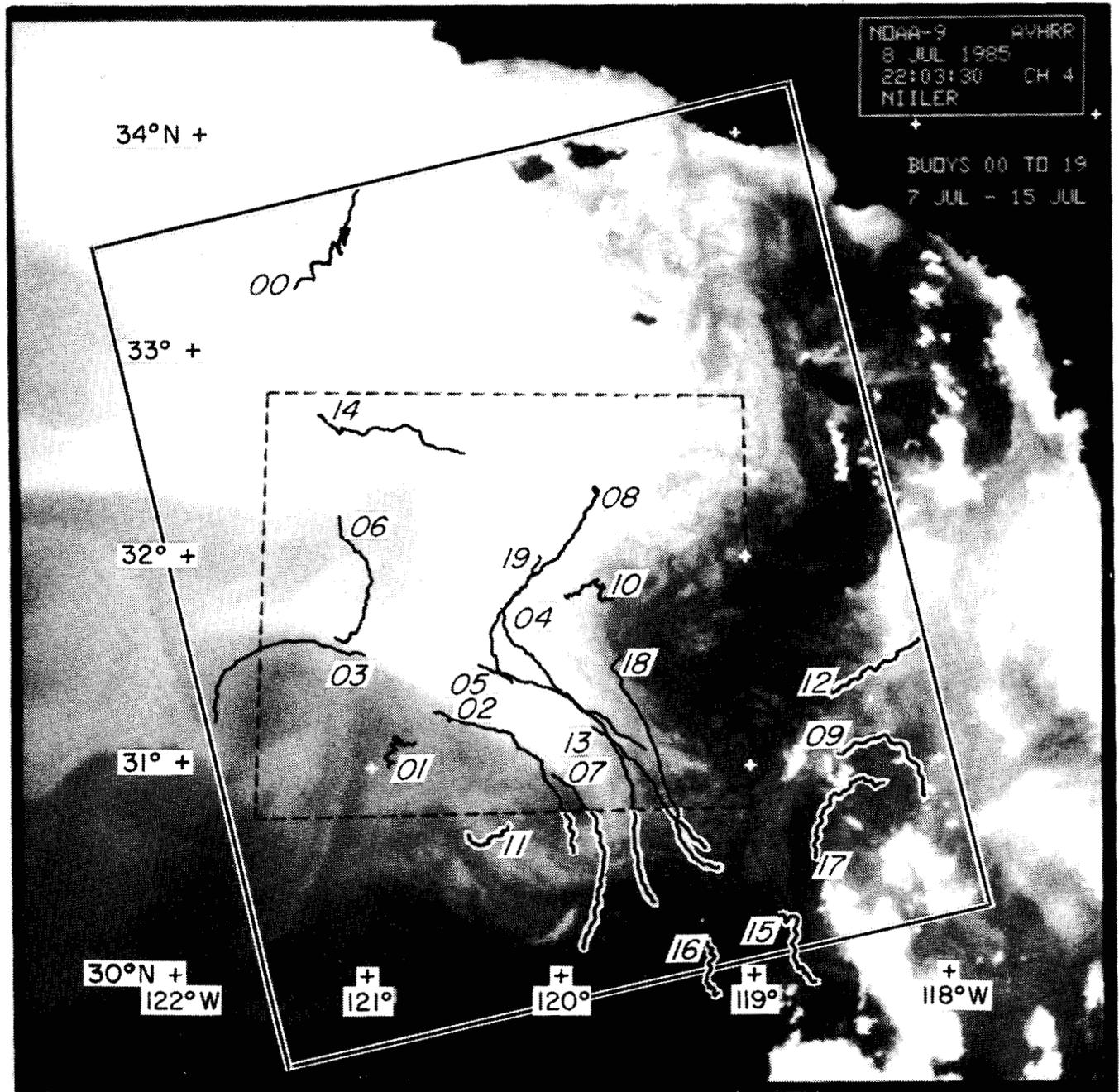


Figure 3. Satellite infrared image of the California Current system south of Point Conception taken on 8 July 1985 at 2204 UT. Light grey shades correspond to relatively cold water. Drifter tracks, numbered at launch site, from deployment time through 15 July are overlaid in black. The solid and dashed boxes denote the study area shown in figure 1a and the location of the transects shown in figure 1b. Adapted from Niiler et al. 1989.

southwest-to-northeast-trending boundary between cold ($<16^{\circ}\text{C}$) and warm ($>19^{\circ}\text{C}$) water. By 8 July, the southward-extending tongue of cold water forming the eastern portion of the front had evolved into an anvil-shaped structure (figures 2 and 3) with most of the flow turning eastward, as indicated by the drifter tracks (figure 3). The continuation of the front to the west of this diverging flow was oriented

generally to the northwest, extending out of our survey area. Another tongue of cold water flowed westward from this region, seen as the band of cool water at $32^{\circ}30'\text{N}$ on the left side of figure 3. This water fed the eddy dipole system described by Simpson and Lynn (1990); the eastern half of both these eddies can be seen on either side of the cold water in figure 3. Plate 1 of Simpson and Lynn

(1990), using larger-scale AVHRR images, shows all of these mesoscale structures and traces the development of the flow along the front between 1 and 9 July 1985.

The study of Niiler et al. (1989) summarized in the introduction is augmented here with other ship-board observations. The geopotential anomaly (15/300 db) mapped from Leg I data (figure 4a) showed the narrow and sinuous nature of the dominating current flow through the study area. Divergence, calculated from the geopotential anomaly and from drifter tracks, is illustrated in figure 4b to indicate the inferred regions of potential upwelling. The surface-temperature manifestations of the flow, as evidenced by the 3-m temperature measured every 5 min (1.54 km) while underway during Leg I, are shown in figure 4c. The maximum gradient observed was $0.36^{\circ}\text{C km}^{-1}$ near station 28 (figure 1a) in the edge of the warm-water ($>19^{\circ}\text{C}$) intrusion to the west of the anvil stem. This gradient was the exception, however; the cumulative frequency distribution showed that 75% of all gradients were less than $0.05^{\circ}\text{C km}^{-1}$, 90% less than $0.09^{\circ}\text{C km}^{-1}$, and 99% less than $0.22^{\circ}\text{C km}^{-1}$. The underway measurements made on the four sections of Leg II showed the same small gradients; these results are summarized in table 1. The frontal region, except for a few small areas, was not characterized by sharp temperature gradients. This is very unlike frontal systems nearer shore (Simpson 1985). Despite the low gradients, the region still displayed a complex temperature structure reflecting the underlying physical dynamics (see below).

The surface waters of the filament entering the study area in the northwest corner had a temperature of about 16.5°C , while those exiting the area towards the east (southeast corner) were slightly less than 17.5°C in the core (figure 4c). This suggests that the water warmed by about 1°C as it passed through the area, due to mixing with the surrounding waters and to surface heating.

Three CTD-XBT sections (station spacing 10 km) were made across and normal to the west-to-east-flowing jet during Leg I (stas. 50–60, 63–69, and 73–81; figure 1a). Niiler et al. (1989) illustrate (their figure 8) the temperature, salinity, and geostrophic current relative to 300 db through the first two sections of this onshore-flowing filament. These sections showed a relatively strong thermal-haline front at the southern edge; this density structure was responsible for geostrophic velocities as high as 70 cm s^{-1} . The sections also showed a shallow salinity minimum extending southward between 50 and 100 m under the front, confirming the

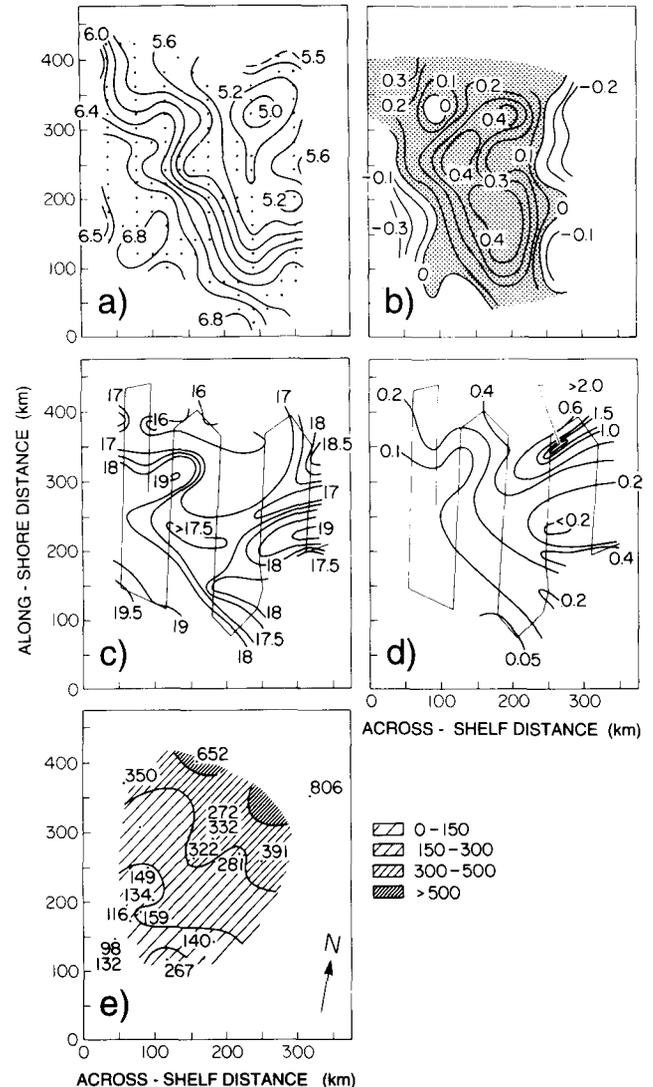


Figure 4. a, Objective map of the 15/300 db geopotential anomaly from FRONTS 85 Leg I data. Contour interval is $0.2\text{ m}^2\text{ s}^{-2}$. Station positions after binning are indicated by dots (from Niiler et al. 1989, fig. 3). b, Geostrophic divergence calculated from the 15/300 db geopotential anomaly. Regions of positive divergence are stippled; units are 10^{-7} s^{-1} (adapted from figs. 10b and 14b of Niiler et al. 1989). c, Temperature (contour intervals 0.5°C) and d, chlorophyll a ($\mu\text{g l}^{-1}$) at 3 m measured underway at 5-min intervals (1.5 km) along the portion of the Leg I cruise track shown by the light straight lines. e, Primary productivity ($\text{mgC m}^{-2}\text{ exp}^{-1}$) integrated over the euphotic zone) estimated from noon-to-dusk ^{14}C incubations at stations occupied during Leg I and II.

intrusion and subduction of low-salinity water to the southwest. The third, easternmost section showed the flow to have spread and dampened, leaving no evidence of an intense current or subduction.

Figures 5 and 6 present the two geostrophic current sections from Niiler et al. 1989 and the corresponding underway surface data for all three sections to describe in more spatial detail (data points every 1.5 km) the surface structure of the front and the current filaments and the surface structure's relation to deeper features. As expected, the

TABLE 1
 Temperature and Chlorophyll Gradients (First Differences; °C km⁻¹ and mg m⁻³ km⁻¹)
 from Underway Measurements* during FRONTS 85

	Leg I		Leg II							
	T	Chl	Section 1 stas. 2-10		Section 2 stas. 10-18		Section 3 stas. 18-26		W-E Section stas. 27-37	
			T	Chl	T	Chl	T	Chl	T	Chl
Maximum gradient	0.36	0.14	0.28	0.13	0.27	0.05	0.38	0.06	0.31	0.04
75% less than ^b	0.05	0.01	0.03	0.01	0.06	0.01	0.04	0.01	0.06	0.01
90% less than ^b	0.09	0.02	0.08	0.01	0.10	0.03	0.06	0.03	0.10	0.01
99% less than ^b	0.22	0.09	0.27	0.06	0.16	0.04	0.17	0.06	0.22	0.02

See figure 1 for cruise track and station positions for each leg.

*Made at 3-m depth every 5 min (1.5 km)

^bPercentage of gradients less than table value

underway temperature and salinity data for the first two sections indicated that the highest gradients were associated with the strongest flows. In the first section (figure 5, stas. 50-60), the two coldest temperatures (<17.5°C) were associated with strong southeastward flows and a weak boundary between southeastward and northwestward flows; the very-low-salinity water (<33.4 psu), however, was found only in the strongest southeastward flow. The second section (figure 5, stas. 63-69) had warmer minimum and maximum temperatures, this time with the warmest water to the north of the filament; salinity again was lowest in the strong southern edge of the flow. Although the surface signatures of the two crossings of the filament were similar, the deeper measurements reveal that only the first section had northwest flows; all the second-section flow above 100 m (with respect to 300 db) was to the southeast. The rich detail and relatively large gradients in the underway data for both sections, however, suggest that the structure of the flow is much more complex than indicated by the CTD-XBT sections, with potential consequences for transport and biology (see below). The weakened and dispersed flows of the easternmost section have much lower temperature fluctuations (figure 6; temperature range of 19.1 to 20.3°C), but the same salinity range as the strong-flow sections (33.2 to >33.5 psu), indicating an apparent rapid warming of the advecting water masses.

During FRONTS 85 Leg II, the hydrographic station separation on the N-S sections was 24 km (37 km for the terminal stations), slightly more than the 10 km between alternate CTD and XBT stations of Leg I, so there is less detail in the depth profiles of properties (figures 7-9). The original intention of these transects was to repeat the sections across the strong west-to-east jet as was done on Leg I. The lack of warmer and more saline water on the northern ends of these three transects, satellite imagery

evidence of the southeasterly drift in the "stem" of the anvil-shaped flow, and an abrupt salinity front found just to the east of the transects (see below) suggest that the Leg II transects were made down the axis of the southward-flowing "stem" and crossed the front near the point where the flow diverged to the west and east. It is likely, as shown below, that each N-S transect was progressively closer to the center of the cold axis of the N-S filament.

The three sections along the same geographical track illustrate the structure and variability in the system over the week of sampling; the relatively weak gradients shown in the transects (figures 7-9 and table 1) probably resulted from the failure of the sections to cross perpendicular to the high-velocity filaments. Underway surface data obtained as on Leg I, however, showed considerable small-scale (<5 km) variability in the properties (figure 10). Subduction at the front of the low-salinity (<33.3 psu) and cool northern water is clear in the three sections (figure 7). All sections show discontinuities in the layer of minimum salinity at the vicinity of the front between 31.5° and 32°N; whether this is a result of undersampling, episodic subduction, or variability in the properties of the southward-flowing water cannot be determined.

The reduction in more-saline (≥33.4 psu) water with time (figure 7) indicates the advection of the southward-flowing stem to the southeast. In view of this possible advection, a remarkable feature of the geostrophic velocity sections (figure 7) is the consistency displayed in the location and intensity of the westerly flows over a period of almost 7 days. The northern region of westerly flow (stas. 8-9, 11-12, 23-24) was probably associated with a meander of the strong southerly flow of the filament. The southern region of westerly flow (stas. 3-4, 16-17, 19-20) perhaps was associated with entrainment of waters into the northern limb of the eddy (center at

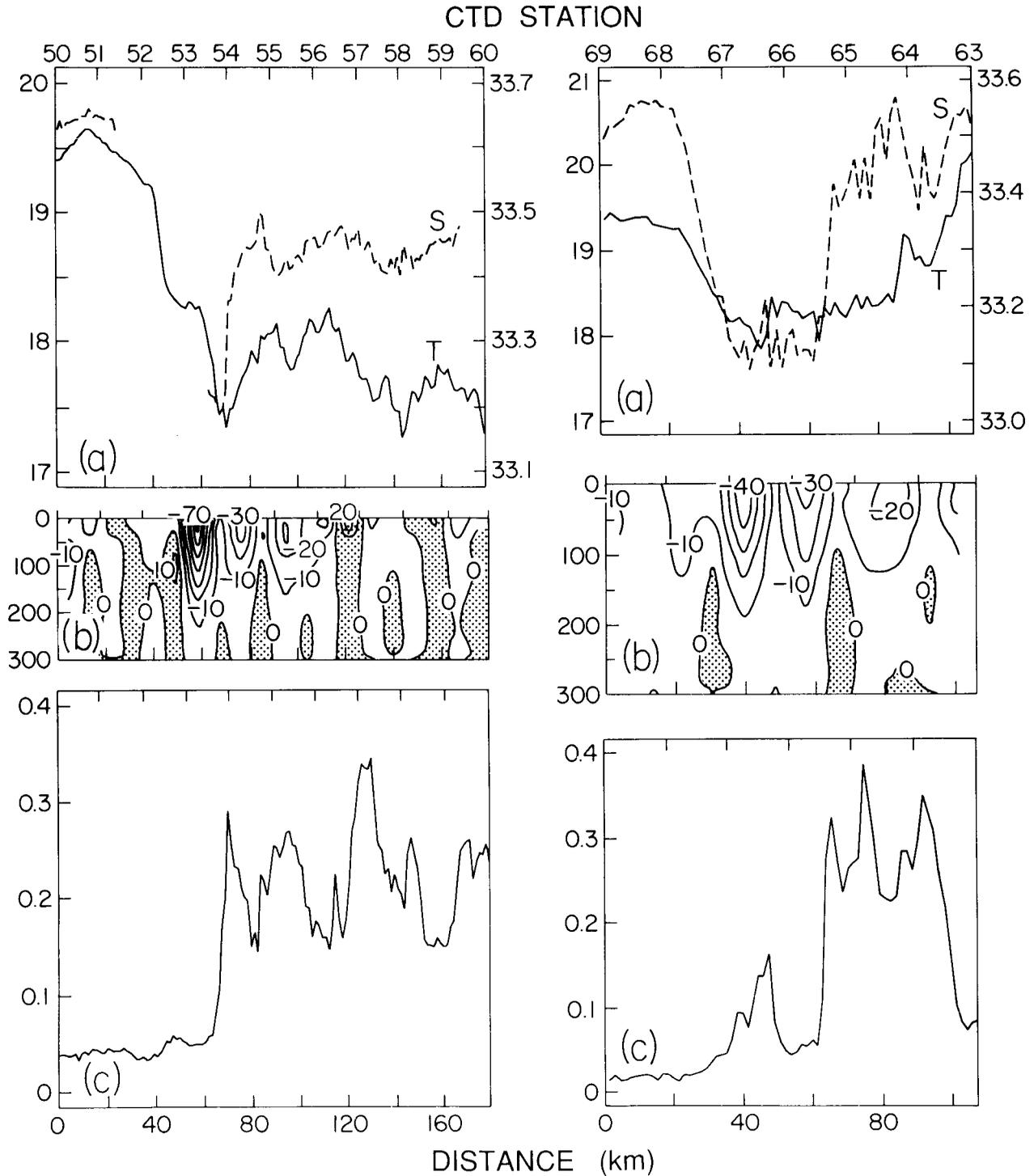


Figure 5. a, Surface (3-m) temperature ($^{\circ}\text{C}$) and salinity (psu); b, geostrophic currents relative to 300 db; and c, surface chlorophyll ($\mu\text{g l}^{-1}$) for two sections (CTD stations 50–60 and 63–69; figure 1a) across the shoreward-flowing jet during FRONTS 85 Leg I. Northwestward flow is indicated by stippling. Note that the high chlorophyll peaks are associated with the high-gradient regions between the cores of the filaments.

$31^{\circ}20'N$, $121^{\circ}40'W$) forming the southwestern portion of the front (figure 3).

Comparisons of the averaged physical properties and other physical characteristics at the terminal stations of the three sections are presented in table 2.

The W-E transect that followed the N-S sections (figure 1b) had narrower station spacing (20 km) except for the two easternmost stations (50 km). From the profiles obtained (figure 11), it is apparent that the section ran from the western side of the

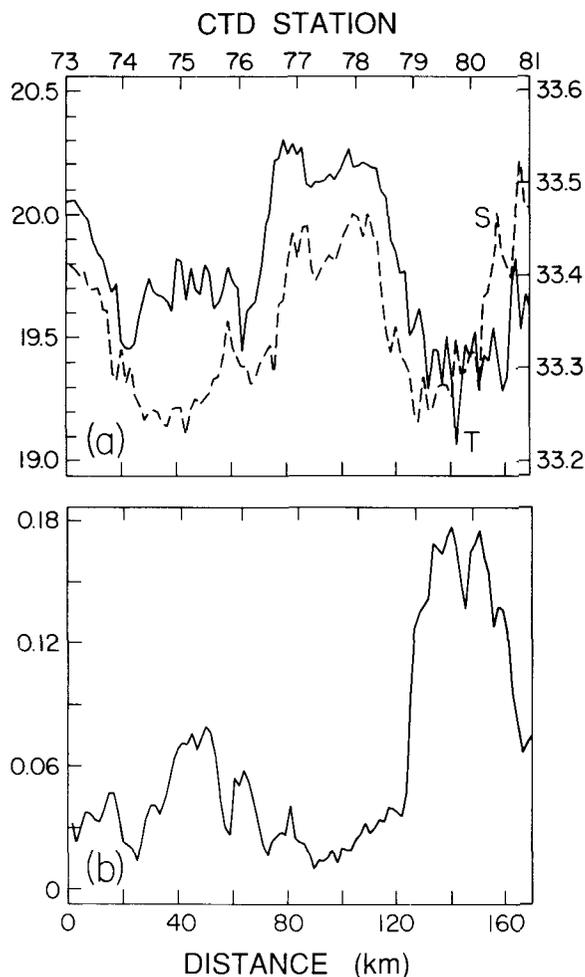


Figure 6. a, Surface temperature (°C) and salinity (psu), and b, surface chlorophyll ($\mu\text{g l}^{-1}$) from the easternmost section (stations 73–81; figure 1a) across the shoreward-flowing jet. The strong filaments seen in figure 5 have weakened and dispersed.

southward-flowing filament into the region of warm water ($>19^{\circ}\text{C}$) nearer the coast. The peak southward velocity of more than 40 cm s^{-1} occurred to the east (between stas. 31 and 32) of the preceding N-S transects, again evidence that the southward filament may have drifted eastward during Leg II.

The infrared image (figure 3) shows the eastern edge of the filament broken up into smaller jets, much like the structure of the shoreward-flowing portion of the filament (figure 5). Evidence for this is seen in the hydrographic section (figure 11) between stations 30 and 33 and in the underway surface temperature (figure 12).

Biology

Underway chlorophyll fluorescence and seven primary-production stations (with nutrient and chlorophyll/phaeophytin profiles to the 0.4% light level) were the only biological measurements made on Leg I (see figure 1b). Therefore the main focus of the following discussion is on the Leg II sections.

Nutrients. The N-S and W-E nutrient sections for nitrate, nitrite, phosphate, and silicate are shown in figures 8 and 11. The transition between a nutricline depth of about 35 m to the north and 100 m to the south (table 2) was gradual over the first two transects. The last transect, however, appears to have a higher horizontal gradient between stations 20 and 23, another indication that this section ran closer down the center of the filament than did the previous two, as suggested by the physical data (see above). On the W-E transect, the nutricline shoaled to the east to a similar depth as that at the north end

TABLE 2
 Comparisons of Averaged Properties at Stations North and South of the Ensenada Front, and Single Values at the Ends of the West-to-East Transect (Figure 1)

	North sta. 10, 26	South sta. 2, 8	N/S ratio	West sta. 28	East sta. 37
Surface temp. ($^{\circ}\text{C}$)	16.6	19.0		16.8	19.0
Surface salinity (psu)	33.32	33.57		33.32	33.65
Salinity minimum (psu)	33.23	32.28		33.20	33.42
Salinity min. depth (m)	43	96		63	42
Mixed-layer depth (m)	~25	~25		~25	~20
Nutricline depth (m)	~35	100		70	32
Surface Chl. <i>a</i> ($\mu\text{g/l}$)	0.17	0.09		0.32	0.16
Deep Chl. max., DCM ($\mu\text{g/l}$)	0.35	0.23		0.36	0.74
DCM depth (m)	51	100		22	42
Integr. Chl. <i>a</i> , 0–200 m (mg/m^2)	23	23	1.0	31	30
Primary production ($\text{mg/m}^2/\text{exp}$)	604	230	2.6	—	—
Zoopl. biomass					
0–210 m day ($\text{ml}/1000\text{ m}^3$)	335	117	2.9	133	89
Zoopl. biomass					
0–210 m night ($\text{ml}/1000\text{ m}^3$)	474	149	3.2	—	—
Zoopl. biomass night/day ratio	1.4	1.3		—	—

Zooplankton biomass (wet displacement volume) from oblique net tows to 210 m.

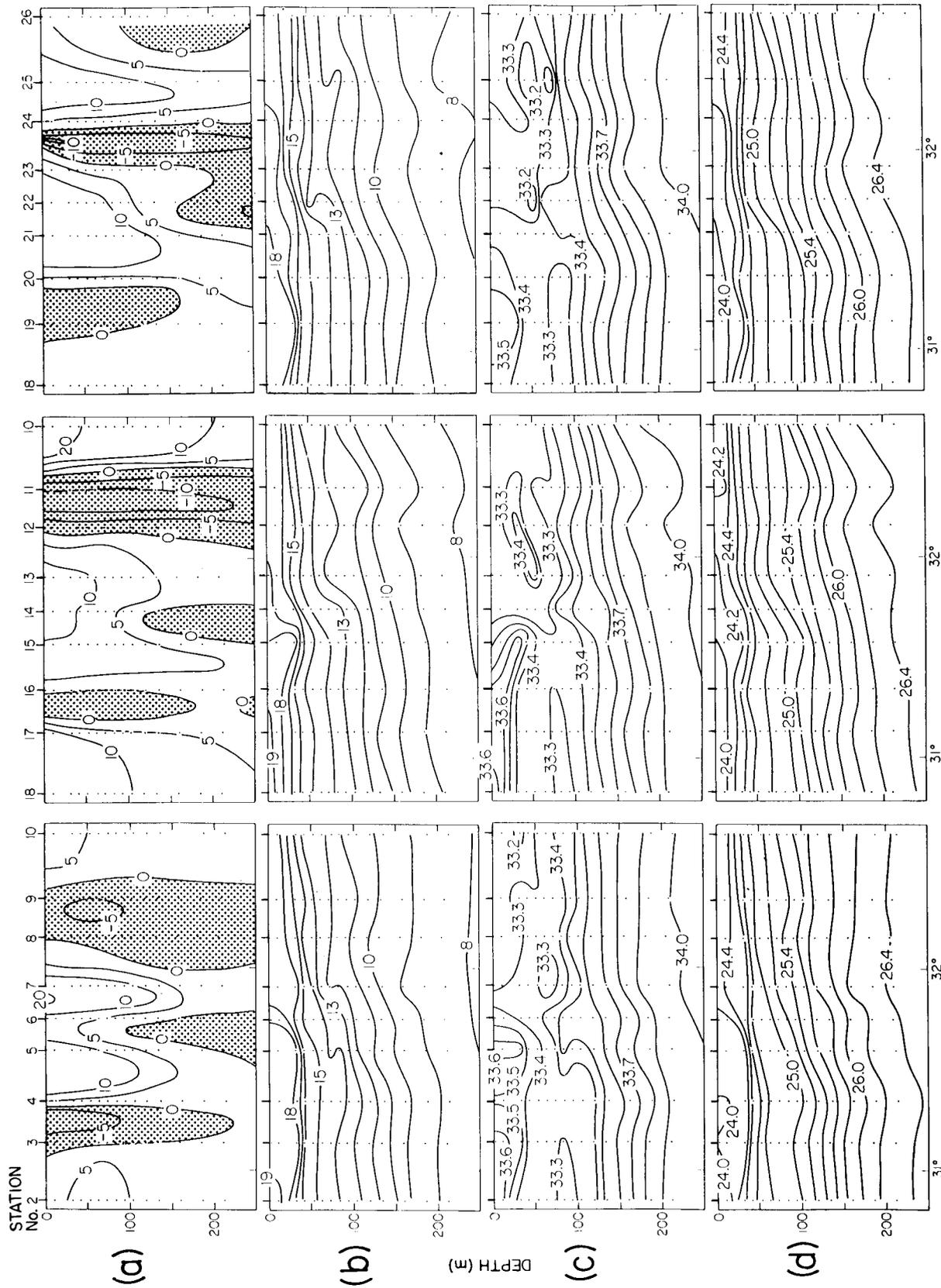


Figure 7. Hydrographic sections across the Ensenada Front from the three transects made on FRONTS 85 Leg II. Left column, stations 2-10 (0907 LT, 14 July to 0742 LT, 16 July); center, stations 10-18 (0306 LT, 17 July to 0724 LT, 18 July); right column, stations 18-26 (0203 LT, 19 July to 0134 LT, 21 July). a, Geostrophic velocity (cm s^{-1}); negative (stippled) velocity indicates westerly flow; b, temperature ($^{\circ}\text{C}$); c, salinity (psu); and d, density (σ_t).

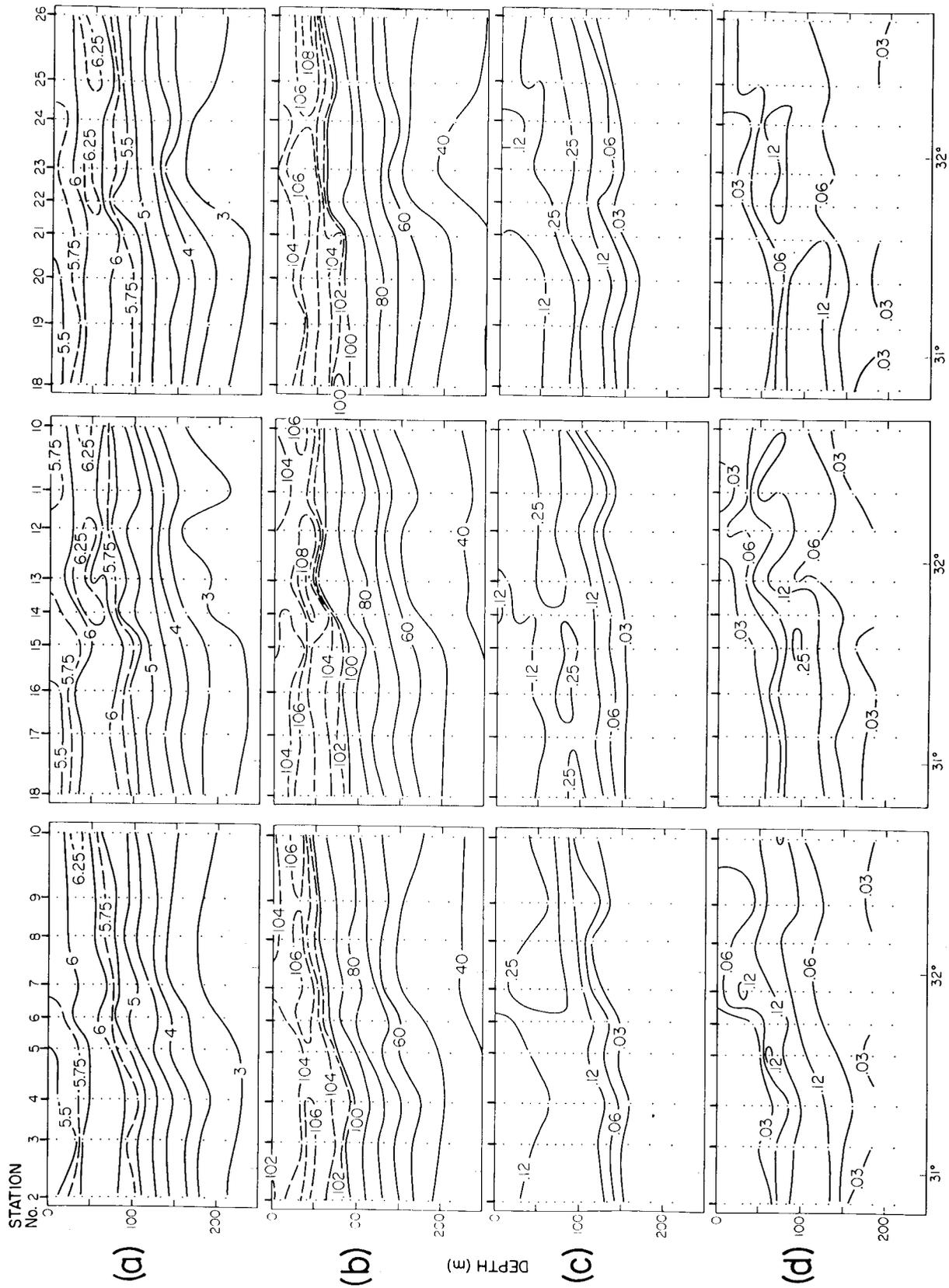


Figure 8. Similar to figure 7, except that a indicates oxygen (ml l⁻¹); b, oxygen saturation (%); c, chlorophyll a (µg l⁻¹); and d, phaeophytin (µg l⁻¹).

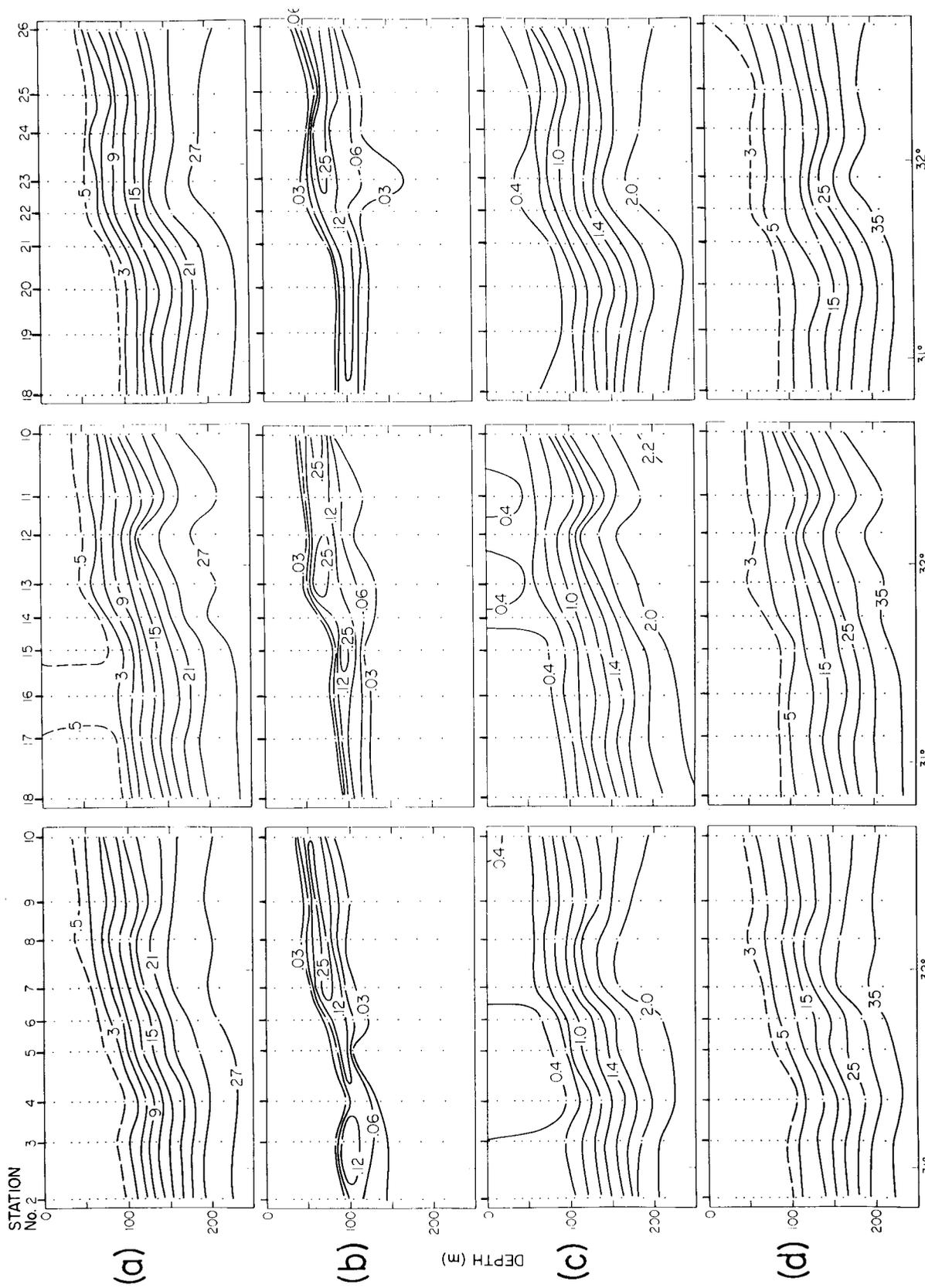


Figure 9. Similar to figure 7, except that a indicates nitrate, b, nitrite, c, phosphate, and d, silicate (all units $\mu\text{M l}^{-1}$).

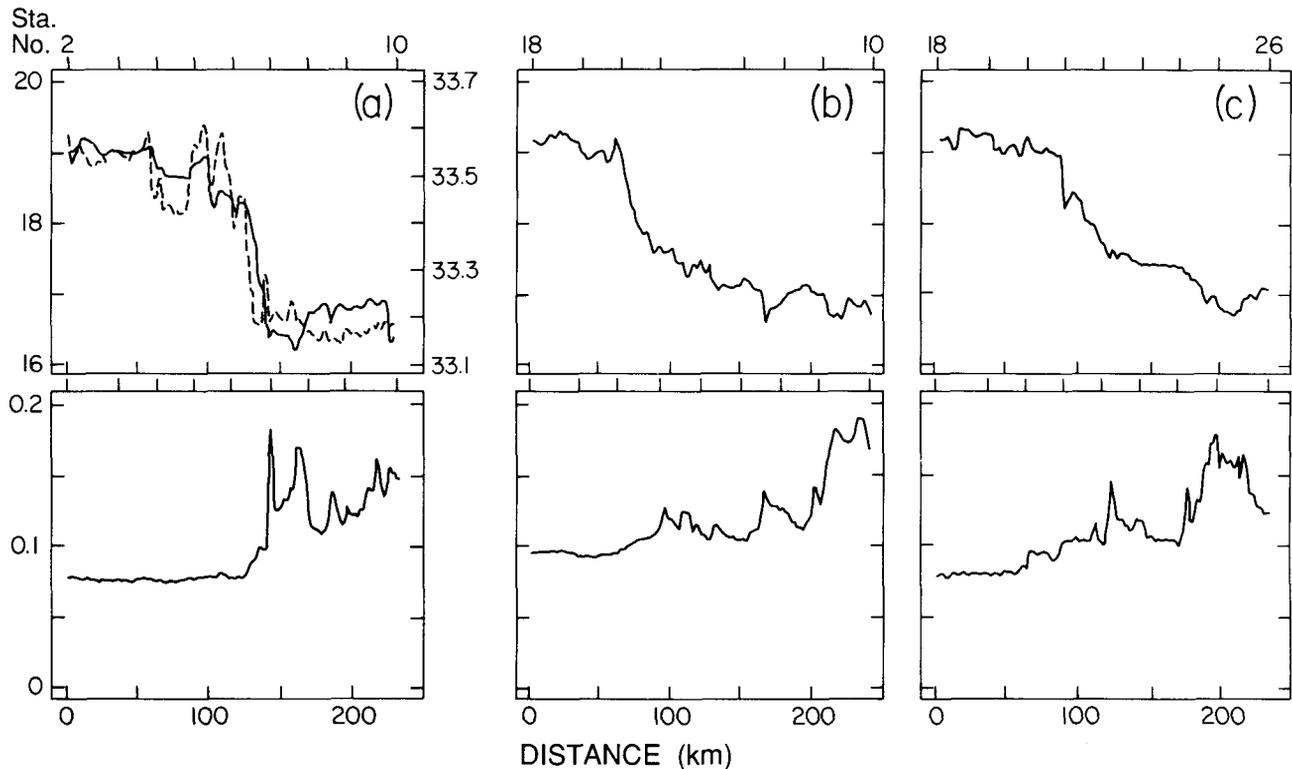


Figure 10. Underway measurements of near-surface temperature ($^{\circ}\text{C}$) and chlorophyll ($\mu\text{g l}^{-1}$) on the three north-south transects across the Ensenada Front (figure 1b). a, section 1, stations 2–10; b, section 2, stations 10–18; c, section 3, stations 18–26. See figure 7 for times and dates. Salinity values (psu; dashed line) for the first section (stations 2–10) are overlaid on the temperature trace.

of transects 1–3; the vertical gradient in the nutricline was much greater, however, so that equivalent deeper values were about 50 m shallower to the east than to the north. The transition from west to east occurred abruptly at the thermohaline front between stations 31 and 32, marking the eastern edge of the southward-flowing filament.

Chlorophyll and primary production. The vertical distributions of chlorophyll and phaeophytin obtained from the Leg II sections are shown in figures 8 and 11. Of note in these sections are the general low gradients in chlorophyll/phaeophytin in the N-S sections and the strong gradient in the W-E section. Plots of integrated chlorophyll over the depth of sampling as a function of station position (figure 13) show how this results in no change in chlorophyll standing stock in the N-S direction, whereas the strong deep chlorophyll maximum (figure 11 and table 2) under the warm waters to the east yields a larger average standing stock than in the north or west.

Surface chlorophyll fluorescence measured underway on Leg I is mapped in figure 4d; primary production integrated over the euphotic zone from both legs is mapped in figure 4e. Chlorophyll in the surface waters of the filament appears to decrease by a

factor of about three during the transit through the study area. Primary production, although there is a strong NE-to-SW gradient, does not appear to be enhanced in the filament waters.

Table 2 shows that the production was approximately three times greater to the north of the front, yet the standing crop of chlorophyll was similar on both sides (see also figure 13), as were the assimilation numbers of the phytoplankton (Gaxiola-Castro and Alvarez-Borrego 1991). The vertical distributions of chlorophyll with respect to the 1% light level and the nutricline (defined as the depth where NO_3 reaches $0.5 \mu\text{M}$) are shown in figure 14.

Comparisons of the patterns of chlorophyll and primary production with temperature and geopotential anomaly show a general broad agreement in overall form, but differences in detail (figure 4). The northeast-southwest gradient from high to low values of chlorophyll and primary production reflects the boundary formed by the southeastward flowing jet (figure 4a). Higher values of chlorophyll ($>0.4 \mu\text{g l}^{-1}$) correspond better to regions with geopotential anomalies of less than about $5.4 \text{ m}^2 \text{ s}^{-2}$ than they do to cold temperatures. The highest values of primary production ($806 \text{ mgC m}^{-2} \text{ exp}^{-1}$), chlorophyll ($>1.5 \mu\text{g l}^{-1}$), and chlorophyll gradients correspond

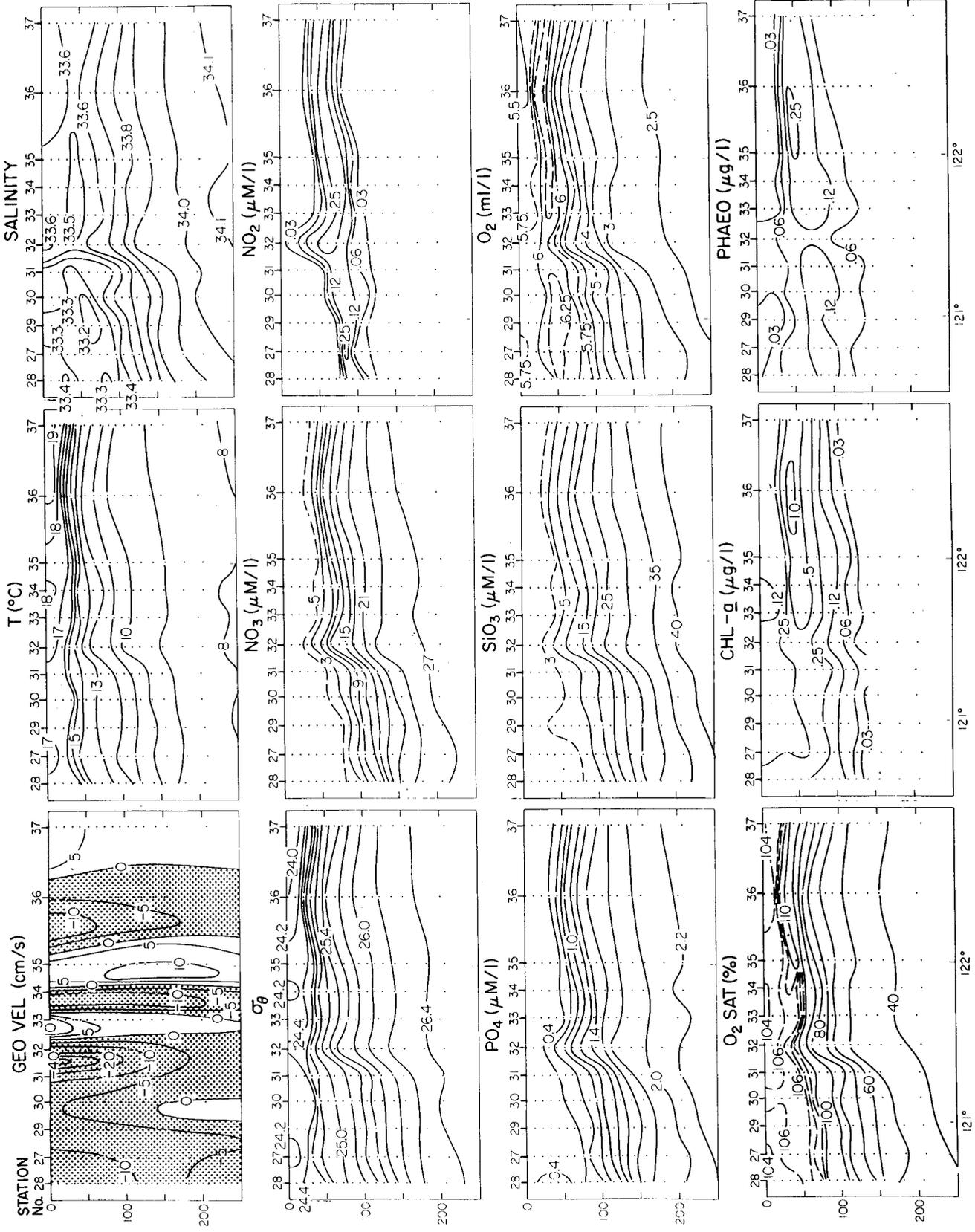


Figure 11. Hydrographic section perpendicular to the three north-south sections shown in figures 7-9 at stations 28-37, 1045 LT, 21 July, to 1639 LT, 22 July. Negative (stippled) velocity indicates southerly flow.

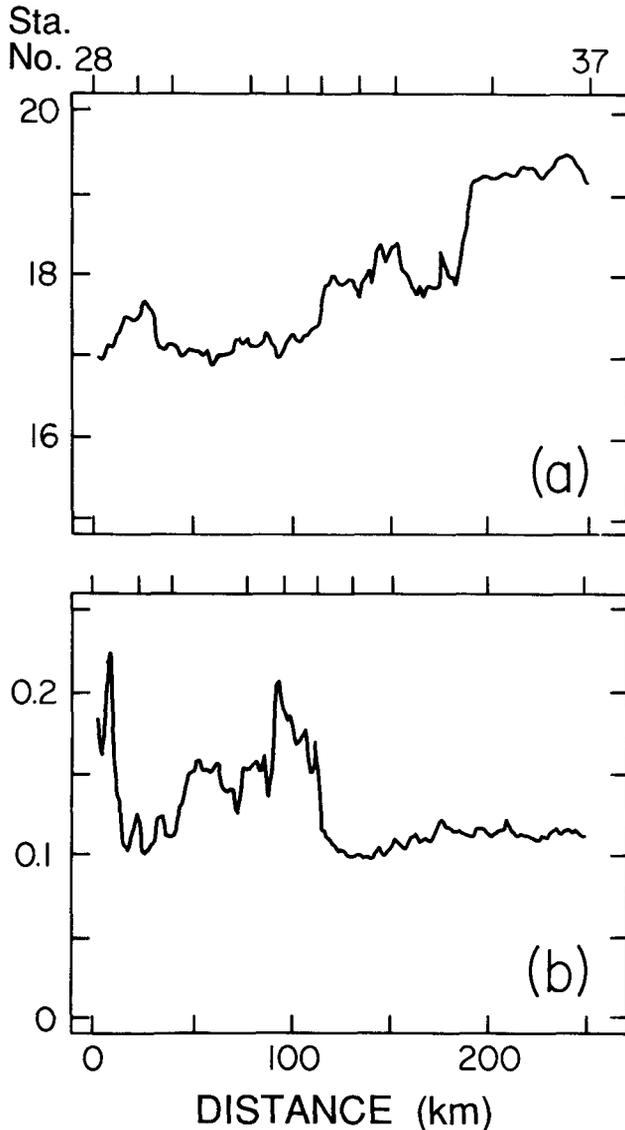


Figure 12. Underway measurements of a, near-surface temperature ($^{\circ}\text{C}$) and b, chlorophyll ($\mu\text{g l}^{-1}$) on the west-to-east transect shown in figure 11.

to the lowest geopotential anomaly ($<5.2 \text{ m}^2\text{s}^{-2}$) in the northeast corner of the survey area, but this region is also associated with shallow topography in the vicinity of San Nicholas Island and with a warm-water intrusion from the east (figure 4c). The N-S-trending ridge of high positive divergence ($>3 \times 10^{-7} \text{ s}^{-1}$) in the middle of the study area (figure 4b) approximately follows the eastern side of the jet axis (figure 4a); surface chlorophyll in general follows this pattern, but in detail, the high-chlorophyll regions are not closely related to highs in positive divergence, as might be expected if the divergence estimate were a good measure of the biological consequences of upwelling. Productivity does not seem well matched at all.

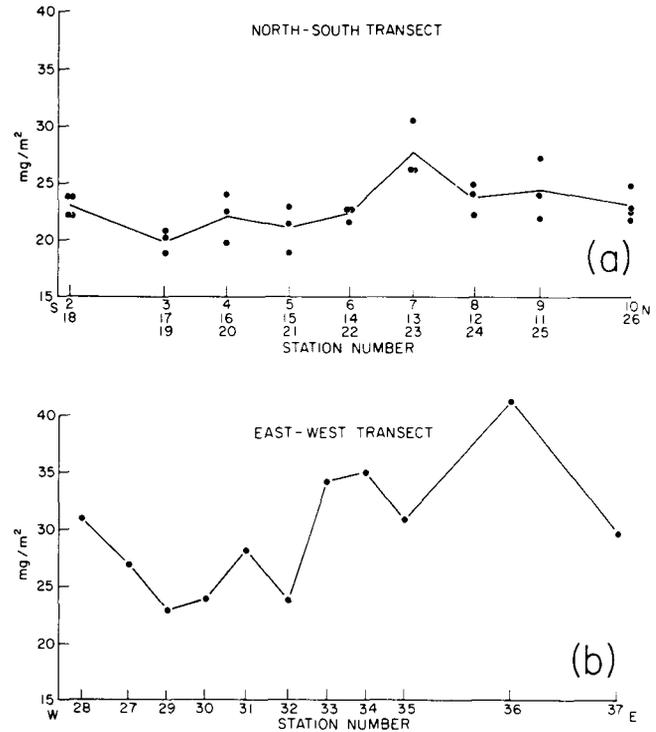


Figure 13. Integrated chlorophyll along the north-south (a) and east-west (b) transects. The solid lines connect the average values for the data at each station.

The relationship of surface chlorophyll to the geostrophic velocities measured on the two Leg I sections across the eastward-flowing jet (figure 5) shows that the high chlorophyll values are associated with the high-velocity-gradient regions between the jets and not with the core of the jets. For example, in the first section (figure 5) the 70-cm s^{-1} jet core has a chlorophyll minimum between a slightly higher value on the south side and a sharp peak to the north. The regions between both northward- and southward-flowing components show chlorophyll peaks.

The sequence of Leg II chlorophyll sections (figure 8) shows an increasing extension of the $>0.25 \mu\text{g l}^{-1}$ subsurface maximum to the south, lending support to the suggestion that the sections were progressively closer to the axis of the southward-flowing filament. This may also indicate the consequences of the subduction of the southward-flowing waters that is suggested by the layer of lower-salinity water. The extent of the low salinity (and other nutrients) did not differ much between the sections to the south of the front, but the chlorophyll definitely was greater. Perhaps the third section passed down the core of the subducting water. The Leg II measurements of surface chlorophyll fluorescence (figure 10) also show an extension of high chloro-

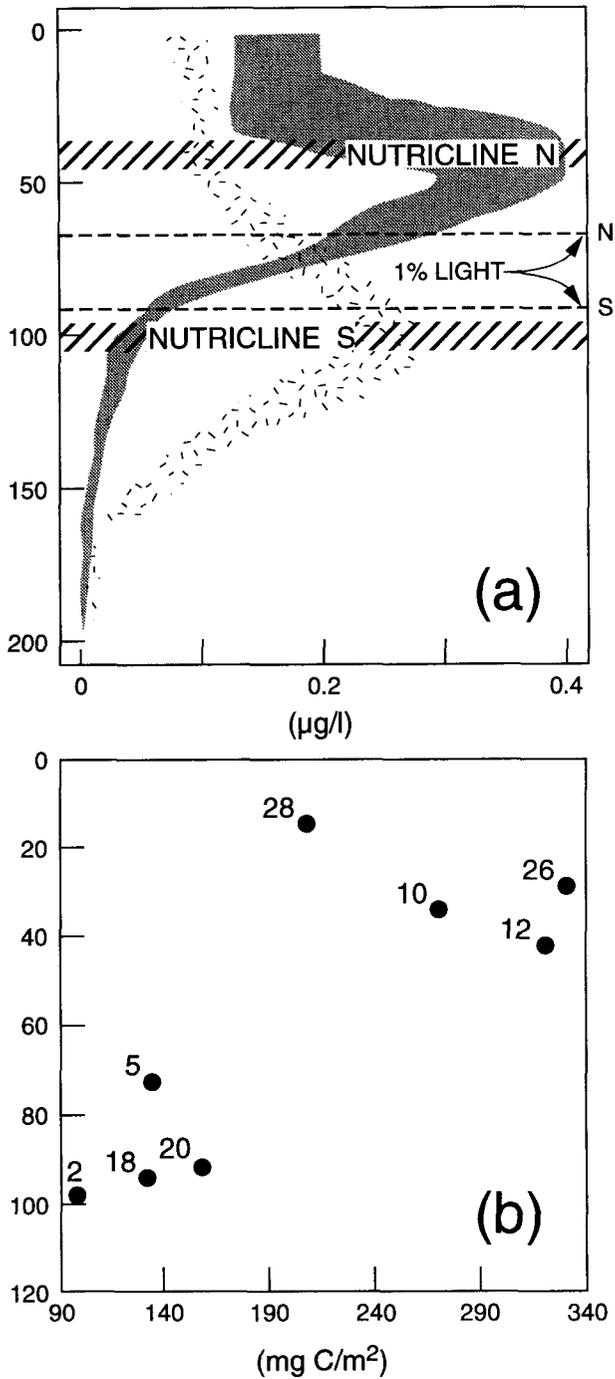


Figure 14. a, Depth (m) profiles of chlorophyll ($\mu\text{g l}^{-1}$) from all casts taken at the northern stations (10, 26; shaded) and southern stations (2, 18; stippled). b, Primary production plotted as a function of the nutricline depth (depth where nitrate exceeds $0.5 \mu\text{M}$). Station numbers are indicated at each point.

phyll south of the front in sections 2 and 3 that is not evident in section 1.

Although the chlorophyll profile of the W-E section (figure 11) shows little detail in the upper 20 m, there is rich pattern in the underway measurements of surface chlorophyll fluorescence (figure 12).

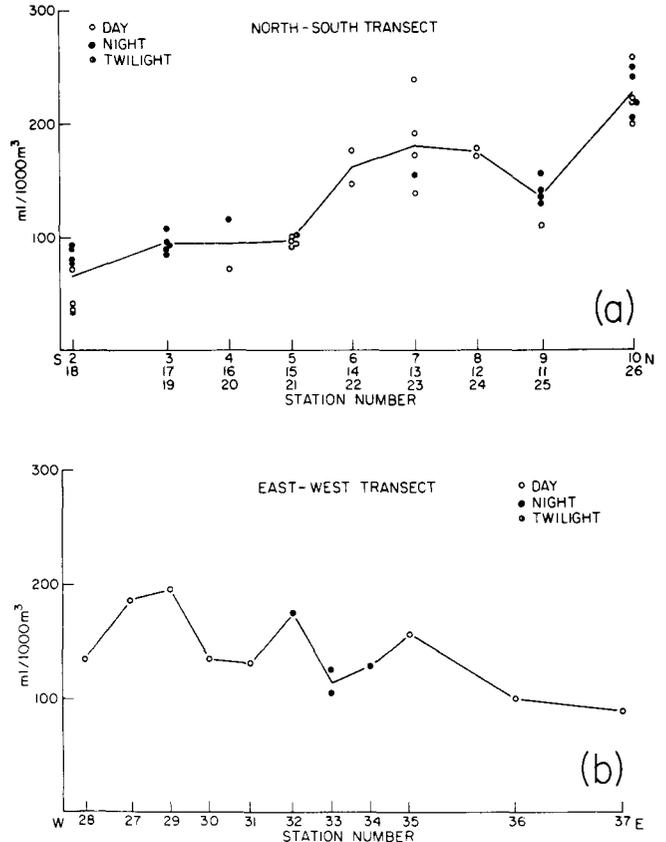


Figure 15. Macrozooplankton displacement volume in the upper 210 m along the (a) north-south and (b) east-west transects. The solid lines connect the average values for the data at each station.

There are also interesting similarities to the structure observed in the three N-S sections from Leg I. Comparison of the fluorescence section (figure 12) with the geostrophic velocity section (figure 11) shows that the high chlorophyll values between stations 32 and 33 are associated with the high shear region east of the strong ($>40 \text{ cm s}^{-1}$) southward flow and with the western edge of the northward filament. The relatively strong ($>10 \text{ cm s}^{-1}$) and warm ($>18^\circ\text{C}$) southward filament near station 34 had the lowest surface chlorophyll ($<0.12 \mu\text{g l}^{-1}$) of the eastern half of the section. The westernmost southward flow of $>10 \text{ cm s}^{-1}$ was also warmer ($>17.5^\circ\text{C}$) and associated with chlorophyll values of $<0.12 \mu\text{g l}^{-1}$; this feature appears to be the anticyclonic intrusion of warmer water from the west seen in the vicinity of $32^\circ\text{N } 121^\circ\text{W}$.

Zooplankton. Zooplankton biomass (displacement volume, including fish eggs and larvae) integrated over the upper 210 m for the N-S and W-E sections is plotted in figure 15. The northernmost station is characterized by a biomass about three times higher than that of the southern terminal station (table 2). The break between the high biomasses of the north

and lower biomasses in the south occurs abruptly between stations 5/15/21 and 6/14/22, a distance of about 13 km; this is the region of the front with the highest gradients in other properties (figures 7–10). The W-E section shows a general decrease of zooplankton biomass to the east beyond station 28; this station appears to have been taken in the warmer waters to the west of the filament.

Zooplankton biomass in the upper 210 m of the water column from the N-S sections varied directly with integrated chlorophyll, while that from the W-E section varied inversely (figure 16). The variation in the W-E section is due to the transition from a western, weakly stratified water column with low integrated chlorophyll and relatively high zooplankton biomass, to highly stratified waters with a strong DCM overlaid by zooplankton-poor waters in the east. The macrozooplankton day-night displacement-volume ratio of about 1.4 (table 2) both north and south of the front suggests a similar day-night difference in grazing pressure on the phytoplankton.

The day and night vertical distributions of zooplankton biomass (displacement volume) over the

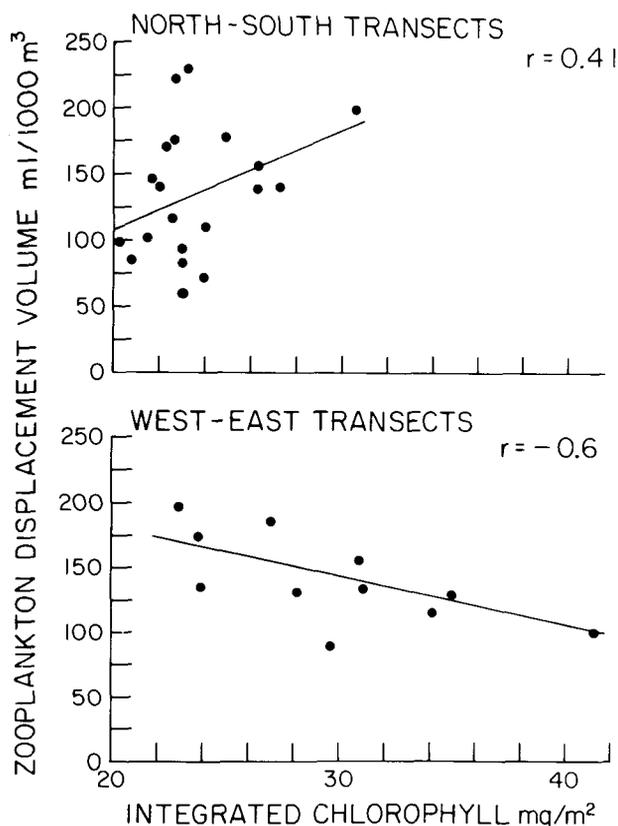


Figure 16. Relation of macrozooplankton displacement volume to integrated chlorophyll on the north-south and west-east transects.

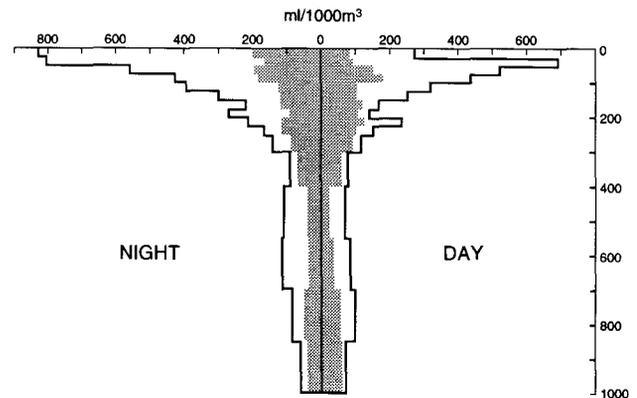


Figure 17. Vertical profiles (depth in meters) of day and night zooplankton biomass (wet-displacement volume) to the north (stations 10, 26; solid lines) and south (stations 2, 18; shaded) of the Ensenada Front. The values shown are the averages of two samples taken at each depth. At the northern station, a layer of abundant detrital material (flocculent aggregates and large fecal pellets) was present between 400 and 850 m, with a peak at about 600 m.

upper 1000 m of the water column at the north and south terminal stations of the sections are presented in figure 17. These distributions clearly show the increased biomass at all depths at the northern station, both day and night. The concentration of the highest biomasses in the upper 100 m results in north/south biomass ratios between the upper 100 m of the terminal stations of 4.2 for night, and 3.8 for day, as compared to 3.2 and 2.9 for the 210-m integrating bongo tows (table 2).

At the northern stations below about 400 m, biomass increased slightly with depth to peaks at 550–700 m during the night and 700–850 m during the day; a small fraction (unmeasured) of this was due to a layer of grey-green flocculent organic aggregates and large fecal pellets, similar to those of salps, between 400 and 850 m. The peak abundance of this material was about 600 m. No such feature was noted for the southern stations.

Total fish eggs and larvae counted in the net samples describe the way that ichthyoplankton varies across the front and in its vertical distributions at the terminal stations of the sections. Figure 18 presents the results from the 210-m integrating bongo net tows along each of the four sections. Except for the samples collected at station 2 (figure 18a), both eggs and larvae in the three N-S sections decreased in abundance to the north; regressions of eggs and larvae against stations using the combined data for the three sections showed, however, that only eggs had a significant negative relationship to station position ($r = -0.63$, $p < 0.0001$). On the W-E section, the larvae decreased in abundance across the southward-flowing filament, but eggs did not (figure 18d). Regression of fish larvae against eggs from the three

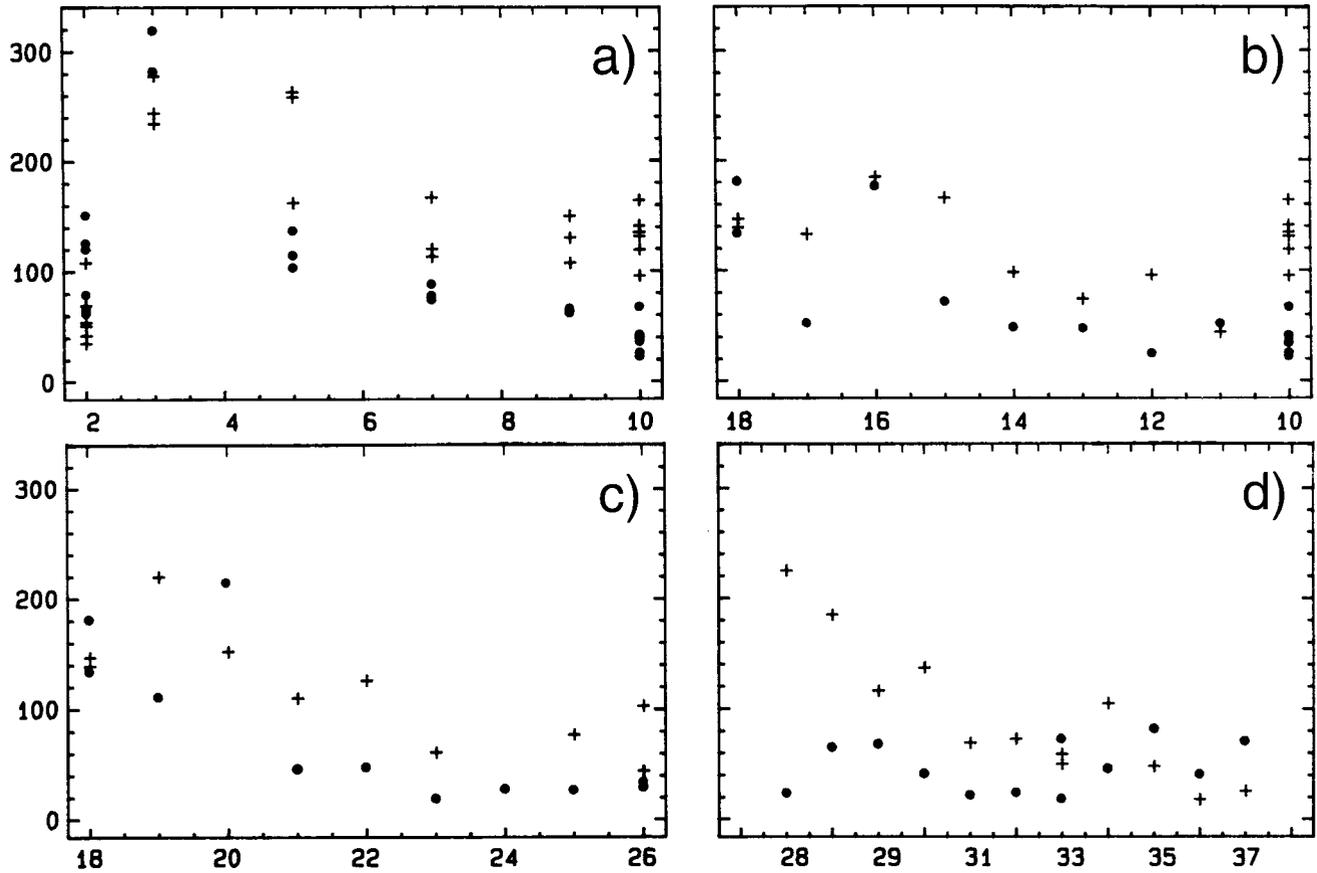


Figure 18. Abundance (numbers/1000 m³) of fish eggs (·) and larvae (+) from the 0–210-m oblique CalBOBL net tows at each station of three north-south (a–c) and one west-east (d) transects (see figure 1b); station numbers are indicated at bottom of each plot. Day values have been multiplied by 1.2 for eggs and 1.5 for larvae to correct for consistent day-night differences in abundance.

N-S sections (figure 19) showed a significant relationship between larvae and eggs ($r = 0.57$, $p < 0.0001$).

The day and night vertical distributions of fish eggs and larvae at the terminal stations are shown in figure 20. Fish eggs in the south were much more abundant than to the north, both day and night; larval abundances were about equal in both areas, except in surface waters to the north at night. Diel shifts in vertical distribution and abundance are clear only for eggs south of the front, and larvae north of the front.

DISCUSSION

Satellite imagery has shown the Ensenada Front to be one of the dominant features of the California Current off southern California and northern Baja California (Pelaez and McGowan 1986; Strub et al. 1990; Thomas and Strub 1990). Many large-scale oceanographic surveys, especially the CalCOFI program, have covered the area of the frontal system, but few have focused enough on the frontal area to provide detailed physical, biological, and chemical

information on the nature of the frontal system. The ship-tracked drogoue measurements of Reid et al. (1963) confirmed the shoreward sweep of surface waters and revealed the mesoscale eddies associated

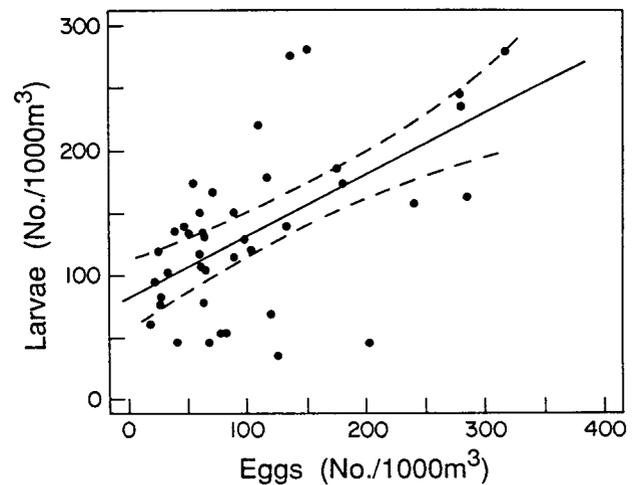


Figure 19. Regression of total fish larvae on total fish eggs for all 0–210-m oblique CalBOBL net tows taken on FRONTS 85 Leg II. Dashed lines are the 95% confidence intervals.

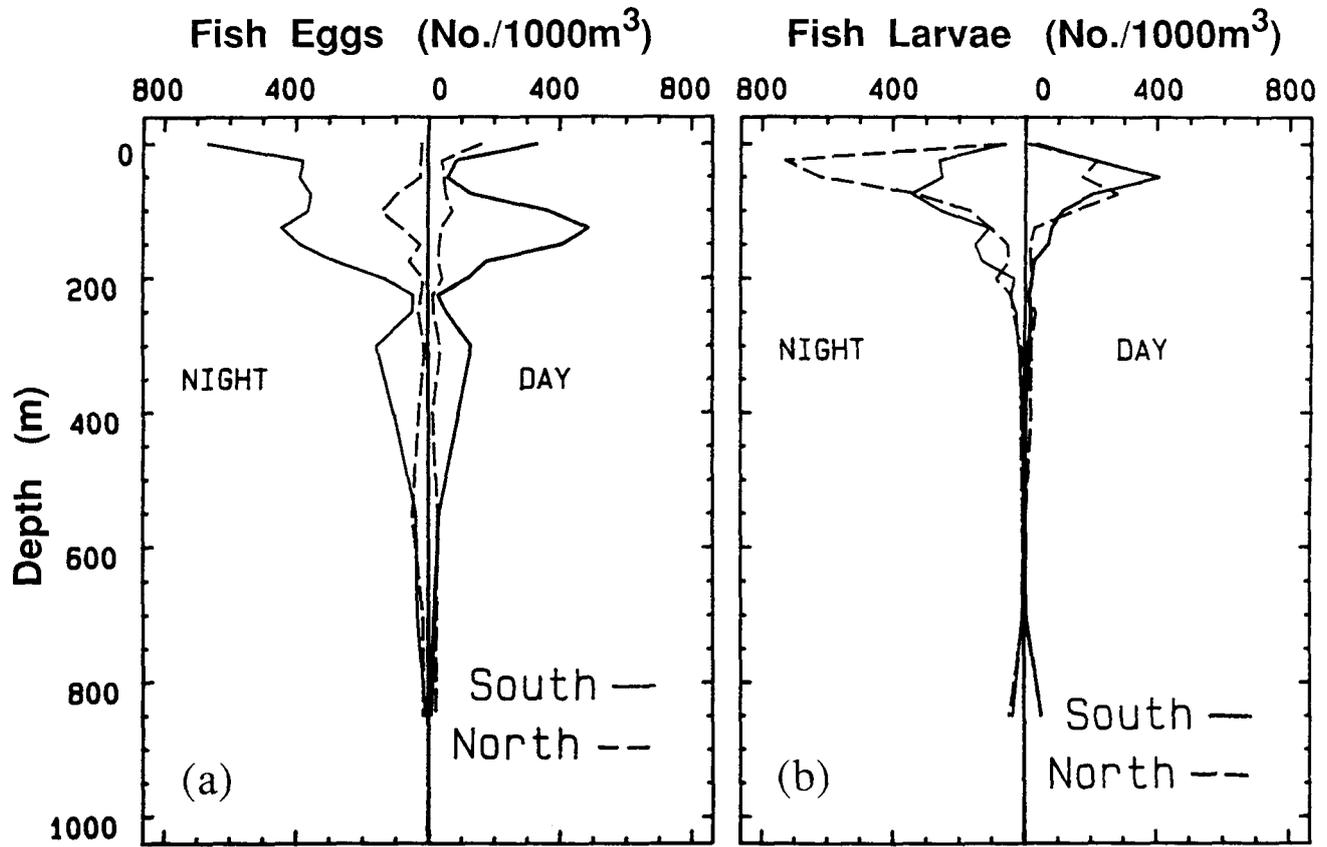


Figure 20. Vertical profiles of abundance of a, all fish eggs and b, all fish larvae from the MOCNESS samples taken to the north (stations 10, 26; dashed lines) and south (stations 2, 18; solid lines) of the Ensenada Front. The values shown are the averages of two samples taken at each depth.

with the flow. A study by Simpson and Lynn (1990), nearly contemporaneous with the one described here, surveyed the same area but reported primarily on the mesoscale eddy dipole to the northwest of our study area.

The flow within our study area, localized within a narrow, intense filament forming only a small part of the large-scale classical picture of the southward-flowing California Current, transports a volume of water (relative to 300 db) comparable to that calculated on the basis of much larger areal averages (Bernal and McGowan 1981; Haury and Shulenberger 1982). Its transport is similar to that of the equatorward jet off northern California surveyed by Huyer et al. (1991). It also transports volumes of the same order as those of offshore-directed jets (Flament et al. 1985; Washburn and Armi 1988).

The large volume of water transported by the filament is relatively rich in chlorophyll and zooplankton. When this water exits the filament system by entering the Southern California Bight or the numerous eddies to the south and east, much of the biological richness has disappeared. The biological and physical mechanisms for the changes observed

are not well understood. Some fraction of these waters appears to be subducted beneath the warm, oligotrophic waters to the south of the front. Whether this is an important mechanism for the loss of organic material from the California Current is the subject of continuing study.

Also not understood is the nature of the processes contributing to the relative richness of the filament waters. Advection from upwelling centers and other loci of enrichment processes to the north may contribute most of the nutrients and organisms, but the complexity of the flow structure in the filament may be a significant *in situ* source. For example, enhanced vertical mixing should result from the large shears between the multiple "strands" of the filament revealed by the CTD and hydrographic sections (figures 5, 7, 11) and satellite imagery (figure 3). Interactions between the wind field and these small-scale velocity structures can also cause upwelling and downwelling (Paduan and Niiler 1990; Lee et al., in press). The enhanced chlorophyll in these high-shear zones (figure 5) seen in the underway measurements suggests that enrichment or convergence does occur.

Thomas and Strub (1990), using CZCS imagery from 1981, have shown the seasonal character of the surface manifestations of the Ensenada Front (their figure 3). Our chlorophyll values from the under-way measurements (figures 5, 6, 10) and from surface bottles of the hydrographic sections (figure 8) agree both in quantity and in the position of the frontal region between 31° and 32.5°N during the summer period. As Thomas and Strub (1990, p. 13,036) caution, however, the near-surface values do not well represent the water column biomass; this is graphically illustrated by comparing our figures 7–10 to the integrated chlorophyll value from the sections (figure 13a). There is clearly no front evident in the water-column-averaged standing crop of phytoplankton.

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REPRODUCTION BY THE OCEANIC COPEPOD *RHINCALANUS NASUTUS* OFF SOUTHERN CALIFORNIA, COMPARED TO THAT OF *CALANUS PACIFICUS*

MICHAEL M. MULLIN

Marine Life Research Group
Scripps Institution of Oceanography
University of California, San Diego
9500 Gilman Drive
La Jolla, California 92093-0218

ABSTRACT

Measuring zooplankters' rate of egg production can provide estimates of secondary production and of the availability of food for many larval fish. Superficially, *Rhincalanus nasutus* and *Calanus pacificus* have similar ecologies; conditions for successful rearing in the laboratory are similar, as are rates of egg production when females are held in the laboratory with excess food; also, the abundances of the two species are positively correlated through space and time. Rates of egg production by these two species in the southern California sector of the California Current were measured in the winters and springs of 1991–93 by holding females in the ambient seawater and in seawater enriched with phytoplanktonic food. At many locations, female *Calanus* produced eggs when in the unenriched seawater; they almost always did so when food was enhanced with cultured phytoplankton. In contrast, *Rhincalanus* seldom produced more than 10 eggs·(female·day)⁻¹ except when incubated with excess food for 2 days, and even then, the spatial/temporal patterns of egg production differed from those of *Calanus*. Future work should focus on whether there are conditions (season, food, etc.) permitting high reproductive rates in *Rhincalanus* feeding on the natural seston off southern California; i.e., >10 eggs·(female·day)⁻¹.

RESUMEN

La disponibilidad de alimento para muchas larvas de peces, así como la producción secundaria, pueden ser estimadas con mediciones de tasas de producción de huevos de zooplancton. Superficialmente, las ecologías de *Rhincalanus nasutus* y *Calanus pacificus* se asemejan. Las condiciones para su cultivo en laboratorio son similares y las tasas de producción de huevos en laboratorio (con dietas de saciedad) son asimismo similares. Además, la abundancia de éstas especies se encuentran correlacionadas positivamente, espacial y temporalmente. En los inviernos y primaveras de 1991–93, en la corriente de

California (frente a California sur), se midieron las tasas de producción de huevos de las dos especies; se pusieron hembras en aguas “no tratadas” y en “aguas enriquecidas con fitoplancton cultivado”. *Calanus* hembra produjeron huevos en varias estaciones con “aguas no tratadas”. Por otro lado, hubo producción de huevos en casi todas las estaciones con “aguas enriquecidas con fitoplancton cultivado”. En contraste, *Rhincalanus* raramente produjeron más de 10 huevos (hembra·día)⁻¹. La excepción fué el tratamiento de dieta de saciedad durante dos días, y aun así, los patrones espacio-temporales de producción de huevos difirieron a los de *Calanus*. Estudios futuros deberán enfocarse en discernir si para *Rhincalanus* (con dieta de seston natural) existen condiciones (estación del año, alimento, etc.) en los mares de California sur que produzcan altas tasas de reproducción; es decir, >10 huevos (hembra·día)⁻¹.

INTRODUCTION

The rate of reproduction by planktonic copepods is an important indicator of population growth and secondary production. Comparing rates in ambient seawater and in the presence of excess food indicates how much these demographic rates are limited by the natural food supply (e.g., Durbin et al. 1983; Ayukai 1988). But it is difficult to determine the effective natural concentration of food because neither the small-scale spatial distribution of copepods relative to where point samples of seston (potential food) are taken nor the property of seston that is most significant to reproduction (e.g., chlorophyll, particulate organic carbon or nitrogen, a critical amino acid, a particular size and type of particle) are usually known. Further, the genetic constitution and past nutrition of female copepods used in experiments is also unknown, though both can affect reproduction and the response to food. Finally, different species may respond differently to the supply of food, or to the proxy variable for food, even if their trophic type, seasonality, and biogeography seem the same.

To compare the reproductive geography of two similar species of large, planktonic, particle-graz-

ing, calanoid copepods, as well as their responses to chlorophyll biomass, I measured the egg production of female *Rhincalanus nasutus* at several locations in the southern California sector of the California Current system, and contrasted the patterns of reproduction to those of the more intensively studied species *Calanus pacificus* (see Mullin 1991a, and references therein) at the same locations.

Earlier work (Mullin and Brooks 1967, 1970; Hakanson 1987) compared metabolic and demographic properties of the two species, including feeding and growth when the diatom *Thalassiosira weissflogii* (= *fluviatilis*) was provided as food. In these studies, the similarities between the two species were more striking than their differences. Both extend into the southern California sector from farther north, not south or west, and both can range farther south to the tip of Baja California (Fleminger 1964), but the southern limits of reproduction and recruitment are not known. This zoogeography led me to expect that *Rhincalanus* would reproduce most readily in the northern part of the region I studied.

Longhurst et al. (1966) found the vertical distribution of *Rhincalanus* to overlap that of *Calanus* in the upper 150 m off San Diego in May, but to extend deeper, to at least 500 m. Populations of the two species were studied concurrently off La Jolla, California, in 1967. From this set of data, Koslow and Ota (1981) found indirect evidence of a difference between the species in the seasonal pattern of diel vertical migration relative to diatom blooms, and Mullin (1991b) found that though rates of juvenile mortality of both populations were density-dependent, the space/time distributions of these rates were uncorrelated between the species.

METHODS

Similarity in the mesoscale distributions of *Rhincalanus* and *Calanus* imply ecological similarity. I therefore counted females of both species in samples taken by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) from January and April 1989 and March and April 1990 (cruises 8901, 8904, 9003, and 9004) and tested whether the abundances correlated.

In June 1969, I found spermatophore-carrying (i.e., newly mated) female *Rhincalanus* in net tows made off La Jolla. I placed 13 of these individually in 1-liter beakers of filtered seawater with cultured *Thalassiosira* added as food. No precautions were taken against cannibalism. The beakers were kept at 15°C for up to 4 months, and every 1–4 days I removed and counted eggs and nauplii, replaced the seawater, and added fresh food.

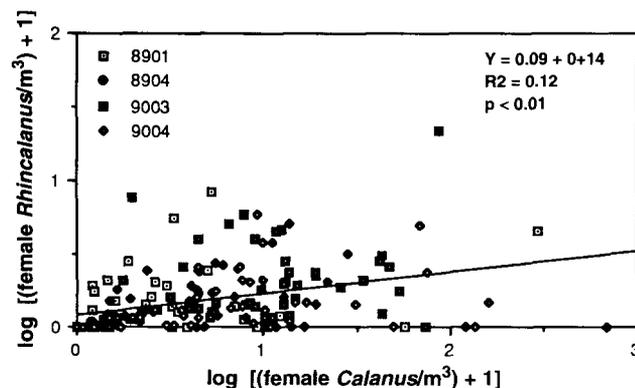


Figure 1. Abundances (log-transformed) of female *Rhincalanus* and *Calanus* in the upper 200 m of the region of study in January and April 1989 and March and April 1990 (cruises 8901, 8904, 9003, and 9004). See figure 3 for region. The correlation is significant at $p < 0.01$.

On several CalCOFI cruises, I measured the production of eggs during 2 days' incubation in seawater plus natural seston ("unfed"), and in the same seawater enriched with *Thalassiosira* ("fed"), by female *Rhincalanus* captured in net tows at various stations, with methods described in Mullin 1991a. The measurements were made irregularly in April and August of 1990 (cruises 9004 and 9008), and at all stations where sufficient animals were captured in January and March 1991 (cruises 9101 and 9103), February and April 1992 (cruises 9202 and 9204), and January 1993 (9301). I measured the per capita reproduction of *Calanus* similarly. In addition to determining the daily production rate of both species with and without supplemental food, I used two ratios (from Mullin 1991a) to express the degree by which food limited production: the ratio (b) of the total production over 2 days of unfed females to that of fed ones, and the ratio (c) of the production of fed females during the second day to that of the same copepods during the first day. Ratio b increases, and c decreases, as food becomes less limited.

Female *Rhincalanus* eat the dinoflagellate *Gymnodinium splendens* and naupliar *Artemia* (Mullin and Brooks 1967, 1970), so I tested how these two alternate foods stimulate fecundity, although neither is as convenient to use at sea as is *Thalassiosira*. Neither resulted in egg-laying rates as high as those when *Thalassiosira* was the supplemental food.

RESULTS

As shown by the example in figure 1, the areal distributions of the two populations in the southern California sector of the California Current are similar on the large scale (the statistically significant trend) but far from identical on smaller scales (the scatter). *Calanus* is the more widespread (fewer absences) and generally the more abundant of the two.

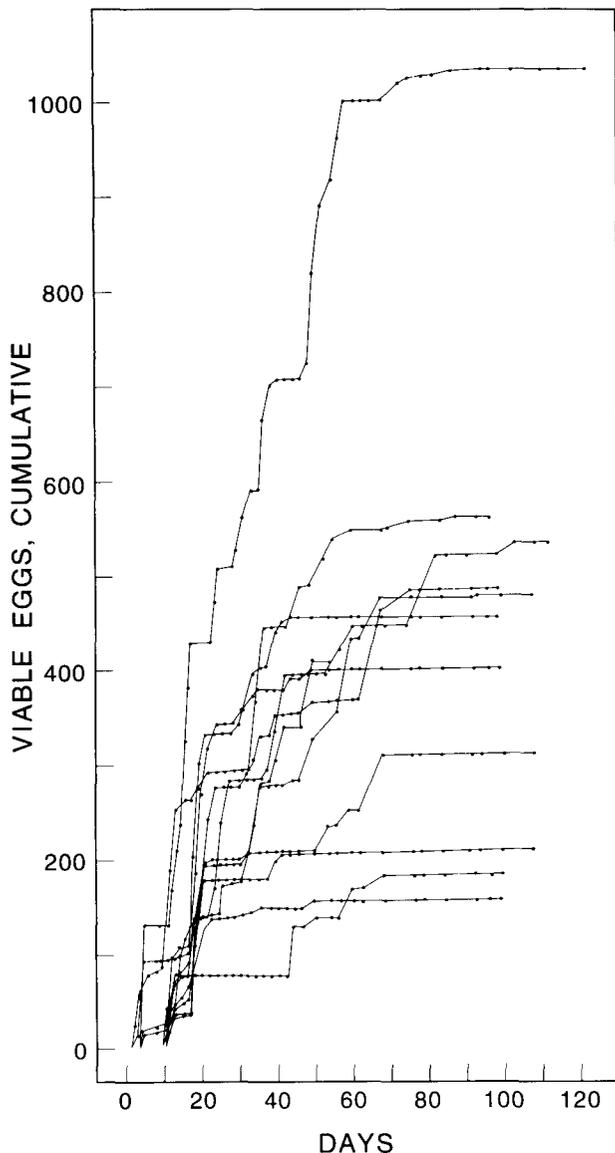


Figure 2. Cumulative production of eggs by 12 newly mated female *Rhincalanus nasutus* fed *Thalassiosira* in the laboratory. The history of another female which produced a total of 1042 eggs is not shown.

Individual female *Rhincalanus* maintained in the laboratory could produce up to 95 eggs in 1–2 days, and over 1000 eggs during adult life (figure 2). The maximal daily production rate slightly exceeded greatest rates by *Calanus* from the same area (Mullin 1991a, figure 18). Mean lifetime fecundity of *Rhincalanus* was 478 eggs; the median was 449 (compared to about 650 for *Calanus*; Mullin and Brooks 1967). Because of the possibility of cannibalism in the 1-liter containers in which females were held, these estimates must be considered minimal. Thus, female *Rhincalanus* are reproductively active at 15°C as far south as La Jolla, at least at times, when fed *Thalassiosira* over long periods.

In April 1990 *Rhincalanus* produced very few eggs south of Palos Verdes unless food was supplemented, and even then did not approach the reproductive rate of *Calanus* at these stations (Appendix). Reproduction did not equal that of *Calanus* even farther north (unfortunately, no samples were taken north of Point Conception during this cruise). Similarly, there was little reproduction by *Rhincalanus* south of Palos Verdes in August, and only one station in the entire area where eggs were laid in the absence of added food, although *Calanus* was reproductively active at several stations (Appendix). With one exception on the two cruises, *Rhincalanus* produced ≥ 10 eggs·(female·day)⁻¹ only when fed for more than 24 hours. The impressions resulting from these two cruises, where sampling of *Rhincalanus* was sporadic, are that conditions at many stations (or the condition of the females themselves), though suitable for *Calanus* to reproduce, were unsuitable for *Rhincalanus*, especially in August.

Figures 9 and 10 of Mullin 1991a show the reproductive geography of *Calanus* during these two periods more completely. They also show the temperatures at 10 m (approximately the temperature of the shipboard incubations) and integrated biomasses of chlorophyll; comparison with the Appendix table suggests that *Rhincalanus*'s reproduction was more inhibited by scarcity of food (as indicated by sparse chlorophyll) or high temperature than was *Calanus*'s reproduction. In April there was no clear relation between *Rhincalanus*'s reproduction and the chlorophyll biomass at the same stations; in August the only reproduction was at three stations where chlorophyll exceeded 80 mg·m⁻². As noted above, this could be either an experimental artifact or a symptom of longer-term limitation: perhaps reproduction would have been greater with other conditions of incubation, or perhaps the females were physiologically incapable of intensively producing eggs within two days under any conditions.

I will present the more extensive measurements of egg production made in January and March 1991 (cruises 9101 and 9103) and February and April 1992 (9202 and 9204) as if they had been made in consecutive months of one year, thus emphasizing seasonality and suppressing interannual variability. Interannual variability might well be important, since the winter of 1992 was characterized by El Niño conditions (Hayward 1993). The distributions of temperature and chlorophyll biomass during these cruises are shown in figure 3, and the actual daily rates of per capita egg production in the Appendix.

In only one case in January 1991 did unfed *Rhincalanus* produce eggs; only once did fed *Rhincalanus*

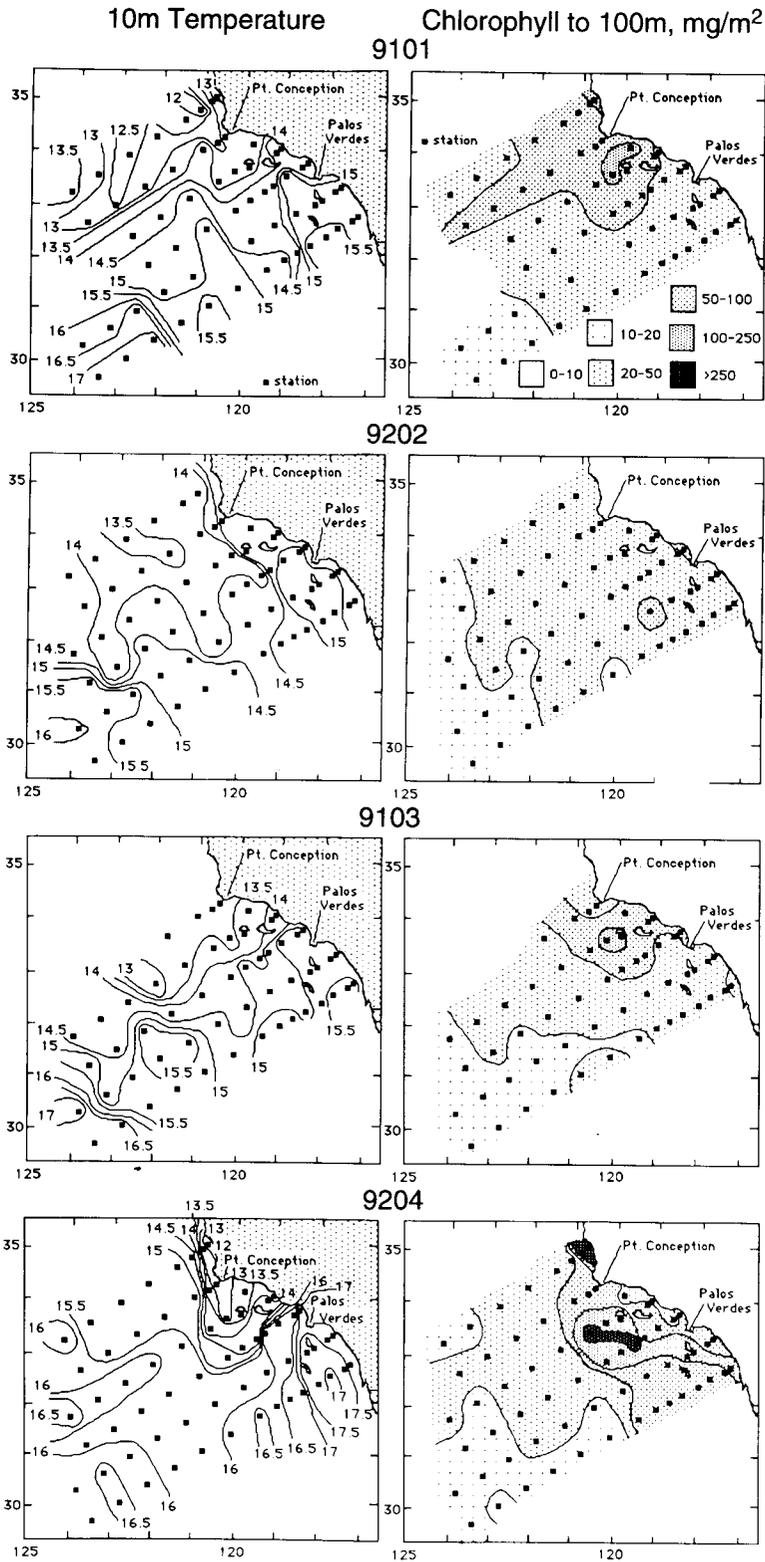


Figure 3. Distributions of temperature at 10 m, and integrated chlorophyll ($\text{mg}\cdot\text{m}^{-2}$, to 100 m) in January 1991 (9101), February 1992 (9202), March 1991 (9103), and April 1992 (9204).

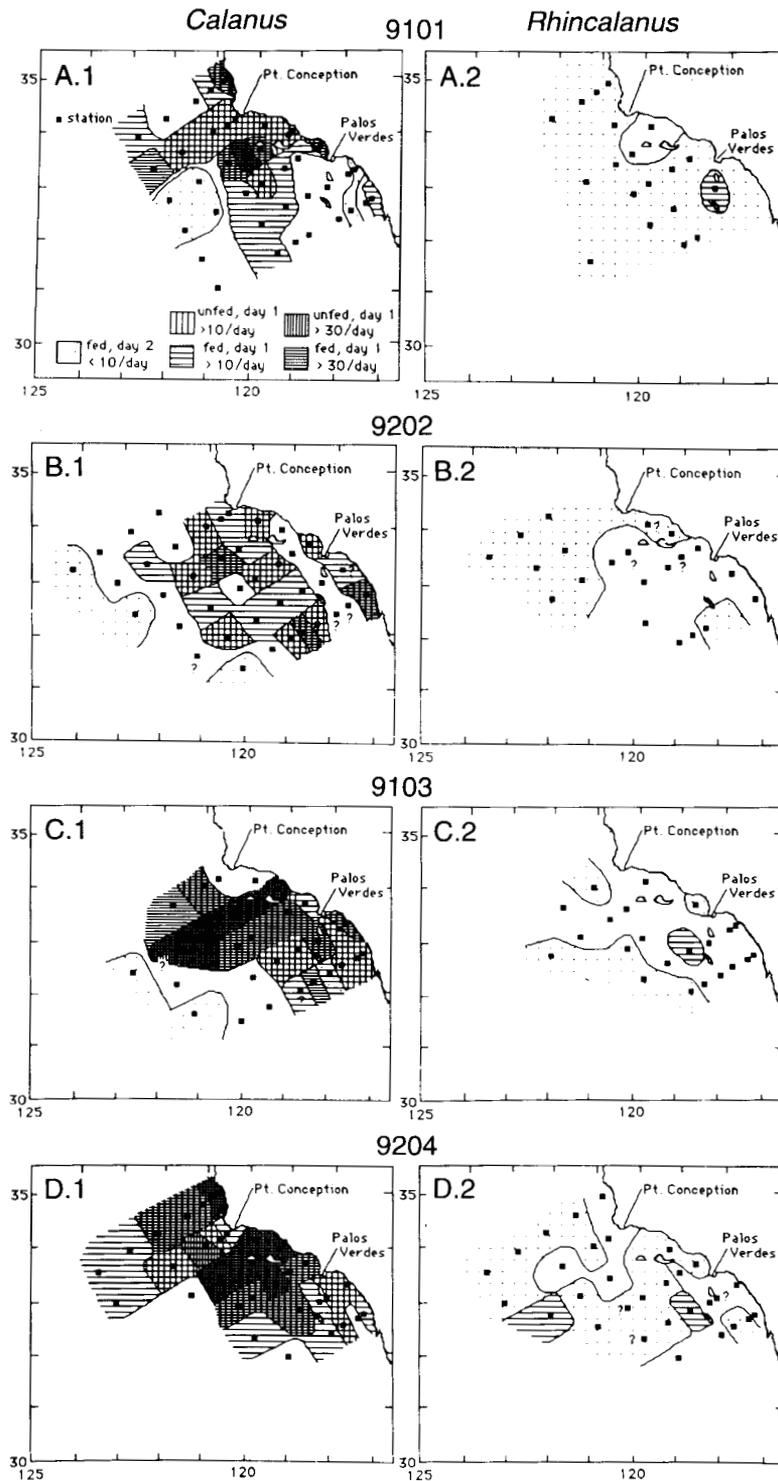


Figure 4. Contour maps of egg production by *Calanus* (1) and *Rhincalanus* (2) on cruises 9101 (A), 9202 (B), 9103 (C), and 9204 (D). Poorest production is in stippled regions; clear regions represent rates of <10 eggs \cdot (female \cdot day) $^{-1}$ on the first day, with or without supplemental food, but production exceeding this on the second day with food.

produce as many as 10 eggs \cdot (female \cdot day) $^{-1}$ on the first day (horizontally striped area in figure 4A.2), and at only two additional stations did the per capita rate exceed this value on the second day (nonstippled

areas in figure 4A.2). The rate of production by *Calanus* in unsupplemented seawater south of Palos Verdes was generally small, but, unlike *Rhincalanus*, female *Calanus* were ready to reproduce at much

EGGS/FEMALE-DAY, FED, DAY 2

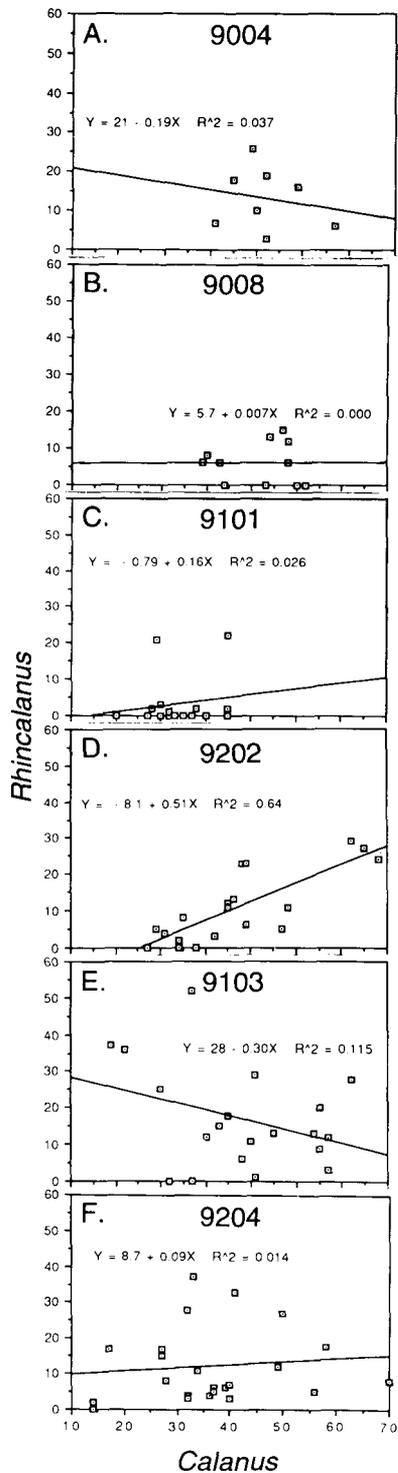


Figure 5. A-F. Egg production of fed *Rhincalanus* on the second day of incubation versus that of *Calanus*, for 6 cruises. Only the correlation for cruise 9202 was statistically significant ($p < 0.01$).

greater rates in the presence of excess food (horizontal striping in figure 4A.1). North of Palos Verdes, *Calanus* was reproductively active at many stations,

even in the unsupplemented seawater, where *Rhincalanus* was not (figure 4A.1 and 2; see also figure 5C). *Rhincalanus*'s reproduction was food-limited everywhere; food limitation affected *Calanus*'s reproduction much less north of Palos Verdes than south of it (figure 6A.1 and B.1).

The lack of egg production by *Rhincalanus* at even the northernmost stations of 9101 makes it unlikely that high temperature, per se, caused *Rhincalanus*'s failure to reproduce at many southern stations where *Calanus* did reproduce.

In February 1992 (9202; figure 4B.1 and 2) no measurements were made north of Point Conception. The distribution of chlorophyll was relatively uniform (figure 3), the absence of elevated biomass around Point Conception perhaps being due to El Niño. There were no stations at which female *Rhincalanus* produced ≥ 10 eggs \cdot day $^{-1}$ on the first day of incubation, with or without supplemental food, even though *Calanus* exceeded this rate at several stations. When food was supplemented for 2 days, however, *Rhincalanus* produced ≥ 10 eggs \cdot (female \cdot day) $^{-1}$ at almost half the stations (nonstippled areas in figure 4B.2), primarily those in the Southern California Bight where *Calanus*'s reproduction was also strong (see also figure 5D). *Calanus*'s reproduction was food-limited more often than in January, at least as indicated by ratio b (figure 6C.1), but there was less obvious geographic pattern to this limitation. *Rhincalanus*'s reproduction was again food-limited over much of the area (figure 6C.2 and D.2).

Again in March 1991 (9103; figures 4C.2 and 5E) *Rhincalanus* on their second day of supplemental food (but, with one exception, only then) produced more than 10 eggs \cdot (female \cdot day) $^{-1}$ at several stations. This was true even at rather warm temperatures along the southernmost line of stations, again suggesting that temperature had not caused the poor reproduction there two months earlier (9101). Also, females incubated at 12.5°–13°C were no more fecund than those incubated at ambient surface temperatures in the southern part of the area. As on cruise 9202, no measurements were made north of Point Conception. *Rhincalanus* reproduced at stations where the concentration of chlorophyll was < 80 mg \cdot m $^{-2}$, a range in which little or no reproduction had occurred on cruises 9008 and 9101 (compare figure 4C.2 with 3; figure 7C.2). Again, however, *Rhincalanus* produced many fewer eggs on the first day of incubation than *Calanus* at most stations (figure 4C.1 and 2), and *Rhincalanus* was more food-limited (figure 6E and F).

Similar results were obtained in April (9204; figure 4D.2), even though several stations north of

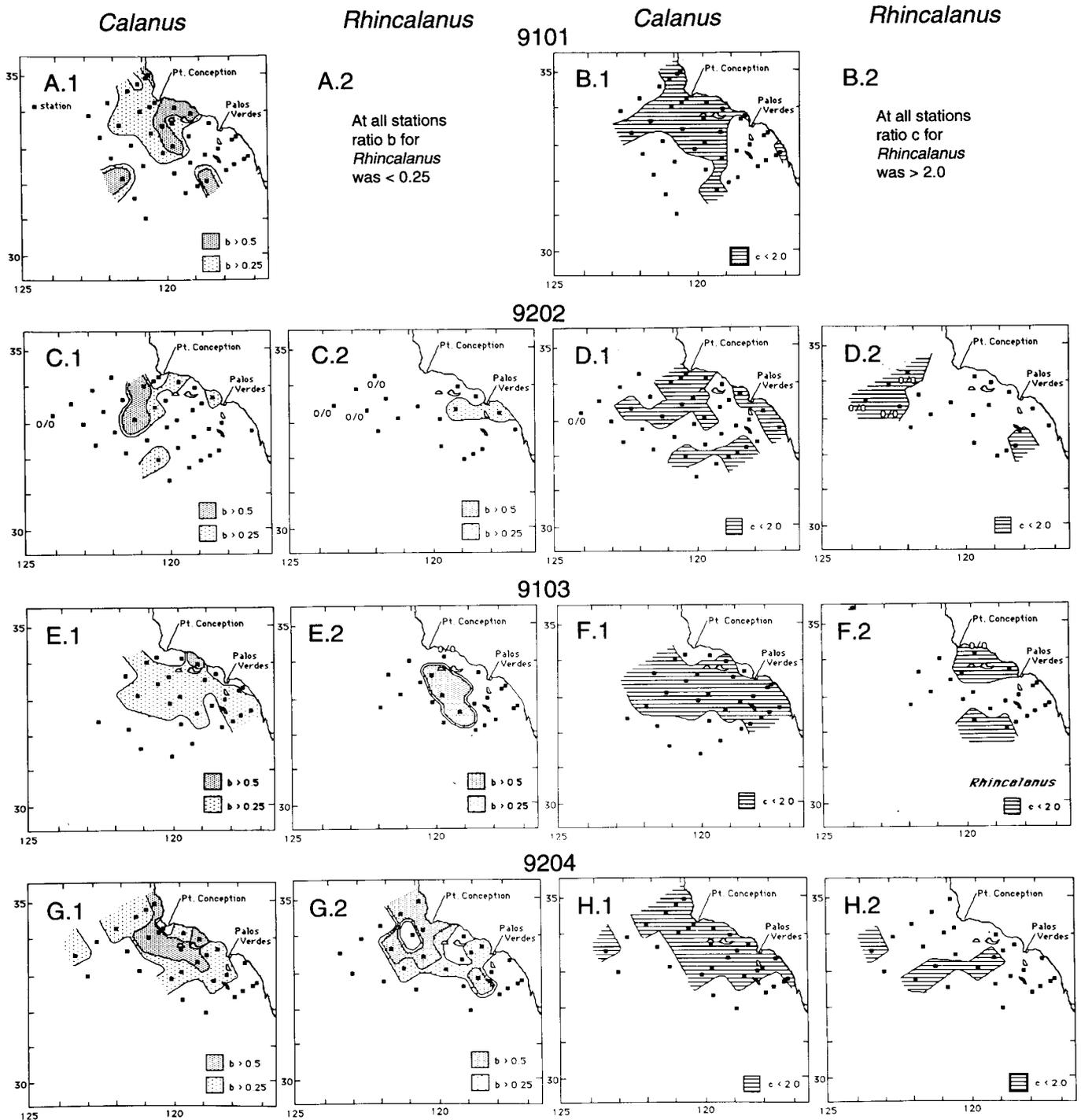


Figure 6. Maps of food limitation of egg production in *Calanus* (1) and *Rhincalanus* (2). In each case, shaded areas mean less limitation by food, as measured by ratios b (A, C, E, and G) and c (B, D, F, and H). See text for explanation of ratios.

Point Conception were sampled, and the biomass of chlorophyll was relatively great north and south of Point Conception. *Rhincalanus*'s rate of egg production was $\geq 10 \cdot \text{day}^{-1}$ at a minority of stations, and then generally as a result of two days' feeding. Again, reproduction was more likely to be stimulated by supplemental food (nonstippled areas in fig-

ure 4D.2) in the Southern California Bight than elsewhere. The reproductive rate of *Calanus* was high over much of the area (figure 4D.1).

At three northern, inshore stations of cruise 9204, *Rhincalanus* on the second day in unsupplemented seawater produced $>10 \text{ eggs} \cdot (\text{female} \cdot \text{day})^{-1}$ (the same rate as with supplemental food), and more than

Rhincalanus

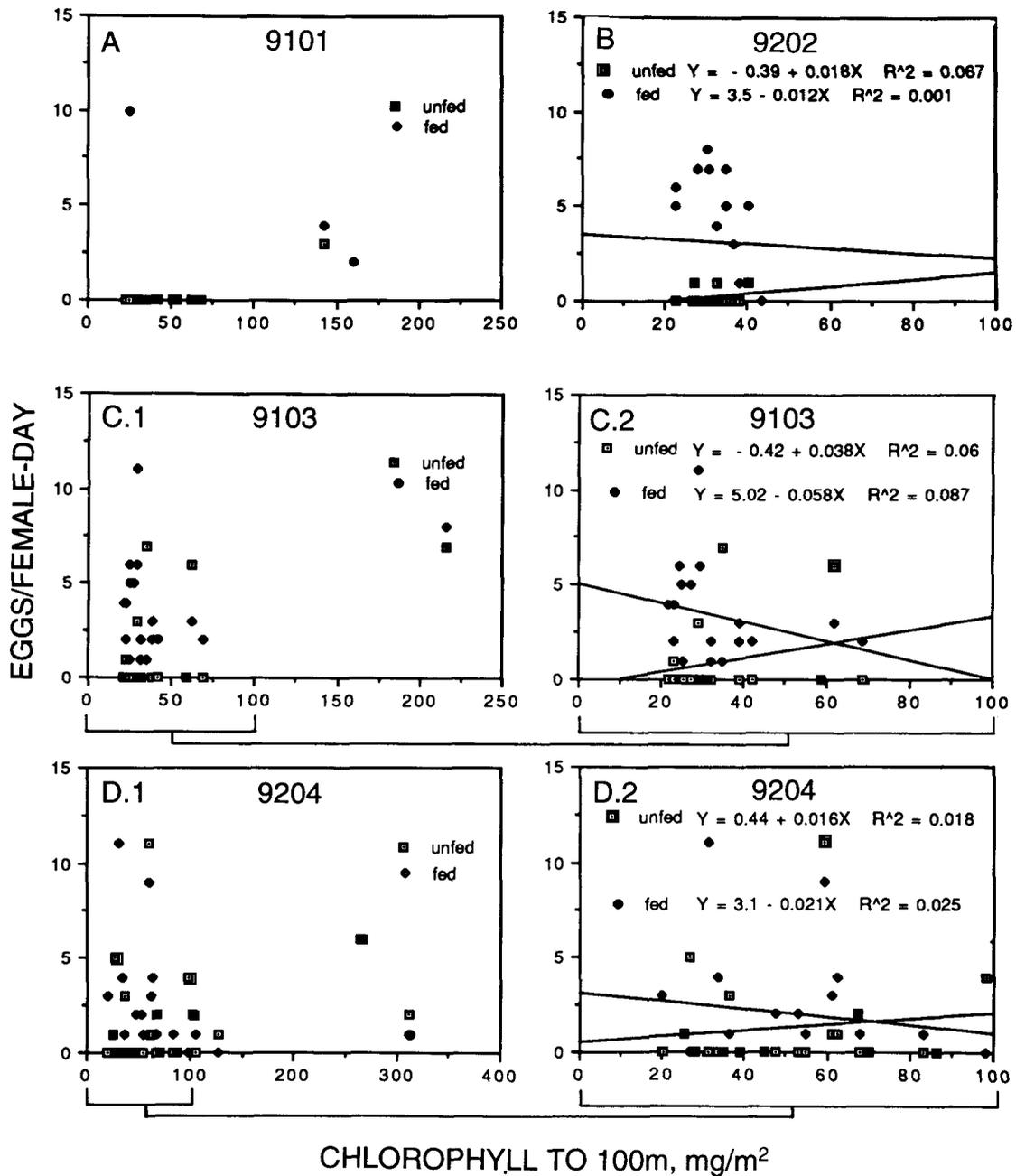


Figure 7. Relations of egg production by *Rhincalanus* on the first day of incubation, with (fed) or without (unfed) supplemental food, to the biomass of chlorophyll (see figure 3) in A, January 1991 (9101); B, February 1992 (9202); C, March 1991 (9103); and D, April 1992 (9204). For cruises 9103 and 9204, correlations were calculated only for those stations where the biomass of chlorophyll was ≤ 100 $\text{mg}\cdot\text{m}^{-2}$ (graph 2 in each case), because nonlinearities might occur at greater biomasses. All correlations are nonsignificant ($p > 0.05$).

five times the first-day rate. This increase virtually never occurs in *Calanus* (Appendix, and Mullin 1991a, figures 3–10), in which depleted food in un-supplemented seawater by the second day results in a rate that is either less than the first-day rate, or < 10 $\text{eggs}\cdot(\text{female}\cdot\text{day})^{-1}$, or (most often) both. A single station on cruise 9204 near Palos Verdes was the only

exception for *Calanus*. This result suggests that *Rhincalanus*'s reproduction is more divorced from the immediate supply of food than is that of *Calanus*.

Based on the ratios indicating the extent that the ambient food supply limits egg production at each station, *Rhincalanus*'s reproduction was more widely limited by food (unshaded areas in figure 6) on all

cruises than was that of *Calanus*. Further, most of the shaded areas for *Rhincalanus* in figure 6 were not due to strong reproduction by unfed females (as the shaded areas for *Calanus* usually were), but to very low rates even after two days with supplemental food. Since the measures of food limitation were based on the copepods' response to supplemental phytoplankton, this conclusion depends on the assumption, drawn from experimental rearing, that both species are particle-grazers, eating primarily phytoplankton.

Egg production by *Calanus* usually correlates positively with chlorophyll biomass, though there is much unexplained variability (Mullin 1991a, figure 15). However, on none of the four cruises in 1991–92 was there a significant relation between production of eggs on the first day of incubation by female *Rhincalanus*, either with or without supplemental food, and the chlorophyll biomass in the water column (figure 7). Analogous relations for *Calanus* were highly significant ($p < 0.01$) for cruises 9101 and 9103, and positive but nonsignificant for cruises 9202 and 9204. Only on 9204 was there a significant relation between *Rhincalanus*'s egg production on the second day of feeding and the biomass of chlorophyll; this relation was positive.

In January 1993 *Rhincalanus*'s reproduction was poor over much of the region, as it had been in January 1991 (compare figure 8A with 4A.2; stippled areas represent poorest reproduction) and was again food-limited at most stations (figure 8B). Unfed *Calanus* produced >10 eggs·day⁻¹ at fewer stations in 1993 than in 1991, and food limitation was more widespread, but *Calanus*'s reproduction was as strong in 1993 in the presence of excess food as in 1991. Had I made more extensive measurements of *Rhincalanus*'s reproduction in April 1990 (Appendix), it might have been possible to discuss interannual variability caused by anomalies in physical properties during winter-spring 1992 (Hayward 1993). In fact, the reproductive rates of *Calanus*, and their food limitation, did not differ greatly from the situation in springs of other years (compare figures 4D.1 and 7G.1 and H.1 with figures 11, 12, and 13 of Mullin 1991a).

DISCUSSION AND CONCLUSIONS

Though additional months and years should be sampled to test the seasonality of reproduction in *Rhincalanus*, the present results suggest that it may be more marked than in *Calanus*, which produces eggs in at least the coastal parts of the region in all seasons (Mullin 1991a). In January 1991 and 1993,

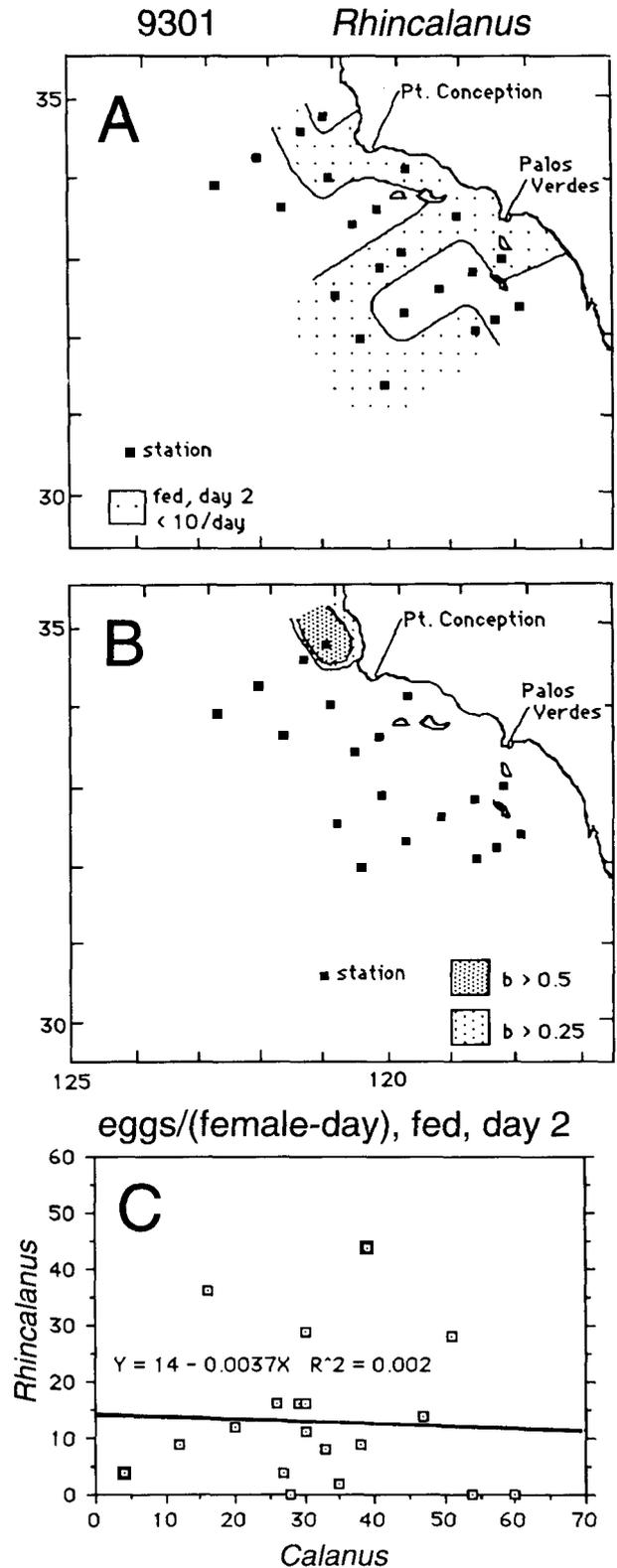


Figure 8. January 1993. A, Contour maps of per capita egg production by *Rhincalanus*; B, degree of limitation by food as reflected in ratio b . C, relation of egg production by *Rhincalanus* to that of *Calanus* after 2 days' feeding. Compare to figures 4A.2, 6A.2, and 5C.

Rhincalanus not only failed to lay eggs in unsupplemented seawater, but also failed, over much of the area, to respond to the presence of excess food. February–April seems to be a more favorable season, at least in terms of the potential to respond to excess food (nonstippled areas in figure 4A–D.2), and late summer is somewhat less favorable (Appendix). However, figure 2 shows that females can be stimulated to reproduce as late as June.

The production of eggs on the second day of incubation with supplemental food, more than the other measurements I made, is a measure of the reproductive potential not limited by food, reflecting the effects of the females' nutritional history and reproductive state over a longer term. If *Rhincalanus* is reproductively affected by the environment in the same way that *Calanus* is, a testable (alternative) hypothesis is that the second-day rates of production by fed females of the two species are positively correlated. As shown in figure 5A–F and 8C, this was the case only on cruise 9202, suggesting that in spite of the overall zoogeographic similarity in the area (figure 1), the two populations often differ on the scale sampled in respect to the aspects of the environment that lead to the most fecund females. On smaller scales, Mullin (1991b) concluded that the two populations also differed in sources of juvenile mortality.

These relations could arise simply from differing rates of response to food if *Calanus* females responded on the first day, and were to some degree spent on the second, while *Rhincalanus* required two days to respond (as seems to be the case). But since the relation between the rates of production by fed female *Calanus* on the first and second days of incubation is never negative (e.g., Mullin 1991a, figure 18), this alternative explanation is untenable.

Though the positive relation between *Calanus*'s egg production and the local biomass of chlorophyll varies considerably, the lack of any positive relation between *Rhincalanus*'s production and chlorophyll is striking, given the apparent similarities in the two species and the fact that food availability frequently limits production (figure 6), as shown by the stimulatory effect of supplementary phytoplankton.

Smith and Lane (1991) argued that reproduction in another large copepod, *Eucalanus californicus*, off central California depends in the summertime on females living in the cold, chlorophyll-rich waters of coastal upwelling or in jets originating in the coastal zone. The CalCOFI stations are too coarsely spaced to define such mesoscale features off southern California, where upwelling is generally weaker than off central California. But the results shown in

figure 7 are not consistent with a similar dependency by *Rhincalanus* in winter and spring.

For the reproductive rate of *Rhincalanus* to approach that of *Calanus* in the studied region, the females must encounter supplies of food (or perhaps other conditions) generally not represented in my experiments, or at times must respond differently. The adequacy of *Thalassiosira* for long-term production (figure 2), and for rearing from egg to adult, demonstrates that *Rhincalanus* can thrive solely on plants, but there may be other food sources, perhaps highly patchy ones in time or space, that were not present in most of my incubations but that some *Rhincalanus* can locate in the natural water column to achieve high rates of production. Future work obviously should focus on this issue — whether there are conditions (season, food, etc.) permitting *Rhincalanus* to reproduce at a high rate on the natural seston; i.e., $>10 \text{ eggs} \cdot (\text{female} \cdot \text{day})^{-1}$; vertical striping in figure 6A.2–D.2. Alternatively, the distribution of *Rhincalanus* off southern California must be explained either by very low mortality rates or by advective immigration of immature stages.

ACKNOWLEDGMENTS

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APPENDIX

Station*	Day	9004				9008				9101				9103			
		Calanus		Rhincalanus		Calanus		Rhincalanus		Calanus		Rhincalanus		Calanus		Rhincalanus	
		Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed
93.100	1	0	0	—	—	0	10.2	—	—	—	—	—	—	—	—	—	—
	2	0	29.2	—	—	1	44.9	—	—	—	—	—	—	—	—	—	—
93.90	1	4.6	32.4	—	—	2.7	8.4	0	0	—	—	—	—	—	—	—	—
	2	3.3	59.6	—	—	5	34.3	0	0	—	—	—	—	—	—	—	—
93.80	1	—	—	—	—	—	—	—	—	0	0	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	0	35.8	—	—	—	—	—	—
93.70	1	—	—	—	—	—	—	—	—	—	—	—	—	0	0	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—	0	25	—	—
93.60	1	0	32.9	—	—	—	—	—	—	6.4	17.5	—	—	0	3.6	—	—
	2	3.1	85.3	—	—	—	—	—	—	0.8	20.7	—	—	0.8	31.9	—	—
93.55	1	—	—	—	—	1.5	—	—	—	0.3	2.7	0	0	—	10.9	0	2
	2	—	—	—	—	0	—	—	—	0	23	0	0	—	40.9	0	0.7
93.50	1	31.9	66.8	—	—	—	—	—	—	1.2	0	0	0	—	—	—	—
	2	1.1	57.6	—	—	—	—	—	—	4.2	9.8	0	0	—	—	—	—
93.45	1	28.4	58.7	—	—	17.8	48.3	—	—	—	—	—	—	4.5	34.5	0	4.2
	2	3	58.7	—	—	0	61.1	—	—	—	—	—	—	0.5	45.4	0	13.1
93.40	1	—	—	—	—	14	37	—	—	0	0	—	—	5.5	11	0.8	4.1
	2	—	—	—	—	5.4	37.2	—	—	0	20	—	—	4.6	9.3	2.8	37.1
93.35	1	26.8	75.3	—	—	0.2	5.6	—	—	0	0	—	—	19.3	24.8	—	2.4
	2	19.5	87.8	—	—	4.3	53	—	—	0	1.5	—	—	2	20	—	25.4
93.30	1	22.4	61.7	—	—	2.4	23.2	—	—	0	—	—	—	12.3	21.8	0	5.6
	2	6.8	63.1	—	—	1	48.3	—	—	0	—	—	—	0.5	11.5	0	35.9
93.28	1	21.7	60.3	—	—	13.3	52.2	—	—	6.3	22.7	—	—	12.5	—	0	5.6
	2	3.8	75.8	—	—	1.6	60.7	—	—	0.3	29.7	—	—	0.5	—	0	36.8
90.110	1	—	—	—	—	4	13.8	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	0.9	19.1	—	—	—	—	—	—	—	—	—	—
90.90	1	0	14.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	2	1	51.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—
90.80	1	0	0	—	—	0	3.1	—	—	0	1.4	0	0	0	0	—	—
	2	0	24.9	—	—	1.2	27	—	—	0	26	0	0.4	0	3.7	—	—
90.70	1	10.6	34.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	2	1.9	30.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—
90.60	1	31	47.9	—	—	5.4	32.3	0	0	5.8	16.3	0	0.2	6.8	4.8	0	0.7
	2	4.6	37.8	—	—	0.1	33.9	0	0	2.3	35.1	0	1.7	0	26.7	0	0
90.53	1	56.6	70.5	0	0.4	13.7	22.2	0	0	3.4	16.7	0	0	16.1	21.2	6.8	0.7
	2	11.8	56.9	0.3	6.2	2.7	43.1	0	0	0.4	20	0	3.3	5.8	30.3	3.9	12.4
90.45	1	30.7	48.1	—	—	10.8	26.3	—	—	1	8	—	—	11.3	26.4	3	11.4
	2	3.5	61.5	—	—	0.4	47.4	—	—	0	22.5	—	—	0	26.8	7	52.5
90.37	1	—	—	—	—	7.2	40.9	—	—	0.3	0	0	10	15.4	33.9	0.2	5.9
	2	—	—	—	—	0	64.2	—	—	0.9	19	0	20.7	4.1	41.3	0	29.5
90.35	1	25.9	38.4	0	3.5	—	—	—	—	—	—	—	—	—	—	—	—
	2	9.8	42.1	0	2.9	—	—	—	—	—	—	—	—	—	—	—	—
90.30	1	8.4	38.2	—	—	2	14.3	0	0	0.7	2.5	—	—	14.7	23	0	5.4
	2	1.1	46.4	—	—	0	33	0	6	1.2	38.9	—	—	0.7	32.6	0	15.1
90.28	1	—	—	—	—	20.7	58.6	—	—	0.9	1.2	—	—	15.5	31.4	0	0.2
	2	—	—	—	—	0.4	44.5	—	—	0	9	—	—	0	35.4	0	17.8
87.110	1	—	—	—	—	1.7	1.5	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	0	34.6	—	—	—	—	—	—	—	—	—	—
87.90	1	1.2	4.3	—	—	0.4	5.8	—	—	—	—	—	—	—	—	—	—
	2	2.4	39.5	—	—	4	34.8	—	—	—	—	—	—	—	—	—	—
87.80	1	0	0.4	—	—	—	—	—	—	6.3	0	—	—	0	0.3	—	2.7
	2	0.5	28	—	—	—	—	—	—	0.6	0.1	—	—	0	36.7	—	16.4
87.70	1	—	—	—	—	—	—	—	—	0	0	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	0	0	—	—	—	—	—	—
87.60	1	5	19.2	—	—	3.8	15.7	—	—	6.6	14.9	0	0	27.7	36	0.1	1.9
	2	5.2	58.1	—	—	10.1	65.4	—	—	1.8	17.3	0	0	3.1	39.8	0	11.4
87.55	1	20.3	20.3	0	1.3	20.5	45.7	—	—	11.5	15.7	0	0	17.8	39.4	6.4	2.7
	2	4.4	40	0	10.4	5.4	68.5	—	—	1.5	10.1	0	0	7.3	38.5	5.9	5.9
87.50	1	20.4	30.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	2	2.2	44.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—
87.45	1	—	—	—	—	—	—	—	—	5.7	19.8	—	0	—	—	—	—
	2	—	—	—	—	—	—	—	—	4.2	30.3	—	0	—	—	—	—
87.39.5	1	17.2	27.8	—	—	—	—	—	—	0	—	0	—	11.7	30.8	—	—
	2	5.9	34	—	—	—	—	—	—	0	—	0	—	15.6	24.7	—	—

*For CalCOFI Basic Station Plan, see inside back cover.

MULLIN: REPRODUCTION BY RHINCALANUS
 CalCOFI Rep., Vol. 34, 1993

Station	Day	9202				9204				9301			
		Calanus		Rhincalanus		Calanus		Rhincalanus		Calanus		Rhincalanus	
		Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed
93.100	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
93.90	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
93.80	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
93.70	1	0	0	—	—	—	—	—	—	0	0	—	0
	2	0	8.5	—	—	—	—	—	—	0	4.2	—	4.3
93.60	1	0	0	—	—	—	—	—	—	—	—	—	—
	2	0	11.3	—	—	—	—	—	—	—	—	—	—
93.55	1	10.6	21.6	0	6.9	3.3	7.9	0	2.4	—	—	—	—
	2	0	39.3	0	23.4	1.9	49.8	0.5	26.6	—	—	—	—
93.50	1	17.2	42.4	0	7.3	—	—	—	—	12.4	20.1	0	1.4
	2	2	67.9	0	24.3	—	—	—	—	2.9	37.7	0.1	9.3
93.45	1	11.7	25.9	0	7.6	—	—	—	—	12.8	58.4	0.5	5.8
	2	1.5	39.5	0	5.6	—	—	—	—	6.4	50.7	0	27.9
93.40	1	—	6.8	—	—	0	16.7	0	0.7	0	7.9	0	0
	2	—	19.3	—	—	0.5	58.2	0.2	18.5	2.7	46.9	1.2	13.8
93.35	1	1.8	—	—	—	15	27	0	0	0	0	—	—
	2	0	—	—	—	0.3	69.6	0.2	8	0	21.1	—	—
93.30	1	—	—	—	—	0	0	0	0	2.7	2.3	—	—
	2	—	—	—	—	2.3	40	0	3.3	0	11.3	—	—
93.28	1	14.2	53.7	0	5	0.5	19.9	1.2	0	0	0	—	—
	2	3.6	61.8	0	28.7	3.6	34.4	0	10.8	0	31.8	—	—
90.110	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
90.90	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
90.80	1	0	—	—	—	—	—	—	—	—	—	—	—
	2	0	—	—	—	—	—	—	—	—	—	—	—
90.70	1	15.8	23.5	—	—	—	—	—	—	0	18.7	0	0
	2	0.2	41.4	—	—	—	—	—	—	0	53.6	0	0
90.60	1	5.5	26	0	6.3	7	20.3	0.2	—	0	15.1	0	0.6
	2	0	64.7	0	26.8	8.6	46.7	0	—	0	28.8	0.5	15.5
90.53	1	0	12.9	—	—	—	—	0.3	1.3	0	—	—	3.9
	2	0	69	—	—	—	—	0.3	9.3	0	—	0.6	18.2
90.45	1	0	20.4	—	—	24.8	41.1	10.6	8.8	0	0	0	1.6
	2	0.5	51.7	—	—	5.7	40.7	27.3	32.6	0	16.1	0	35.7
90.37	1	0	4.6	—	—	9.1	16.5	0	0.9	6.2	18.7	0	0
	2	0	40.8	—	—	7	26.6	0.1	14.9	0	32.9	0.1	9.8
90.35	1	—	—	—	—	—	29.2	0	—	—	—	—	—
	2	—	—	—	—	—	27.9	0.1	—	—	—	—	—
90.30	1	—	27.6	1.4	0.9	—	—	—	—	2.7	11	—	—
	2	—	48.2	1.6	10.6	—	—	—	—	0	33	—	—
90.28	1	—	—	—	—	21.1	33.5	0	2.4	—	—	—	—
	2	—	—	—	—	6	32.6	0	36.7	—	—	—	—
87.110	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
87.90	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
87.80	1	1.2	0	—	—	—	—	—	—	—	—	—	—
	2	0.6	32.8	—	—	—	—	—	—	—	—	—	—
87.70	1	7.4	11.7	—	—	—	—	0	0	1.4	5.6	0	0
	2	1.4	33.7	—	—	—	—	0.2	2.2	0	27	0	4.2
87.60	1	4.2	1.5	—	—	27.8	60.8	0.8	—	0.5	5	0	0.8
	2	0	22.7	—	—	0.4	37.9	5.6	—	0	33	0	7.7
87.55	1	11.9	35	0	7.5	9.9	44.3	1.8	2.3	2.4	15.8	0	0
	2	3.9	38.2	0	23.3	6.4	14.1	2.9	1.7	0.5	60.3	0	0
87.50	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
87.45	1	11.3	17.4	1.4	3.5	42.7	48.2	0.6	3.1	—	—	—	—
	2	1.1	35.2	4.8	11.6	14.4	32.2	0.8	4.2	—	—	—	—
87.39.5	1	1.6	5.1	0	—	14.9	30.6	1.3	3.6	0	14.6	0	0
	2	0	31.6	0	—	1.5	27.3	7.4	17.2	0	28.3	0	0

continued on next page

APPENDIX (continued)

Station	Day	9004				9008				9101				9103			
		Calanus		Rhincalanus		Calanus		Rhincalanus		Calanus		Rhincalanus		Calanus		Rhincalanus	
		Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed
87.35	1	23.8	49.6	8.3	6.3	26.2	67.7	—	—	0	11.6	—	—	6.2	21.2	0	2.9
	2	1.5	42	9.3	19.3	4.1	61.2	—	—	0	27.6	—	—	0.2	45.8	0	4.3
87.33	1	—	—	—	—	—	—	—	—	—	56.6	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	30.4	—	—	—	—	—	—
83.90	1	0	0	—	—	—	—	—	—	—	—	—	—	0.2	2.1	—	—
	2	0	7.5	—	—	—	—	—	—	—	—	—	—	0	6.2	—	—
83.80	1	2.8	5.5	1.2	0	—	—	—	—	0	1.9	—	—	—	35.5	0	0.4
	2	1.7	30.6	0	6.8	—	—	—	—	0	7.6	—	—	—	57.1	0	3.1
83.70	1	—	—	—	—	1	10.5	0	0	0	3.9	0	0	37.1	57.5	0	0.7
	2	—	—	—	—	1.4	29.3	0	6	0	8.1	—	—	2.5	56.6	0	12.5
83.60	1	33.8	51.3	5.6	12.8	10.4	42.6	—	—	15.8	34.4	0	0	35.5	49.6	0.2	1.5
	2	2.3	34.7	10	18.5	5.6	39	—	—	3.1	22.1	0	0	4.5	55	0.8	19.8
83.55	1	43.3	48.1	2.7	9	15.4	35.3	0	9	48	68.8	—	2.5	39.6	62.7	7.5	7.8
	2	18.5	39.1	3.8	26.5	0	30.2	0	8	5.4	17.8	—	20.9	6.3	54.5	13.2	13
83.51	1	—	—	—	—	—	—	—	—	23.1	46.7	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	6.7	32.3	—	—	—	—	—	—
83.42	1	40.9	53.2	—	—	21.4	45	0	0	26.1	27.4	—	—	50.6	53.3	—	—
	2	10.1	50.9	—	—	0	48.3	0	6	20.7	38.2	—	—	8.6	28.5	—	—
83.40	1	—	—	—	—	—	—	—	—	16	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	2.5	—	—	—	—	—	—	—
82.47	1	32.9	43.4	1.1	1.2	25.6	27.7	—	—	29.8	23.6	3.3	4.2	0	0	0	0
	2	3.7	49.6	1.7	15.6	4.4	44.3	—	—	4.7	35.3	3.8	22.5	0	22.3	0	0
80.90	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
80.80	1	—	—	—	—	0.7	8.3	—	—	8.1	40.8	—	—	—	—	—	—
	2	—	—	—	—	0	26.7	—	—	3.3	28.1	—	—	—	—	—	—
80.70	1	—	—	—	—	25	26.4	0	1	19	18.9	—	—	8.4	62.8	0	3.3
	2	—	—	—	—	13.5	47	0	15	0.8	28.8	—	—	0	62.5	0	27.9
80.60	1	—	—	—	—	—	—	—	—	23.8	29.6	—	—	26.1	47.7	0.3	2.2
	2	—	—	—	—	—	—	—	—	1.7	42.1	—	—	1.1	55.2	2.1	9.4
80.55	1	57.4	53.5	—	—	32.4	40	—	—	13.6	20.4	0	0	1.7	0	—	—
	2	9.6	52.8	—	—	1	43.7	—	—	7.8	35.1	0	0	0	25.5	—	—
80.51	1	2.5	10.6	—	—	32.9	27.7	—	—	18	24.8	—	—	—	—	—	—
	2	0.1	15.2	—	—	4.9	44.3	—	—	0	35.3	—	—	—	—	—	—
77.100	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
77.90	1	—	—	—	—	0	0	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	0	54.3	—	—	—	—	—	—	—	—	—	—
77.80	1	—	—	—	—	0	15.7	—	—	0	12.5	0	—	—	—	—	—
	2	—	—	—	—	0	50.9	—	—	0	36.7	0	—	—	—	—	—
77.70	1	—	—	—	—	4.3	27.5	0	0	0.3	7.3	0	0	—	—	—	—
	2	—	—	—	—	2.8	52.1	0	0	2.8	24.5	0	0	—	—	—	—
77.60	1	—	—	—	—	2.5	12.3	0	0	8.6	8	0	0	—	—	—	—
	2	—	—	—	—	0	47.6	0	12	1.7	28.1	0	1.8	—	—	—	—
77.55	1	—	—	—	—	—	—	—	—	1.7	16.9	0	0	—	—	—	—
	2	—	—	—	—	—	—	—	—	0	27.2	0	0	—	—	—	—
77.51	1	—	—	—	—	22	—	0	1	26.7	38	0	0	—	—	—	—
	2	—	—	—	—	5.1	—	0	2	2.3	22.3	0	0	—	—	—	—
77.49	1	—	—	—	—	13.2	43	4	3	9.4	55.3	—	—	—	—	—	—
	2	—	—	—	—	13	43.8	5	13	13.5	38.7	—	—	—	—	—	—

Station	Day	9202				9204				9301			
		Calanus		Rhincalanus		Calanus		Rhincalanus		Calanus		Rhincalanus	
		Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed
87.35	1	17.5	21	0.1	2.7	13.8	45.2	0	0.1	0.8	1.6	—	—
	2	3.6	35.8	0	13.3	22.6	36.6	1.3	5	0.3	24.7	—	—
87.33	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
83.90	1	0	0	—	—	—	—	—	—	—	—	—	—
	2	0	4.1	—	—	—	—	—	—	—	—	—	—
83.80	1	0.9	1.2	0	0	—	—	0.3	11.2	—	—	—	—
	2	0.7	21.2	0	3.9	—	—	0	13.2	—	—	—	—
83.70	1	13.4	17.8	0	0	4.3	9.4	0.2	4.2	—	—	—	—
	2	9	25.7	0	8.2	2.8	35.8	1.8	3.8	—	—	—	—
83.60	1	13.7	30.7	1.1	5.4	53.2	—	5.7	5.6	11.7	28	0	3.3
	2	7.2	35.3	1.6	12.5	13	—	28.5	38.5	2.9	30	1.1	29.1
83.55	1	0	24.8	0	—	—	—	—	—	0	23.8	0	2.1
	2	0	38	0	—	—	—	—	—	0	29.8	0	11.2
83.51	1	—	—	—	—	51	51.5	—	—	9.3	26.8	—	—
	2	—	—	—	—	6.8	27.2	—	—	0	40	—	—
83.42	1	0	5.7	0	0.3	48.6	72.8	0	1.4	1.5	3	—	—
	2	0	47.3	0	5.2	8	37.1	0.1	5.6	0	15	—	—
83.40	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
82.47	1	12.6	28.3	—	0	38.4	41.9	—	—	0	3.9	0	0.3
	2	1.7	24.1	—	1.8	0.2	46.6	—	—	0	34.7	0.3	2.2
80.90	1	0	5.4	—	—	3.7	16	1	0.6	—	—	—	—
	2	0	33.8	—	—	1.1	39.8	0	7.1	—	—	—	—
80.80	1	8.7	26.5	0	0	—	—	—	—	—	—	—	—
	2	0	17.8	0	0	—	—	—	—	—	—	—	—
80.70	1	0	4.8	0	0.5	11.1	24.4	4.6	0.4	16	12.2	0	0
	2	0	18.7	0	4.9	0.2	49.1	2.4	11.6	0.1	29.9	0.1	15.8
80.60	1	20.2	20.1	—	—	30.8	24.6	2.1	1.7	3.7	10	0	0
	2	8	28.7	—	—	9	28.2	0.2	7.6	0.1	28.1	0	0
80.55	1	2.6	18.3	—	—	24	21.8	3.8	0.3	7.6	18.8	—	—
	2	1	16	—	—	6.9	32.1	28.2	28.4	0.7	16.8	—	—
80.51	1	9.2	19	—	—	5.8	24.6	—	—	0	4.7	—	—
	2	0	21.4	—	—	0.1	21.9	—	—	0	21.4	—	—
77.100	1	0	0	—	—	—	—	—	—	—	—	—	—
	2	0	0	—	—	—	—	—	—	—	—	—	—
77.90	1	0	1.3	0	0.4	4.7	13.5	0	0	—	—	—	—
	2	0	24.2	0	0	6.7	14.2	0	0.3	—	—	—	—
77.80	1	0	1	0	4.6	1.6	14.9	0	0	6.2	36	0	1.4
	2	0	32.5	0	3.3	4.7	39.1	0	6.3	1.2	26.3	1.5	15.7
77.70	1	0.4	5.9	0	0	18.3	34.1	0	0.4	32.4	66.3	0.4	4.1
	2	0	28.4	0	0	8	50.4	0	5	2.3	19.9	0.6	12
77.60	1	—	—	—	—	20.2	33.4	3.1	0.6	18.3	28.4	0.8	0.1
	2	—	—	—	—	6.2	31.6	4.2	2.6	7.3	11.7	0.5	9.2
77.55	1	—	—	—	—	11.6	29.6	—	—	29.5	24.2	4.7	6.6
	2	—	—	—	—	8.4	18.8	—	—	5.6	38.9	14.4	44.3
77.51	1	—	—	—	—	31.2	33.2	2	1.4	0.2	11.8	—	—
	2	—	—	—	—	11.5	17.2	15.4	16.5	0.1	23	—	—
77.49	1	—	—	—	—	65	—	—	—	0	11.8	—	—
	2	—	—	—	—	9.4	—	—	—	0.3	28.5	—	—

THE EFFECT OF NATURAL VARIABILITY OF LIFE-HISTORY PARAMETERS ON ANCHOVY AND SARDINE POPULATION GROWTH

JOHN L. BUTLER, PAUL E. SMITH, AND N. CHYAN-HUEI LO

Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, California 92038

ABSTRACT

The northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*) populations were modeled with a stage-based matrix to examine how natural variation of life-history parameters affects per capita growth. In the model northern anchovy (*Engraulis mordax*) population, the greatest change in growth results from natural variation in the duration of, and the instantaneous mortality rate of, the early and late larval stages. In the model Pacific sardine (*Sardinops sagax*) population, the greatest change in growth results from natural variation in the duration of, and the instantaneous mortality rate of, the late larval stage. Temperature determines the duration of both egg and yolk-sac larval stages and the rate at which prerecruit sardine and anchovy mature. We believe that changes in the duration of both egg stages and yolk-sac larval stages may have greater effects on population growth than changes in any single stage.

RESUMEN

Se modelaron las poblaciones de anchoveta nor- tēna (*Engraulis mordax*) y de sardina Monterrey (*Sar- dinops sagax*). Usando matrices basadas en estadios de vida, se examinó como la variación natural de los parámetros de las fases vitales afecta el crecimiento per capita. En las poblaciones modelo de anchoveta, el mayor cambio en crecimiento fué resultado de la variación natural de la duración y de la tasa instan- tánea de mortalidad de los estadios tempranos y tardíos de las larvas. En la población modelo de sardina, el cambio mayor en crecimiento fué resul- tado de la variación natural de la duración y tasa instantánea de mortalidad de los estadios larvales tardíos. La temperatura determina la duración de los estadios huevo y saco vitelino, así como la tasa a la cual las sardinas y anchovetas pre-reclutas maduran. Creemos que cambios en la duración de estadios huevo y de saco-vitelino podrían tener efectos ma- yores en el crecimiento poblacional que cambios en cualquiera de los estadios individuales.

INTRODUCTION

The Pacific sardine population (*Sardinops sagax*) in the northeast Pacific Ocean has greatly fluctuated during this century. Biomass peaked in 1932 at about 3,600,000 MT (Murphy 1966) and then fell to about 6,000 MT in 1975 (Barnes et al. 1992); it remained low for the rest of the decade. Recently the sardine has begun to recover off California and northern Baja California. Since the early 1980s the population has grown steadily at about $50\% \cdot y^{-1}$ (Smith et al. 1992) to reach a biomass of about 340,000 MT in 1991 (Barnes et al. 1992).

The northern anchovy (*Engraulis mordax*) popula- tion off California and Mexico has also undergone large changes. Stock size was low in the 1950s and 1960s, grew rapidly in the early 1970s, and reached a maximum biomass of about 1,700,000 MT in 1974 (Lo and Methot 1989). In the early 1970s, the north- ern anchovy's population growth rate was also about $50\% \cdot y^{-1}$.

Scale-deposition rates in anaerobic sediments indi- cate that both populations have undergone similar wide fluctuations before and since the development of modern fisheries (Soutar and Isaacs 1974; Smith and Moser 1988). Sardines appear to fluctuate more rapidly than anchovy, although Lasker and MacCall (1983) pointed out that calibrating scale-deposition rate to population size may exaggerate changes in total abundance of the species. Nevertheless the scale data indicate that large population fluctuations are common among these clupeoid stocks in the absence of fisheries, and that these fluctuations must be due to changes in the physical and biotic environment.

Global climate change will significantly affect the physical environment of marine ecosystems. Potent- ial effects include changes in sea-surface tempera- ture and in the intensity of upwelling (Bakun 1990). These physical changes will affect the distribution and dynamics of fish stocks. The stage-based matrix described here provides a means to test hypotheses concerning how environmental change will affect fish populations.

A number of important life-history parameters of marine fish are directly affected by changes in tem- perature. Temperature and food densities affect

growth at all stages. Instantaneous mortality of eggs and larvae are also a function of temperature (Houde 1989), and the size and age of first reproduction varies with temperature (Methot 1986). Because all of these parameters are linked by temperature, it is possible that some of the effects of global climate change can be investigated by means of stage-based population models and existing knowledge.

Previous attempts to model anchovy or sardine populations using stage-based models have been hampered by (1) a lack of theoretical framework (Smith 1985) or (2) an incomplete understanding of the range of variation for important life-history parameters (Smith 1985; Smith et al. 1992). Our objective in this paper is to model anchovy and sardine populations by using a stage-based matrix (Lefkovich 1965) as a theoretical framework and to examine how natural variation of stage-specific vital rates affects population growth rates.

Vital rates for each stage of the model were obtained from the literature. For some stages the vital rate is unknown; in such cases we obtained a vital rate from literature on other populations of sardines and anchovy, or estimated by the methods described below. We have thus compiled the most comprehensive estimates of life-history parameters to date. We also examined the effect of fishing mortality on the two populations.

METHODS

The matrix (**A**) describes the transition of a population from time t to time $t+1$ in terms of vital rates of each life stage:

$$\mathbf{A}n_t = n_{t+1} \quad (1)$$

where n_t is a vector describing the population at each stage at time t , and **A** is the transition matrix:

$$\mathbf{A} = \begin{matrix} P_1 & m_2 & \dots & \dots & m_q \\ G_1 & P_2 & 0 & \dots & 0 \\ 0 & G_2 & P_3 & 0 & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & G_{q-1} & P_q \end{matrix} \quad (2)$$

where P_i is the probability of surviving and staying in stage i , G_i is the probability of surviving and growing into the next stage, and m_i is the maternity per fish per unit time (d); $i = 1, \dots, q$.

Both P_i and G_i are functions of the survival probability (p_i) and the growth probability (γ_i) (Caswell 1989):

$$p_i = e^{-z_i} \quad (3)$$

and $P_i = p_i(1 - \gamma_i) \quad (4)$

and $G_i = p_i \gamma_i \quad (5)$

where $\gamma_i = [(1 - p_i)p_i^{d_i-1}]/[1 - p_i^{d_i}] \quad (6)$

where z_i is the daily instantaneous mortality rate (IMR) and d_i is the duration (d) within the i th stage. The derivation of P_i , G_i , and γ_i follow Crouse et al. (1987) and Caswell (1989).

The maternity parameter m_i is computed as:

$$m_i = \frac{\sum_j [f_j w_{ij}]}{\sum_j [w_{ij}]} \quad (7)$$

where f_j (the age-specific fecundity rate) is the number of eggs per fish of age j per unit time, and w_{ij} is the proportion of fish that are of age j :

$$w_{ij} = \exp(-z_i t_{1j}) - \exp(-z_i t_{2j}) \quad (8)$$

where t_{1j} is the beginning and t_{2j} is the ending age for the fish of age group j . Briefly, total annual production of eggs was estimated for each size class and apportioned on an average daily basis.

Anchovy spawn each day from sunset to midnight, with the peak at 2200 (Lo 1983). Sardine spawn between 2000 and 0400, with the peak near midnight (Smith 1973). In the model, the fecundity estimates of sardine were assumed to be knife-edged at 0000 h, and the fecundity estimates of anchovy were corrected for mortality from spawning (2200) to census at the end of day one (2400) by: $F_i = Q_i m_i$, where Q_i is the probability of surviving from spawning to the first census and $Q_i = e^{-zt}$, where z is the daily instantaneous mortality rate and t is the time from peak spawning to the time of census.

The dominant eigenvalue λ of the matrix represents the population growth rate. If $\lambda = 1.0$, the population is stationary, and if $\lambda = 1.5$, the population is growing at $50\% \cdot d^{-1}$. The results are given in annual growth of the population, which is equal to λ^{365} , since the duration of stages was measured in days. We estimated λ from the dominant eigenvalue of the matrix **A** using MathCAD.

We measured the importance of natural variability in mortality, duration, and fecundity parameters at each stage by calculating λ for a series of values for each parameter. Initial conditions were a stationary population, and we examined changes of λ with known deviations of each stage-specific vital rate.

Anchovy Vital Rates

The northern anchovy is a multiple spawner (Hunter and Goldberg 1980). Annual fecundity is

the number of eggs released per spawning (batch fecundity) times the number of spawnings in a season. The variation in batch fecundity and the variation of spawning rate with age are well known (Hunter and Goldberg 1980; Hunter and Macewicz 1980; Parrish et al. 1986; Alheit, in press), but little is known of the interannual variation in number of spawnings per year. The spawning rate for northern anchovy varies interannually from once every 6.25 days to once every 10.6 days (Bindman 1985). At that rate the average female would spawn 5 to 10 times during the March–April spawning season. Some spawning occurs all year long, and Parrish et al. (1986) found evidence that the number of spawnings per year increases with age. The fecundity used in the model was a daily rate that apportioned spawning equally over the year (table 1). In reality, spawning is seasonal, but modeling the seasonality of spawning is beyond the scope of this paper. The daily fecundity was divided by two to estimate the number of female eggs.

The anchovy population was modeled on the basis of nine stages, as defined by Smith (1985). We derived minimum, maximum, and best estimates of daily instantaneous mortality rates and duration of each stage from literature values (table 2). The durations of the egg and yolk-sac stages are derived from incubation experiments at different temperatures (Lo 1983). Mean duration was based on the development rate at 16°C, which is about the average temperature for anchovy eggs. Mortality rates of egg, yolk-sac, and larval stages were estimated from field studies (Stauffer and Picquelle 1981; Bindman 1985). Durations of the larval and juvenile stages are from field studies of growth rates derived from daily increments in the otoliths (Methot and Kramer 1979; Butler 1987, 1989).

TABLE 1
 Fecundity Schedule of Northern Anchovy

Year	Wt (g)	Spawns per year	Batch (eggs)	$M(x)$	$L(x)$ $z = .76$	$LxMx$	Daily
0	0.0	0.0					
1	8.7	5.3	4237.8	22460.3	1000	11230170	30747
2	14.6	11.9	7860.4	93538.8	468	21888070	59926
3	18.3	19.2	10132.2	194538.2	216	21010130	57523
4	21.2	23.5	11912.8	279950.8	102	14277491	39090
5	24.5	23.5	13939.0	327566.5	48	7861596	21524
6	24.5	23.5	13939.0	327566.5	22	3603232	9865
7	24.5	23.5	13939.0	327566.5	10	1637833	4484

	Female eggs per female per day mean	90% maturity at year one*
Juveniles	11.7	10.5
Small adults	199.2	199.2
Large adults	448.4	448.4

*Assuming that 90% of females mature at age 1 and that the batch fecundity is given by the formula: $Batch = -1104 + 614 \cdot wt$ (Hunter et al. 1985).

Mortality rates of the late larval and early juvenile stages are unknown. We estimated these rates from the relationship of mortality rate to body size (Peterson and Wroblewski 1984) and adjusted them to achieve a stationary population. The relationship between dry weight and mortality rate is given by Peterson and Wroblewski (1984): $M_{(w)} = (1.92 \cdot \gamma^{-1}) w^{-0.25}$, and the relation between length and dry weight for northern anchovy is dry weight = $0.000488 \cdot SL^{3.73}$, where SL is measured in cm (Butler 1987). For a 72.5-mm juvenile $M = 2.04$, and the daily rate is $z = 2.83/365.25 = 0.00557$. This value was adjusted to a "best" value of 0.0044 to obtain a lambda of 1.0. We chose the late juvenile stage for this adjustment because at present little is known about natural mortality in this stage.

TABLE 2
 Stage-Specific Life-History Parameters of Northern Anchovy

Stage	Size (mm)		Daily natural mortality			Duration (days)			Daily fecundity/female		
	Min.	Max.	Min.	Best	Max.	Min.	Best	Max.	Min.	Best	Max.
Egg			0.12 ^a	0.231 ^a	0.45 ^b	1.4 ^c	2.9 ^c	3.9 ^c	0	0	0
Yolk-sac larvae	hatch	4	0.19 ^d	0.366 ^d	0.59 ^d	1.4 ^c	3.6 ^c	3.9 ^c	0	0	0
Early larvae	4	10	0.187 ^d	0.286 ^d	0.345 ^d	8 ^e	12 ^e	23 ^e	0	0	0
Late larvae	10	35	0.0470 ^f	0.0719 ^f	0.087 ^f	35 ^e	45 ^e	71 ^e	0	0	0
Early juvenile	35	60	0.0009 ^f	0.0141 ^g	0.017 ^f	45 ^e	62 ^e	100 ^e	0	0	0
Late juvenile	60	85	0.0029 ^f	0.0044 ^f	0.0053 ^f	60 ^e	80 ^e	138 ^e	0	0	0
Prerecruit	85	110	0.0020 ^f	0.0031 ^f	0.0037 ^f	200 ^h	287 ^h	632 ^h	0	10.1	19.4
Early adult	110	135	0.0011 ^j	0.0021 ^j	0.0036 ^j	750 ^h	1000 ^h	1250 ^h	143.8	199.2 ⁱ	230.7
Late adult	135	160	0.0011 ^j	0.0021 ^j	0.0036 ^j	1000 ^h	1250 ^h	1500 ^h	284.2	448.2 ⁱ	529.0

^aBindman 1985
^bStauffer and Picquelle 1981
^cLo 1986
^dPeterman et al. 1988
^eMethot and Kramer 1979
^fPeterson and Wroblewski 1984

^gButler 1987, Waldron et al. 1989
^hFiedler et al. 1986
ⁱHunter et al. 1985
^jMethot 1989
 *Used to tune model to lambda = 1.0

Adult natural mortality rates are assumed to be constant with age and were derived from the stock synthesis model (Methot 1989). We also examined the effect of an annual fishing mortality rate of 0.6 on all adult stages. We derived adult growth rates from fisheries data (Fiedler et al. 1986).

Sardine Vital Rates

Pacific sardine is also a multiple spawner. Batch fecundity estimates were based on MacGregor (1957) and Clark (1934). Little is known about the number of spawnings per year. Off Chile, the Pacific sardine (*S. sagax musica*) spawns every 7 days (Oliva et al. 1989), a rate similar to that of the northern anchovy. The South African pilchard, *Sardinops ocellatus*, spawns every 2–5 days, and older fish may spawn up to 80 times per year (Le Clus 1989). Fecundities in the life table (table 3) were estimated from batch fecundity times a total of 40 spawnings per year for the oldest age classes (the maximum rate is 80 spawnings per year, and the minimum is 24; table 4). We divided the daily fecundity by two to account for the number of female eggs.

We modeled the sardine population with thirteen stages as defined by Smith et al. (1992). The minimum, maximum, and mean daily instantaneous mortality rates and duration of each stage are derived from the literature (table 4). The durations of the egg and yolk-sac stages are derived from incubation experiments at different temperatures (Lasker 1964). Mean duration was derived from the development rate at 16°C, which is about the average temperature for sardine eggs (15.6°C; Butler 1987).

TABLE 3
Fecundity Schedule of Pacific Sardine

Age	Wt (g)	Spawns	Batch	M(x)	Daily	L(x)	Survivors to day 1
1	52.7	0	13860	0	0	1000	0
2	93	6	24459	146754	402	670	201
3	123	12	32349	388188	1063	449	238774
4	152	15	39976	599640	1642	301	247239
5	170	19	44710	849490	2326	202	234783
6	193	23	50759	1167457	3196	135	216288
7	202	28	53126	1487528	4073	91	184730
8	205	30	53915	1617450	4428	61	134644
9	205	35	53915	1887025	5166	41	105297
10	205	40	53915	2156600	5904	27	80666
11	205	40	53915	2156600	5904	18	54072
12	205	40	53915	2156600	5904	12	36245
13	205	40	53915	2156600	5904	8	24296

	Female eggs per female per day	Survivors to first census
Prerecruit	134	80.5
Juveniles	647.6	388.9
Small adults	1576.3	946.6
Large adults	2811.5	1688.3

Batch fecundity = 263 eggs per gram (MacGregor 1957).

We estimated mortality rates of yolk-sac and larval stages from the field (Butler 1991). The best estimates of egg mortality rates are from unpublished data (N. C. H. Lo). Durations of the larval and juvenile stages are from field studies of growth rates calculated from daily increments in the otoliths (Butler and Rojas de Mendiola 1985; Castillo et al. 1985; Butler 1987). The mortality rates of the late larvae through stage III juveniles are unknown. We estimated these rates from the general relation-

TABLE 4
Stage-Specific Life-History Parameters of the Pacific Sardine

Stage	Size (mm)		Daily natural mortality			Duration (days)			Daily fecundity/female		
	Min.	Max.	Min.	Best	Max.	Min.	Best	Max.	Min.	Best	Max.
Egg			0.31 ^a	0.72	2.12 ^b	1.4 ^c	2.5 ^c	3.9 ^c	0	0	0
Yolk-sac larvae	hatch	4	0.394 ^d	0.6698 ^d	0.971 ^d	1.4 ^c	3.1 ^c	3.9 ^c	0	0	0
Early larvae	4	10	0.1423 ^d	0.2417 ^d	0.3502 ^d	5 ^e	11 ^e	21 ^e	0	0	0
Late larvae	10	35	0.057 ^d	0.0964 ^d	0.139 ^d	20 ^e	35 ^e	50 ^e	0	0	0
Early juvenile	35	60	0.029 ^d	0.056 ^d	0.081 ^d	17 ^e	25 ^e	40 ^e	0	0	0
Juvenile I	60	85	0.0116 ^b	0.0197 ^{b,*}	0.0285 ^b	30 ^e	50 ^e	80 ^e	0	0	0
Juvenile II	85	110	0.0023 ^b	0.0040 ^b	0.0058 ^b	80 ^e	110 ^e	146 ^{e,i}	0	0	0
Juvenile III	110	135	0.0016 ^b	0.0028 ^b	0.0040 ^b	105	146 ^{e,i}	185	0	0	0
Juvenile IV	135	160	0.0012 ^j	0.0022 ^j	0.0032 ^j	110	170 ^j	220	0	0	0
Prerecruit	160	185	0.0006 ^l	0.0011 ^l	0.0015 ^l	110	175 ^j	220	0	80 ^k	161 ^k
Early adult	185	210	0.0006 ^l	0.0011 ^l	0.0015 ^l	190 ^m	381 ^m	570 ^m	286 ^k	389 ^k	489 ^k
Adult	210	235	0.0006 ^l	0.0011 ^l	0.0022 ^l	400 ^m	663 ^m	920 ^m	730 ^k	946 ^k	1114 ^k
Late adult	235	260	0.0006 ^l	0.0011 ^l	0.0022 ^l	1908 ^m	2773 ^m	3473 ^m	1064 ^k	1688 ^k	3123 ^k

^aSmith 1973
^bSmith et al. 1989
^cLasker 1964
^dButler 1991
^eButler and Rojas de Mendiola 1985
^fCastillo et al. 1985
^gButler 1987

^hPeterson and Wroblewski 1984
ⁱKimura and Sakagawa 1972
^jBy analogy to northern anchovy
^kMacGregor 1957, Clark 1934, Le Clus 1989
^lMurphy 1966, MacCall 1979
^mWalford and Mosher 1943, Phillips 1948
ⁿUsed to tune model to lambda = 1.0

ship of mortality rate to body size (Peterson and Wroblewski 1984). The relationship between dry weight and length is given by: dry weight = $0.0122 \cdot SL^{3.35}$, where standard length is measured in cm (Butler 1987). The predicted mortality rate was 0.0053 for stage I juveniles, and we adjusted this value to 0.0197 to achieve a theoretically stationary population. The mortality rates of stage IV juveniles and prerecruits are assumed to be the same as the mortality rates for northern anchovy of the same body size. Adult growth rates were derived from otolith readings (Phillips 1948); adult mortality rates were derived from the cohort analysis (Murphy 1966; MacCall 1979). Natural mortality was set at $0.4\% \cdot y^{-1}$. We also examined the effect of annual fishing mortality rates of 0.25 and 0.6.

RESULTS

Anchovy

Natural variations in individual stage-specific mortality or duration (table 5) result in changes of population growth from equilibrium to an annual increase or decrease of about threefold. The most influential stage appears to be the early larval. Natural variation in instantaneous mortality rates or duration of this stage lead to the largest changes in the population growth rate. The fastest growth rate of the early larvae results in a 278% increase in the population, whereas the slowest growth rate results in a 74% decrease (table 5). The least sensitive is the late adult stage: at that point, variations in growth and mortality have minimal effect on population growth. The sensitivity of the model to natural variations in fecundity may be an underestimate. The values in the literature are largely taken from biomass estimate studies, and none of these studies has encompassed a major environmental perturbation.

TABLE 5
Eigenvalue (λ^{365}) of Lefkovitch Matrix after Change in the Stage-Specific Life-History Parameters of Northern Anchovy

Stage	Natural mortality		Duration		Fecundity	
	Min.	Max.	Min.	Max.	Min.	Max.
Egg	1.27	0.66	1.30	0.85		
Yolk-sac larvae	1.65	0.60	1.93	0.93		
Early larvae	2.78	0.64	2.67	0.26		
Late larvae	2.57	0.65	1.78	0.37		
Early juvenile	1.90	0.88	1.20	0.71		
Late juvenile	1.09	0.95	1.07	0.85		
Prerecruit	1.35	0.84	0.98	0.79	0.95	1.02
Early adult	1.06	0.95	1.06	0.97	0.86	1.12
Late adult	1.00	1.00	1.00	1.00	0.97	1.16

TABLE 6
Eigenvalue (λ^{365}) of Lefkovitch Matrix after Change in the Stage-Specific Life-History Parameters of Pacific Sardine

Stage	Natural mortality		Duration		Fecundity	
	Min.	Max.	Min.	Max.	Min.	Max.
Egg	1.29	0.68	1.21	0.84		
Yolk-sac larvae	1.23	0.85	1.34	0.90		
Early larvae	1.31	0.82	1.47	0.72		
Late larvae	1.43	0.79	1.47	0.79		
Early juvenile	1.17	0.89	1.11	0.89		
Juvenile I	1.15	0.95	1.09	0.89		
Juvenile II	1.04	0.96	1.03	0.97		
Juvenile III	1.04	0.96	1.03	0.98		
Juvenile IV	1.04	0.97	1.03	0.98		
Prerecruit	1.02	0.98	1.01	0.99	0.98	1.00
Early adult	1.04	0.97	1.03	0.98	1.00	1.00
Adult	1.05	0.91	1.01	0.99	1.00	1.01
Late adult	1.05	0.86	0.99	1.00	1.00	1.11

There is some evidence that reproduction is drastically reduced during major El Niño events. Under such conditions the population declines rapidly.

We tested the effect of fishing on the anchovy population by using values of natural mortality of 0.76 and fishing mortality of 0.6 for both adult stages. Under these conditions the anchovy population declined at a rate of $5\% \cdot y^{-1}$.

Sardine

The population growth rate of the Pacific sardine appears to be most sensitive to changes in egg and larval stages (table 6). Reported values for egg mortality vary widely in the literature (Smith 1973; Smith et al. 1989). Extremely high values of egg mortality — 88% in the first day — were reported for the Pacific sardine off Peru (Smith et al. 1989). At this rate the model indicates that the population declines at the rate of 32% per year. The fastest growth of the early and late larval stages results in population growth rates of $43\% \cdot y^{-1}$, whereas the slowest growth rate of the early larval stage results in a population decrease of $28\% \cdot y^{-1}$ (table 6). The population is least sensitive to changes in the vital rates of the older stages, prerecruit through late adult.

Fishing affects the mortality rate of all adult sardine stages. If fishing mortality is 0.25, then the population declines at a rate of $18\% \cdot y^{-1}$. During the decline of the sardine fishery, fishing mortality was as high as 0.8 (Murphy 1966). At this level, the population declines at $50\% \cdot y^{-1}$. High fishing mortality reduces the abundance of the oldest age classes, which have the highest reproductive potential because of their larger size and greater number of spawnings.

DISCUSSION

For the northern anchovy, natural variation in the duration of, and the instantaneous mortality rate of the early and late larval stage has the greatest effect on population growth (table 5). These results are similar to those of Smith (1985), who used a stage-based model to examine the role of vital rates in the dynamics of anchovy recruitment. Smith concluded that changes in the late larval stage have the greatest potential to affect survival and recruitment. Our results indicate that the anchovy population is also sensitive to changes in the early larval stage (table 5). The difference between our model and Smith's (1985) is largely due to the low mortality rate (0.16) that Smith used for this stage. The higher mean mortality rate (0.29) in our model leads to greater sensitivity, since faster or slower growth rates have a greater cumulative effect. High abundance of the early larval stage is a prerequisite to strong recruitment, but high larval abundance does not necessarily indicate strong year classes (Peterman et al. 1988).

In this model, we have also tried to examine the role of changes in fecundity. The variation in batch fecundity and spawning rate with age are well known, but little is known of interannual variability in the number of spawns per year. Estimated spawning rates for northern anchovy have varied from once every 6.25 days to once every 11 days. However, the Japanese anchovy, *Engraulis japonica*, spawns once every 1.4 days, and the Cape anchovy, *Engraulis capensis*, spawns as seldom as once every 16 days. Clearly, the number of spawns can vary significantly.

The sensitivity of the anchovy population matrix to changes in the vital rates of both early and late larvae is due to the dynamics of these stages. Natural mortality is high (Peterman et al. 1988), and the duration is long relative to egg stages. Changes in either value produce large effects. The observed natural variation in mortality rate of the early stage is quite large. Smith (1985) also identified the late larval stage of anchovy as important to recruitment variation. Variation in the duration of this stage is largely due to changes in temperature rather than difference in food densities (Methot and Kramer 1979; Owen et al. 1989).

Most life-table parameters do not change independently. The development rate of northern anchovy eggs and yolk-sac larvae is temperature-dependent (Zweifel and Lasker 1976, Lo 1986), as are larval growth rates (Methot and Kramer 1979). At about 22°C the egg, yolk-sac, and early larval stages would be brief. If all these stages are at their lower limits, the model population more than doubles

each year. The population model can be stabilized if reproduction is restricted to the prerecruit stage (85–110 mm), with fecundity reduced to only 7 eggs per female per day. In other words, these life-history parameters are then similar to those of a small tropical anchovy, *Encrasicolina purpurea* (Clarke 1989; Somerton, in press).

From 1922 to 1942, temperatures at Scripps Pier averaged 17.1°C; from 1943 to 1974, temperatures averaged 16.6°C, excluding El Niño years 1957–59. The duration of both incubation and the yolk-sac stage are a function of temperature (Lasker 1964; Zweifel and Lasker 1976). Given these relationships, the Lefkovitch model, adjusted to stability at colder temperatures (11°C), predicts that the northern anchovy population would grow at an annual rate of 7% during warmer years (22°C), and that the sardine population would grow at 4%·y⁻¹. Thus, temperature effects on the early stages alone cannot explain the difference in abundance of the two species from 1922 to 1942 and from 1943 to 1973. Temperature's effect on spawning rates in both species is unknown, as are its effects on the age of maturation and on the growth rate of juveniles.

The sardine population appears to be less sensitive to changes in vital rates than the anchovy population by an order of magnitude. Changing the duration of the early larval stage changes growth rates by +40% or -27%·y⁻¹. The addition of fishing mortality results in a 44%·y⁻¹ decline in the population. Clark and Marr (1955) debated whether the environment or fishing caused the decline of the sardine population. Our results indicate that either the environment or fishing can produce these changes.

Some discussion of the assumptions of this model is warranted. The stage-specific model assumes that the population reaches a stable age distribution. In reality, stage-specific life-history parameters vary from year to year, and the population probably never achieves a stable age distribution. The fecundity estimates are averaged over all seasons and assumed to be constant on a daily basis. In reality, fecundity has a seasonal component, and most fecundity estimates are made during the peak season. It is also important to note that these fecundity estimates have been made during the course of biomass estimates and that few, if any, long-term studies exist. There is some indication that fecundity may be near zero during extreme environmental conditions (Csirke 1980; Ware and Tsukayama 1981).

The model also does not treat density-dependent effects. Growth rates predicted by the model are not sustained indefinitely in nature. Density-dependent effects on the population could be modeled by

changing fecundity, mortality, or duration with population size. The model's sensitivity to changes in the larval stages suggests that cannibalism may be an important density-dependent feedback mechanism. Density-dependent influences are usually weak compared to density-independent factors, but MacCall (1981), Alheit (1987), Valdés et al. (1987), and Valdés Szeinfeld (1991) have indicated that cannibalism is an important density-dependent effect in clupeoid fishes. Cannibalism on eggs may, in fact, be largely density-independent (Smith et al. 1989), whereas cannibalism on larvae from different schools, because of the population's sensitivity to larval mortality rates, may be density-dependent.

CONCLUSIONS

Natural variation in stage-specific vital rates can account for the large changes in population size observed in nature. The Lefkovitch model predicts changes in population growth that are as great as those indicated by the time series of these populations. Both populations are more sensitive to variation in the parameters of larval stages than to adult parameters. However, more research is needed on interannual variation of adult reproductive parameters, since these variations may have greater impact than indicated in the present model.

The sensitivity of the models to larval duration and mortality rate does not, however, indicate that these stages can be used to predict recruitment. Variance of postmetamorphic stages is sufficient to mask the relation between larval abundance and subsequent recruitment. These results are in accordance with those of Bradford (1992).

The sensitivity of the models to larval duration and mortality rate does not, however, indicate that these stages can be used to predict recruitment. Variance of postmetamorphic stages is sufficient to mask the relation between larval abundance and subsequent recruitment. These results are in accordance with those of Bradford (1992).

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SPAWNING FREQUENCY AND BATCH FECUNDITY OF JACK MACKEREL, *TRACHURUS SYMMETRICUS*, OFF CALIFORNIA DURING 1991

BEVERLY J. MACEWICZ AND J. ROE HUNTER

Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, California 92038

ABSTRACT

In southern California waters, during March–April 1991, the average mature female jack mackerel, *Trachurus symmetricus*, spawned every 5 days, and eight percent of the females spawned at 1–3 day intervals. The average relative batch fecundity was 112 oocytes per gram female weight (without ovary). Batch fecundity was lower for females that had spawned within the last 3 days than for females in which no evidence existed for a previous spawning.

RESUMEN

En aguas de California sur, durante Marzo–Abril de 1991, los especímenes maduros promedio del charrito (*Trachurus symmetricus*) desovaron cada 5 días; ocho por ciento de las hembras desovó en intervalos de 1–3 días. La fecundidad relativa promedio por cada puesta fué de 112 ovocitos por gramo (peso corporal de hembra libre de ovarios). La fecundidad por cada puesta en las hembras que habían desovado en los últimos 3 días fué menor que en las hembras en las que no se observó evidencia de desove previo.

INTRODUCTION

Jack mackerel, *Trachurus symmetricus* (Ayres, 1855), range from Baja California to the Gulf of Alaska and from coastal waters up to 1000 miles offshore (MacCall and Stauffer 1983). The southern California fishery usually takes fish 10–30 cm (FL, fork length). No fishery presently exists for larger fish (FL >40 cm), which occur predominantly offshore and to the north (MacCall et al. 1980; MacCall and Stauffer 1983; Mason 1991). The potential value of an offshore trawl fishery for *T. symmetricus* has attracted some interest lately, and if such a fishery were to develop, estimates of *T. symmetricus* biomass from California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton data would be a valuable management tool.

MacCall and Stauffer (1983) used CalCOFI data and reproductive information on *T. symmetricus* to estimate the average biomass off western North

America. Their chief barrier for estimating a time series of *T. symmetricus* biomass from CalCOFI data was the lack of information on daily rates of spawning (spawning frequency) and numbers of oocytes released per spawn (batch fecundity). The object of this paper is to provide new estimates of these two reproductive parameters for *T. symmetricus*.

Relatively little is known about the reproductive biology of *T. symmetricus* from the California Current. Gonad development and sexual maturity were studied by Wine and Knaggs (1975), and some preliminary fecundity estimates are available in MacGregor (1976). Lisovenko and Andrianov (1991) estimated the spawning frequency of *Trachurus murphyi* from Peruvian waters. Other works related to reproduction of *Trachurus* include various analyses of CalCOFI ichthyoplankton data to estimate the seasonality of reproduction, diel time of spawning, and distribution of eggs and larvae (Ahlstrom and Ball 1954; Farris 1961; Kramer and Smith 1970; Moser et al. 1993). Temperature-specific egg incubation rates are also known for *T. symmetricus* (Zweifel and Lasker 1976).

METHODS

Jack mackerel, *Trachurus symmetricus*, were collected about 200 nautical miles off the southern California coast (figure 1) from March 23 to April 9, 1991, during a cooperative cruise on the R/V *Novodrutsk* (from Vladivostok, Russia). A large, nearly square, pelagic trawl with a vertical and horizontal opening of 75–80 meters was towed at 4.2 to 5.5 knots to collect the fish. Most of the 36 trawls were made at night; they lasted from 50 minutes to 8 hours and 40 minutes (Macewicz and Abramenkoff 1993). Surface water temperature ranged from 13.5°C to 14.7°C.

T. symmetricus were randomly sampled from the catch. Up to 100 fish from each haul were sexed, and measured (FL) to the nearest millimeter; their gonads were also classified (Macewicz and Abramenkoff 1993). From each trawl, 5 to 22 females were selected, not on the basis of maturity, but at random. The females were individually weighed (to the nearest gram) and their ovaries were removed and pre-

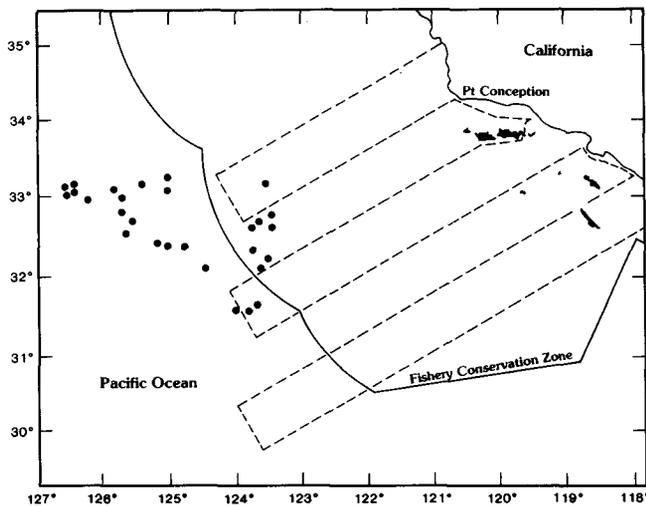


Figure 1. Location of the jack mackerel survey during March 23–April 9, 1991. Circles = trawls in which *Trachurus symmetricus* were taken; dotted line = the CalCOFI survey pattern.

served in 10% neutral buffered Formalin. Analysis of the preserved ovaries of these female *T. symmetricus* is the subject of this paper.

Histological Classification

The preserved ovaries were weighed to the nearest milligram in the laboratory. A piece of each ovary was removed, dehydrated, and embedded in Paraplast. Histological sections were later cut at 5–6 μm and stained with Harris hematoxylin followed by eosin counterstain (H&E).

Each ovary was classified histologically in the manner developed for northern anchovy, *Engraulis mordax*, by Hunter and Goldberg (1980) and Hunter and Macewicz (1985a,b) with a few modifications for the ovarian structure of *T. symmetricus*. Oocytes in *T. symmetricus* ovaries develop asynchronously; that is, oocytes in many stages of development occur simultaneously in reproductively active ovaries (Wallace and Selman 1981). In each ovary we recorded the presence or absence of the following characters: oocytes that had not begun vitellogenesis; oocytes in early vitellogenic stages (0.28–0.54 mm in diameter); advanced yolked oocytes (smallest about 0.42 mm in diameter) in which any stages of nucleus migration (precursor to hydration) or hydration (>0.95 mm in diameter) were noted; and postovulatory follicles.

Unlike the developing oocytes of northern anchovy, those of *T. symmetricus* contain lipid droplets. The lipid first appears in oocytes about 0.19 mm in diameter (before vitellogenesis starts) and then eventually surrounds the nucleus and begins to fuse. Just before the nucleus migrates, partially fused lipid

droplets begin moving to the side of the nucleus opposite the direction of migration. This location of the oil droplets on one side of the nucleus is a unique character that signals the onset of the migratory-nucleus stage. For this reason, oocytes in the migratory-nucleus stage can be detected much earlier in *T. symmetricus* than in species lacking an oil droplet, such as the northern anchovy.

Ovarian atresia in most teleosts seems to follow a similar sequence of stages (α , β , γ , and δ), as defined by Bretschneider and Duyvene de Wit 1947; Lambert 1970; and Hunter and Macewicz 1985b. We examined the ovarian sections for the presence of alpha (α) atresia of yolked oocytes and grouped them as follows: none, $\alpha < 50\%$ (1 oocyte to 49% of the yolked oocytes were in α atresia), or $\alpha \geq 50\%$ (50% or more of the yolked oocytes were in α atresia). The presence of beta (β) atresia was also noted. Alpha atresia of *T. symmetricus* was essentially similar to that described and illustrated for northern anchovy by Hunter and Macewicz (1985b); however, β atresia in *T. symmetricus* differed from northern anchovy because numerous vacuoles were scattered between the follicle cells. The vacuoles are probably remnants of the lipid droplets, which take longer than yolk to resorb, and in H&E slides appear empty. Ovarian atresia may indicate that the end of a spawning season is approaching (Hunter and Macewicz 1980, 1985b).

Spawning Frequency

To measure spawning rate from postovulatory follicles, one must be able to estimate the age of the postovulatory follicles on the basis of their deterioration (Hunter and Goldberg 1980; Hunter and Macewicz 1985b). The best way to develop criteria for estimating the age of postovulatory follicles is to spawn fish in the laboratory and sample at known times after spawning. Alheit et al. (1984) were able to estimate age of postovulatory follicles for *Engraulis ringens* by sampling fish at sea through the day and night. They then reconstructed the degeneration rate of the postovulatory follicles by analyzing the time series. This alternative method requires a diel rhythm of spawning so that the elapsed time from spawning to capture can be used to assign ages to postovulatory follicles. Farris (1961) demonstrated that *T. symmetricus* spawn only at night, with a peak around midnight, which indicates that the method of Alheit et al. is possible.

It was not practical for us to spawn *T. symmetricus* females in the laboratory, so we used the method of Alheit et al. (1984). We used the time of day of the

trawls (table 1) to estimate the age of *T. symmetricus* postovulatory follicles. Although some gaps existed in the time series (0600–1200 and 1500–2000), we were able to discriminate between postovulatory follicles 0–6 h old, 12–30 h old, 36–54 h old, and older than 60 h. Because degeneration and resorption of postovulatory follicles is a continuous process, we estimated ages based on the extent of changes in the following: the size and apparent shape of the follicle (from large and convoluted to V-shaped and 1/10 of the original size); appearance of the granulosa cells (from many healthy cells with nuclei linearly arranged, to a few cells containing pycnotic nuclei, cytoplasmic vacuoles, and granules); appearance of the lumen; and the size of the thecal layer. The histological characteristics are very similar to those described for *Scomber japonicus* (Dickerson et al. 1992) and northern anchovy (Hunter and Goldberg 1980; Hunter and Macewicz 1985a).

Batch Fecundity

Batch fecundity (*F*, number of oocytes per spawn) was considered to be the number of oocytes in the

ovary that either contained migratory nuclei or were hydrated. We used the gravimetric method (Hunter et al. 1985, 1992) to estimate the mean number of such oocytes that each ovary contained. Dioses et al. (1989) showed that location of tissue samples does not affect estimates of batch fecundity in *T. murphyi*, which indicates that such oocytes are dispersed randomly throughout the ovary. We teased apart oocytes in a few drops of 50% glycerin and then identified, counted, and measured them, using a digitizer linked by a video camera system to a dissection microscope. Hydrated ovaries containing new postovulatory follicles were not used to estimate batch fecundity.

In Formalin-preserved material, migratory-nucleus-stage and hydrated oocytes are easily identified. Hydrated oocytes are very large and translucent, with faint segmentations resulting from the fusing of yolk globules into “large plates.” Oocytes with late-stage migratory nuclei are larger and less opaque than the other yolked oocytes and have a wide, clearish band on the periphery resulting from fusing of some yolk globules. In addition, a reflective oil drop (or several if lipid droplets are still fusing) is prominent in the migratory-nucleus and hydrated-oocyte stages. Oocytes at the migratory-nucleus stage are detectable in whole oocyte material only after most of the lipid droplets have come together and begun to fuse. Early stages of the movement and fusion of lipid droplets in migratory-nucleus oocytes can be accurately identified in histological sections, but in whole oocytes the early stages are difficult to see. Our examination of the ovaries of 42 females (33 in which the migratory-nucleus stage was distinct, and 9 in which it was difficult to see) indicated that the stage could be consistently detected when the mean diameter of the migratory-nucleus-stage oocytes was 0.69 mm or larger. This detection criterion may, however, be different for other microscope imaging systems. Only when the migratory-nucleus-stage oocytes averaged 0.69 mm or larger did we use them to estimate batch fecundity.

To compare the number and size of oocytes in the spawning batch to the other oocytes in the ovary, we measured oocyte size–frequency distributions in three females. We measured about 200 oocytes, and identified them by four developmental stages:

1. unyolked but with lipid droplets
2. early yolking
3. advanced yolked
4. about to be spawned — hydrated or with migrating nuclei

TABLE 1

Number of Mature Female Jack Mackerel, *Trachurus symmetricus*, from Trawl Samples Taken off Southern California in 1991

Trawl number	Date		Trawling midpoint hour	Mature females		
	Mo	Day		Total	Non-spawn	Spawn*
1	03	23	1500	11	5	6
2	03	23	2000	20	12	8
3	03	24	2400	18	10	8
6	03	25	2000	20	5	15
7	03	25	2400	20	6	14
8	03	26	1400	21	3	18
9	03	26	2100	10	2	8
10	03	27	0300	10	0	10
11	03	27	2200	20	2	18
13	03	28	2100	21	6	15
15	03	29	2100	20	5	15
17	03	30	2000	19	4	15
18	03	31	2400	21	3	18
19	03	31	2000	20	2	18
20	04	01	0100	10	0	10
22	04	01	2000	20	4	16
23	04	02	0300	5	0	5
24	04	02	2000	5	0	5
26	04	03	0600	10	3	7
27	04	03	2200	22	12	10
28	04	05	2200	21	8	13
29	04	06	1200	6	5	1
31	04	07	0200	5	5	0
32	04	07	2100	18	10	8
33	04	08	0400	10	5	5
34	04	08	2100	20	12	8
36	04	09	2400	10	8	2
All			N	413	137	276
			%		33	67

*Sum of the females identified as having spawned in the last 54 hours or as able to do so within 24 hours.

We counted the rest of the oocytes in the weighed subsample by stage. For ovaries with oocytes in stages 3 and 4, we measured 30–50 oocytes in each stage, and counted the remaining in each stage.

We estimated the batch fecundity of 33 females: 6 on the basis of counts of hydrated oocytes, and the rest on counts of migratory-nucleus-stage oocytes. In all, 40 females with ovaries containing hydrated oocytes were collected, but 34 of these had ovaries containing new postovulatory follicles, which indicated that they had just begun to spawn and thus were not suitable to be used for estimating batch fecundity.

RESULTS

Spawning Frequency

Of the 415 female jack mackerel ovaries collected and preserved, 413 were histologically classed as mature because they had ovaries containing yolked oocytes or beta atresia. Two females (one from trawl 11 and one from trawl 36) were classed as immature because their ovaries contained no yolked oocytes and no stages of atresia. The ovaries of 67% of the mature females contained postovulatory follicles (≤ 54 hours old), or hydrated oocytes, or migratory-nucleus-stage oocytes, indicating that these females had spawned within the last 54 hours or would do so within the next 0–24 hours (table 1).

Spawning frequency was calculated on the basis of histological evidence of three different nights:

Spawned on night of capture: late migratory-nucleus-stage oocytes, hydrated oocytes, or new postovulatory follicles in the ovary

Spawned the night before capture: postovulatory follicles 12 to 30 hours old in the ovary

Spawned two nights before capture: postovulatory follicles 36 to 54 hours old in the ovary.

Some histological stages were not used to estimate spawning frequency because we were not confident that their incidence could be consistently determined. We did not use oocytes in the early migratory-nucleus stage, because we were not confident of the time of day when females became fully recruited into this stage. We show the data, however (spawning night A, table 2). It is interesting that the migratory-nucleus stage was first detected at 2000 hours, about 24 hours before the batch would be expected to spawn. We also did not use postovulatory follicles considered to be older than 55 hours, because they can be confused with very late stages of β atresia.

The percentage of mature females spawning per day is estimated from daily spawning rates computed for three different spawning nights: spawning night B, determined on the basis of females with ovaries containing hydrated oocytes or postovulatory follicles, and spawning nights C and D, based on females with ovaries containing postovulatory follicles of different ages. The percentages of mature females spawning on nights B, C, and D were 20.1%, 23.5%, and 16.9% (table 2). The mean of the three estimates was 20.2%, indicating that the average female *T. symmetricus* spawned every 5 days during the 18-day sampling period.

The ovaries of 8% of the mature females contained histological evidence of two spawnings: that is, a single ovary contained postovulatory follicles of two different ages; or postovulatory follicles and hydrated or migratory-nucleus-stage oocytes; or some other combination. Because we knew the approximate age for each of these characters, we were able to calculate the interval between spawnings. The data indicated that 8% of the population spawned at intervals of one to three days (table 3).

Batch Fecundity

The relation between female weight (W , without ovary) and batch fecundity (F) for 33 females with batch fecundity estimates (table 4) was determined by linear regression analysis. In the resulting equation, $F = -11436 + 126W$ with $r^2 = 0.48$, the intercept for the regression of F on W did not differ from zero ($t = -0.62$, $df = 32$, $P = 0.541$). Therefore, the regression line was forced through 0, yielding the relation $F = 112W$, where W ranged from 586 to 1,262 g (figure 2).

Covariance analysis indicated that the relation between batch fecundity and female weight was different when the ovary contained postovulatory follicles > 11 hours old ($F_{1,30} = 20.94$, $P < 0.001$), and the r^2 improved to 0.68 in the multiple regression equation with the presence of past spawning as a variable. Thus females that had spawned within the last 12–54 hours had lower batch fecundity than those in which no evidence of past spawning was detected. The mean adjusted fecundity for the average (791 g, without ovary) female in our fecundity data set was 73,655 oocytes (SE = 1,116) when evidence existed for past spawning, and 103,797 oocytes (SE = 1,181) when no such evidence existed.

T. symmetricus ovaries usually contained substantially more advanced yolked oocytes than are released in a single spawning batch. This is in sharp contrast to the northern anchovy, in which most of the advanced-yolked oocytes become hydrated and

TABLE 2
 Spawning Frequency of *T. symmetricus* on Four Nights (A–D) and the Presence
 of Histological Characters Indicating Spawning

Midpoint hour	Trawl ID number	Spawning nights						Total number mature females
		A	B		C	D		
		Early migratory- nucleus-stage oocytes	Hydrated oocytes	Hydrated oocytes & new postovulatory follicles	Postovulatory follicles 0–6 hours old	Postovulatory follicles 12–30 hours old	Postovulatory follicles 36–54 hours old	
1200	29	0	0	0	0	1	0	6
1400	8	0	4	9	0	4	2	21
1500	1	0	1	1	0	3	1	11
2000	17	2	0	2	5	7	2	19
	6	3	0	4	1	2	6	20
	22	1	0	2	3	9	2	20
	24	1	0	0	0	2	3	5
	2	4	0	0	2	1	1	20
	19	3	0	5	1	7	5	20
2100	13	1	1	2	0	7	4	21
	15	4	0	1	1	4	6	20
	32	5	0	0	0	2	2	18
	9	3	0	1	3	0	2	10
	34	3	0	1	1	2	1	20
2200	11	2	3	0	4	5	6	20
	28	5	0	0	1	4	5	21
	27	2	0	0	0	5	5	22
24/0	36	0	0	0	0	1	1	10
	7	3	0	0	4	4	5	20
	3	5	0	1	0	1	2	18
	18	4	1	0	7	7	3	21
0100	20	3	0	0	2	3	3	10
0200	31	0	0	0	0	0	0	5
0300	10	1	0	1	4	4	2	10
	23	1	0	0	1	4	0	5
0400	33	0	0	0	1	3	1	10
0600	26	3	0	0	2	5	0	10
All	N	59	10	30	43	97	70	413
Females spawning per night	% SE	14.3 1.8		20.1 3.5		23.5 2.6	16.9 1.9	

Some females have more than one histological character, but no female is counted more than once per given spawning night.

are spawned as a single batch. In the 33 females used to estimate batch fecundity, we also measured the size and estimated the number of the remaining advanced-yolked oocytes (not included in the spawning batch). We determined that the ratio of the number of oocytes in the fecundity batch to the remaining advanced-yolked oocytes was 1.01 (SD = 0.41) and that the average mean diameter of the remaining advanced-yolked oocytes was 0.55 mm (SD = 0.026). Thus, just before spawning, there existed the equivalent of about two batches of advanced-yolked oocytes, one of which would definitely be spawned. Under some circumstances (such as higher water temperature, reduced food availability, or the last spawn) all the advanced oocytes may be hydrated and spawned at once, thus doubling the

batch fecundity. Our results also indicated that size modes of oocytes, or an oocyte size threshold should not be used as an alternative to counts of oocytes in the hydrated or migratory-nucleus stages, because they may yield inaccurate estimates of batch fecundity in *T. symmetricus*.

To estimate how many batches of yolked oocytes an ovary contained, we counted all the oocytes larger than 0.25 mm in the ovaries of the three females (A, B, and C) illustrated in figure 3. Histological criteria indicate that 0.25 mm is about the diameter of an oocyte at the onset of vitellogenesis. By dividing the total number of oocytes larger than 0.25 mm by their batch fecundity, we obtained estimates of 6, 4, and 7 batches for females A–C, respectively. Thus *T. symmetricus* ovaries may contain

TABLE 3
 Occurrence (+) of Histological Criteria in the Ovaries of 33 Spawning *T. symmetricus* Females
 Indicating Different Spawning Events

Trawl #	Fish number ^a	Migratory-nucleus oocytes	Postovulatory follicles			Elapsed time between spawnings (day)
			≤6 hours old ^b	12–30 hours old	36–54 hours old	
11	1604	—	+	+	—	1
17	1633	—	+	+	—	1
3	1617	+	—	+	—	2
7	1610	+	—	+	—	2
17	1601	+	—	+	—	2
18	1608	+	—	+	—	2
18	1620	+	—	+	—	2
19	1647	+	—	+	—	2
19	1649	+	—	+	—	2
23	1628	+	—	+	—	2
26	1603	+	—	+	—	2
26	1605	+	—	+	—	2
26	1607	+	—	+	—	2
27	1613	+	—	+	—	2
28	1617	+	—	+	—	2
32	1618	+	—	+	—	2
8	1619	—	+	—	+	2
10	1607	—	+	—	+	2
18	1617	—	+	—	+	2
22	1611	—	+	—	+	2
6	1618	+	—	—	+	3
7	1605	+	—	—	+	3
9	1610	+	—	—	+	3
10	1604	+	—	—	+	3
11	1602	+	—	—	+	3
15	1612	+	—	—	+	3
17	1625	+	—	—	+	3
18	1628	+	—	—	+	3
19	1608	+	—	—	+	3
20	1618	+	—	—	+	3
24	1699	+	—	—	+	3
27	1620	+	—	—	+	3
28	1602	+	—	—	+	3

^aFemales are listed in order of time elapsed between spawnings.

^bOvary may also contain hydrated oocytes; ovaries of two females (11–1604 and 18–1617) contained only hydrated oocytes. Because spawning was imminent, they are included in this group.

the equivalent of 4–7 spawning batches of yolked oocytes, if one includes oocytes in the earliest vitellogenic stages.

Annual Spawning Cycle and Ovarian Atresia

The atretic state of *T. symmetricus* ovaries taken in this study is best considered within the context of the annual spawning cycle. According to monthly averages of the standing stock of jack mackerel larvae in the California Current from 1951 to 1984 (Moser et al. 1993), about 27% of the season's production had been completed by the end of the cruise. During the cruise period, about 10% of the average number of larvae produced in a year were spawned (shaded area in figure 4).

Our analysis of ovarian atresia indicates that about 5% of the *T. symmetricus* in the collection area had ended or were close to ending spawning for the year.

The ovaries of 3 (0.7%) of the 413 mature females were classified as inactive and were judged not able to spawn at the time of capture or in the near future because they contained beta atresia but no yolked oocytes. The presence of beta atresia in these ovaries indicated that the ovaries may have been active during the current season (Hunter and Macewicz 1985b). An additional sign of season completion, for 4% of the females, was the presence in their ovaries of the alpha stage of atresia in 50% or more of the yolked oocytes (Hunter and Macewicz 1980, 1985b). This lends credence to our assumption that this highly atretic condition is related to the end of spawning for female *T. symmetricus*. Finally, the small loss (4.7%) of females to the spawning population seems reasonable, since only about a fourth of the production for the spawning season had been completed.

TABLE 4

Batch Fecundity (Number of Oocytes to Be Spawned in the Batch) of 33 *T. symmetricus* Females Taken March 23–April 9, 1991, and 2 Females Taken May 27, 1970

Year	Fork length (mm)	Weight without ovary (g)	Ovary weight (g)	Batch fecundity	Postovulatory follicles*
1991					
	383	586.4	24.612	51,987	+
	393	598.2	44.786	52,965	+
	395	605.5	21.508	52,147	—
	415	632.9	31.102	63,997	+
	398	637.7	26.343	52,736	+
	382	638.5	47.462	75,915	—
	396	643.8	41.250	56,395	—
	400	654.6	62.410	82,476	+
	394	659.3	31.707	73,392	+
	406	665.0	47.000	109,593	—
	412	668.8	25.230	61,628	+
	403	671.4	22.568	31,752	+
	406	697.6	29.357	72,269	—
	417	706.2	27.754	86,400	—
	413	722.5	25.455	48,360	+
	405	735.8	33.952	70,205	+
	423	739.9	32.126	59,946	+
	422	744.8	29.226	91,661	—
	429	755.5	42.482	129,838	—
	417	756.7	35.283	100,267	—
	423	761.7	99.310	115,847	—
	422	775.4	32.637	81,073	+
	432	776.7	40.255	123,961	—
	421	793.5	35.530	85,795	—
	435	826.8	54.153	120,063	—
	454	902.3	39.669	72,685	+
	445	904.3	64.735	112,648	—
	440	945.8	63.191	134,716	—
	485	1105.9	46.083	94,654	+
	493	1160.8	64.237	164,711	+
	492	1162.8	58.214	116,788	+
	504	1194.3	58.669	94,543	+
	488	1262.4	123.550	171,466	—
1970					
	543	1576.2	141.8	192,000	*
	540	1602.0	120.0	159,000	*

*+ = presence of postovulatory follicles 12 to 54 hours old, indicating these females had spawned recently.

* = unknown if postovulatory follicles were present, data are from MacGregor 1976.

About a third of the females had ovaries containing minor levels of alpha-stage atresia (less than 50% of yolked oocytes affected). This condition seemed surprisingly common (35% of the mature females), since only a fourth of the season's production had been completed. In comparison, during the peak months of the northern anchovy spawning season, females classed in this state — i.e., containing minor levels of alpha atresia — constitute only about a twentieth of the population (Hunter and Macewicz 1985b).

DISCUSSION

This study indicates that jack mackerel, *Trachurus symmetricus*, females spawn many times during the

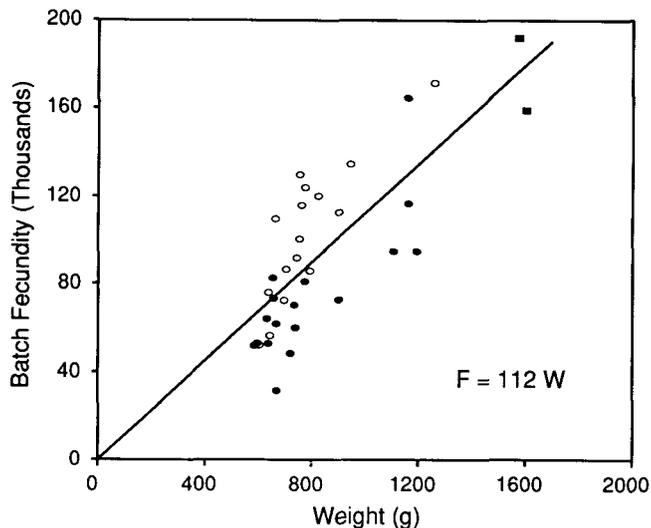


Figure 2. Batch fecundity (F) of *Trachurus symmetricus* as a function of female weight (W, without the ovary); the batch was estimated from numbers of migratory-nucleus-stage oocytes or hydrated oocytes; regression line was forced through zero. Closed circles = females that had spawned 12 to 54 hours before capture; open circles = females with no histological evidence of a past spawning; Squares = females with unknown spawning history, from MacGregor 1976.

year. The average *T. symmetricus* female spawned 3.6 times during the 18-day sampling period. Over the same period about 10% of the annual crop of *T. symmetricus* larvae were produced (figure 4), according to the annual larval production curve from Moser et al. (1993). Thus the average female may spawn 36 times per year according to these data.

Data from two other studies indicate high spawning rates in *T. symmetricus*. The frequency of *T. symmetricus* females with ovaries containing hydrated oocytes ranged from 0 to 24% in monthly sets of samples compiled over several years by Wine and Knaggs (1975) from southern California data. Wine and Knaggs did not intend for their data to be used to estimate spawning frequency, and biases could exist because of sampling during inappropriate times of day (DeMartini and Fountain 1981; Schaefer 1987). Lisovenko and Andrianov (1991) used the hydrated-oocyte method to estimate spawning frequency for *Trachurus murphyi* taken off Peru in 1980–85. Our interpretation of their data indicate that the average *T. murphyi* female may spawn about 15 times per year. Wine and Knaggs's data indicate about 21 spawnings for *T. symmetricus*, whereas our initial guess for *T. symmetricus*, based on our point estimate and the average larval production curve, was about 36 spawnings. All data considered, 25 spawnings per year seems a reasonable guess of the annual number of spawnings for the average female *Trachurus*. This means that the average *T. symmetricus* female may spawn about 2,800 oocytes per gram

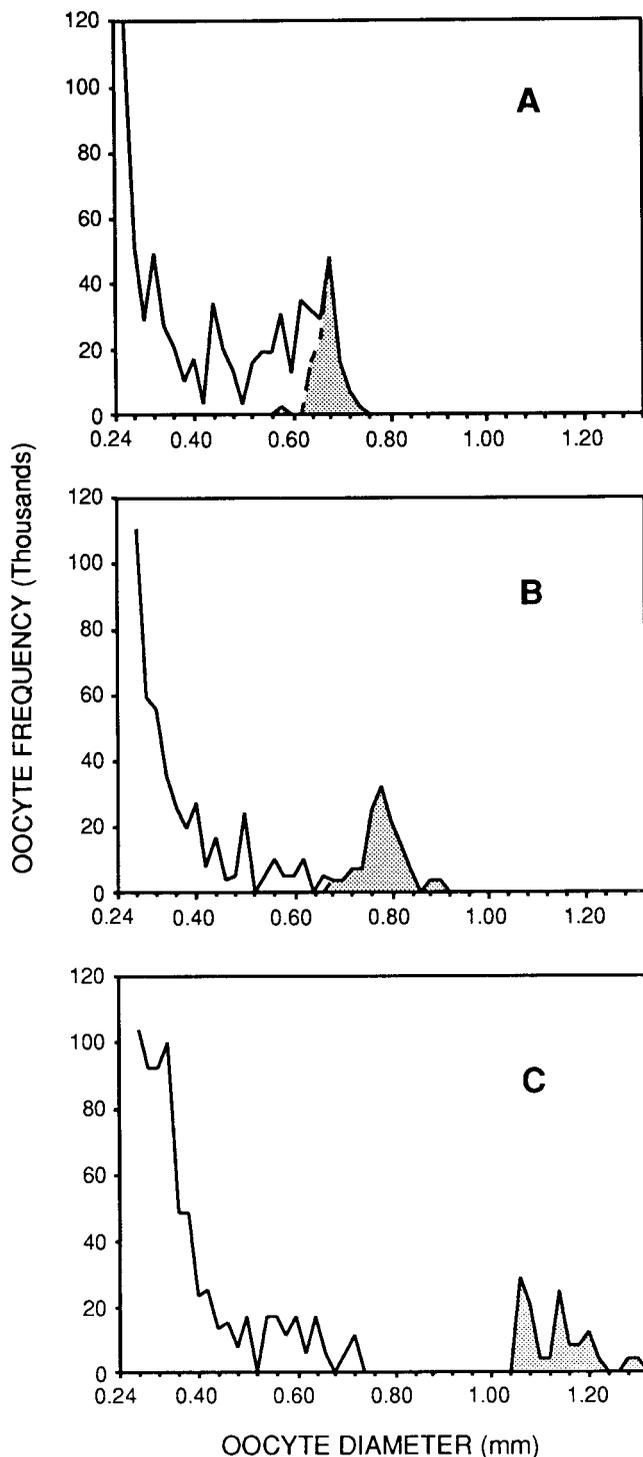


Figure 3. Oocyte size-frequency distributions of three *Trachurus symmetricus* females showing progressive maturation of a spawning batch from female A to female C. Shaded area = batches about to be spawned: in A, early migratory-nucleus-stage oocytes (mean diameter = 0.67 mm); in B, well-advanced migratory-nucleus-stage oocytes (mean diameter = 0.78 mm); and in C, hydrated oocytes (mean diameter = 1.13 mm).

body weight per year (25×112). More accurate data, particularly age-specific data, would be highly desirable.

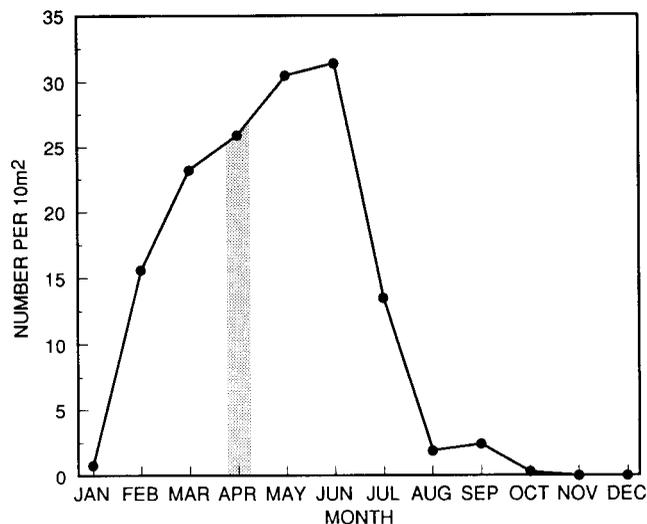


Figure 4. Annual spawning season as indicated by the average number of *Trachurus symmetricus* larvae per 10 m² taken in the CalCOFI surveys 1958–84, from Moser et al. 1993. Shaded area indicates portion of spawning season considered in this paper.

The potential annual fecundity of various *Trachurus* species has been estimated over the years (Chirginskiy 1970; Kaiser 1973; Macer 1974; Andrianov 1985; Arruda 1986), but we suspect these data are a loss. Owing to the high spawning rates of *Trachurus* indicated by this study and the two cited above, and the limited number of batches of yolked oocytes in the ovary, it seems unlikely that the standing stock of yolked oocytes in the ovary at the beginning of the spawning season is an accurate measure of annual fecundity in any *Trachurus* species. In other words, it is probably preferable to consider annual fecundity as being indeterminate in *Trachurus*. Thus the only accurate way to measure annual fecundity is to measure spawning frequency and batch fecundity throughout the spawning season.

Only a few studies of batch fecundity exist for *Trachurus*, and most of these are not particularly useful for making comparisons. We believe that only the two determinations based on hydrated oocytes are useful in MacGregor's (1976) preliminary study of *T. symmetricus*; for the other 28 of his specimens, MacGregor may have used inaccurate criteria (all dense-yolked oocytes) to identify the oocytes composing the batch in *T. symmetricus*. Paschenko¹ identified the spawning batch as all oocytes above 0.50 mm (as shown in MacGregor 1976, figure 2) so his fecundities are probably overestimated. It is obvious

¹Paschenko, V. M. Distribution, biology and biomass assessment of the jack mackerel *Trachurus symmetricus* (Ayers). Presented to the 1979 U.S.–U.S.S.R. Bilateral Meeting on Fisheries Assessment in the North Pacific, Seattle, June 5–8, 1979.

from our few oocyte size-frequency distributions that all the dense-yolked oocytes are not spawned at once, because only about half of them undergo final maturation synchronously. Chigirinskiy (1970) also used an inaccurate oocyte criterion for identifying the spawning batch of *T. japonicus* (yolked oocytes >0.38-mm diameter). Although Lisovenko and Andrianov (1991) used hydrated oocytes to identify the oocytes composing the spawning batch in *T. murphyi*, they do not give the weight or length of the females; consequently, comparison to their study is difficult. The most useful study is that of Dioses et al. (1989), who used hydrated oocytes to estimate batch fecundity of *T. murphyi* off Peru. The relative batch fecundity of *T. murphyi* in his study—about 235 oocytes per gram female weight—is about twice that of *T. symmetricus* in this study (112 oocytes per gram).

Batch fecundity may change seasonally in *T. symmetricus*, as it does in a number of other fishes (Conover 1985; Alheit 1987; Kjesbu 1989). Two kinds of indirect evidence suggest a possible seasonal change in batch fecundity. First, females with low levels of ovarian atresia were more prevalent than expected, considering that only 27% of the year's spawnings had been completed. These females appeared to continue spawning at undiminished rates, but atretic losses may have reduced the batch size. Second, batch fecundity was lower in females with evidence of past spawning, indicating that there may be a link between batch fecundity and spawning rate.

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REPRODUCTIVE BIOLOGY OF THREE CALIFORNIA SPECIES OF PARALABRAX (PISCES: SERRANIDAE)

DEBRA L. ODA, ROBERT J. LAVENBERG, AND JAMES M. ROUNDS

Natural History Museum of Los Angeles County
Section of Fishes
900 Exposition Boulevard
Los Angeles, California 90007

ABSTRACT

Paralabrax clathratus, *P. maculatofasciatus*, and *P. nebulifer*, common off California, spawn in the warm summer months. All three species are capable of daily spawning, but our data indicate that the mean interval between spawning events is about two days. In general, *P. clathratus* and *P. maculatofasciatus* appear to spawn most frequently in the late afternoon and evening hours; *P. nebulifer* may spawn most often at midday. Our data indicate that batch fecundity (BF, number of eggs) is approximately related to the ovary-free body weight (OFW, grams) of *P. clathratus*, according to the equation $\log_{10} BF = 0.91 * \log_{10} OFW + 5.26$ ($n = 25$). Preliminary data are provided that relate batch fecundity to ovary-free body weight in *P. maculatofasciatus* and *P. nebulifer*. Evidence of hermaphroditism occurs in each species: *P. maculatofasciatus* is a protogynous hermaphrodite; the reproductive patterns of the other two species remain unclear.

RESUMEN

Paralabrax clathratus, *P. maculatofasciatus* y *P. nebulifer*, comunes frente a California, desovan en los meses cálidos de verano. Las tres especies son capaces de desovar diariamente; sin embargo, nuestros datos indican que el intervalo promedio entre eventos de desove es de alrededor dos días. En general, pareciera que el desove de *P. clathratus* y *P. maculatofasciatus* es más frecuente en horas avanzadas de la tarde y al anochecer, mientras que el desove de *P. nebulifer* pareciera ocurrir a menudo al mediodía. Nuestros datos indican que la fecundidad de cada puesta (BF, en número de huevos) en *P. clathratus* se relaciona aproximadamente con el peso corporal libre de ovarios (OFW, en gramos) de acuerdo a la ecuación $\text{LOG}_{10} BF = 0.91 * \log_{10} OFW + 5.26$ ($n = 25$). Se proveen datos preliminares que relacionan la fecundidad por puesta con el peso corporal libre de ovarios en *P. maculatofasciatus* y *P. nebulifer*. Se observa evidencia de hermafroditismo en las tres especies: *P. maculatofasciatus* es un hermafrodita pro-

togínico; los patrones reproductivos de las otras dos especies son poco claros.

INTRODUCTION

Three species of *Paralabrax* are common in the waters off southern California: *P. clathratus* (kelp bass) and *P. nebulifer* (sand bass) in nearshore coastal waters, and *P. maculatofasciatus* (spotted sand bass) in harbors and bays. *Paralabrax nebulifer* and *P. clathratus* have been recognized as important game fish in southern California since 1916 (Collyer 1949). They remain one of the most frequent catches for sport-fishers, ranking second and third, respectively, in number of fish taken in the state in 1989 (Oliphant 1990).

Aspects of spawning and reproduction in the species of *Paralabrax* have been variously reported. All three species spawn in the warm summer months (Clark 1933; Limbaugh 1955; Smith and Young 1966). *Paralabrax clathratus* (typically solitary) and *P. nebulifer* are known to gather in large schools during spawning (Limbaugh 1955). All three species are multiple spawners, although this has not always been clearly stated in previous literature. Quast (1968) suggested that *P. clathratus* may spawn more than once a season and that sex products are not completely released at spawning. Smaller *P. clathratus* were thought to spawn less frequently—only once each season—and to mature later than the multiply spawning larger individuals (Frey 1971). DeMartini (1987) reported that *P. clathratus* and *P. nebulifer* are multiple spawners, and estimated batch fecundity for specimens of both species collected between 1982 and 1985. Hastings (1989) has established that *P. maculatofasciatus*, from the northern Gulf of California, is a protogynous hermaphrodite. Most other members of the family Serranidae are hermaphroditic. Hermaphroditic characters were found in *P. clathratus*, but because of a lack of transitional individuals, the species was identified as a secondary gonochorist—i.e., having separate sexes but derived from a hermaphroditic ancestor (Smith and Young 1966).

For the past decade the reproductive biology of multiply spawning marine fishes has come under

scrutiny. Techniques have been established to estimate spawning frequency and batch fecundity. Spawning frequency is estimated from the percentage of mature female fish with postovulatory follicles of a known age, or from the percentage of mature females with a full complement of hydrated oocytes (Hunter and Macewicz 1985). Eggs of the most advanced stage—typically hydrated oocytes—from an ovary sample of known weight are counted to estimate the number of ova that will be spawned in a single batch (Hunter et al. 1985). Our objectives were to estimate the spawning frequency and batch fecundity of *P. clathratus*, *P. nebulifer*, and *P. maculatofasciatus* using these techniques, and to determine at what time of day and in which season they spawn. Preliminary evidence for hermaphroditism is examined for each species.

MATERIALS AND METHODS

Adult and juvenile *Paralabrax* were collected between Ventura and Mission Bay, California, in spring and summer 1988. Fish were taken by hook and line, trawls, and entrainment during the initial phase of a heat treatment at the Los Angeles County Scattergood Generating Station, Playa del Rey, California. Most fish were sacrificed to obtain field data (*P. clathratus* $n = 84$, *P. maculatofasciatus* $n = 79$, *P. nebulifer* $n = 81$); some fish were transported live to the R & D Laboratory at the Southern California Edison Redondo Beach Generating Station. Time of collection, standard length (SL, mm), and weight (grams) were recorded for all field-collected specimens. Gonads were removed from sacrificed fishes, weighed, and preserved in 10% buffered Formalin.

Transported fish were allowed to acclimate to ambient conditions in 1,100-liter outdoor tanks equipped with flow-through seawater systems. Water temperature varied between 14.7° and 19.9°C during the *P. maculatofasciatus* experimental time period, between 15.3° and 20.9°C for *P. clathratus*, and between 16.9° and 19.9°C for *P. nebulifer*. On June 12–13, 1989, each fish was catheterized to determine spawning status, and tagged with a colored, numbered “spaghetti tag.” All *P. clathratus* females, 97% of the *P. maculatofasciatus* females, and 26% of the *P. nebulifer* females were reproductively active (largest oocytes at least 0.4–0.5 mm). *Paralabrax nebulifer* females were reexamined on July 12; 73% were active. Each tank contained about equal numbers of mature specimens of each sex. Reproductively active females were injected with the hormone LHRHa (des-Gly¹⁰-[d-Ala⁶]-LHRH) to induce the maturation of oocytes (*P. clathratus* $n = 17$, *P. maculatofasciatus* $n =$

29, *P. nebulifer* $n = 20$). A dosage of 50 µg LHRHa per kg of fish weight was injected into the dorsal muscle tissue between the pectoral fin and anus. All tanks were visually and quantitatively inspected at least every hour for the presence of running ripe individuals or freshly spawned eggs. The time at which each female spawned was noted, and the fish were then sacrificed at predetermined time intervals. Each was weighed and measured (SL) before sacrifice, and ovaries were removed, weighed (wet weight), and preserved in 10% Formalin.

Samples of the preserved ovaries were embedded in Paraplast, sectioned (ca. 6 µm) and counterstained with hematoxylin-eosin for histological examination (Hunter and Macewicz 1985).

The appearances of postovulatory follicles in the specimens for the timed sacrificial series were used as a standard upon which to estimate spawning times in field-collected material. A general histological classification of the ovaries for all three species is as follows:

Hydrated: Hydrated or migratory-nucleus-stage oocytes in the ovary, and no new postovulatory follicles (figure 1A–C).

Day 0 (age ≤4-hour-old postovulatory follicles): New postovulatory follicles, typically convoluted with a well-defined lumen, ranging in size to ca. 300 µm. The granulosa epithelial cell and thecal connective cell layers may be separate; little or no degeneration of the cells is apparent (figure 1D and E).

Day 1 (age >4- to ≤24-hour-old postovulatory follicles): Postovulatory follicles reduced in size, generally 150–300 µm, zero to few folds in the granulosa cell and thecal cell layers, and small lumen. Granulosa cells often with pycnotic nuclei, vacuoles, and degenerating cytoplasm (figure 2A–C).

Nonspawning (mature): Ovaries with many yolked oocytes, no postovulatory follicles, and no hydrating oocytes (figure 2D and E).

The degeneration of postovulatory follicles in *Paralabrax* is generally similar to that found in most other multiply spawning marine fishes that have been investigated (Hunter and Goldberg 1980; Hunter and Macewicz 1980; Goldberg et al. 1984; Hunter et al. 1986; Schaefer 1987). But we could confidently identify only postovulatory follicles that were ≤24 hours old.

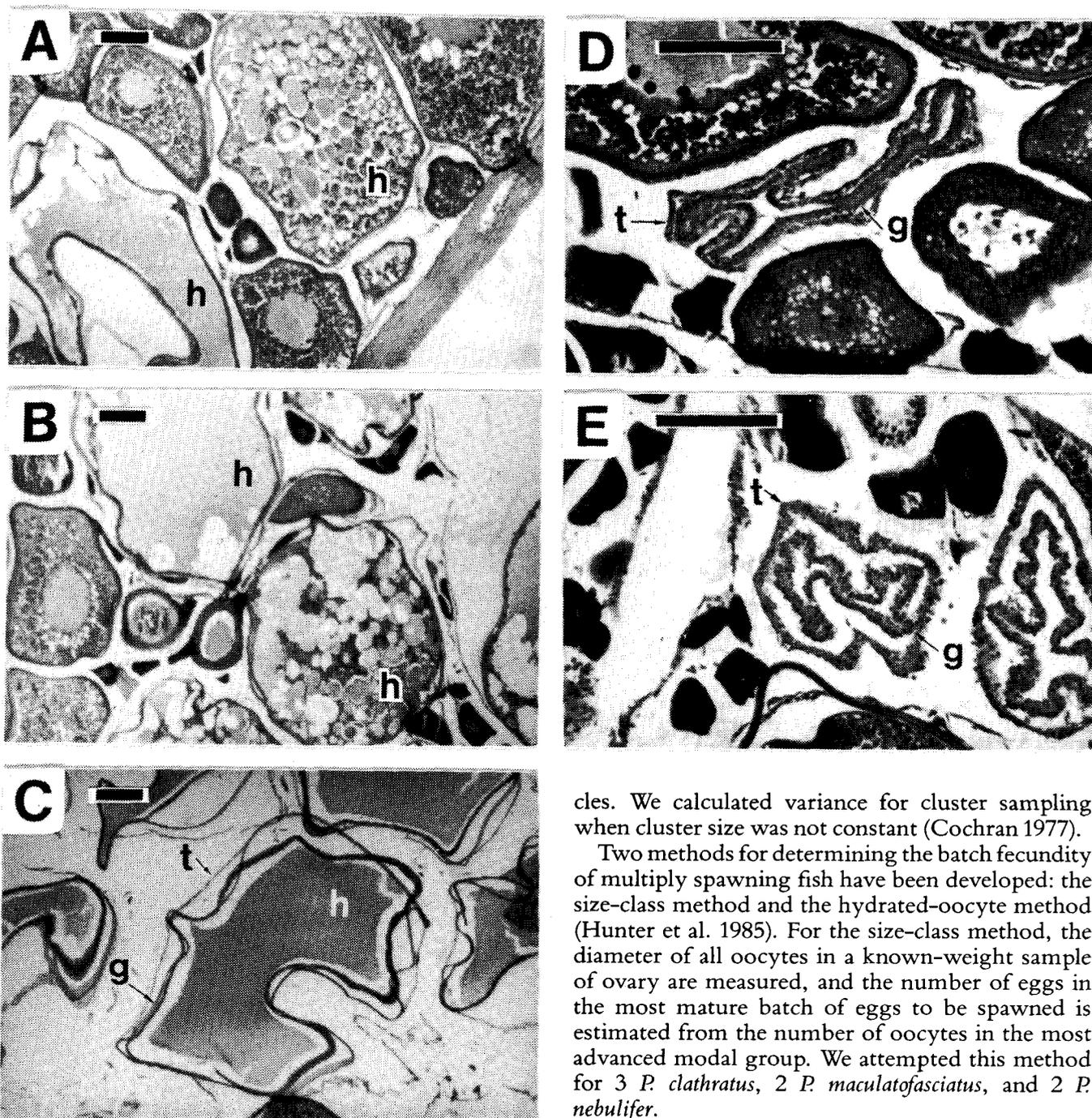


Figure 1. Hydrating oocytes: A, *Paralabrax maculatofasciatus*; B, *P. clathratus*; C, *P. nebulifer*. Postovulatory follicles, age day 0 (≤ 4 hrs old); D, *P. clathratus*; E, *P. nebulifer*. h = hydrating oocytes; g = granulosa epithelial cell layer; t = thecal connective cell layer. Bar = 0.1 mm.

Following the methodology of Hunter et al. (1986), we considered the data from our field collections of *Paralabrax* gonads as statistical clusters of samples from the population. We estimated spawning frequency on the basis of the number of females whose ovaries contained day-1 postovulatory folli-

cles. We calculated variance for cluster sampling when cluster size was not constant (Cochran 1977).

Two methods for determining the batch fecundity of multiply spawning fish have been developed: the size-class method and the hydrated-oocyte method (Hunter et al. 1985). For the size-class method, the diameter of all oocytes in a known-weight sample of ovary are measured, and the number of eggs in the most mature batch of eggs to be spawned is estimated from the number of oocytes in the most advanced modal group. We attempted this method for 3 *P. clathratus*, 2 *P. maculatofasciatus*, and 2 *P. nebulifer*.

For the hydrated oocyte method, hydrated oocytes in a weighed sample of ovarian tissue are counted, and the ratio of hydrated oocytes to grams of ovary is extrapolated to total ovary weight in order to estimate the number of eggs in the most mature batch to be spawned. Specimens used in this method must have ovaries with oocytes that have sufficiently begun hydration, and show no evidence of ovulation of the batch. Initially, we used samples from 12 *P. clathratus*, 9 *P. maculatofasciatus*, and 4 *P. nebulifer* to test whether the location of tissue sam-

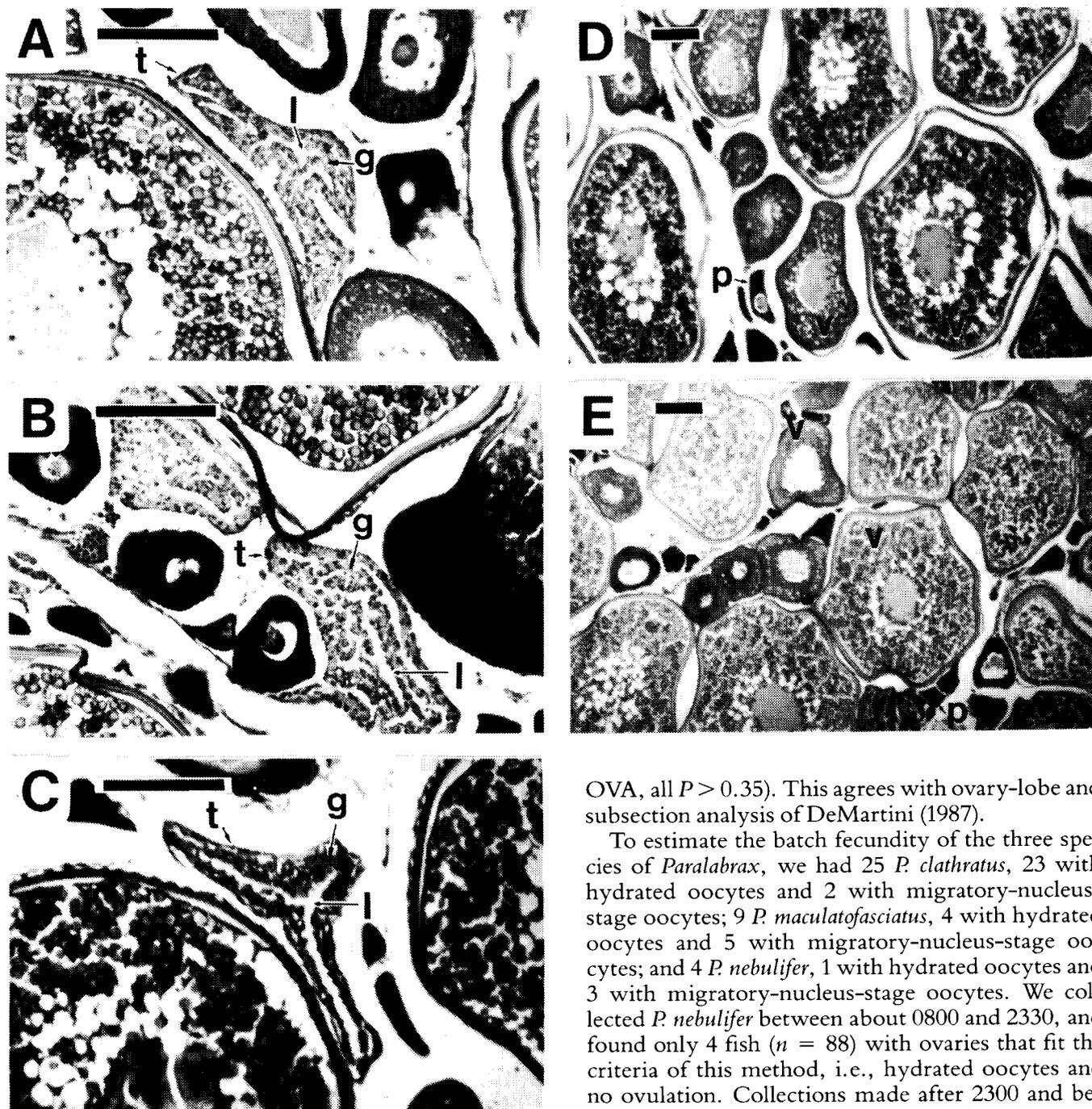


Figure 2. Postovulatory follicles, age day 1: A, *Paralabrax clathratus* (12–18 hrs old); B, *P. maculatofasciatus* (ca. 18 hrs old); C, *P. nebulifer* (12–18 hrs old). Nonspawning (mature) ovaries: D, *P. clathratus*; E, *P. maculatofasciatus*. g = granulosa epithelial cell layer; l = lumen; p = primary oocytes; t = thecal connective cell layer; v = vitellogenic oocytes. Bar = 0.1 mm.

ples (right or left ovarian lobe, position of the sample on the ovary lobe) would affect the estimate of batch fecundity in these species (Hunter et al. 1985). We found no statistically significant location difference in the number of mature oocytes (two-way AN-

OVA, all $P > 0.35$). This agrees with ovary-lobe and subsection analysis of DeMartini (1987).

To estimate the batch fecundity of the three species of *Paralabrax*, we had 25 *P. clathratus*, 23 with hydrated oocytes and 2 with migratory-nucleus-stage oocytes; 9 *P. maculatofasciatus*, 4 with hydrated oocytes and 5 with migratory-nucleus-stage oocytes; and 4 *P. nebulifer*, 1 with hydrated oocytes and 3 with migratory-nucleus-stage oocytes. We collected *P. nebulifer* between about 0800 and 2330, and found only 4 fish ($n = 88$) with ovaries that fit the criteria of this method, i.e., hydrated oocytes and no ovulation. Collections made after 2300 and before 0800 may yield larger numbers of *P. nebulifer* to use for estimating batch fecundity.

Our data provide two estimates of diel spawning period. We histologically examined ovaries of field-collected fish and categorized them according to the developmental stage of the most advanced oocytes. We followed oocyte development temporally to estimate a probable spawning time for each species. We estimated the age of postovulatory follicles by comparing them with our laboratory series, and back-calculated the time of spawning from capture time.

RESULTS AND DISCUSSION

Annual Spawning Period

Paralabrax are recognized as summer spawners off southern California. Clark (1933) reported a June-through-August spawning period for rock bass (*P. clathratus* and *P. nebulifer*), which was substantiated by Collyer and Young (1953) and Limbaugh (1955). Limbaugh (1955) also found that *P. maculatofasciatus* were ripe in July. Yearlong, monthly examinations of the gonads of *P. clathratus* by Smith and Young (1966) indicate that oocytes mature from May through September and that spermatocytes develop between April and September (no samples from October). Quast (1968) reported that the relative gonadal weight of *P. clathratus* increased in April and decreased in November, and spawning rate peaked from May to July.

Larval *Paralabrax* occur in ichthyoplankton samples collected in the nearshore Southern California Bight in early summer (Lavenberg et al. 1986). From 1978 to 1984, larval abundance peaked inshore of the 36-m contour between June and September, coinciding with reported peak spawning times. Generally, spawning occurs in the warm summer months when water temperatures typically exceed 16°C. When summer water temperatures drop, oocyte maturation or embryonic development may be affected. In July 1980, when sea temperatures were below 16°C, significantly fewer *Paralabrax* larvae were collected (Lavenberg et al. 1986; Petersen et al. 1986).

Diel Spawning Period

Estimated spawning times from both temporal oocyte development and postovulatory follicle ageing are generally comparable for each species. Spawning in *P. clathratus* probably begins in the late afternoon: migratory-nucleus-stage oocytes begin to develop in the morning; hydration and ovulation occur throughout the day; and individuals with new (0 to 4 hrs old) postovulatory follicles were collected in the evening (figure 3A). Age classification of postovulatory follicles (figure 3B) supports this estimate: our peak spawning estimates are from the late afternoon into the evening. During our limited collection periods for *P. maculatofasciatus*, we observed no spawning. We found hydrated oocytes throughout the day, and a few ovulating females in the afternoon (figure 3C). Spawning probably occurs late in the day: studies of postovulatory follicles indicate peak spawning in the afternoon and night (figure 3D). Evidence exists for prolonged day-long spawning in *P. nebulifer*: we collected ovulating fe-

males throughout the day, from 0800 to 1100, 1330 to 1500, and 1900 to 2300 (figure 3E). Age classification of postovulatory follicles also suggests prolonged daily spawning for *P. nebulifer*, with a noticeable peak at midday (noon–1400, figure 3F).

Our data support DeMartini's (1987) suggestion that the prolonged presence of hydrated oocytes in *P. nebulifer* resulted from a lengthy process of hydration. Oocyte maturation may be as long as 15 hours in *P. clathratus*. The earliest migratory-nucleus stages develop by ca. 0600 (females whose ovaries contained migratory-nucleus-stage oocytes, not at the earliest stage, were collected beginning at 0830), and spawning appears to peak at 2100 (figure 3B). Evidence of the length of time involved in oocyte maturation is less clear in *P. nebulifer* and *P. maculatofasciatus*.

Spawning Frequency

All three species — *P. clathratus*, *P. maculatofasciatus*, and *P. nebulifer* — are capable of daily spawning. Histological examination of ovaries of each species revealed individuals with both migratory-nucleus-stage or hydrating oocytes and postovulatory follicles that indicated ovulation had occurred 8 to 24 hours prior to collection (table 1, figure 4). These fish had all spawned before being collected (within 24 hours) and were hydrating a new batch of eggs to spawn, presumably within 15 hours. Two *P. nebulifer* had ovaries that contained early migratory-nucleus-stage oocytes, postovulatory follicles that were less than 4 hours old, and postovulatory follicles that were 18 to 24 hours old. These fish had recently spawned (<4 hours before capture), spawned the day before collection, and were maturing a new batch of oocytes that would have been spawned on the day after capture. Not all fish captured demonstrated evidence of daily spawning: 32% of the *P. clathratus* females ($n = 84$), 20% of the *P. maculatofasciatus* females ($n = 79$), and 31% of the *P. nebulifer*

TABLE 1
 Evidence of Daily Spawning in Three Species
 of *Paralabrax**

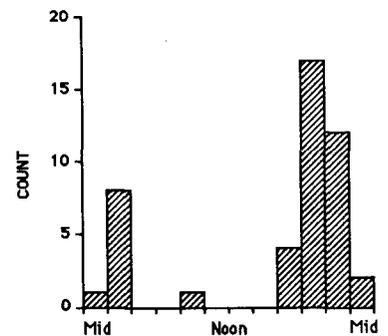
Stages present in ovary	Numbers of female <i>Paralabrax</i>		
	<i>P. clathratus</i>	<i>P. maculatofasciatus</i>	<i>P. nebulifer</i>
POF _i + MN	0	13	10
POF _i + H	17	2	3
POF _i + O	6	0	0
POF _i + POF _o	1	0	16

*Each *Paralabrax* female had day-1 postovulatory follicles (8 to 24 hours old, POF_i) and either migratory-nucleus-stage oocytes (MN); hydrated oocytes (H); initial stages of ovulation (hydrated oocytes and new postovulatory follicles, O); or new (≤ 4 hours old) postovulatory follicles (POF_o).

Paralabrax clathratus

	Mid	0200	0400	0600	0800	1000	Noon	1400	1600	1800	2000	2200	Mid
Collection Times					xxxxxxxxxxxxxxxxxxxx	xxxxxxxxxxxxxxxxxxxx				xxxxxxxxxxxxxxxxxxxx	xxxxxxxxxxxxxxxxxxxx		
Migratory Nucleus Stage					xxxxxxx								
Hydrated Oocytes					xxxxxxxxxxxxxxxxxxxx					xxxx			
Ovulation							xxx			xxx			
Recently Spawmed (< 4 hour old postovulatory follicles)											xxxxxxxxxxxx		

A

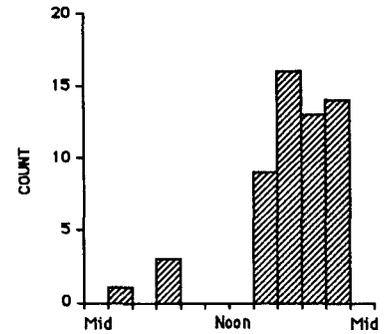


B

Paralabrax maculatofasciatus

	Mid	0200	0400	0600	0800	1000	Noon	1400	1600	1800	2000	2200	Mid
Collection Times					xxxxxxxxxxxxxxxxxxxx	xxxxxxxxxxxxxxxxxxxx							
Migratory Nucleus Stage					xxxxxxxxxxxxxxxxxxxx								
Hydrated Oocytes					xxxxxxxxxxxxxxxxxxxx								
Ovulation							xxxx						
Recently Spawmed (< 4 hour old postovulatory follicles)													

C

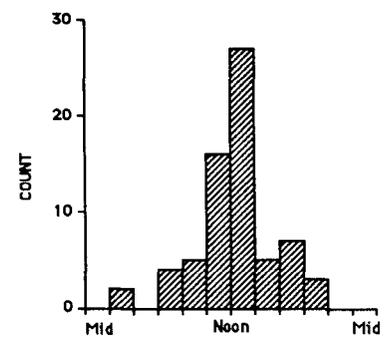


D

Paralabrax nebulifer

	Mid	0200	0400	0600	0800	1000	Noon	1400	1600	1800	2000	2200	Mid
Collection Times					xxxxxxxxxxxxxxxxxxxx	xxxxxxxxxxxxxxxxxxxx				xxxxxxxxxxxxxxxxxxxx	xxxxxxxxxxxxxxxxxxxx		
Migratory Nucleus Stage					xxxxxxxxxxxx					xxxxxxxxxxxx			
Hydrated Oocytes					xxxxxxxxxxxxxxxxxxxx								
Ovulation						xxxxxxx		xxxxxxx			xxxxxxx		
Recently Spawmed (< 4 hour old postovulatory follicles)						xxxxxxxxxxxx							

E



F

Figure 3. Time periods at which fish in various developmental stages were collected (A, C, E) and frequency distribution of estimated spawning times based on ages of postovulatory follicles (B, D, F).

females ($n = 81$) showed evidence of spawning on two consecutive days. There was no statistically significant difference in the average size of specimens that exhibited evidence of daily spawning, com-

pared to those that had spawned the day before collection (but showed no evidence of maturing a new batch to be spawned the next day), those with hydrated oocytes in the ovary, or nonspawners (one-

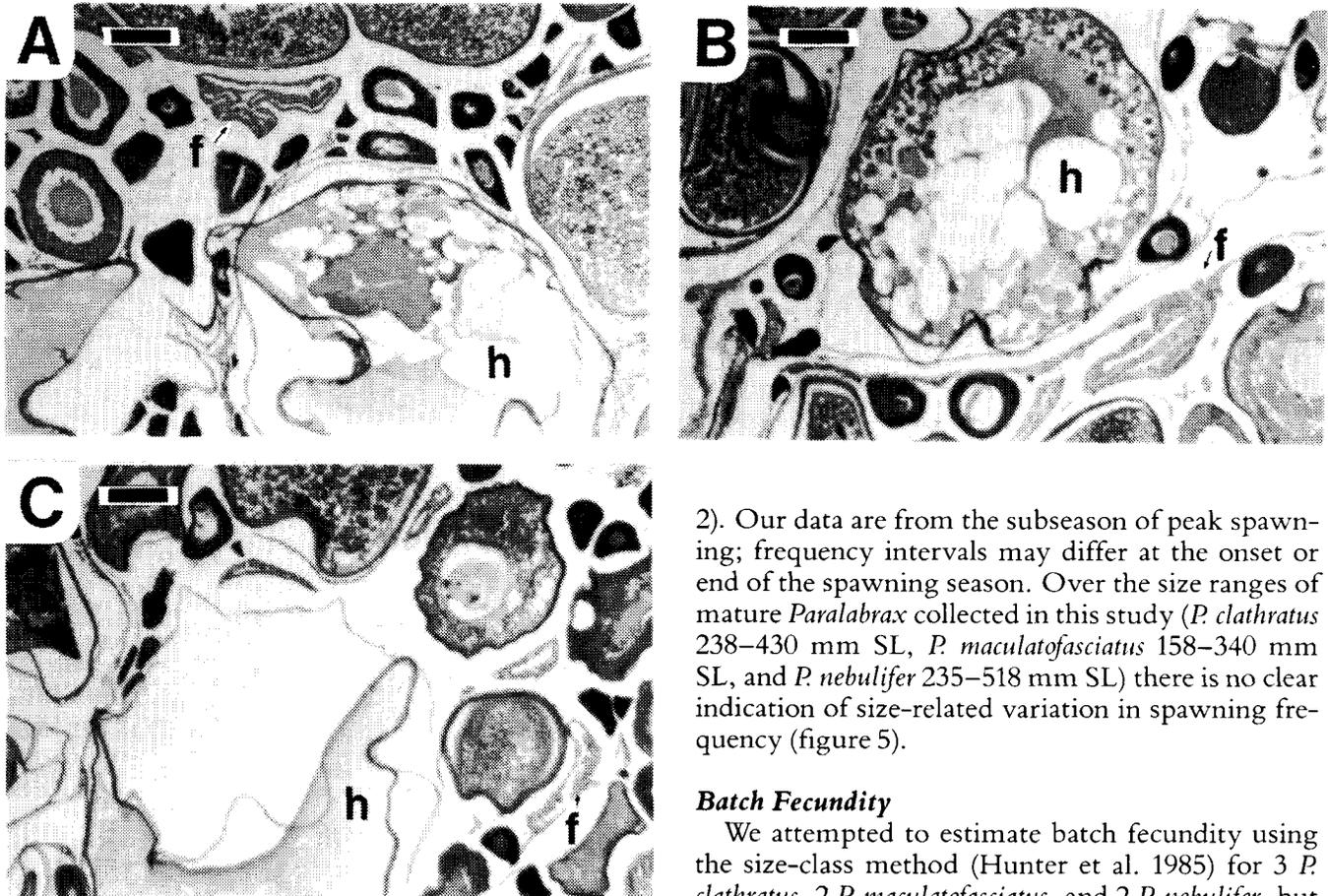


Figure 4. Evidence of daily spawning: presence of both day-1 postovulatory follicles and hydrating oocytes. A, *Paralabrax clathratus*; B, *P. maculatofasciatus*; and C, *P. nebulifer*. h = hydrating oocytes, f = day-1 postovulatory follicle. Bar = 0.1 mm.

way ANOVA, *P. clathratus*, $P = 0.221$, $n = 80$; *P. maculatofasciatus*, $P = 0.959$, $n = 79$; and *P. nebulifer*, $P = 0.554$, $n = 74$).

The proportion of females with day-1 postovulatory follicles was calculated as the total number of day-1 females divided by the total number of mature females. Spawning frequency is estimated by assuming that the proportion of females with day-1 ovaries is the proportion of fish that will spawn each day. The fraction of mature female *Paralabrax clathratus* collected with day-1 postovulatory follicles was 0.42 (standard deviation = 0.04; table 2), indicating an average of 2.4 days between each spawning event. An interval of 1.5 days between spawns was estimated for *P. maculatofasciatus* because the fraction of mature females collected with day-1 postovulatory follicles was 0.68 (standard deviation = 0.19; table 2). The average interval between spawning for *P. nebulifer* was estimated at 1.6 days; the fraction of mature females collected with day-1 postovulatory follicles was 0.63 (standard deviation = 0.19; table

2). Our data are from the subseason of peak spawning; frequency intervals may differ at the onset or end of the spawning season. Over the size ranges of mature *Paralabrax* collected in this study (*P. clathratus* 238–430 mm SL, *P. maculatofasciatus* 158–340 mm SL, and *P. nebulifer* 235–518 mm SL) there is no clear indication of size-related variation in spawning frequency (figure 5).

Batch Fecundity

We attempted to estimate batch fecundity using the size-class method (Hunter et al. 1985) for 3 *P. clathratus*, 2 *P. maculatofasciatus*, and 2 *P. nebulifer*, but

TABLE 2
Numbers of *Paralabrax* Females Collected in Various Spawning States

Collection	Day 0		Day 1	Nonspawning	Total
	Hydrated	≤4 Hours			
<i>Paralabrax clathratus</i>					
19 July	0	1	1	0	2
27 July	3	5	7	5	20
28 July	12	0	19	18	49
17 Aug.	1	0	8	4	13
Total	16	6	35	27	84
<i>Paralabrax maculatofasciatus</i>					
2 Aug.	0	0	37	3	40
3 Aug.	1	0	5	3	9
4 Aug.	4	0	11	13	28
8 Sep.	1	0	1	0	2
Total	6	0	54	19	79
<i>Paralabrax nebulifer</i>					
19 July	1	0	21	1	23
21 July	0	0	22	1	23
26 July	6	0	5	5	16
27 July	1	0	0	1	2
28 July	2	2	3	10	17
Total	10	2	51	18	81

Day 0 females had hydrated oocytes in the ovary (hydrated) or postovulatory follicles ≤4 hours old. Day-1 females had postovulatory follicles >4 and ≤24 hours old. The ovaries of nonspawning females contained yolked oocytes, but no hydrating oocytes or postovulatory follicles.

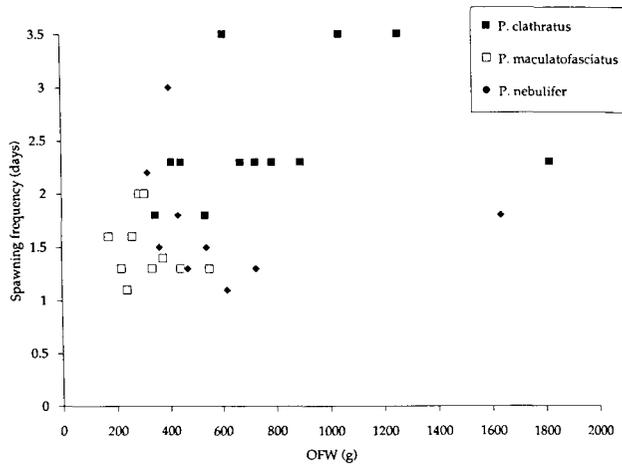


Figure 5. Relation between spawning frequency and size (ovary-free weight) of *Paralabrax clathratus*, *P. maculatofasciatus*, and *P. nebulifer*. Collections of each species were ranked by size (OFW) and partitioned into groups of equal numbers (*P. clathratus*, 12 groups, $n = 7$; *P. maculatofasciatus*, 10 groups, $n = 8$; and *P. nebulifer*, 9 groups, $n = 9$) represented on the graph by the mean OFW.

were unable to consistently determine a most-advanced mode; in cases where a most-advanced mode was identifiable, the estimates ranged from 3 to 8 times the estimates determined with the hydrated-oocyte method. Size ranges for the developing oocytes of these *Paralabrax* spp. were determined (table 3, which also includes chorion diameters of field-collected *Paralabrax* eggs from the ichthyoplankton collection of the Natural History Museum of Los Angeles County).

In our collections only 25 specimens of *P. clathratus* (collected in the Ventura/Port Hueneme area), 9 of *P. maculatofasciatus* (from Mission Bay), and 4 of *P. nebulifer* (collected at the Huntington Flats, off Seal Beach) fit the criteria required to use the hydrated-oocyte method for determining batch fecundity. Log transformation of the data improved the fit of the batch fecundity to ovary-free weight, and of the batch fecundity to standard-length linear relationships of *P. clathratus*, as it did for DeMartini (1987).

TABLE 3
**Oocyte Size Ranges at Developmental Stages for
Paralabrax Spp. (*P. clathratus*, *P. maculatofasciatus*, and *P. nebulifer*, $n = 200$)**

Primary oocytes	to 0.16 mm
Partially yolked oocytes	0.14–0.31 mm
Fully yolked oocytes	0.24–0.58 mm
Migratory-nucleus-stage oocytes	0.55–0.82 mm
Hydrated oocytes	0.72–0.84 mm
Water-hardened eggs (5% Formalin)	0.86–0.90 mm
Water-hardened eggs (70% ethanol)	0.79–0.90 mm

Table also includes chorion diameter ranges for field-collected *Paralabrax* eggs, preserved in 5% buffered Formalin and 70% ethanol (from the Natural History Museum of Los Angeles County ichthyoplankton collection).

TABLE 4
**Linear Regression Parameters for Log₁₀-Transformed
 Batch Fecundity (BF)–Ovary-Free Weight (OFW), and
 Log₁₀-Transformed BF–Standard Length (SL)
 Relationships of Female *Paralabrax***

	<i>P. clathratus</i>	<i>P. maculatofasciatus</i>	<i>P. nebulifer</i>
$\log_{10} BF = a + b \cdot \log_{10} OFW$			
N	25	9	4
Intercept (a)	5.26	7.19	3.40
Coefficient (b)	0.91	0.56	1.25
Standard error	0.445	0.227	0.328
R ²	0.454	0.257	0.737
P	<0.001	0.163	0.141
$\log_{10} BF = a + b \cdot \log_{10} SL$			
N	25	9	4
Intercept (a)	-5.57	-1.41	-6.78
Coefficient (b)	2.93	2.17	3.17
Standard error	0.430	0.217	0.342
R ²	0.491	0.325	0.714
P	<0.001	0.109	0.155

The number of samples available for *P. maculatofasciatus* and *P. nebulifer* are quite low and are included only as preliminary information (table 4, figure 6); linear regression analyses for these two taxa indicate no statistically significant relationship between size and batch fecundity at these low n values. The log-transformed linear relationship of ovary-free weight to batch fecundity in *P. clathratus* is statistically significant, $P = <0.001$ (table 4, figure 6). A standard-weight female (ca. 700 g OFW and 300 mm SL for this collection) would average 81,000 eggs per batch applying this regression equation. The average batch size per spawning by a standard-weight female varied by a factor of 2 in seven years of estimates for *Engraulis mordax* (Hunter et al. 1985). Because of this interannual variation, Hunter et al. (1985) recommended that when the egg production method is used to estimate biomass for *E. mordax*, batch fecundity must be recalculated for each biomass estimation. Our estimations of batch fecundity for *Paralabrax* are higher than those reported by DeMartini (1987) and may indicate the variability possible in these species of *Paralabrax*. Batch fecundity estimates calculated for *Seriphys politus* (Sciaenidae) from southern California did not vary like those for *Engraulis mordax* (DeMartini 1991). DeMartini concluded that batch fecundity estimates for *S. politus* were relatively invariant over four years (1979, 1980, 1985, and 1986) but significantly lower in 1984, during a major El Niño event. In 1987, DeMartini estimated batch fecundity for *Paralabrax* that were collected, in part, during the same El Niño event. Estimates of the batch fecundity of *Paralabrax* should be calculated over several years to determine whether fecundity is relatively invariant as in *S. politus*, or fluctuates among years as in *E. mordax*.

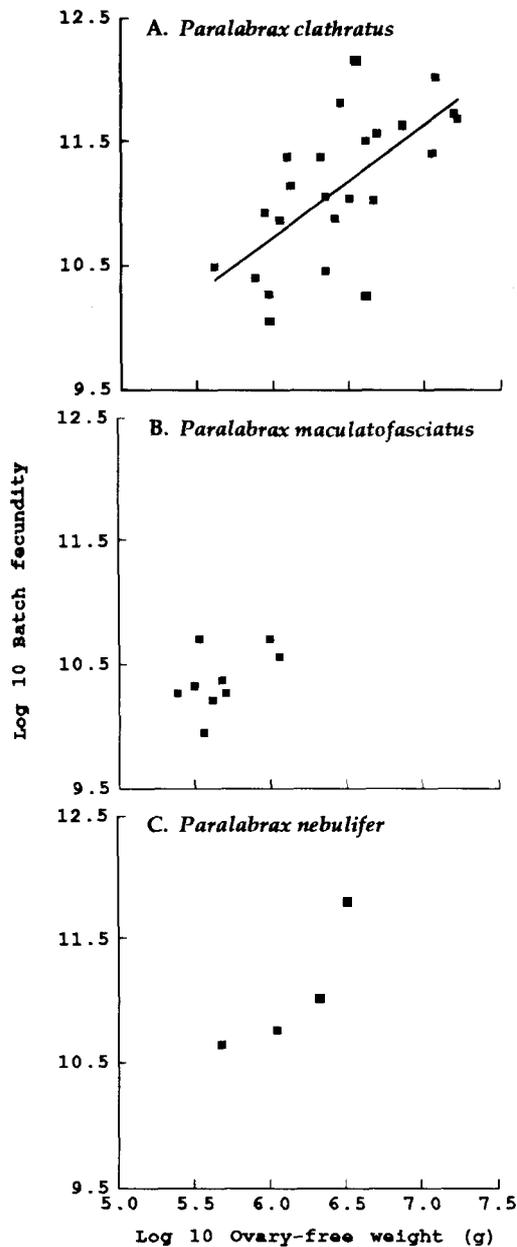


Figure 6. Relations between \log_{10} -transformed batch fecundity and ovary-free weight for our collections of *Paralabrax clathratus*, *P. maculatofasciatus*, and *P. nebulifer*.

The relative fecundity (batch fecundity/ovary-free weight) of *Paralabrax clathratus* does not seem to be influenced by body size (ovary-free weight; figure 7), and the average relative fecundity of *P. clathratus* that would have spawned on consecutive nights did not differ significantly from that of fish which had not spawned the night before collection (independent *t* test, *df* = 16, *p* = 0.475).

Hermaphroditism

Smith (1965) indicated that many serranids are specialized in their "reproductive mechanisms":

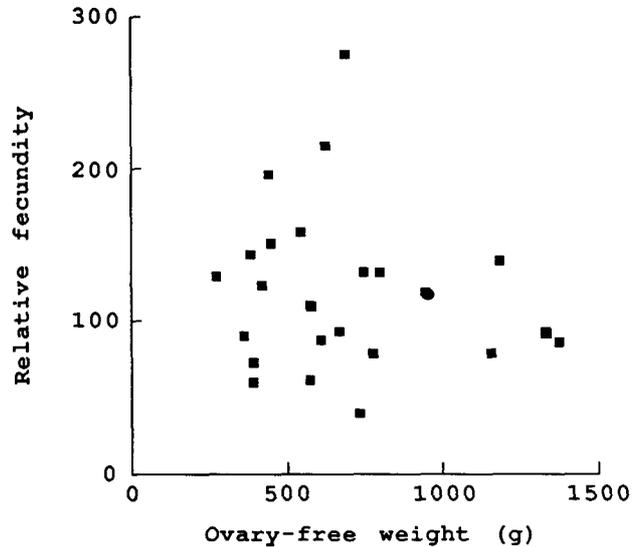


Figure 7. Relative fecundity (number of hydrated oocytes per gram of ovary-free weight) versus ovary-free weight (g) of *Paralabrax clathratus*.

some are gonochoristic, some are synchronous hermaphrodites, and others are protogynous hermaphrodites. Sadovy and Shapiro (1987) list five features of fishes that clearly indicate protogynous hermaphroditism: a membrane-lined central cavity in the testes; sperm sinuses in the gonadal wall; transitional individuals; stage 1, 2, or 3 atretic oocytes in the testes; and experimentally induced sex change. In our studies we found that these three species of *Paralabrax* share two characters: a central membrane-lined cavity in the testes, and sperm sinuses in the gonadal wall.

Gonads of six specimens of *P. nebulifer* contained both testicular and ovarian tissue. Of these, four were active males with primary oocytes in the testes (figure 8A). Proliferating testicular tissue, in the area corresponding to the testicular islet (Hastings 1989), was present in two specimens: one was immature (121 mm SL) and had only primary oocytes in the ovarian tissue (figure 8B), the other (278 mm SL; figure 8C) had vitellogenic oocytes. This suggests the possibility of protogynous hermaphroditism in *P. nebulifer*, which would mean that *P. nebulifer* is capable of both prematuration and postmaturation sex change. No signs of oocyte degeneration were detected in any of the six fish; therefore we believe that, on the basis of the criteria of Sadovy and Shapiro (1987), insufficient evidence exists to call *P. nebulifer* a protogynous hermaphrodite, although other evidence is certainly suggestive.

None of the *P. clathratus* specimens that were collected had both tissue types in the gonad. Smith and Young (1966) examined the gonads of *P. clathratus* and labeled them as secondary gonochores based on

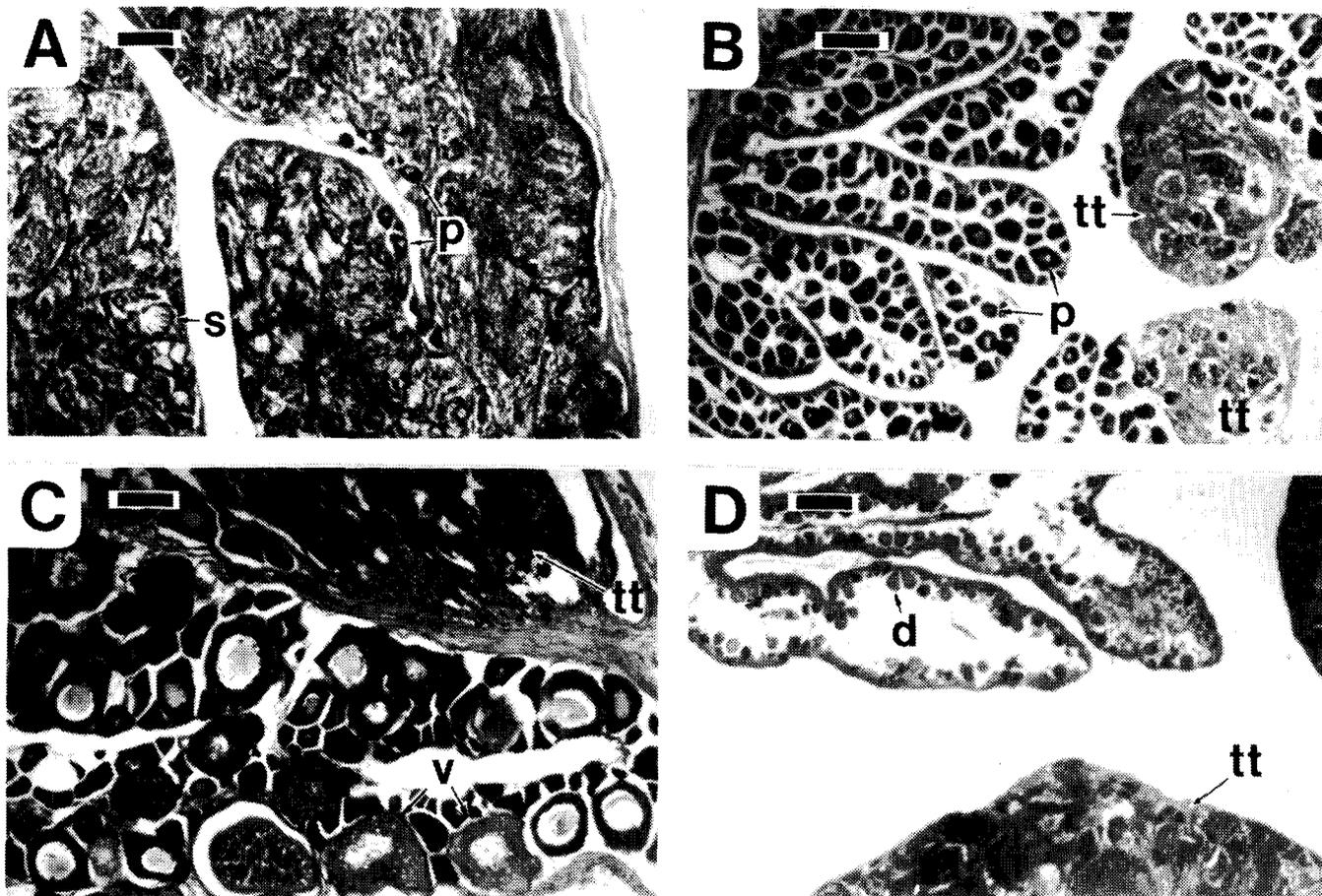


Figure 8. *Paralabrax nebulifer* (A-C) and *P. maculatofasciatus* (D) gonads with simultaneously occurring testicular and ovarian tissues: d = degenerating oocytes; p = primary oocytes; s = sperm crypts; tt = testicular tissue; v = vitellogenic oocytes. Bar = 0.1 mm.

the presence of a membrane-lined central cavity in the testes, sperm sinuses in the gonadal wall, a lack of transitional individuals, and no observed differences in the size ranges of males and females. Transitional individuals may be more prevalent at times different from those of our collections; sex change is seasonal in some species, occurring primarily at the end of the spawning season (Sadovy and Shapiro 1987).

One *P. maculatofasciatus*, which had been maintained at the King Harbor Laboratory for one year, was catheterized (cellular material not clearly male or female) and injected with LHRHa on June 30, 1989, at 0810 and sacrificed on July 3, 1989, at 0800. Active testicular tissue occupied 80%–85% of the gonad, but was enclosed in lobes that attached to about 25% of the gonadal wall (columnar nature of the epithelial lining was not evident). Attached to the remaining 75% of the gonadal wall were regressing ovarian lobes lined with columnar epithelium

and containing degenerating primary oocytes (figure 8D). These characters support Hastings's (1989) identification of *P. maculatofasciatus* as a protogynous hermaphrodite.

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OCEANIC FACTORS INFLUENCING DISTRIBUTION OF YOUNG ROCKFISH (*SEBASTES*) IN CENTRAL CALIFORNIA: A PREDATOR'S PERSPECTIVE

DAVID G. AINLEY,
WILLIAM J. SYDEMAN
PRBO International Biological Research
4990 Shoreline Highway
Stinson Beach, California 94970

RICHARD H. PARRISH
Pacific Fisheries Environmental Group
NOAA, National Marine Fisheries Service
P.O. Box 831
Monterey, California 93942

WILLIAM H. LENARZ
Tiburon Laboratory
NOAA, National Marine Fisheries Service
3150 Paradise Drive
Tiburon, California 94920

ABSTRACT

We used the diet of a seabird, the common murre (*Uria aalge*), to assess the abundance of juvenile rockfish (*Sebastes* spp., mostly *S. jordani*) in the Gulf of the Farallones, California, 1973–90. On the basis of an exploratory analysis of the data and of several oceanographic factors, we hypothesize that availability of fish in the study area during June–July was a function of advection during the January–February period of rockfish parturition. When upwelling or downwelling was persistent in winter, there were few juveniles in late spring, but when upwelling had been mild or pulsed, juveniles were abundant. Rockfish availability also decreased when turbulence, sea level, and sea-surface temperature were high during winter. Stepwise multiple regression analyses indicated that, among these variables, advective transport significantly affects the distribution of juvenile rockfish.

RESUMEN

Usamos la dieta del ave marina alca piquilarga (*Uria aalge*) para estimar la abundancia de rocot juveniles (*Sebastes* spp., principalmente *S. jordani*) en el Golfo de Farallones, California, 1973–90. Basándonos en un análisis exploratorio de los datos así como en factores oceanográficos, presentamos la hipótesis que la disponibilidad de peces en Junio–Julio fué función de la advección durante Enero–Febrero (la temporada de cría los rocot). Cuando hubo surgencias o hundimientos de masas de agua persistentes en invierno, disminuyó la abundancia de juveniles en primavera tardía, mientras que cuando las surgencias fueron poco intensas u ocurrieron intermitentemente, la abundancia de los juveniles incrementó. La disponibilidad de los rocot disminuyó cuando en invierno hubo valores altos de turbulencia, nivel del mar o temperatura superficial. Análisis de regresión múltiple por pasos indicaron que de entre esas variables, la advección afecta significativamente la distribución de rocot juveniles.

INTRODUCTION

Eastern boundary currents contribute roughly a third of the world's fishery resources (Thompson 1981). Such productivity is attributable, in part, to the dominant oceanographic feature of these areas — upwelling of cold, nutrient-rich waters to the surface, which in turn leads to enhanced phytoplankton growth. Parrish and MacCall (1978) examined the relations between several environmental variables and the recruitment success of Pacific mackerel (*Scomber japonicus*) in southern California, and found the highest correlation with the upwelling index (Bakun 1973) at 30°N during the early part of the spawning season. The correlation was positive, and Parrish and MacCall stated that “upwelling is obviously related to recruitment, because it determines the basic productivity of the California Current.”

Associated with upwelling, however, is wind-generated turbulence, which could lead to impaired nutrient and carbon transfer to higher trophic levels. For example, Peterman and Bradford (1987) found a negative linear relationship between the mortality rate of northern anchovy (*Engraulis mordax*) during the first 15 days of the larval period and a measure inversely related to turbulence, i.e., the number of periods of calm at 33°N during the main spawning season. Neither cannibalism, as measured by the biomass of adults, nor advection, as measured by offshore Ekman transport, improved the explanation of variability in early mortality. Further, as noted by Methot (1983), even though advection may not have increased mortality during the first 15 days of the larval period, it may have reduced the proportion of larvae that remain in favorable habitat, thereby contributing to late mortality.

Bailey and Francis (1985) found strong year classes of Pacific whiting (*Merluccius productus*) only when sea-surface temperature (SST) in the Los Angeles Bight was relatively high, and when upwelling at 36°N was relatively low at the beginning of the spawning season. They showed that whiting larvae are found farther offshore and to the south in cold years and in years of relatively high upwelling. They concluded that this could be either because spawning takes place farther offshore and to the south or

because of advection. They cited evidence that the larvae grow more slowly during cold years and that prey densities are relatively low offshore and to the south.

Fishery oceanographers have long believed that advection could be an important factor in the reproductive success and recruitment of fish. Bakun (1986) and Simpson (1987) discuss some of the physical mechanisms involved in advection and some physical phenomena that would retain eggs and larvae in favorable habitat.

In order to deter the offshore transport of larvae, fishes in eastern boundary currents tend to reproduce when advection (Ekman transport) is low. They also tend to bear their young alive; relatively large larvae are more capable of swimming than, for instance, newly hatched northern anchovies (Parrish et al. 1981). We found that prevalence of the young-of-the-year (YOY) of one genus of live-bearing fish, *Sebastes*, varies from year to year in the diet of an apex predator, the common murre (*Uria aalge*), in California (Ainley and Boekelheide 1990). To determine what factors might explain the availability of rockfish, we analyzed the relations between several oceanographic factors and the prevalence of rockfish in the murre diet.

METHODS

A seabird, the common murre, was our fish-sampling tool. We studied murre diet at Southeast Farallon Island (SEFI), 42 km offshore of central California (figure 1), each June and July for 18 years, 1973–90. Murres carry fish in their beaks, in full view, to feed their offspring. From within a blind that overlooked a group of approximately 100 pairs of breeding murres within 10 m of the blind, we observed birds returning from the sea with fish (Ainley and Boekelheide 1990). Observations were made every 3 to 5 days throughout the chick-rearing season, from late May to early July. Using 8× binoculars (for a “frame-filling” view of each murre), we identified, to the closest taxon possible, 800 to 4000 prey items per year (Ainley and Boekelheide 1990). Years when sample sizes were smaller were oceanographically anomalous years, such as during El Niño events, when fewer pairs were breeding (Ainley and Boekelheide 1990).

We used the proportion of juvenile rockfish in the diet as an index to rockfish availability within the foraging range of the murres. Murres' preferred prey were juvenile rockfish (Ainley and Boekelheide 1990). When rockfish were not available, the murres fed along the mainland coast on other species of fish, principally anchovies. Murres dive to a depth of

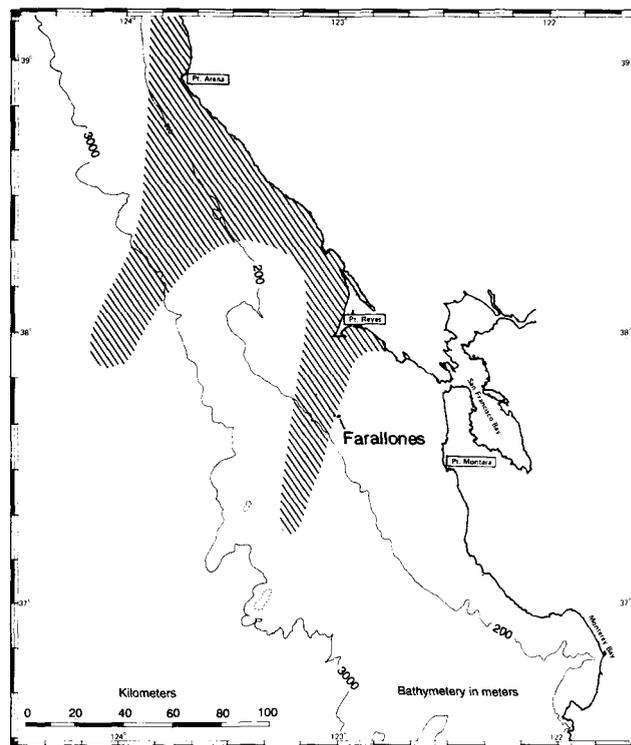


Figure 1. Upwelling plumes of a size and shape typical of early spring in central California, and the location of the Gulf of the Farallones study area (shape of the plume drawn according to figure 4.2.2-27 in SAIC 1987).

about 100 m, which corresponds to the depth of the continental shelf in the study area. They forage up to 80 km from breeding sites. Thus, allowing for the shape of the mainland coastline and the fact that it lies only about 40 km from SEFI, the murre population can sample about 7000 km² of ocean during the summer breeding season, including the entire volume of water overlying the continental shelf and upper slope.

During June 1985 and 1986, we collected 24 and 42 common murres, respectively, at various locations within the study area. Gut contents analysis revealed 274 juvenile rockfish in the 1985 sample, and 87 in the 1986 sample (PRBO unpubl. data), and many rockfish were fresh enough to identify to species. These data provided a check for the identifications made at SEFI.

From 1983 to 1991, the National Marine Fisheries Service, Tiburon Laboratory (NMFS), estimated the abundance and distribution of juvenile rockfish in waters off central California, including those surrounding the Farallon Islands (our murres were collected on these cruises). The more classical research method used by NMFS—a grid of trawl stations during late May and June (Wyllie Echeverria et al. 1990; Adams 1992)—overlapped the time of our observations at SEFI. The proportion of juvenile rock-

fish in the murre diet (as a measure of annual variability in the abundance of the fish) correlated with the NMFS trawl data during overlapping years when trawl results were consistently derived from year to year (1986–91, including 1991 to increase the sample size); a regression between murre diet and log-transformed trawl results for fishes in the size classes appropriate to murre foraging (>39 mm; see Results) was highly significant ($R^2 = 0.87$, $t = 5.27$, $P < 0.01$; figure 2). Therefore, we believe that the bird diet serves as a valid index to the availability of juvenile rockfish in the Gulf of the Farallones region during early summer. We use the diet data for comparison with oceanographic conditions because this time series is much longer than that of the trawl data.

We related the proportion of rockfish in the murre diet to indices of upwelling ($m^3/sec^{-1}/100 m^{-1}$ of coastline; Bakun 1973) and turbulence (wind speed³), SST, and sea level. We used the upwelling index as a surrogate measure of Ekman transport (advection). Monthly upwelling indices were taken from Bakun (1973), Mason and Bakun (1986), and unpublished updates. A turbulence index consisting of monthly wind-speed-cubed values was derived from 6-hr wind-speed values that were inferred by Bakun from atmospheric pressure fields supplied by the U.S. Navy's Fleet Numerical Oceanography Center. A preliminary analysis with these data indicated that the upwelling index and turbulence estimates derived for 36°N are more representative of conditions in the study area than those at 39°N (F. Schwing, Pacific Fisheries Environmental Group, NMFS, Monterey, pers. comm.). At SEFI we measured SST daily. We used sea level measured at San Francisco (units in mm) as an index to the strength of northerly flow in the California Current and an integration of temperature by depth and region —

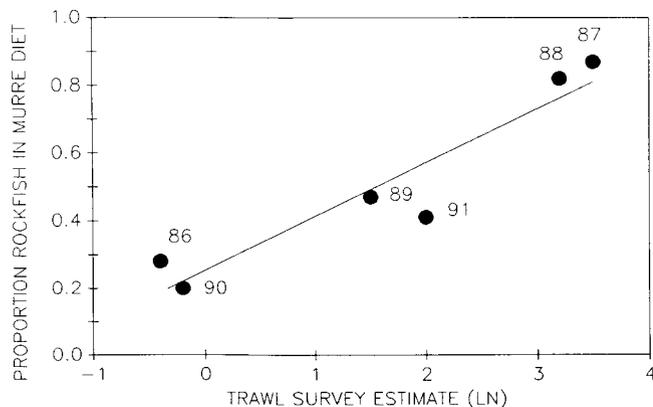


Figure 2. The relation between the proportion of the murre diet contributed by rockfish and the log of the number of juvenile rockfish (>39 mm) in NMFS trawl samples, 1983–91. The relation is described by the equation, $Y = 0.272 + 0.165X$.

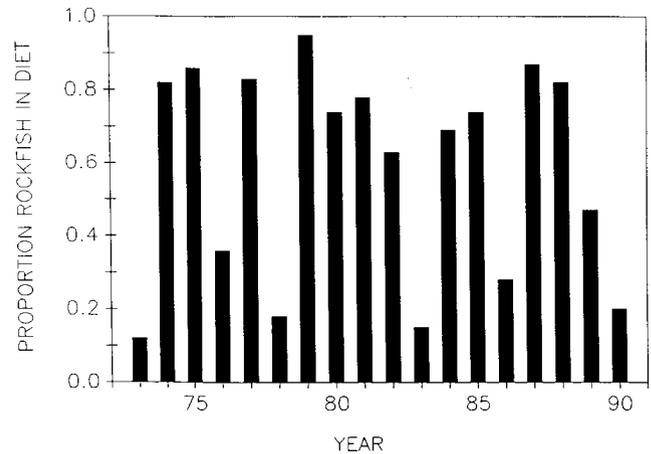


Figure 3. Annual variability in the proportion of rockfish in the diet of the common murre, Southeast Farallon Island, June and July 1973–90.

factors known to affect the marine climate of eastern boundary currents (Norton et al. 1985). Finally, we related rockfish values to measures of wind pulsation, defined as the number of wind events (velocity >9 kts terminated by winds <9 kts) per month. At SEFI we measured winds daily at 0800 PST.

We correlated the percentage of rockfish in the birds' diet with the above oceanographic and meteorological values averaged for individual and combined monthly periods, October to June, preceding the June–July chick-feeding period. Initially, we used simple regression analyses to investigate relations among these variables; we also tested for correlations among the measures. We used quadratic values of upwelling, turbulence, and SST to model apparent curvilinear relations. To examine the relative effect of each oceanographic variable on rockfish availability, we used forward and backward stepwise multiple regression. Statistical significance was assumed if nominal $P < 0.05$. We recognized that the large number of tests increases the probability of failing to reject false hypotheses, and thus consider this an exploratory analysis.

RESULTS

Rockfish in the common murre diet varied substantially from one year to the next (figure 3). Regression analyses of rockfish in the diet against the upwelling index, turbulence, SST, and sea level indicated which values provided significant correlations (figure 4). The average January-plus-February upwelling index ($UJ + F$) related to rockfish availability in a parabolic fashion (figure 5) and explained 61% of the variation in interannual abundance ($Y = 79.54 + 1.51(UJ + F) - 0.11((UJ + F)^2)$); separately, neither month was significantly related to rockfish abundance. Rockfish were most available when the

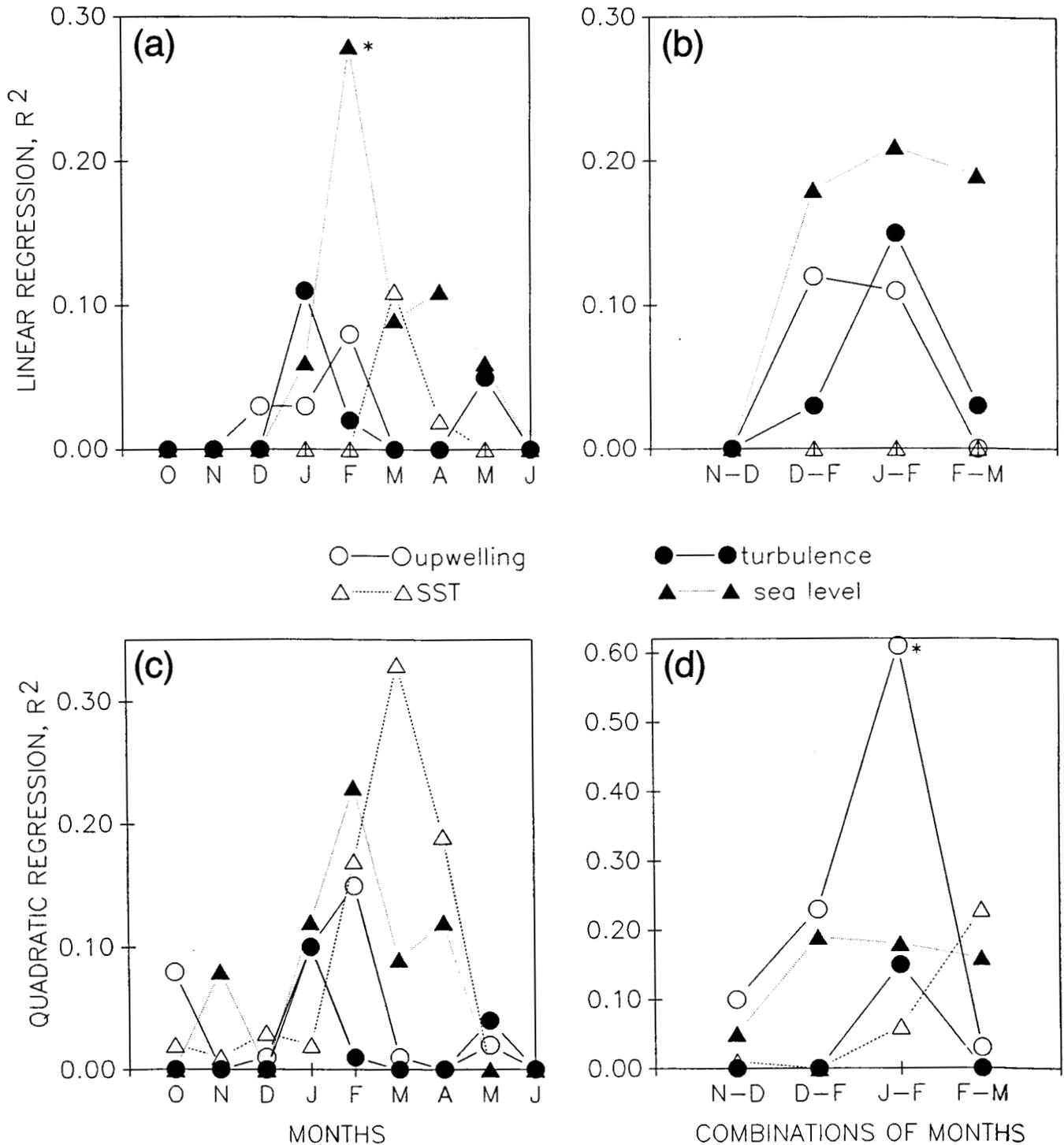


Figure 4. Values of R^2 for regressions between prevalence of rockfish in the murre diet and four oceanographic parameters: a, linear regression by month, and b, by combinations of months; c, quadratic regression by month, and d, by combinations of months. Significant values are indicated by an asterisk (*).

average January–February upwelling index was slightly above zero. During years of prevalent winter downwelling (1973, 1978, 1983, and 1986), or years when winter upwelling was overly persistent (1976, 1989, 1990), rockfish were less abundant (fig-

ure 3; see also Ainley and Boekelheide 1990). We found no significant relations between rockfish abundance and monthly upwelling indices later in the spring and summer, when upwelling reaches its maximum intensity in the California Current sys-

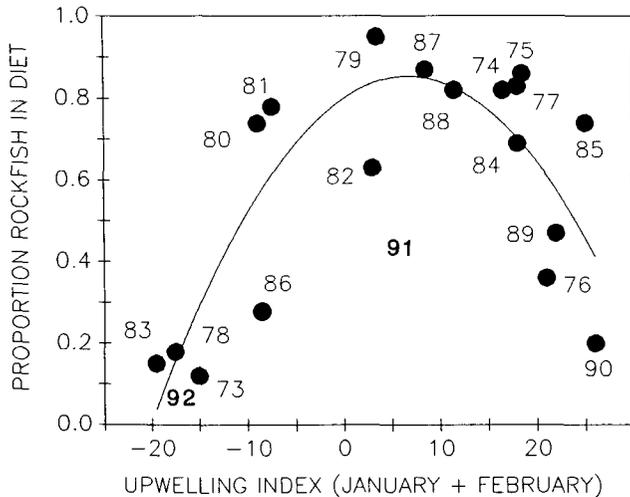


Figure 5. Parabolic relation between rockfish in the diet of mures in the Gulf of the Farallones during June and July and the upwelling index during the preceding January and February, 1973-90. The relation is described by the equation $Y = 79.54 + 1.51(UJ + F) - 0.11((UJ + F)^2)$.

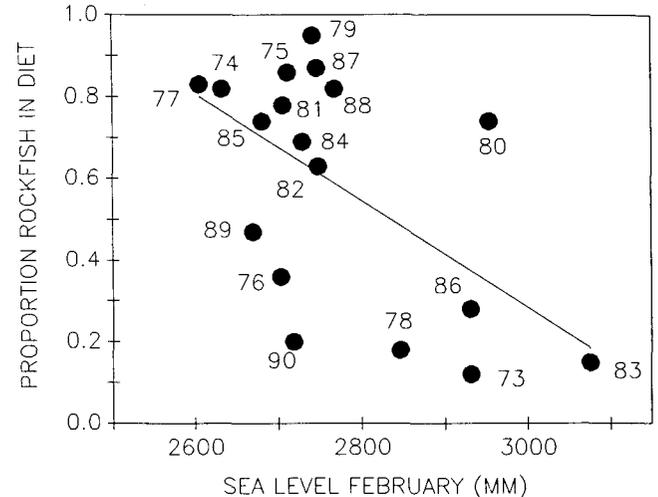


Figure 6. The relation between rockfish in the diet of mures in the Gulf of the Farallones during June and July and sea level during the preceding February, 1973-90.

tem (Breaker et al. 1983). Neither did we find any relation with wind pulsation.

Rockfish availability was negatively, but not significantly, correlated with turbulence during January-February (figure 4; $P = 0.0635$). This variable accounted for only 15% of the yearly variation in fish prevalence. Again, separate turbulence values for January or February were even more weakly related to rockfish availability. Turbulence was greatest during 1978, 1980, 1983, and 1986; the winters of 1978, 1983, and 1986 were also characterized by intense downwelling and elevated sea level. We detected no departure from linearity ($P > 0.10$) between turbulence and rockfish availability.

In March, SST was negatively, but weakly, correlated with rockfish abundance. The quadratic of March SST accounted for 33% of the variation in annual rockfish prevalence, but was again not significant (figure 4; $P = 0.052$). The warmest March SSTs were noted in 1978, 1983, and 1986.

Sea level during February was negatively and significantly correlated with rockfish prevalence (figures 4 and 6; $P = 0.014$), when it accounted for 28% of the yearly variation in rockfish abundance. Sea level was highest in 1973, 1978, 1980, 1983, and 1986. Although sea level in 1976, 1989, and 1990 was low, rockfish were scarce. A linear relation was more significant and explained more of the variance than did a quadratic relation.

The January-February upwelling index, March SST, February sea level, and January-February turbulence values correlated significantly (table 1). The upwelling index was negatively correlated with SST, sea level, and turbulence. SST was positively

correlated with sea level and turbulence, and sea level and turbulence also were positively associated. Forward multiple regression indicated that January-February turbulence ($F = 0.10$), March SST ($F = 0.25$), and February sea level ($F = 0.80$) were insignificant when January-February upwelling was first entered into the model. A backward regression analysis confirmed these findings (table 2). The explan-

TABLE 1
 Correlation Coefficients among Four Environmental Factors in Central California, 1973-90

	1	2	3	4
1. Upwelling, Jan.-Feb.	1.000			
2. Temperature, Mar.	-0.8416	1.000		
3. Sea level, Feb.	-0.8192	0.7455	1.000	
4. Turbulence, Jan.-Feb.	-0.7736	0.6823	0.7964	1.000

Each value alone had significant or nearly significant correlation to the prevalence of rockfish in the diet of mures at the Farallon Islands.

TABLE 2
 Backward Regression of January + February Upwelling Index (UI), February Sea Level (SL), and March Sea-Surface Temperature (SST) with Rockfish Prevalence in the Murre Diet

Model	R ²	F	P
UI, UI ² , SST, SL	0.58	6.81	0.0035
UI, UI ² , SST	0.59	9.17	0.0013
UI, UI ² , SL	0.60	9.50	0.0011
UI, UI ²	0.61	14.03	0.0004
SL, SST	0.23	3.55	0.0547
UI	0.11	3.11	0.0971
SL	0.28	7.54	0.0144
SST	0.11	3.08	0.0986

R² values were adjusted by the degrees of freedom and sample size ($n = 18$ years).

atory power of the model was greatest when only the upwelling index was included. SST and sea level contributed little to explaining variation in rockfish prevalence in the diet and could be dropped from the model with no effect on R^2 values.

DISCUSSION

Most of the rockfish eaten by murrets at Southeast Farallon are YOY shortbelly rockfish (*S. jordani*) — on average, 70% of rockfish in the summer diet (Ainley and Boekelheide 1990). This species has also dominated midwater trawl catches of YOY rockfish in the study area (Wyllie Echeverria et al. 1990; Adams 1992), as well as the fish contained in murre stomachs during the two years of collections (Briggs et al. 1987; Ainley, unpublished data). The shortbelly constitutes the largest biomass of any rockfish off California and is a species of the continental shelf and upper slope (Pearson et al. 1991). January and February are the peak months of parturition for this and most other abundant rockfish species that inhabit offshore central California (Wyllie Echeverria 1987), and are the months just before the spring transition from winter conditions to the upwelling period (Breaker et al. 1983). Murrets begin to feed on these fish, along with other prey of the same size, as soon as the prey appear in winter (PRBO unpublished data). By the time the rockfish have increased from about 1 cm to 4 cm they are big enough to be carried to chicks at SEFI breeding sites.

The correlation with the upwelling index indicates to us that intense and persistent midwinter winds, either onshore (negative upwelling) or offshore (positive upwelling), transport larvae and perhaps small juveniles away from the foraging range of murrets at the Farallones. It is at this time, just after birth and when they are smallest, that YOY rockfish are most vulnerable to advection. Figure 1 depicts an upwelling plume typical of this coast during the early upwelling period (March–April; see also figure 3 in Parrish et al. 1981). Later (June), when upwelling is intense and continuous, plumes in this area of the coast are much broader and extend much farther offshore (SAIC 1987). Along this coast, murrets tend to feed at the periphery of upwelling plumes, because there are no prey in recently upwelled water (Briggs et al. 1988). On the basis of this pattern and our analysis herein, we conjecture that large, intense plumes may completely displace YOY rockfish from the foraging range of Farallon-based murrets. Advection outside of the murre foraging range — i.e., away from the continental slope (the main habitat of shortbelly and certain other rockfish) — may remove young rockfish from the popu-

lation unless they can compensate by swimming, or survive until fortuitous currents carry them back to suitable habitat. Whether or not such advection strongly affects recruitment of rockfish, however, remains to be determined (and is being investigated by NMFS). Hobson and Howard (1989) reported mass mortality of YOY shortbelly rockfish on the California shore, not the usual shortbelly habitat (and certainly outside of murre foraging habitat), and conjectured that they had been transported in waters propelled by intense shoreward winds.

Upwelling has the potential to increase primary production in coastal waters of eastern boundary currents, as well as to decrease the egg and larval survival of spawning pelagic fishes because of turbulence and advection (Bakun 1990; Cury and Roy 1989). Our analysis indicates that increased transport of young (larval and small) juvenile fish away from traditional areas for recruitment is an important factor. We base our hypothesis — “The observed pattern of presence or absence of fish is explained by advection” — partly upon the reasoning of Cury and Roy (1989): fish (in this case, rockfish) should bear their young within the central upwelling area of the California Current just before the seasonal onset of intense upwelling. By eliminating the passive (planktonic) egg and reducing the early larval stage, they should be better able to cope with turbulence and advection, which are also caused by the intense, upwelling winds that are the nemesis of smaller developmental stages of the fish. Indeed, by bearing their young alive, rockfish eliminate about 40 days' free existence in the passive stages. This idea assumes that incubation time would be the same as gestation time if rockfish spawned eggs rather than bearing viable larvae. If it is assumed that incubation time of (hypothetical) egg-laying rockfish would be similar to that of other egg layers, then only about one week of passive drifting would be eliminated.

On the other hand, many rockfish species apparently bear their young when they do in order to avoid the intense offshore transport characterizing late spring in the California Current region, as well as perhaps to take advantage of spring plankton blooms. Through natural selection, the release of rockfish larvae during late winter may have evolved because upwelling events are usually intermittent at that time. Upwelling events that are mild or short lead to an enhanced food web. Resulting upwelling plumes may displace the fish slightly offshore, but the young fish are able to return because, between the upwelling events, slack or onshore winds propel them or allow them to return shoreward. We failed to find a correlation with wind pulsation because

years of extended weak transport and intermittent strong winds were those in which YOY rockfish were abundant. In such conditions the swimming ability of the young, but relatively well developed, rockfish larvae is sufficient to accommodate to the food dispersal caused by turbulence.

Our analyses suggest that advection is an important factor determining the occurrence patterns of YOY rockfish in central California. Other factors that perturb the oceanic environment in which these rockfish live also appear to play a role. These factors are represented by SST and sea level in our analyses and, like upwelling, correlated most closely with variability of YOY rockfish during late winter.

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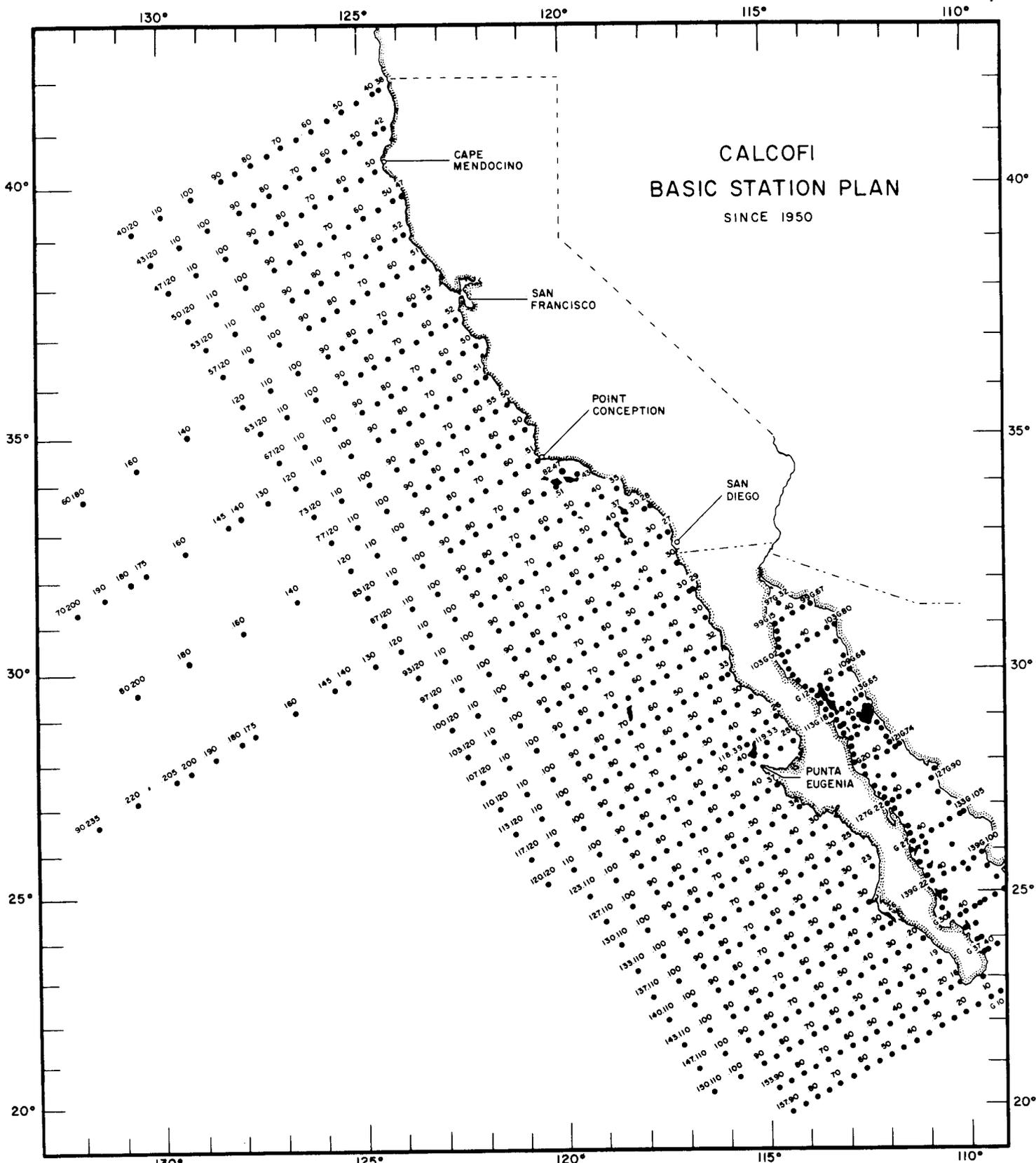
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